

Detecting species interactions using remote cameras: effects on small mammals of predators, conspecifics, and climate

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Abstract. Effective conservation management requires an understanding of the source and direction of the many interactions that occur within ecological communities. Without this understanding, management interventions such as control or eradication of introduced species can have unexpected and undesirable outcomes. One of the challenges for wildlife managers is to garner relevant information for their site of management. In this paper we describe how images of mammals captured on remote cameras can be used to uncover behavioral interactions that can in turn help to identify and prioritize areas for more explicit research or management. Our cameras were set repeatedly at four sites over three years in Tasmania, Australia, and we used a series of generalized linear mixed models to interpret relative changes in count data of three species of small mammals: the introduced black rat *Rattus rattus*, and the native long-tailed mouse *Pseudomys higginsii* and swamp rat *Rattus lutreolus velutinus*. We also included two potential predators, the introduced feral cat *Felis catus* and the native Tasmanian devil *Sarcophilus harrisii*. We found that counts of the two species of native small mammals were correlated positively with each other, that swamp rats had a negative effect on black rats, and that black rats had a negative effect on the long-tailed mouse. Devils were important effects in most small mammal models. Despite their effect probably being underestimated by the remote camera survey method, feral cats were included in models for the long-tailed mouse. On the basis of the inclusion of native and both species of introduced mammals in long-tailed mouse models, we propose that the long-tailed mouse is a priority for further research. This research should clarify the competitive dominance and predatory pressure exerted by the black rat and feral cat, respectively, on this species, and also the potential for management of either introduced species to increase the impact of the other. We conclude that remote cameras can help to uncover cryptic or unsuspected interactions within ecological communities, and hence provide an informed basis for developing targeted research questions to increase the effectiveness of wildlife management.

Key words: animal behavior; ecological interactions; *Felis catus*; generalized linear mixed models; invasive species; predator and prey interactions; *Pseudomys higginsii*; *Rattus lutreolus velutinus*; *Rattus rattus*; remote cameras; *Sarcophilus harrisii*; wildlife management.

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INTRODUCTION

Understanding the source and direction of ecological interactions is an important precursor to the effective conservation of threatened species and to the management of invasive species or native pests. Although single species may often be targeted for conservation or control, a relatively low return for management effort, or unexpected outcomes, may arise if the broader ecological context is not considered (Caughley and Gunn 1996). For example, removals of invasive black rats *Rattus rattus* and common brushtail possums *Trichosurus vulpecula* in New Zealand led to unexpected and undesirable outcomes in which house mice *Mus musculus* and black rats were released from competition, respectively (Ruscoe et al. 2011). Similarly, on sub-Antarctic Macquarie Island, a dramatic increase in numbers of rabbits *Oryctolagus cuniculus* followed the eradication of feral cats *Felis catus*, which may have resulted in increased grazing pressure on vegetation (Bergstrom et al. 2009, but see also Dowding et al. 2009). Such unintended consequences have occurred following management interventions in many systems (e.g., Caughley and Gunn 1996, Martin and Murray 2011), but appear to be particularly prevalent in systems with introduced mammals (Glen and Dickman 2005, Clout and Williams 2009).

Predation and inter- and intraspecific competition are among the most pervasive interactions between introduced mammals and their native counterparts (Dickman 2011) and, together with factors such as resource availability and disturbance, can markedly affect species' activity and abundance (Bruno et al. 2003). Disentangling these factors and identifying their relative influence are important generally for understanding the drivers of population dynamics (Ward et al. 2010), and are even more crucial for predicting the outcomes of management interventions (Caughley and Gunn 1996, Fox and Monamy 2007).

Population size is often the parameter of interest for conservation management, but behavioral interactions can indirectly affect species' abundances and distributions by influencing opportunities for foraging, mating, and dispersal (Sih 1988, Winnie and Creel 2007, Sherriff et al.

2011, Greenville et al. 2014). Remote cameras provide a relatively low-cost and low-invasive means of recording multiple species, including predators, prey, and potential competitors, over periods of months or years (Towerton et al. 2011, Meek et al. 2012). Chronological records of the patterns of multiple species visitations can be constructed from the date and time information recorded with each photograph. These records can then be used to explore the effect of subtle cues such as integumental or fecal odors, which can change individual behavior in many species (Boonstra et al. 1982, Dickman and Doncaster 1984, Banks 1998, Brown et al. 1999), on the pattern of visitation of animals that follow. As a result, observations of behavior at cameras can in the least be used to guide more specific research, and may of themselves inform the outcomes of management interventions.

Our study, using remote cameras, was conducted in the cool temperate forests of southern Tasmania, a large (64,519 square kilometers) island south of the continental mainland of Australia. Feral cats are an important threat to biodiversity in many parts of the world (Medina et al. 2011, Nogales et al. 2013), and have established populations across the island. In Australia, feral cats are formally recognized as a key threat to biodiversity under the *Environment Protection and Biodiversity Conservation Act* 1999 (DEWHA 2008). Small mammals, including endemic species, may be at high risk of predatory impact because they are frequently eaten by feral cats, and are selectively targeted in many areas (Nogales et al. 2013, Yip et al. 2014). Although it has not been experimentally demonstrated as yet, introduced small mammals such as the black rat may support higher numbers of feral cats, which then leads potentially to higher predatory impacts of feral cats on native wildlife (Banks and Hughes 2012).

Tasmanian devils *Sarcophilus harrisii* are a predator endemic to Tasmania that co-occur with feral cats and have experienced large population declines as a result of devil facial tumour disease (Hawkins et al. 2006). Their interactions with native and introduced small mammals are largely unknown; however, as a native carnivore they have co-occurred with Tasmanian small mammals for thousands of generations and therefore these mammals are likely to have

adapted to their presence (Carthey and Banks 2012). In addition, the frequency of occurrence of small mammals is much lower in the diet of devils compared to that of feral cats (Lazenby 2012). There is some evidence of a mesopredatory relationship between devils and feral cats, with an island-wide increase in spotlight counts of feral cats being associated with declines in devil populations (Hollings et al. 2014). In addition, feral cats are detected less frequently at remote camera sites that devils have visited in comparison to camera sites where devils have not been recorded (Lazenby and Dickman 2013).

The long-tailed mouse *Pseudomys higginsii* and swamp rat *Rattus lutreolus velutinus* are small mammals endemic to Tasmania. Both are generalist omnivores and the latter is the larger of the two based on average adult body weight (Taylor and Calaby 1988, Driessen 1999, Driessen and Rose 1999, Menkhorst and Knight 2001). These species vary inversely in space, with the larger swamp rat likely to be dominant and driving what appears to be an asymmetrical competitive relationship (Monamy and Fox 1999) most likely based on interference competition (Grant 1972, Glazier and Eckert 2002). Introduced black rats are also omnivorous, but their interactions, if any, with the long-tailed mouse and swamp rat are unknown. Black rats are larger than both of these Tasmanian endemic small mammals, and have occurred in Tasmania for at least 200 years (Menkhorst and Knight 2001). They negatively affect native fauna (especially small mammals) in other ecosystems in Australia (Stokes et al. 2009) and worldwide (King 1984, Banks and Hughes 2012).

