The Effect of Density-Dependence on Foraging Dominance between Two Pest Species

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Authors
Ross, James G.
Sam, Shona

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The Effect of Density-Dependence on Foraging Dominance between Two Pest Species

James G. Ross
Department of Ecology, Lincoln University, Lincoln, New Zealand
Shona Sam
Marlborough District Council, Blenheim, New Zealand

ABSTRACT: Possum numbers have been significantly reduced in many regions of New Zealand. However, research has indicated some unexpected consequences of possum control. At some sites, rat numbers have more than doubled 2 years after possum control. What this suggests is that the removal of a direct competitor has enabled a rapid increase in rat numbers relative to slower possum recovery. This has serious implications, as high rat numbers could inhibit ongoing possum ground control. To investigate this, an experimental trial was run where we tested the following research hypotheses by manipulating the rat density: i) Null hypothesis (H0) rat density has no influence on possum foraging behaviour around bait stations, ii) Alternative hypothesis (H1) rat density indirectly influences possum behaviour by removing all bait before possums can access it, and/or iii) Alternative hypothesis (H2) rat density directly influences possum behaviour by physically excluding them from bait stations. The experimental site was divided into 2 parts, a treatment block and a control (non-treatment) block. Rat control was undertaken using Victor® kill traps and 96 rats were removed over 6 nights (density estimated at 4.6 rats/ha). To quantify the effect of rat density on possum foraging behaviour, non-toxic bait stations were stapled to a tree every 10 m along 18 monitoring lines (n = 50). Possum behaviour was then monitored using both modified tracking cards and IR camera traps. Prior to trapping, 92% of all the baits were removed by rats on the first night. Following trapping, this reduced down to 8% in the treatment block. Rats turned up earlier than possums at the majority of the monitored sites (~1 hour before sunset). Before trapping, baits were only available 33% of the time when a possum visited a bait site (n = 15), and no baits were removed. After trapping, baits were available 100% of the time and 2 baits were removed by possums. These results support H1 and suggest that the smaller-bodied competitor can dominate food resources in NZ forests. This has the potential to make possum ground control more difficult when using control techniques that do not target rodents.

KEY WORDS: brushtail possum, field rodents, kill traps, monitoring, Rattus rattus, ship rat, Trichosurus vulpecula, vertebrate pest control

INTRODUCTION

Introduced mammalian predators are a significant problem in New Zealand (NZ) for both agricultural and conservation reasons (Coleman and Caley 2000). Possums (Trichosurus vulpecula), for example, require ongoing suppression and local eradication because they are vectors for bovine TB. To reduce the infection of cattle and deer herds requires sustained control of possums, and significant amounts of money are spent each year on possum control activities (AHB 2012a). Whilst this has resulted in declining TB cattle infection rates (AHB 2012b), recent research investigating trophic interactions has indicated some unexpected consequences of possum control (Ruscoe et al. 2011). For example, at 4 sites where possums were removed, ship rat (Rattus rattus) numbers more than doubled by Year 2 when compared to sites where possums had not been removed. What this indicates is that the removal of a direct competitor has facilitated a rapid increase in rat numbers (competitive release theory) relative to the slower possum recovery, suggesting that possums are the dominant competitor of rats only when their numbers are at pre-control levels.

Once possums have been removed in a control operation, they can take 5 years or longer to recover to the original population size; there is usually ongoing maintenance control, targeting any survivors and reinventing animals, thus keeping possum numbers at artificially low levels (Veltman and Pinder 2001). However, rats can rapidly increase in numbers, and at high levels they could remove and cache possum bait from fixed bait stations and/or bait bags attached to trees (Morriss et al. 2012). Private possum contractors have indicated that this is a real problem which, in some areas, increases their labour and bait costs, because they are having to initially target rats before they can undertake any serious possum control (Martin Brenstrup, Central Districts Pest Control Ltd, pers. comm. 2010). This suggests that rats are capable of dominating foraging opportunities, and perhaps rats in this situation become the dominant competitor when possums are in the recovery phase after control.

Little is known about inter-species pest interactions in New Zealand, particularly at bait stations, where interactions may cause a reduction in bait availability for one or more pest species. Competitive inter-species interactions surrounding food is common across most mammalian groups where dietary and habitat conditions overlap. For example, (Brown 1971) found one chipmunk species (Eutamias dorsalis) will aggressively compete for food with another chipmunk species (E. unbrinus) when found in the same habitat. Within a group of avian scavengers, there was both intra-species and inter-species competition at food carcasses (Wallace and Temple 1987), whereby those birds with a larger body mass were found to aggressively exclude others.
from the food resource. Chimpanzee (*Pan troglodytes schweinfurthii*) foraging was found to be negatively affected by competition from the invasion of yellow baboons (*Papio cynocephalus cynocephalus*) into an area of Tanzania (Matsumoto-Oda and Kasagula 2000).

