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Research

Trophic rewilding establishes a landscape of fear: Tasmanian devil introduction increases risk-sensitive foraging in a key prey species

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Global declines of large carnivores have reduced the 'landscape of fear' that constrains the behaviour of other species. In recent years, active and passive trophic rewilding have potentially begun restoring these lost top–down controls. The Tasmanian devil *Sarcophilus harrisii* has declined severely due to a novel transmissible cancer. In response to extinction fears, devils were introduced to the devil-free Maria Island, where their abundance rapidly increased. We tested how this introduction influenced risk-sensitive foraging in the common brushtail possum *Trichosurus vulpecula*, a major prey species for devils, using giving-up densities (GUDs). Before the introduction of devils, possum GUDs on Maria Island were indistinguishable from the long-diseased region of Tasmania, where devils have been rare since ~2000. Three years after devil introduction, GUDs were 64% higher on Maria Island than the control region, demonstrating that after an initial period of high mortality, possums quickly adopted risk-sensitive foraging behaviours. Devil activity across Maria Island was variable, leading to a heterogeneous landscape of fear and highlighting that top predators must be at functional densities to elicit behavioural responses from prey. Our study provides strong evidence that top predators modify the behaviour of prey by instilling fear, causing rapid ecological change following recoveries.

Key words: apex predator, giving-up densities, landscape of fear, predator–prey, trophic cascade, trophic rewilding

Introduction

Large carnivores have declined severely across much of the earth (Ripple et al. 2014), leading to weakened landscapes of fear (Ritchie and Johnson 2009). Fear alone is capable of structuring communities. For example, racoons *Procyon lotor* exposed to large-carnivore vocalisations reduced their foraging, which led to an increase in their prey, and a decrease in the prey of racoons' prey (Suraci et al. 2016). Trophic rewilding has gained recent popularity and aims to restore natural top–down processes to promote self-regulating, biodiverse ecosystems (Svenning et al. 2016, Derham et al. 2018). Passive rewilding has occurred too, as top predators have begun recovering

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across parts of Europe (Chapron et al. 2014), North America (Gompper et al. 2015) and Asia (Athreya et al. 2013), and this has brought hope that predators may once again exert top–down control on ecosystems (Svenning et al. 2016). Although rewilding is now popular, empirical research on its effects are rare, with the literature dominated by opinion pieces and essays (Svenning et al. 2016).

Tasmania's top predator, the Tasmanian devil *Sarcophilus harrisii*, has suffered severe population declines over a ~25-year period following the emergence of a transmissible cancer, devil facial tumour disease (DFTD). DFTD has spread across ~80% of the devil's range (Fig. 1), causing average population declines of 80% (Lazenby et al. 2018) and up to 95% in some long-diseased areas (Hollings et al. 2014). Where devils have declined severely, the common brushtail possum *Trichosurus vulpecula*, a key prey species of devils, now shows relaxed risk-sensitive foraging behaviour, as measured by a giving-up density (GUD) experiment (Hollings et al. 2015). In GUD experiments, animals are offered artificial food patches in areas with varying predation risk, and the amount of food remaining when the forager 'gives-up' foraging is used to measure the perceived risk of predation (Brown 1988, Bedoya-Perez et al. 2013). GUDs of possums declined so strongly in the long-diseased region that they were indistinguishable from possum GUDs on Maria Island, a devil-free island. The indistinguishable GUDs in the two regions suggest that possums no longer perceive devils as a predation threat in long-diseased habitat (Hollings et al. 2015).

In response to modelling that suggested devils could go extinct in the wild (McCallum et al. 2009) and the listing of the species as endangered (Hawkins et al. 2008), a free-ranging 'insurance population' of devils was introduced to Maria Island in 2012 (Thalmann et al. 2016), a 116 km² National Park off Tasmania's east coast. The devil population rapidly grew (Fig. 1) to about 90 individuals by 2016 (DPIPWE 2018), nearing the estimated carrying capacity of the island. Although possums were first introduced to Maria Island in the 1950s, and other species have also been introduced (Rounsevell 1989), Maria Island contains a mammal community that is broadly representative of the mainland of Tasmania. The introduction of devils provides an ideal natural experiment to test the effects of introducing a top predator into a system with a prey species that has been isolated from its major predator, the devil, for 40–60 years. Here, using a multiple before–after control-impact (mBACI) GUD experiment, we test whether the introduction of devils to Maria Island has increased risk-sensitive foraging behaviours in possums.