Species interactions vary with context, with ecosystem productivity (or surrogate measures of productivity, such as rainfall) being particularly important (Elmhagen and Rushton 2007). Rainfall is a key determinant of food availability in many Australian systems and, in consequence, can have marked effects on the reproductive output and population dynamics of small mammals (Dickman et al. 1999, Orians and Milewski 2007). Differences in the magnitude of these responses between species can also change the source and direction of species interactions. Indeed, broad-scale changes in climate, including rainfall, have been identified as a major source of change in ecosystem interactions such as compe-

tition, intensity of pathogen infection, mutualism, and herbivory in other systems around the world (Tylianakis et al. 2008). Consequently it is important that observations of behavioral interactions over a given time frame are placed into the broader ecosystem context to include such drivers as rainfall.

Here, we trialled the use of remote cameras to uncover interactions among introduced and native predators, small mammals, and food availability. We did this by deploying 15–18 remote cameras at four spatially independent study sites twice a year over a three-year period in a cool temperate forest system. We carried out a 13-month cull of feral cats at two sites to increase variation in cat activity at cameras and maximize our ability to detect potential interactions between species (Lazenby et al. 2014). Generalized linear mixed models (GLMMs) were used to model counts of species recorded at cameras. Within our system we aimed specifically to observe interactions between the introduced feral cat and black rat, the Tasmanian devil, and the long-tailed mouse and swamp rat. We used rainfall in our models as a surrogate for food availability.

Based on the mode of operation of remote cameras, and the power of subtle cues to alter animal behavior, we hypothesized that records of species' visitations to cameras would be useful for detecting patterns consistent with behavioral interactions. In our study system, we expected that small mammals with greater adult body mass would reduce the count at cameras of those that weighed less (e.g., Monamy and Fox 1999). Thus, we hypothesized that black rats would negatively affect both native small mammals, and that the swamp rat would negatively affect the long-tailed mouse. In addition, we hypothesized that feral cats would have an important effect on small mammal counts, whereas devils would have relatively little effect given the low frequency of occurrence of small mammals in their diet compared to feral cats. We accepted that devils could obscure the effect of feral cats on small mammals given the reduced detectability of cats at camera sites visited by devils (Lazenby and Dickman 2013). We use the results to develop more targeted research questions to improve management effectiveness and decrease the likelihood of unexpected outcomes of man-

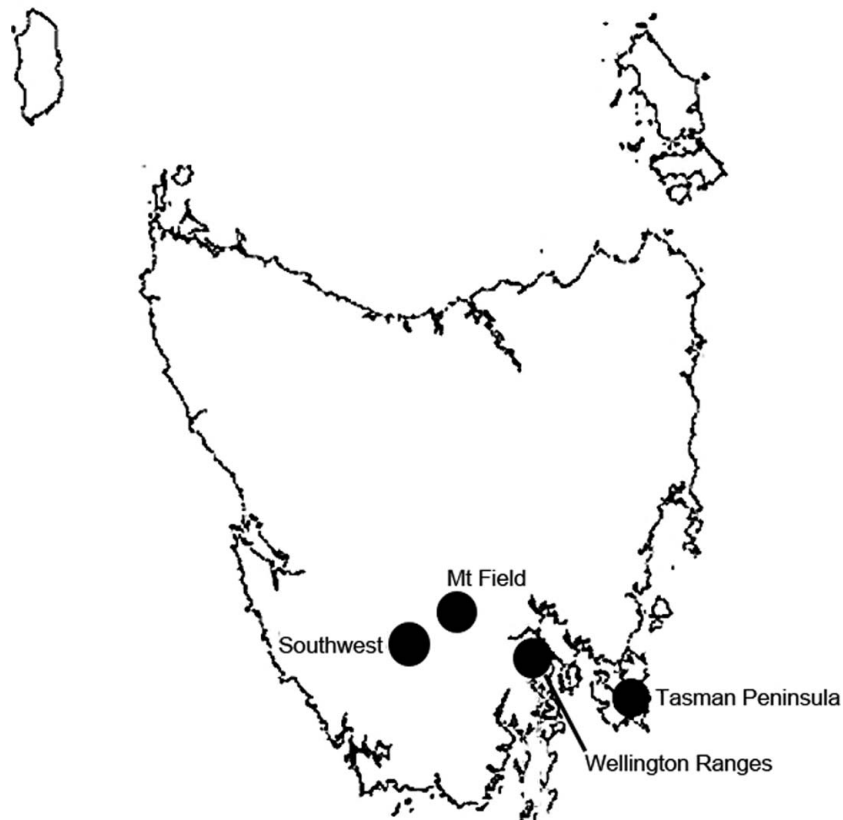


Fig. 1. Map of Tasmania showing study sites. The four study sites were monitored with remote cameras twice a year from 2009 to 2011 (excluding the Wellington Ranges site, which was monitored only once in 2009).

agement interventions on invasive species.

METHODS

Study sites

Four study sites, referred to henceforth as Southwest, Mt Field, Tasman Peninsula and Wellington Ranges, were selected in southern Tasmania between the 51 and 55 northing grid on the GDA 94 map datum based on similarities in flora, fauna and land use (Fig. 1). Yearly average rainfall in the 10 years preceding our first survey, collected by the Bureau of Meteorology (www.bom.gov.au), and recorded at the closest weather station to our study sites, was: Southwest, 145 cm; Mt Field, 78 cm, Tasman Peninsula, 67 cm; and Wellington Ranges, 84 cm. Tasmanian devils with facial tumour disease have been recorded in the Southwest, Mt Field, and the Wellington Ranges, but there were no records from the Tasman Peninsula before or during the course of

our study. Further study site details can be found in Lazenby and Dickman (2013).

Camera surveys

Standardized remote camera surveys were carried out at all sites from 2009 to 2011. The protocol has been described in detail by Lazenby and Dickman (2013) but, in brief, we deployed 15–18 DigitalEye 7.2 trail cameras (Pixcontroller) in a systematic grid pattern 1–1.5 km apart at the four study sites, allowing them to operate for seven nights per survey in 2009, and 14 nights per survey in 2010 and 2011. Cameras were deployed at the same locations for each of the surveys. Surveys commenced in April and June in each of the three years of the study. We did not deploy cameras in the Wellington Ranges in April 2009, resulting in 23 site surveys in total (Table 1).