Possums and rats have a large dietary overlap (~60%), and possums are considered the dominant competitor due to their larger body size (Sweetapple and Nugent 2007, Ruscoe et al. 2011). Generally the larger body-massed species is the dominant competitor, and this size advantage is also observed in NZ forests between ship rats and mice (Ruscoe et al. 2011). During winter, when most possum control operations take place, there is a limited natural food supply for possums and rats. Accordingly, artificially modifying the winter food supply by placing out control baits means that both possums and rats are being drawn into small areas for food, and it seems highly likely that there would be competition for that food resource. However, in situations where there are very low densities of the dominant competitor (possum) and high densities of the smaller-bodied rat, could the smaller species be superior and actually dominate food resources? The smaller competitor dominating has been observed for birds, where the smaller hooded crow (*Corvus cornix*) constrains the larger common raven (*C. corax*) until the crows were removed using traps (Bodey et al. 2009). In these situations, is competition dominance driven by density-dependence rather than by body size-dependence, and is this the case for possums and ship rats in NZ?

To test this research question, we developed a series of research hypotheses: (H₁) Rat density has no influence on possum behaviour around bait stations, and manipulating rat numbers would not influence possum foraging behaviour. The alternative hypotheses were that: (H₂) High rat density indirectly influences possum behaviour by removing all available bait before possums can access it, and/or: (H₃) Rat density directly influences possum behaviour, with them physically defending and excluding individual possums from bait stations.

**METHODS**

**Study Site**

This study took place at Patuha Forest (~39.204989, 173.954086), New Zealand, in July-August 2012. The forest is dominated with mixed broadleaf/hardwood with a scattering of isolated large podocarps. The site (~55 ha) was divided into 2 parts, a treatment block and a control (non-treatment) block with a 200-m buffer zone in between.

**Population Indices**

To estimate the numbers of rats and possums, both blocks were monitored using ChewCards (rats; Connovation Ltd, Auckland, NZ) and WaxTags® (possums; Pest Control Research Ltd, Christchurch, NZ) following standardised protocols (Sweetapple and Nugent 2011, NPCA 2008). There were 2 sample periods conducted: prior to the rodent trapping, and after rodent trapping. ChewCards (8 lines in control block, 10 lines in the treatment block) and WaxTags® (5 lines in each block) were placed every 10 m along lines spaced ~200 m apart. Both devices were left out for 4 nights. The mean percentage of ChewCards and WaxTags® bitten per line for each block over each sampling period was to be calculated to provide relative indices of rat and possum abundance before and after rodent trapping. Changes in these indices were then used to calculate percentage reductions in rodent activity, and these were adjusted for natural changes in the control block (Hix et al. 2012).

Rat control in the treatment block was undertaken using 42 Victor kill traps (Pest Control Solutions, Christchurch, NZ) with 3-4 traps per monitoring line in the treatment block. To prevent immigration from the control block immediately following trapping, 3 additional trapping lines were also established in the buffer zone using a further 10 traps. All traps were baited and left unset for 2 nights. Following this, all traps where then rebaited, set, and checked daily for 14 nights.

**Feeding Behaviour**

To quantify the effect of rat density on possum feeding behaviour, 50 biodegradable bait bags containing non-toxic Ferafeed 213 that is used with encapsulated cyanide possum bait (Feratox®; Connovation Ltd) were nailed at shoulder height every 20 m along each WaxTag® monitoring line (5 per line) in each block. Possum behaviour was then monitored at the bait bags using modified tracking cards (Figure 1) and 24 IR trail cameras.

The cameras (Bushnell Trail Cam # 119455; Bushnell Outdoor Products, Overland Park, KS, USA) were deployed at 12 bait bag locations in each block, with at least one camera located on each monitoring line. The camera was placed in a position that allows the bait bag to be in the middle of the field of view. Cameras were set on the quickest setting, which allowed a photo to be taken approximately every 1.5 sec continuously whilst the animal remained present at the station.

The bait bags, tracking cards, and cameras were all deployed for 4 nights during each sampling period (before and after rat control). All bait bags, tracking cards, and cameras were checked daily and replaced daily if necessary.