Material and methods

Giving-up density experiment

GUDs – the density of food remaining in a patch when an individual 'gives-up' foraging – are a powerful experimental approach used to study perceived predation risk (Brown 1988, Bedoya-Perez et al. 2013). In a single measure, GUDs quantify the decisions made by a forager when it trades off between the benefits of obtaining food and the risk of being killed (Brown and Kotler 2004). As food becomes increasingly difficult to locate, an optimal forager should give-up foraging at a GUD that balances the metabolic, predation and opportunity cost of foraging (Brown 1988).
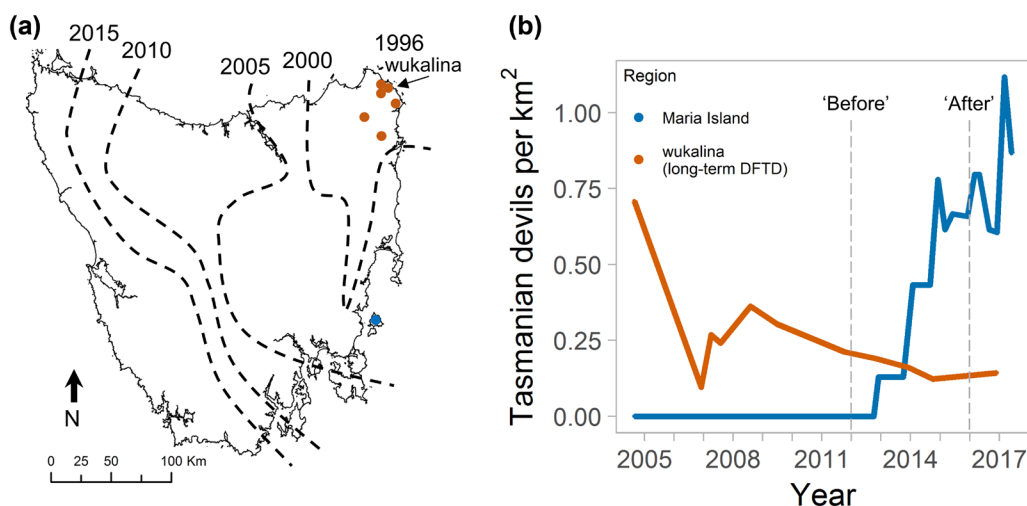

Figure 1. (a) Map showing the spread of DFTD across Tasmania, Australia. Dashed lines represent the estimated disease front. Study site locations for the long-term DFTD region are shown in orange and Maria Island in blue. (b) Devil densities declined and stabilised at low density in north-east Tasmania following DFTD onset in 1996, while they rapidly increased on Maria Island following introduction in 2012. The GUD experiment was conducted when devils were absent from Maria Island and again when devils were at high density (dashed vertical lines). Devil densities were stable in the long-term diseased region over this period. Density estimates for wukalina are from (Lazenby et al. 2018). Maria Island density estimates are based on island-wide abundance estimates from regular trapping by the Save the Tasmanian Devil Program (DPIPWE 2018), divided by the area of Maria Island.

We conducted a GUD experiment at six study sites in Tasmania's long-diseased north-east and six study sites on Maria Island (Fig. 1). We performed the experiment in 2011–2012 ('before'), when devils were absent on Maria Island and were at very low densities in the long-diseased region (Hollings et al. 2015). We repeated the experiment in 2016 ('after'), when devils were at high density on Maria Island but remained at stable low densities in the long-diseased region.