The cameras featured an infrared flash, were triggered to take a photograph by motion and

Table 1. Survey effort with remote cameras for surveys conducted at four study sites from 2009 to 2011, where SW = Southwest, Mt F = Mt Field, TP = Tasman Peninsula, WR = Wellington Ranges. Minimum no. camera trap nights were calculated by taking the date of the last recorded photograph on a camera that was not operational on the day of collection as the last operational day of the camera for that survey. The Mt F Jun 2009 survey was repeated in July 2009 to account for the low number of camera trap nights; however, access to a portion of the site was still limited, resulting in a similarly low minimum number of camera trap nights.

Study site survey	Start date	Total no. nights used for analysis	No. cameras deployed	Minimum no. camera trap nights†
SW Apr 2009	30/3/2009	7	18	120
SW Jun 2009	17/6/2009	7	17	105
SW Apr 2010	26/3/2010	14	18	226
SW Jun 2010	25/6/2010	14	17	221
SW Apr 2011	25/3/2011	14	16	222
SW Jun 2011	14/6/2011	14	16	205
Mt F Apr 2009	7/4/2009	7	18	106
Mt F Jun 2009	9/6/2009	7	15	64
Mt F Apr 2010	20/4/2010	14	16	216
Mt F Jul 2010	16/7/2010	14	17	201
Mt F Apr 2011	9/4/2011	14	17	229
Mt F Jul 2011	30/6/2011	14	16	177
TP Apr 2009	19/4/2009	7	16	96
TP Jun 2009	28/6/2009	7	17	98
TP May 2010	6/5/2010	14	17	236
TP Aug 2010	2/8/2010	14	16	200
TP Apr 2011	26/4/2011	14	17	226
TP Jul 2011	17/7/2011	14	16	221
WR Sep 2009	19/9/2009	14	17	223
WR May 2010	24/5/2010	14	16	210
WR Aug 2010	26/8/2010	14	16	228
WR May 2011	11/5/2011	14	16	225
WR Aug 2011	3/8/2011	14	16	210

† Accounting for malfunctions.

heat, and were set to record in 'trail mode' so that photographs were taken at least once every second after they had been activated by an animal. They recorded photographs for the full 24-hour cycle each day. A scent lure and food reward consisting of Juro tuna emulsion (Juro Oz Pro tackle, Australia) and fish-based tinned cat food in jelly was placed 1.5–2.0 m from each camera unit for each survey. Two dessert spoons of tinned cat food and 50–75 mL of tuna emulsion were spread in a 0.25-m² area that was the focal point for the camera. Tuna emulsion was also applied on 1–2 branches up to 2 m off the ground above the focal point of the camera to maximize the chances of the lure scent entering air streams. Additional tuna emulsion was placed in a perforated film canister that was staked into the ground after the first two standard camera surveys conducted in 2009. We checked baits one week after the initial setup during the 2010 and 2011 survey seasons to re-bait, and to replace camera batteries and memory cards.

We collected >58,500 photographs over the

course of our surveys. These were stored in an Access database that consisted of six relational tables, and included information pertaining to the species of animal photographed, surety of species identification, 24-h survey period, survey and site identification. None of the small mammals that we photographed exhibited individual-specific markings such as coat patterns, and therefore our analyses were restricted to estimates of species activity rather than abundance. Surety of species identifications was scored 1, 2, or 3 based on the visibility of the key characteristics of each species, as follows: swamp rats—an approximately equal head-body and tail length, and ears set close to the head (Taylor and Calaby 1988); long-tailed mice—large rounded ears, tail longer than the head-body length, with a convex head profile (Driessen and Rose 1999); black rats—long elongated ears, tail longer than the head-body length, with a concave head profile (Menkhorst and Knight 2001). A score of 1 was given when all characteristic features were visible and consistent with a species, and 2 when most characteristic features were visible. Unidentified

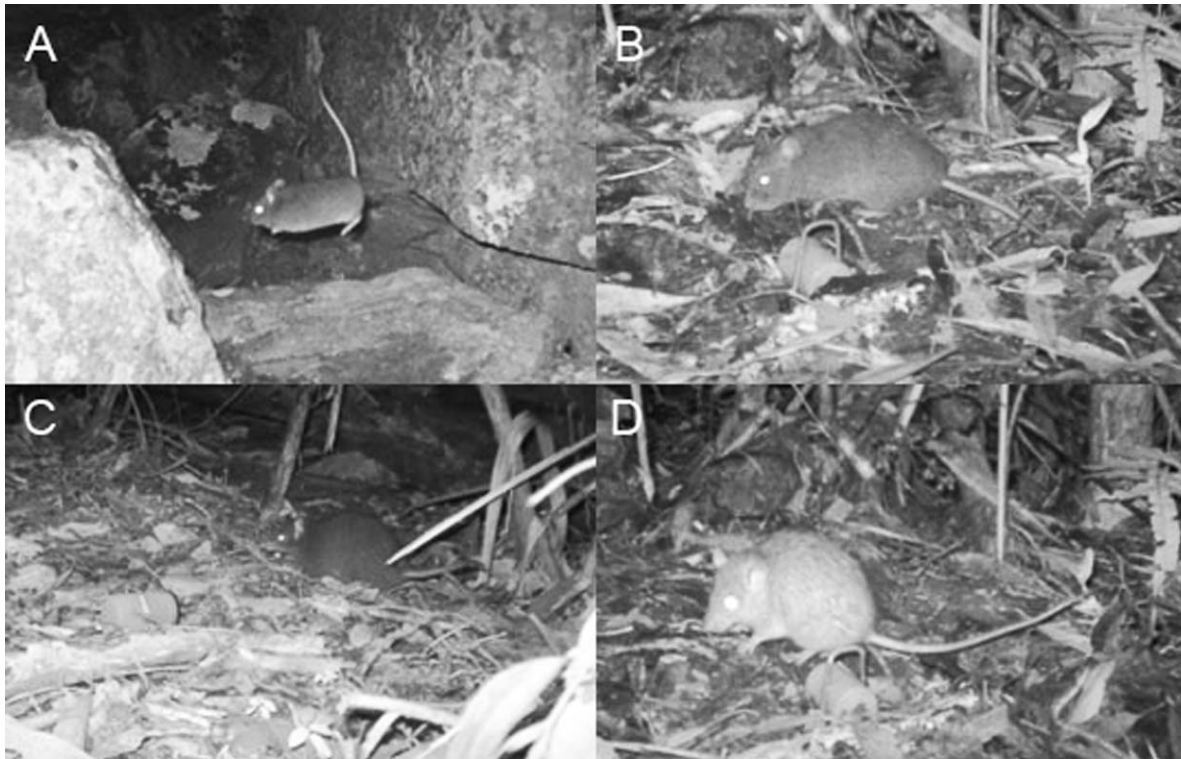


Fig. 2. Examples of photographs of small mammals taken on remote cameras that were identified with a high level of confidence to species. Species are (A) long-tailed mouse, *Pseudomys higginsi*, (B) swamp rat, *Rattus lutreolus velutinus*, (C) dusky antechinus, *Antechinus swainsonii*, and (D) black rat, *Rattus rattus*. The above photos constitute examples of high-confidence identifications because there is a clear view of head profile and body to tail-length ratio. Photographs have been cropped.