**Data Analysis**

We had initially intended to use a generalised linear model (GLM) to detect any significant change in mean possum activity around the bait bags in the presence (control block) and absence (treatment block) of rats. However, given the low number of possum interactions both pre-and-post trapping, this was amended to a GLM investigating differences in the times that rats and possums were first observed by the cameras each night.

An assessment of the rodent population density in the treatment block was undertaken using the “Zippin Removal” method (Zippin 1958). This method uses plots of nightly catch against cumulative catch to estimate the number of rodents left untouched. For this calculation, we only used the total number of rats caught over the first 6 nights of trapping (Brown et al. 1996). This is believed to
be a more reliable estimate when we assume that the population is closed (Watkins et al. 2010).

RESULTS
Population Indices
The ChewCard and WaxTag indices indicated high rat activity in the control and treatment blocks prior to trapping. Following trapping, the ChewCard index reduced by 80% in the treatment block and this converts to an activity reduction of 82.4% after considering natural changes in the control block (Table 1). Possum activity levels remained low before and after rodent trapping.

A total of 96 rats was trapped over the first 6 nights of trapping in the treatment block, and this converts to a population estimate of 101 (+ 4.86 SE) rats in the treatment block prior to trapping with a density of 4.6 rats/ha (95% CI estimate 4.2 - 5.0).

Table 1. Relative indices of rat and possum activity pre- and post rat trapping.

<table>
<thead>
<tr>
<th>Species</th>
<th>Block</th>
<th>Pre-trapping</th>
<th>Post-trapping</th>
<th>Change</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rat</td>
<td>Control</td>
<td>85.7% ± 6.9</td>
<td>97.1% ± 1.8</td>
<td>13.3%</td>
</tr>
<tr>
<td>Rat</td>
<td>Treatment</td>
<td>62.5% ± 5.3</td>
<td>12.5% ± 5.9</td>
<td>-80.0%</td>
</tr>
<tr>
<td>Possum</td>
<td>Control</td>
<td>0.0% ± 0.0</td>
<td>4.0% ± 3.2</td>
<td>-</td>
</tr>
<tr>
<td>Possum</td>
<td>Treatment</td>
<td>0.0% ± 0.0</td>
<td>4.0% ± 3.2</td>
<td>-</td>
</tr>
</tbody>
</table>

Feeding Behaviour
Prior to trapping, 46 out of 50 bait bags were removed by rodents on the first night in both blocks. One additional bag was removed but no clear paw tracks could be identified (Table 2). Following trapping, 25 out of 25 bait bags were removed on Night 1 in the control block whereas only 2 out of 25 were removed in the treatment block.

Pre-trapping rats were first observed at 1400 hrs whereas the first possum was not observed until 1642 hrs. This observation was consistent post trapping with the first rat observed on the camera footage at 1506 and the first possum not turning up until 1644 hrs. Whilst rodents were generally observed first each night, there was considerable variation in the time of first appearance at each camera site, and the differences between rats and possums was not statistically significant (F₁,₂₀ = 2.34; P=0.134; Table 3).

A total of 15 possum visits was observed by the cameras over the 2 nights of observations pre-and-post trapping. On average, bait was only available for 33% of these visits in the blocks where rats had not been removed, and no bait was taken by possums. In the treatment block after trapping bait availability was 100%, and for 2 of these visits baits were removed by possums (Table 4).

Table 2. Total numbers of bait bags removed by rodents after one night pre-and-post rodent trapping.

<table>
<thead>
<tr>
<th>Block</th>
<th>Time</th>
<th>Total No. Bags</th>
<th>Taken by Rats</th>
<th>Change</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>Pre</td>
<td>25</td>
<td>23</td>
<td>92.0%</td>
</tr>
<tr>
<td>Treatment</td>
<td>Pre</td>
<td>25</td>
<td>23</td>
<td>92.0%</td>
</tr>
<tr>
<td>Control</td>
<td>Post</td>
<td>25</td>
<td>25</td>
<td>100.0%</td>
</tr>
<tr>
<td>Treatment</td>
<td>Post</td>
<td>25</td>
<td>2</td>
<td>8.0%</td>
</tr>
</tbody>
</table>

Table 3. Mean time of first appearance (24-hr clock). Sunset c. 1730.