At each site, we deployed 10 food stations, each consisting of one 'safe' artificial food patch at the base of a potential escape tree, and one 'risky' patch 5–12 m from the nearest escape tree (defined as a tree with a diameter at breast height > 10 cm). Across the 12 study sites and two survey periods, this totalled 480 food patches. We positioned food stations at least 100 m apart alongside an unsealed, rarely used road, > 30 m into the forest. Each food patch consisted of a 4 litre round plastic container partially filled with a substrate of 2.5 litre of medium-sized, smooth river pebbles. We evenly mixed 100 sultanas into the substrate of each patch and fitted containers with a lid that had a 10 cm diameter hole in the centre–top. This allowed a possum to put either a head or paw into the container but not both, preventing possums from rapidly depleting the food supply. We selected sultanas because they are highly attractive to possums (Pickett et al. 2005), and maintain their structural integrity when wet, ensuring the remaining sultanas are easily countable. Food patches were deployed for four consecutive nights and checked each morning for evidence of animal visitation. If an animal had visited the patch, we counted all remaining sultanas and replenished the patch with 100 sultanas.

During the 'before' period, we identified the foraging species using hair samples collected with double-sided tape around the rim of the food tray. A sample from each 'clump' of hair was identified to species level based on features of the hair medulla and cross-sectional shape (Triggs and Brunner 2002). Tape was replaced daily if there was evidence of visitation. To verify the accuracy of the hair identification, we used camera traps to record animal activity at 2–4 food patches per site. We assessed whether the species identified using the hair sample was the same as the species recorded on camera. This revealed that identification of possum hair is generally very accurate because possum fur is distinctive (Triggs and Brunner 2002, Hollings et al. 2015), and they typically leave many hairs after feeding at the food tray.

During the 'after' period, we used camera traps (Reconyx PC-800 infrared) at each patch to identify the foraging species. Cameras were positioned on a nearby tree or garden stake ~2–3 m from the food patch and programmed to take five pictures per trigger, with a one second quiet period between subsequent triggers. The use of cameras additionally enabled us to record the number of devil detections at each patch during the 'after' period.

Non-target species visited some food stations; however, foraging by non-target species was limited by the design of the containers and weight of the substrate. Analysis during the 'before' period indicated that non-target species rarely took more than 15% of the food and never more than 25% (Hollings et al. 2015). Foraging by non-target species included Tasmanian pademelon *Thylogale billardierii*, Bennett's wallaby *Macropus rufogriseus*, southern brown bandicoot *Isoodon obesulus*, long-nosed potoroo *Potorous tridactylus* and *Rattus* spp. The considerable weight of the pebble substrate and small space within the container ensured minimal foraging by small mammals. The small hole in the lid requires considerable dexterity to search through the substrate for sultanas, which limited foraging by wallabies, as observed from camera footage and assessed during an initial pilot study on food patch design (Hollings et al. 2015). We discarded foraging data when there was no evidence of possum foraging, where a definitive species identification could not be made, or where there was evidence of substantial foraging by non-target species.

We ensured that all study sites were environmentally comparable, with similar average annual rainfall (Maria Island = ~730 mm, long-diseased = ~750–1100 mm) and elevation (< 200 m a.s.l.). Sites were in dry eucalypt forest or coastal woodland/scrub, and all sites were in reserves, which ensured minimal impact of culling on possum abundance and behaviour. Rainfall differed substantially between the 'before' and 'after' periods, which could affect an individual's energetic state and therefore GUD (Brown 1992, Bedoya-Perez et al. 2013). Rainfall was near the long-term mean in the year preceding the 'before' trials (MI = 109%; north-east = 99%) but was substantially below average for two years preceding the 'after' trials (MI = 60% and 70%; north-east = 72% and 74%).

Statistical analysis

To assess changes in the risk-sensitive foraging behaviour of possums in relation to changing devil densities, we performed two separate analyses using linear mixed-effects models (LMM; lmer from the 'lme4' library in R ver. 3.5.1). Because of the nested structure of the experiment, we included a random effect of nights nested within stations (pairs of food patches) nested within study site.

First, we analysed changes in possum GUD using the mBACI framework to assess whether the GUD of possums changed following devil introduction to Maria Island, relative to the long-diseased region as a control. We investigated this effect by testing for an interaction between 'region' (Maria Island or long-diseased) and 'period' ('before' or 'after' devil introduction). The most complex model included a three-way interaction between 'region', 'period' and 'position' (risky or safe patch) with main effects.