occurrences were scored as 3. Identification of the swamp rat was made on the assumption that the camera sites were outside the known range and habitat of the similar-looking broad-toothed mouse *Mastacomys fuscus* (Menkhorst and Knight 2001), and the presence of only the swamp rat in our earlier live-trapping at each of the study sites (Lazenby and Dickman 2013). Only occurrences that scored 1 were used in analyses because misidentification of species could produce spurious results (Fig. 2). We restricted our analyses to commonly recorded small mammals; other species were recorded occasionally at cameras (e.g., dusky antechinus *Antechinus swainsonii*), but too infrequently to include in our models.

Analyses

We used generalized linear mixed modelling (GLMM) to ascertain which of our nominated factors best described small mammal counts at

cameras. Detectability is an important source of variation in data when detection probabilities are less than one (MacKenzie et al. 2002). Multiple-species occupancy modelling, where detection probability is explicitly modelled after repeat visits for more than one species, is a sound conceptual approach for modelling the potential for one or more species to be associated with changes in the probability of site occupancy or detection of another (MacKenzie et al. 2004, Luiselli 2006, Bailey et al. 2009, Richmond et al. 2010, Waddle et al. 2010, Wagner et al. 2013). However, we were unable to use a multiple-species approach within an occupancy framework, nor model the probability of site occupancy of one species as a factor of the site occupancy of another within single species models because, despite having a relatively low detection probability compared to our other modelled species, feral cats had a high probability of site occupancy.

cy. This meant that we could not effectively model the probability of site occupancy or detection of alternative species in the absence of cats. Estimates of the probability of site occupancy and detection for feral cats and their associated 95% confidence intervals at each site under a supported single species multi-season occupancy model, where the probabilities of site occupancy and detection were held constant (as presented in Lazenby et al. 2014), were: Southwest probability of site occupancy, Ψ 0.64 (0.40–0.82), p -detection 0.08 (0.06–0.12); Mt Field, Ψ 0.50 (0.23–0.75), p -detection 0.09 (0.06–0.13); Tasman Peninsula, Ψ 0.63 (0.44–0.78), p -detection 0.14 (0.11–0.17); Wellington Ranges, Ψ 0.63 (0.42–0.80), p -detection 0.12 (0.09–0.15).

Whilst not explicitly modelling detection probabilities, generalized linear mixed models (GLMMs) can be tailored to investigate relative changes in counts that arise from changes in detection probability between species at sites through different seasons. GLMMs can account for random effects in counts at individual survey devices, as well as potential correlations between counts through time and across replicated sites (Bolker et al. 2008). Thus, use of GLMMs for count data, where sources of variation in detection other than those arising from other species are either held constant (e.g., through standardised survey effort and placement of survey devices at the same locations across seasons) or replicated (e.g., by use of multiple study sites), can be expected to provide robust biological representations of modelled systems.

We constructed an *a priori* list of factors that might reasonably alter small mammal behavior, as follows: above or below average rainfall and minimum and maximum temperature in the 6 or 12 months preceding a survey, and the count of potential predators and competitors during the same camera survey. We included Tasmanian devils and feral cats as potential predators, and the long-tailed mouse, swamp rat, and black rat as potential competitors depending on which small mammal was the dependent variable. Correlation analyses showed the climatic factors to be significantly positively correlated, so we used the difference from the average rainfall in the six months preceding each camera survey as our only climatic factor. Rainfall data were collected by the Tasmanian Bureau of Meteorol-

ogy, and accessed from the nearest weather station to each of our study sites. We calculated above or below average rain for the six months preceding a survey by calculating the 10-year average for relevant six month periods, and then subtracting this from the relevant six months preceding each survey. Data were transformed for inclusion in GLMMs by adding a constant so that all values were positive.

The numbers of 24-h periods in which a species visited a camera within a season at a site were tallied to produce a count; i.e., multiple visits within one 24-h period counted as one, but visits across four 24-h periods to a camera within a season at a site counted as four. Twenty-four-hour periods were defined as the 24 h between 17:00 hours and 17:00 hours the next day (i.e., 5 pm to 5 pm) because, rather than calendar dates, a continuous night is likely to have most biological significance to a wild animal. We limited our counts of species' activity to 24-h periods to reduce the potential for 'trap happy' responses (that is, individuals that respond to food lures by increasing their activity out of proportion to their baseline activity or abundance) to minimize potential skew in the data. Expressing the count of occurrences of any given taxon as an average across survey periods would have accounted for camera failures (such as those caused by flat batteries); however, it would also have resulted in proportional data. Such data, which in our case were skewed towards zero, are challenging to model owing to the difficulty of defining an appropriate distribution for the dependent variable; in addition, transformation of count data may be inappropriate for GLMMs (O'Hara and Kotze 2010). Our emphasis, which was reflected in the structure of the GLMMs and the interpretation of their output, thus was on relative changes in counts between species and seasons at sites so that, despite small differences in camera survey effort, we had the same survey effort for each species. This approach applies also to the increase in camera survey effort from seven nights in 2009 to 14 nights in 2010 and 2011.

We constructed our GLMMs in SPSS 21 (SPSS, Chicago, Illinois, USA) such that each site was treated as a subject with individual cameras nested within each site. We tested and included camera as a random variable to account for

possible differences between cameras within each of the sites (Tobler et al. 2015). We accounted for potential correlation through time by specifying season as a repeated measure. Counts of the long-tailed mouse, swamp rat, black rat, Tasmanian devil, and feral cat, with rainfall, were included as independent variables in full models when they were not the dependent variable. An example of SPSS syntax for a full model is included in the Appendix.

Appropriate distributions for the dependent variables and covariance matrices were selected by comparing AIC_c values for the full GLMMs in SPSS (Cameron and Trivedi 2013). Distributions tested were Poisson and negative binomial, both with a log link. Poisson distributions are generally used to describe counts of occurrences in a fixed period of time, whereas negative binomial distributions are more appropriate when the dependent variable is a count with high variance. Negative binomial distributions yielded the lowest AIC_c values for each dependent variable, consistent with the mean and variance of their counts: long-tailed mouse, mean = 0.360, variance = 1.238; swamp rat, mean = 0.720, variance = 3.668; black rat, mean = 0.700, variance = 3.382. Models that included black rats as either the dependent variable or a fixed effect were restricted to three sites because black rats were never detected at the Southwest study site. As a consequence, we constructed two model sets represented by five GLMMs: one each with the long-tailed mouse and swamp rat as the dependent variable across four sites, and one each with the black rat as either the dependent variable or a fixed effect for the two native small mammals across three sites. We considered it important to include two sets of models rather than focus on three sites because the Southwest was an important source of data, and any lack of congruence between the two sets of models was an important source of information for their interpretation.