<table>
<thead>
<tr>
<th>Species</th>
<th>Pre-trapping</th>
<th>Post-trapping</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rat</td>
<td>1642.9 + 35.6</td>
<td>1671.3 + 38.7</td>
</tr>
<tr>
<td>Possum</td>
<td>1718.6 + 49.6</td>
<td>1746.9 + 47.8</td>
</tr>
</tbody>
</table>

Table 4. Bait availability and removal by possums pre-and-post rat trapping.

<table>
<thead>
<tr>
<th>Block</th>
<th>Time</th>
<th>Visits</th>
<th>Bait gone (%)</th>
<th>Bait Taken (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>Pre</td>
<td>4</td>
<td>1 (25)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Treatment</td>
<td>Pre</td>
<td>2</td>
<td>2 (100)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Control</td>
<td>Post</td>
<td>4</td>
<td>3 (75)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Treatment</td>
<td>Post</td>
<td>5</td>
<td>0 (0)</td>
<td>2 (40)</td>
</tr>
</tbody>
</table>
DISCUSSION

Our trapping data indicated that we had medium-high numbers of ship rats. In this study, we estimated a density of 4.6/ha prior to control, and typically rat densities in NZ podocarp forest are around 4/ha (Morriss et al. 2012) with highs of 6.7/ha (Brown et al. 1996) and 6.5/ha (Innes et al. 2010) recorded in fragmented habitat elsewhere. Our possum density was low and typical of what occurs 2 years following 1080 aerial control. The relative possum and rat densities also matches previous research work which indicates that numbers of rats are known to be high 2 years following lethal control that targets both species (i.e., aerial 1080 cereal bait; Ruscoe et al. 2011).

Prior to rat trapping, bait bags put out for possum control were almost completely removed by rats on the first night out in the field (92%). Also, given that rats appeared to be active earlier than possums, when a possum did actually locate a bait site, the bag had already been removed in the vast majority of cases. In direct contrast, immediately following trapping, all bait remained available and the cameras actually observed 2 possums removing bait. The rapid discovery of the bait bags is not surprising, and previous research investigating possum and rat control suggests that most possums and rats are killed on the first or second night following the deployment of toxic bait (Nugent et al. 2012).

This research suggests that the rapid rat consumption of bait should severely hamper possum control, particularly when rat numbers are high relative to possums. Rats are also known to hoard baits, and 78% of captive ship rats will take and cache non-toxic bait when presented with a surplus of food (Morriss et al. 2012). However, high kills for both species are generally observed following aerial 1080 control, particularly following non-toxic prefeeding (Nugent et al. 2011). With sowing rates of 2 kg/ha there are ~170 baits available per hectare, and it seems that there is plenty of toxic bait remaining for possums even after bait caching by rats. In the same trial with the captive ship rats, the numbers of individual rats hoarding toxic bait reduces to 40% as the rapid 1080 toxicosis removes individuals from the population (Morriss et al. 2012). Recent bait surveys following aerial control also indicate that only 10% of toxic bait is actually consumed, and aerial application rates could go significantly lower using either cluster or strip sowing techniques (i.e., 250g/ha; Nugent et al. 2012).

What this study highlights is that there is danger when using control tools that target individual pest species. Specificity has become a key component of pest control in recent decades in the quest to avoid non-target mortality (Caut et al. 2007), and in NZ this has led to the development of possum-specific tools such as encapsulated cyanide. While many ecological studies have focused on predator release following removal of the top predator, it is the competitive release of rats and mice that is most often observed following the control of possums and/or rats (Ruscoe et al. 2011). What this suggests is that species interactions in NZ forests are driven more by competition than predation. From a control standpoint, there may be the need in some situations to simultaneously control the smaller competitor when targeting the larger competitor.

In conclusion, there is significant dietary overlap between possum and rats (55% as reported by Ruscoe et al. 2011), and the general rule is that the larger-bodied competitor dominates and changes the smaller-bodied competitor’s behaviour and distribution (Gehrt and Prange 2007). However, the smaller-bodied competitor is not always inferior (Bodey et al. 2009), and at high densities rats most likely dominate food resources in NZ forests. Accordingly, it seems that density-dependence rather than by body size-dependence is in operation with rats and possums in NZ forests. Whether rats or possums directly avoid each other is currently unknown, and in future studies it would be useful to observe interaction behaviour around bait stations. Certainly rats act aggressively to mice around food (Bridgman 2012), and this may be the case with possums and rats particularly when food resources become scarce. In this study no interactions were observed, but the likelihood of this occurring becomes more likely as possum numbers increase over time following control.

ACKNOWLEDGEMENTS

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LITERATURE CITED