Second, we investigated whether variation in devil activity across Maria Island and the long-diseased region during the 'after' period created a heterogeneous landscape of fear. To do this, we modelled possum GUD as a function of total devil detections on camera at a site during the four nights of

the experiment. Because a devil could easily travel the length of the transect in minutes, we pooled devil detections at the level of each study site using a 30-min quiet period between the next devil detection, reducing the possibility of double counting a devil at a nearby patch. We hypothesised that the amount of devil activity in an area would influence the likelihood of a possum encountering a devil, and in turn influence possum anti-predator behaviour. We did not attempt to estimate devil density because the 1-km transects are much smaller than the size of a devil's home range (~22 km²) (Comte 2019). We analysed the effect of devil activity on possum GUDs for the 'after' period only because we used camera traps to observe all patches in this survey period only. The most complex model consisted of an interaction between 'devil activity' (devil detections per site) and 'position' (risky or safe) with main effects.

In both analyses, we ran all simpler combinations of explanatory variables, and selected the best models using an information theoretic approach based on small-sample corrected Akaike information criterion (AICc) (Burnham et al. 2011). Some models showed strong signs of containing a 'pretending variable' (sensu Anderson 2007), otherwise known as an uninformative parameter (Leroux 2019). These variables can be identified when the addition of a variable to a simpler nested model does not improve model fit (i.e. the log-likelihood) and increases the AIC value by approximately the penalty of two (Anderson 2007, Leroux 2019). In such cases, we excluded models containing a pretending variable, as recommended by Anderson (2007) and Leroux (2019). For completeness, we present the model selection table containing the pretending variables in Supplementary material Appendix 1 Table A1, A2.

Data deposition

Results

Possum GUDs were initially indistinguishable between Maria Island and the long-diseased region, but following the introduction of devils to Maria Island, possum GUDs were 64% higher on Maria Island than the control region (Fig. 2a). The interaction between region and period was present in the top-performing LMM, which carried 95% model weight, and the interaction term had a relative importance of 0.98 (Table 1), clearly demonstrating that the foraging behaviour of possums became more risk-sensitive on Maria Island following the introduction of devils, relative to the control site. The general downward trend in GUD may be explained by two years of drought preceding the 'after' trials (see Discussion).

For the second analysis describing the spatial variation in GUD during the 'after' period, the index of devil activity carried a variable importance of 0.92 and was present in the top-performing model, which carried a model weight of 0.92 (Table 2), demonstrating that possum GUDs are positively associated with the local activity of devils (Fig. 2b). In both analyses, there was no evidence that possums foraged to a lower GUD at the food trays positioned at the base of an escape tree, compared to risky food trays (variable importance 0.04 in mBACI and 0.00 in 'after'; Table 1, 2). GUDs at one study site on Maria Island appeared to deviate from the
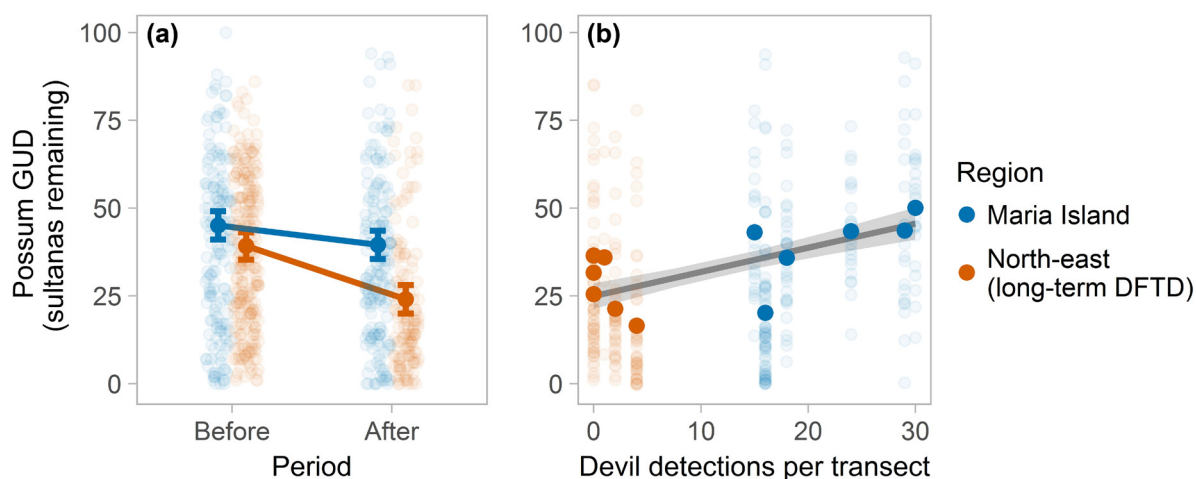