Covariance matrices that we tested for residuals from repeated measures analyses were unstructured (a completely general covariance matrix), diagonal (heterogeneous variances and no correlation between elements) and first order autoregressive (observations on the same subject that are close in time are more highly correlated than measurements at other times). Models with

first order autoregressive covariance structures had the lowest AIC_c values, but the suitability of an unstructured matrix could not be ascertained because these models did not converge. We tested two types of covariance matrix for the random variable, and these were variance components (assigning a scaled identity structure to each of the specified random effects) and first order autoregressive (which could take into account any potential spatial correlation between cameras within sites). GLMMs with a variance component matrix for the random variable for the long-tailed mouse as the dependent variable had the lowest AIC_c value. Variance component matrices when the black rat was the dependent variable did not converge and, therefore, we used a first order autoregressive. Models with either matrix for the random variable for the swamp rat did not converge, so we modelled this species without a random variable.

After ascertaining the structure of our full models, we sequentially trimmed non-significant fixed effects from them (Gruder et al. 1993) such that all effects within two AIC_c points of the lowest value were considered important. Bayesian Information Criteria (BIC_c) are also shown for completeness; all BIC_c results were congruent with those using AIC_c. Two sets of models were constructed; one set where all species excluding black rats were included as a fixed effect across four sites, and the other set where black rats were included as a fixed effect and were themselves modelled as the dependent variable across three sites.

RESULTS

The count of occurrences of modelled species varied across study sites (Table 2). There was a low count of devils in the Wellington Ranges, the Tasman Peninsula recorded the highest counts of native small mammals and feral cats, and Mt Field had the highest count of devils (Table 2). These data were the basis for the subsequent GLMM models.

Long-tailed mouse

Swamp rats and feral cats were the most important factors influencing counts of the long-tailed mouse across the four study sites (Table 3A). The effect of swamp rats was relatively large

Table 2. Occurrences of modelled species from repeated visits to remote camera stations at four study sites in Tasmania from 2009 to 2011. An occurrence is expressed as a visit within a 24-h period.

Species	Southwest	Mt Field	Tasman Peninsula	Wellington Ranges
Black rat	0	39	74	76
Long-tailed mouse	67	12	61	24
Swamp rat	143	12	153	31
Feral cat	58	45	84	76
Tasmanian devil	126	138	26	2

and positive compared to that of feral cats, which was overall negative but with wide confidence intervals (Fig. 3A). Tests for black rats as a fixed effect in long-tailed mouse and swamp rat models at three sites revealed that black rats, feral cats and especially devils had important negative effects, whereas the swamp rat had a positive effect on counts of long-tailed mice (Table 3B, Fig. 3B).

Swamp rat

The long-tailed mouse and devil were important factors for the swamp rat at the same four sites (Table 4A). A model with just the long-tailed mouse had marginally lower AIC_c and BIC_c values than the model that included the devil, but as criterion Δ values were < 2 , the effects of the devil were considered important to include. The long-tailed mouse had a relatively large and positive fixed effect compared to the devil, which had an overall negative effect but with large confidence intervals (Fig. 4A). Devils had an

important negative effect and rainfall a positive effect on swamp rat counts across the three study sites (Table 4B, Fig. 4B).

Black rat

Swamp rats and devils were important negative influences on counts of black rats across three study sites (Table 5, Fig. 5).

DISCUSSION

Our results using remote cameras provide mixed support for our initial hypotheses. As expected, there were correlations in photographic rates between predators, prey, and conspecifics. Of themselves, these observations are not proof of behavioral interactions, but they do show promise for developing testable hypotheses in ecosystems where limited faunal knowledge is available. As discussed below, we uncovered unexpected patterns in species counts that allowed us to develop more targeted research

Table 3. Information selection results for GLMMs describing long-tailed mouse counts in Tasmania at (A) four study sites, and (B) three sites that include the black rat as a fixed effect. Sequential trimming of fixed effects was used to select the final model, whereby effects within two AIC_c points of the lowest value were considered important. Models are listed in decreasing AIC_c order.

Fixed effects	Random effects	AIC _c	BIC _c
(A) Four study sites			
SR, FC, TD, RF	site and camera	1800.157	1815.657
SR, FC, TD, RF	none	1857.338	1865.110
SR, FC, RF	site and camera	1797.803	1813.314
SR, RF	site and camera	1796.472	1811.994
SR, FC	site and camera	1789.420	1804.942
(B) Three sites			
BR, SR, FC, TD, RF	cameras within sites	1355.946	1370.111
BR, SR, FC, TD, RF	none	1395.298	1402.412
BR, SR, RF, TD	cameras within sites	1355.330	1369.511
BR, SR, FC, RF	cameras within sites	1355.123	1369.303
SR, FC, TD, RF	cameras within sites	1356.910	1371.090
BR, SR, FC, TD	cameras within sites	1348.411	1362.595

Notes: SR = swamp rat, FC = feral cat, TD = Tasmanian devil, RF = rainfall, BR = black rat AIC_c = Akaike Information Criterion corrected for small sample size, BIC_c = Bayesian Information Criterion corrected for small sample size. Bold type indicates the best model.

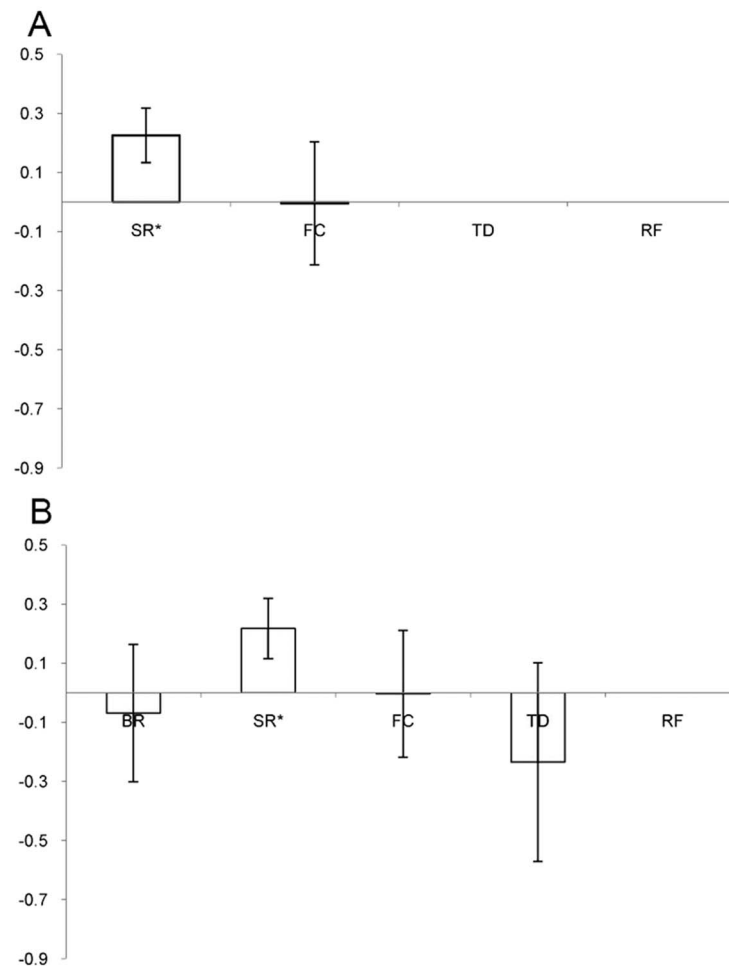


Fig. 3. Estimates of fixed effects from the best fitted GLMM as determined by AIC_c values for the long-tailed mouse across (A) four sites and (B) three sites that include the black rat as a dependent variable. Bars denote 95% confidence intervals. SR = swamp rat, FC = feral cat, TD = Tasmanian devil, BR = black rat, RF = rainfall. Significant effects are marked with an asterisk. For (A), the intercept value was -2.431 ± 0.432 SE, negative binomial value was 5.400. Residual values (camera by site) were: AR1 diagonal = 0.281 ± 0.024 SE, AR1 Rho = 0.008 ± 0.073 SE. Random values (cameras within sites) were: var(intercept) 0.473 ± 0.853 SE, var(camera) 2.783 ± 0.705 SE. For (B), the intercept value was -2.609 ± 0.472 SE, negative binomial value was 4.111. Residual values (camera by site) were: AR1 diagonal = 0.262 ± 0.026 SE, AR1 Rho = 0.028 ± 0.089 SE. Random values (cameras within sites) were: var(intercept) = 0.339 ± 0.597 SE, var(camera) 3.044 ± 0.911 SE.

questions that would not have been possible without the use of remote cameras. Whilst cameras were a useful tool in our system, visitation by multiple species may be a shortcoming, especially where measuring the effect of a subordinate species, such as a mesopredator on prey, is important. The feral cat in our system is a good example of this; it is likely that the extent of behavioral change elicited by feral cats on small

mammals was obscured by devils. This was an a priori expectation that we were able to make because we had previously modelled the pattern of visitation between feral cats and devils (Lazenby and Dickman 2013).

In specific regard to our study system, swamp rats had a positive effect on long-tailed mouse counts, in contrast to our prediction that the ostensibly dominant rats would reduce counts of

Table 4. Information selection results for GLMMs describing swamp rat counts in Tasmania at (A) four study sites and (B) three sites that include the black rat as a fixed effect. Sequential trimming of fixed effects was used to select the final model, whereby effects within two AIC_c points of the lowest value were considered important. Models are listed in decreasing AIC_c order.

Fixed effects	Random effects	AIC _c	BIC _c
(A) Four study sites			
LTM, FC, TD, RF	site and camera	no convergence	no convergence
LTM, FC, TD, RF	none	1661.979	1669.751
LTM, TD, RF	none	1657.862	1665.640
LTM, TD	none	1653.102	1660.885
LTM	none	1651.751	1659.540
(B) Three sites			
BR, LTM, FC, RF	cameras within sites	no convergence	no convergence
BR, LTM, FC, TD, RF	none	1312.105	1319.219
BR, LTM, TD, RF	none	1308.098	1315.220
LTM, TD, RF	none	1308.631	1315.760
TD, RF	none	1280.375	1287.511

Notes: LTM = long-tailed mouse, FC = feral cat, TD = Tasmanian devil, RF = rainfall, BR = black rat, AIC_c = Akaike Information Criterion corrected for small sample size, BIC_c = Bayesian Information Criterion corrected for small sample size. Bold type indicates the best model.

long-tailed mice. In addition, the long-tailed mouse had a positive effect on swamp rat counts in a modelled system without black rats, again contrasting with our expectation that there would be a negative effect, or no effect, of the long-tailed mouse on swamp rat counts. On the other hand, as expected, black rats had a negative effect on the long-tailed mouse although, in contrast to expectations, there was no effect of the black rat on swamp rats and a negative effect of swamp rats on black rats. Feral cats had an important effect in long-tailed mouse models. Surprisingly devils had an important negative effect in all small mammal models, excluding the long-tailed mouse in systems where the black rat was not included.

When looking at the effects that were important in describing counts of small mammals, we found that long-tailed mouse counts were affected by the greatest number of fixed effects, but only one of these effects, the swamp rat, was positive. Swamp rats were the only small mammal to be affected positively by above average rainfall in the six months preceding camera surveys, and this result was restricted to models that included black rats as a fixed effect.

All our GLMM models accounted for variation within sites between seasons, and our black rat and long-tailed mouse models had the capacity to account for variation between cameras (i.e., they included a random variable). This was not the case for swamp rat models, as these did not

converge when a random variable was incorporated. Lack of convergence is a common phenomenon when GLMMs are used in biological applications, and can arise when random effects structures are too complicated, or if there is collinearity between two or more independent variables (Thiele and Markussen 2012). Models that included a random variable converged for other small mammals, perhaps indicating that there may have been collinearity between two or more independent variables in the swamp rat models. We avoided redefining these models to address potential collinearity, instead modelling the swamp rat without a random variable in order to apply a consistent approach across the three small mammal species. As swamp rats were the most commonly recorded small mammals at cameras, we are reasonably confident that our swamp rat models are a robust representation of the effects of the tested variables on the behavior of this species.