Figure 2. (a) Effects plot from the best-supported LMM investigating possum GUDs before and after the introduction of devils to Maria Island. The best-supported model contained an interaction between 'period' and 'region' (Table 1). The solid dots represent the model fit and the transparent dots show the raw data. This demonstrates that GUDs were indistinguishable between the two regions in the 'before' period (Hollings et al. 2015), however following the introduction of devils to Maria Island, GUDs were significantly higher on Maria Island than the control region. Error bars = SE. (b) Effects plot from the best-supported LME model investigating the effect of local devil activity on possum GUDs in the 'after' period. The line represents the model fit with SE, the transparent dots represent the raw data and the solid dots show the mean GUD for the 12 study sites.

Table 1. Model outputs from LMM analysis of the number of sultanas remaining in a food patch in the mBACI GUD experiment. The table shows the model rank based on change in AICc (ΔAICc) from the top model, model weights and model coefficient estimates (SE) for each predictor variable. The relative importance of variables was calculated by summing the weights of all models containing the variable. We present models within seven ΔAICc. Not all models are shown; see Supplementary material Appendix 1 Table A1 for models that we excluded from comparison because we deemed them to contain a 'pretending variable'.

Model rank	Log likelihood	ΔAICc	Weight	df	Intercept	Period (after)	Region (north-east)	Period×Region (after:NE)	Position (risky)	Period×Position (after:risky)	Position×Region	Period×Position ×Region
1	−3254.16	0.00	0.95	8	42.32 (3.91)	−3.92 (1.42)	−10.67 (5.49)	−6.81 (1.98)				
Null	−3286.25	58.08	0.00	5	37.98 (2.84)							
Relative importance						1.00	0.99	0.98	0.04	0.03	0.03	0.03

trend, with possum GUDs consistently lower than the model fit (Fig. 2b). This occurred at the study site closest (~200 m) to the small human settlement of Darlington; at this site, devil activity was about half of the maximum observed on Maria Island (Fig. 2b).

Discussion

The introduction of devils to Maria Island led to a clear increase in risk-sensitive foraging behaviour by possums, supporting the notion that rewilding can establish missing ecological functions. Devil activity on Maria Island was spatially variable, which seemingly led to a heterogeneous landscape of fear, as revealed by variation in GUD (Fig. 2b). Devils were less active at the transect closest to human settlement on Maria Island, and possums here had a GUD as low as the long-diseased region. Although based on one study site, this suggests that the ecological effects of devils might be mediated through human influence and highlights that it is not necessarily enough to simply have a predator in the landscape to elicit a response from prey, but that predators need to be at functional densities if they are to 'retain their claws' (Kuijper et al. 2016). Humans often have a suppressive influence on the density of large carnivores which can mediate the ecological effects of carnivores (Kuijper et al. 2016), and this needs to be considered when predicting the ecological effects of predator recoveries.