There was congruence between our two sets of models (i.e., those that were based on three sites and those that were based on four), with three exceptions. The long-tailed mouse had a positive effect on swamp rat counts across four sites, but was not identified as an effect in models that included the black rat across three sites. Rainfall was an important positive effect in swamp rat models across three but not four sites, and similarly devils were an important effect in long-tailed mouse models that were based on

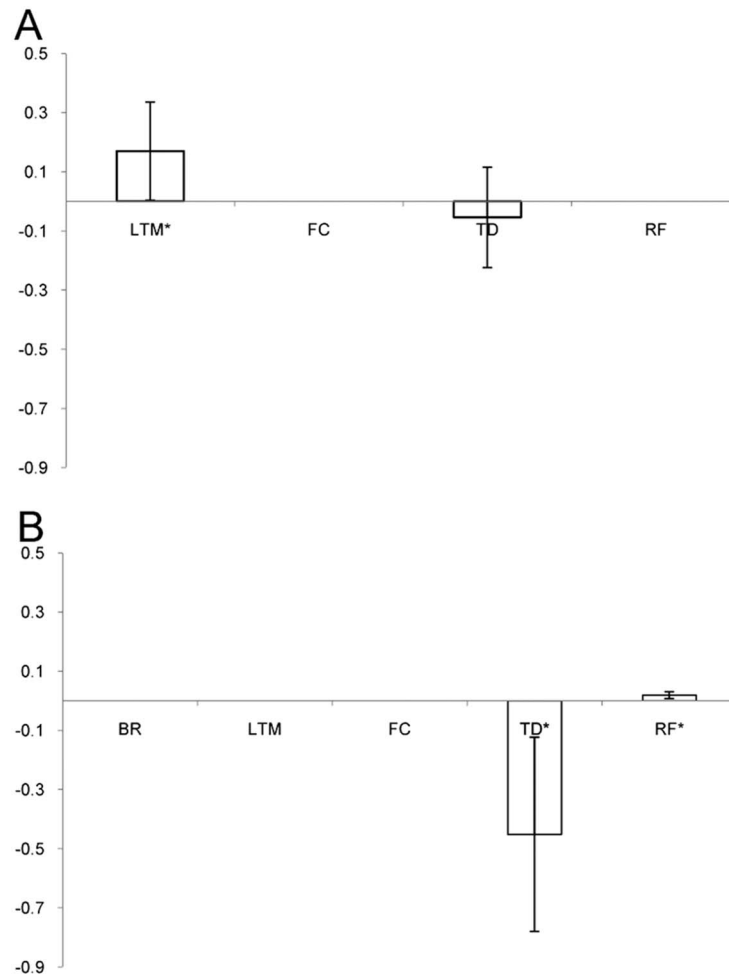


Fig. 4. Estimates of fixed effects from the best fitted GLMM as determined by AIC_c values for the swamp rat across (A) four sites and (B) three sites that include the black rat as a fixed effect. Bars denote 95% confidence intervals. LTM = long-tailed mouse, BR = black rat, FC = feral cat, TD = Tasmanian devil, RF = rainfall. Significant effects are marked with an asterisk. For (A), the intercept value was -0.230 ± 0.192 SE, negative binomial value was 7.237. Residual values (camera by site) were: AR1 diagonal = 0.694 ± 0.059 SE, AR1 Rho = 0.451 ± 0.047 SE. Random effects were not included in this model due to lack of convergence. For (B), the intercept value was -1.156 ± 0.379 SE, negative binomial value was 9.019. Residual values (camera by site) were: AR1 diagonal = 0.623 ± 0.059 SE, AR1 Rho = 0.374 ± 0.059 SE. Random effects were not included in this model due to lack of convergence.

three but not four sites. There are clear explanations for the former two differences between models sets. Firstly, our models may not have been able to determine the importance of the long-tailed mouse in describing swamp rat counts across three sites because relatively low counts were recorded for the long-tailed mouse at two of the three sites, Mt Field and Wellington Ranges. Secondly, in terms of rainfall, the

Southwest experienced the highest average precipitation of all the sites, and therefore rainfall may only be an important determinant of swamp rat counts at drier sites. There is no obvious explanation as to why devils would be an important descriptor of long-tailed mouse counts in models based on three sites and that include black rats rather than models based on four sites that do not include black rats. Perhaps black rats

Table 5. Information selection results for GLMMs describing black rat counts at three study sites in Tasmania. Sequential trimming of fixed effects was used to select the final model, whereby effects within two AIC_c points of the lowest value were considered important. Models are listed in decreasing AIC_c order.

Fixed effects	Random effects	AIC_c	BIC_c
LTM, SR, FC, TD, RF	cameras within sites	1395.384	1409.549
LTM, SR, FC, TD, RF	none	1299.723	1306.837
LTM, FC, TD, RF	none	1300.258	1307.380
LTM, SR, FC, RF	none	1305.652	1312.773
LTM, SR, TD, RF	none	1291.069	1298.190
SR, TD, RF	none	1286.627	1293.756
SR, TD	none	1262.452	1269.588

Notes: LTM = long-tailed mouse, SR = swamp rat, FC = feral cat, TD = Tasmanian devil, RF = rainfall, AIC_c = Akaike Information Criterion corrected for small sample size, BIC_c = Bayesian Information Criterion corrected for small sample size. Bold type indicates the best model.

are an important predictor variable for long-tailed mouse counts, and without them included in models, the full extent of the importance of other predictor variables is not realised. For the remainder of the discussion, we treat devils as important descriptors of long-tailed mouse counts.

GLMMs for the small mammals were indicative of three way interactions. The positive effect of long-tailed mouse counts on swamp rats, and vice versa, may indicate that the two species were responding positively to a similar environmental variable, for example, food. In the case of the long-tailed mouse, the positive effect of swamp rats may also be a result of an interaction

between swamp rats and black rats whereby the swamp rat alters black rat behavior to reduce the negative effect of this species on the long-tailed mouse. Although we had initially expected the larger black rat to dominate the swamp rat in encounters, potential dominance of the swamp rat over its congener is not entirely surprising: swamp rats dominate similar-sized and even larger bush rats *Rattus fuscipes* in enclosures and under field conditions (Maitz and Dickman 2001). In addition, the spatial dominance that has been observed between swamp rats and the long-tailed mouse (Monamy and Fox 1999) was most apparent during the breeding season when female swamp rats apparently excluded male

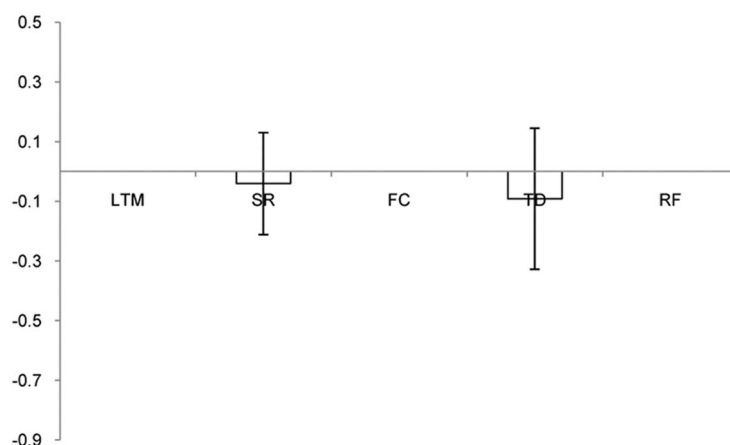


Fig. 5. Estimates of fixed effects from the best fitted GLMM as determined by AIC_c values for the black rat across three sites in southern Tasmania. Bars denote 95% confidence intervals. LTM = long-tailed mouse, SR = swamp rat, FC = feral cat, TD = Tasmanian devil, RF = rainfall. The intercept value was -0.306 ± 0.244 SE, negative binomial value was 7.942. Residual values (camera by site) were: AR1 diagonal = 0.756 ± 0.076 SE, AR1 Rho = 0.445 ± 0.059 SE. AIC_c scores indicated that the random effect of cameras within sites was not important for this model set.

rats and the long-tailed mouse from habitat patches with the greatest cover. We set our cameras in areas of sparse undergrowth to obtain clear photographs of the study species, and to avoid cameras being triggered by moving vegetation. As a result, we probably did not sample the dense habitat from which female swamp rats have been observed to exclude the long-tailed mouse. Black rats also prefer dense leaf litter and understorey vegetation (Cox et al. 2000), and it is possible that they too would face exclusion from such habitats by the swamp rat.

While our results do not have the strength of inference of a manipulative experiment, they do provide an indication that native small mammals could be important in limiting the behavior of the introduced black rat. The swamp rat may be an important guardian against the black rat for the long-tailed mouse, although the balance of competitive advantage over the black rat also may be dynamic. This potential complexity is suggested by the strong positive association between the swamp rat and long-tailed mouse, and the importance of rainfall in swamp rat models. If the source of this positive association, for example food availability (as determined by climate) or habitat quality were perturbed, it may then present a competitive opportunity for the black rat. Our study focussed on relative changes in species counts at the same camera sites through time in study sites where no major disturbances (e.g., timber harvesting or clearing) were taking place, and therefore habitat was a constant variable. However, it has been suggested that black rats are associated with disturbed habitats compared to native Australian small mammals (Banks and Hughes 2012). In this regard, habitat disturbance may affect the dynamics of the interaction between the three species. Environmental changes such as those caused by climate, CO₂ enrichment, biotic invasions, and land use have been shown to affect species interactions including competition, intensity of pathogen infection, mutualism, and herbivory in global ecosystems (Tylianakis et al. 2008).

Clearly, understanding the ecological relationships between our three study species of small mammals would benefit from more detailed investigation. Questions specific to management of black rats that arise from our camera surveys,

and that could be addressed to increase knowledge of the small mammal component of our system, are: do the long-tailed mouse and swamp rat respond positively to the same or similar environmental variables in habitats that contain black rats, and if so how is this affected by microhabitat; does the black rat exert competitive dominance over the long-tailed mouse, and if so what is the impact of this on the long-tailed mouse's population viability; do swamp rats limit black rat distribution and abundance, and if so how is this competitive advantage affected by habitat; if swamp rats do dominate black rats, how is this competitive dominance affected by changes in rainfall? Removal methods are a potential option for addressing some of the above questions. For example, in a different system, the abundance of native bush rats *Rattus fuscipes* increased following the removal of black rats, and black rats were unable to re-establish following increases in the abundance of bush rats (Stokes et al. 2009).

Our results showed that devils had an important overall negative effect on small mammal counts. We did not expect this given devils have co-occurred with native species of small mammals for many thousands of generations, and small mammals are found at a relatively low frequency in their diet compared to feral cats. However, it is likely that avoidance is a key behavior that has been selected for in small mammals (e.g., Kovacs et al. 2012), hence resulting in the negative effect of devils on small mammal counts that we observed. The results highlight the value of monitoring the broader ecological impacts of the decline of this species, and also the localized impacts of devils that are associated with programs such as the establishment of island populations that are carried out to establish viable disease-free populations (DPIPWE 2010).

Effect size estimates for both devils and cats had large confidence intervals, which is not surprising given the dynamics of predator visitation to cameras. Sources of variation include behavioral interactions between devils and cats where devils suppressed cat activity at cameras and may have had an inadvertently positive effect on small mammal counts if the effect of cats otherwise would have been greater than that of devils, and an increase in predator

activity associated with cameras where small mammals were more active. This latter source of variation is possible because we summarized our data to a total count for each species during each session. Therefore, our analytical approach was limited to detecting relative change in small mammal counts between sessions rather than fine-scale behavioral changes that may have occurred within sessions. Notwithstanding the behavioral dominance that may be exerted by devils over cats, it is important to note that devils may be more attracted to, and effective at scavenging from, the bait food and scent sources that we deployed at the remote camera sites (Owen and Pemberton 2005, Denny and Dickman 2010). Despite this, feral cats were still an important effect in models describing long-tailed mouse counts. Questions specific to management of feral cats and devils that arise from our camera surveys within our system of study are: what is the level of predation of devils and feral cats on each of the small mammals studied, and how does this affect the population viability of each of the small mammals; and is feral cat predation mediated by devils?

In terms of prioritizing research, we found that long-tailed mouse models incorporated the most fixed effects, indicating that this endemic species may be particularly susceptible to perturbations in the forest ecosystem. Therefore, we suggest that more explicit research investigations focus first on the long-tailed mouse. Understanding the extent of feral cat and black rat interactions and impacts within our modelled system is important in determining firstly whether management intervention is needed, secondly the extent and form needed to effectively reduce the impacts of these invasive species, and thirdly to identify potentially unexpected outcomes from management intervention. An important component of this research, and one that may not have been identified using remote cameras in our system, is whether feral cats exert downward pressure on black rats, and whether this pressure compensates for the apparent downward pressure that feral cats exert on the long-tailed mouse by reducing the pressure that black rats exert on the long-tailed mouse. Insight into this question could be gained by using methods such as exclusion fencing or replicated removal experiments.

Conclusions

We used remote cameras and then GLMMs to identify factors that best describe counts of commonly recorded small mammals at our camera stations. Our results indicate the potential for ecological interactions among species and their predators and competitors, and serve to identify areas where experimental trials are justified. We propose that the impact of the feral cat on small mammals warrants further research, that black rats may be an important threat to the endemic long-tailed mouse which is moderated in part by swamp rats, and that small mammal populations should be monitored and managed in response to localized recovery efforts for the Tasmanian devil. We show that the long-tailed mouse may be particularly susceptible to changes in the forest system given the broad range of factors that affected counts of this species at cameras. In interpreting our results, we note that additional factors such as avian and reptilian predators, and other climatic variables that were not included in our models, may also have important interactions with the study species. Despite such caveats, we conclude that remote cameras can provide considerable insight into interactions that may occur between species, including interactions that had not been previously suspected, and thus can provide managers with more informed options about how best to intervene to achieve conservation or control outcomes.

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SUPPLEMENTAL MATERIAL

ECOLOGICAL ARCHIVES

The Appendix is available online: <http://dx.doi.org/10.1890/ES14-00522.1.sm>