Isolation from predators can rapidly erode anti-predator behaviours, increasing an individual's susceptibility to predation following carnivore recoveries (Berger et al. 2001, Blumstein and Daniel 2005, Carthey and Banks 2014, Jolly et al. 2018). Devils caused high initial mortality of naive possums on Maria Island; 23% of devil scat on Maria Island contained brushtail possum (Ingram 2018), compared to an average of 6.2% across mainland Tasmania (Andersen et al. 2017). Although mortality was initially high, possums showed a clear anti-predator response after just three years of living with devils – less than a single generation (defined as the average age of parents; Pacifici et al. 2013a, b). Our findings support the rapidity of prey responses following carnivore recoveries elsewhere. In Europe and the USA, recolonising brown bears and wolves caused initially high mortality of predator–naive moose (Berger et al. 2001). Like our study, moose showed a rapid anti-predator behavioural response within a single generation (Berger et al. 2001). With the exception of rare species like those housed on Australia's island refuges or in predator-free sanctuaries (Woinarski et al. 2015), this capacity to rapidly re-learn anti-predator behaviours should negate fears of localised prey extinctions following predator recoveries.

Despite a general downward trend in GUD, the introduction of devils to Maria Island prevented GUDs from decreasing to the levels of the long-diseased region, demonstrating an increase in perceived predation risk following

Table 2. Model outputs from LMM analysis of the number of sultanas remaining in a food patch in the 'after' period. During the 'after' period, we recorded the number of devils detected on cameras at a transect to investigate whether fine-scale, local devil activity is a driver of possum behaviour. The table shows the model rank based on change in AICc (ΔAICc) from the top model, model weights and model coefficient estimates (SE) for each predictor variable. The relative importance of variables was calculated by summing the weights of all candidate models containing the variable. Models worse than the null are not shown; see Supplementary material Appendix 1 Table A2 for models that we excluded from comparison because we deemed them to contain a 'pretending variable'.

Model rank	Log likelihood	ΔAICc	Weight	df	Intercept	Devil detections per transect	Position	Devil detections × Position
1	−1398.38	0.00	0.914	6	24.96 (3.65)	0.69 (0.22)		
Null	−1401.77	4.72	0.086	5	33.98 (3.30)			
Relative importance						0.91	0.00	0.00

devil introduction. We suggest the general downward trend could be driven by two years of drought preceding the 'after' surveys, making food scarcer and therefore more valuable. In addition to predation pressure, energetic state influences an animal's GUD (Brown 1992, Bedoya-Perez et al. 2013). For example, starved foxes forage to lower GUDs that non-starved foxes (Berger-Tal et al. 2009), probably because food is more beneficial to a low-energy individual (Bedoya-Perez et al. 2013). Maria Island and the control region were both exposed to similarly low rainfall preceding the 'after' period, yet the control region saw a significantly larger drop in GUDs, and the two regions had significantly different slopes. This demonstrates that although an external factor seemingly had a downward influence on GUD, possums on Maria Island showed an increase in risk-sensitive foraging following devil introduction, relative to the control.

Empirical research on trophic rewilding is still rare (Svenning et al. 2016), and our large-scale experiment provides evidence that trophic rewilding can establish or restore the landscape of fear. We demonstrate that top predators modify the behaviour of prey by instilling fear, and that behavioural change can occur rapidly following top predator introductions, far more rapidly than demographic change. Other research shows that devils modify the behaviour of mesopredators and prey; for example, spotted-tailed quolls *Dasyurus maculatus* temporally partition activity to avoid devils at high density (Cunningham et al. 2019a), and feral cats *Felis catus* willingly feed on carcasses in areas where devils are rare, but less so in areas where devils are abundant, possibly a response to increased risk of encountering a devil at a carcass (Cunningham et al. 2018). The next important step is to quantify how these behavioural changes affect fitness, demography and the flow-on effects to vegetation. For example, in response to predator recoveries elsewhere, other species modify the areas where they forage (Hernández and Laundré 2005), or the period of the day in which they use risky areas (Kohl et al. 2018), which can have cascading benefits for over-consumed vegetation (Ripple and Beschta 2007, Kuijper et al. 2013). Overall, our study provides empirical support that introducing a top predator can establish missing ecological controls, supporting the ecological case for trophic rewilding.

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Supplementary material (available online as Appendix ecog-04635 at <www.ecography.org/appendix/ecog-04635>). Appendix 1.