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Research

Temporal partitioning of activity: rising and falling top-predator abundance triggers community-wide shifts in diel activity

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Top predators cause avoidance behaviours in competitors and prey, which can lead to niche partitioning and facilitate coexistence. We investigate changes in partitioning of the temporal niche in a mammalian community in response to both the rapid decline in abundance of a top predator and its rapid increase, produced by two concurrent natural experiments: 1) the severe decline of the Tasmanian devil due to a transmissible cancer, and 2) the introduction of Tasmanian devils to an island, with subsequent population increase. We focus on devils, two mesopredators and three prey species, allowing us to examine niche partitioning in the context of intra- and inter-specific competition, and predator–prey interactions. The most consistent shift in temporal activity occurred in devils themselves, which were active earlier in the night at high densities, presumably because of heightened intraspecific competition. When devils were rare, their closest competitor, the spotted-tailed quoll, increased activity in the early part of the night, resulting in increased overlap with the devil's temporal niche and suggesting release from interference competition. The invasive feral cat, another mesopredator, did not shift its temporal activity in response to either decreasing or increasing devil densities. Shifts in temporal activity of the major prey species of devils were stronger in response to rising than to falling devil densities. We infer that the costs associated with not avoiding predators when their density is rising (i.e. death) are higher than the costs of continuing to adopt avoidance behaviours as predator densities fall (i.e. loss of foraging opportunity), so rising predator densities may trigger more rapid shifts. The rapid changes in devil abundance provide a unique framework to test how the non-lethal effects of top predators affect community-wide partitioning of temporal niches, revealing that this top predator has an important but varied influence on the diel activity of other species.

Keywords: apex predator, ecology of fear, invasive species, mesopredator release, predator–prey, temporal partitioning of activity, trophic cascade

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Introduction

Top predators play important roles in structuring the behaviour of mesopredators and prey, sometimes leading to avoidance behaviours (Lima 1998, Laundré et al. 2001). These avoidance behaviours reflect the need to balance the benefits of an activity against its attendant risks, including potentially lethal encounters with a predator (Lima and Dill 1990). One strategy to reduce interference competition with a dominant predator, or reduce the risk of predation, is to partition activity into times of the day when predators are less active (Lima and Dill 1990, Kronfeld-Schor and Dayan 2003, Kohl et al. 2018). Prey species in South Africa, for example, are more diurnal when co-existing with nocturnal top predators (lion *Panthera leo* and spotted hyaena *Crocuta crocuta*), compared to a neighbouring area without these predators (Tambling et al. 2015). Such niche partitioning can be a mechanism that facilitates coexistence (Carothers and Jaksić 1984).

Top predators have declined worldwide (Ripple et al. 2014), leading to a widespread decline in predation risk and the fear it induces in prey, and sometimes triggering trophic cascades and mesopredator release (Crooks and Soulé 1999, Terborgh et al. 2001, Johnson et al. 2007, Ritchie and Johnson 2009, Suraci et al. 2016). After centuries of decline, however, some large carnivores are beginning to recover across parts of Europe (Chapron et al. 2014), North America (Gompper et al. 2015) and Asia (Athreya et al. 2013), bringing hope that predators may once again exert control over the behaviour and abundance of other species.

We use two natural experiments that mirror the global trends of predator declines, as well as recent recoveries. The Tasmanian devil *Sarcophilus harrisii* (hereafter 'devil'), a top predator, has declined severely following the emergence of a novel transmissible cancer, devil facial tumour disease (henceforth 'disease'; Hawkins et al. 2006, McCallum et al. 2007). The disease was first detected in north-east Tasmania, Australia, in 1996, and has since spread across ~80% of the devil's range, causing average population declines of 80%, and up to 95% in some areas (Hollings et al. 2014, Lazenby et al. 2018). In response to the threat of extinction (McCallum et al. 2009), a free-living, disease-free population of devils was introduced to Maria Island (Thalmann et al. 2016), a 116 km^2 National Park off the east coast of Tasmania that was not previously inhabited by devils. The population rapidly increased to its estimated carrying capacity of ~100 (DPIPWE 2018). These independent shifts in devil abundance allow us to test the behavioural effects of falling and rising abundance of a top predator in a single study.

In this paper, we test how changes in devil abundance affect community-level partitioning of the temporal niche, in the context of intra- and inter-specific competition and predator–prey interactions. Devils are the largest predator (6–14 kg) in Tasmania and are nocturnal. They are competitively dominant over two mesopredators, the native spotted tailed-quoll *Dasyurus maculatus* (2–5 kg, hereafter 'quoll'), which is largely crepuscular/nocturnal, and the invasive feral cat *Felis catus* (3–5 kg; hereafter 'cat'), which has variable activity patterns. We also examine temporal partitioning in three major prey species of devils, the Tasmanian pademelon *Thylogale billardierii* (hereafter 'pademelon'), the Bennett's wallaby *Macropus rufogriseus* (hereafter 'wallaby') and the common wombat *Vombatus ursinus*; these prey species are mostly crepuscular/nocturnal. Because circadian rhythms evolve to ensure an animal is active at the most beneficial time (Kronfeld-Schor and Dayan 2003, Kronfeld-Schor et al. 2017), the activity patterns of prey species may respond to a trade-off between avoiding diurnal predators (eagles, humans) and nocturnal predators (devils, quolls). Both devils and quolls feed mainly on pademelon and wallaby (Jones and Barmuta 1998, Andersen et al. 2017), whereas cats prefer smaller prey (Doherty et al. 2015). Thus, if competition for food is the major driver of temporal activity, quolls should show a stronger response than cats. Because pademelon and wallaby are shared prey of both devils and quolls, shifts in the diel activity of quolls could also affect these species.

We compiled a large dataset of 71 666 independent animal records from two simultaneous camera studies conducted over a five-year period, totalling 76 516 camera nights (Table 1), from which we assessed the role of devils in structuring community-wide diel activity. We asked two main questions: 1) how does the temporal activity of conspecifics, competitors and prey respond to changes in devil density, and 2) do these other species alter their overlap with the devil's usual temporal niche in response to changes in devil density? We hypothesised that increasing devil densities would cause other species to reduce their overlap with the devil's temporal niche because of increased risk of death or injury. We hypothesised that declining devil densities would allow other species to increase their use of the devil's usual temporal niche because of substantially reduced risk of encountering a devil. In interpreting our results, we consider whether the response of one species to changes in devil density may affect the response of

Table 1. Summary of remote camera deployment strategy. See Supplementary material Appendix 1 Table A1 for details of site descriptions and camera deployment method.

Survey name (number of study sites)	Cameras per site (total cameras)	Total camera nights	Independent animal records
Devil decline survey 1 (29)	14 (406)	20 048	16 230
Devil decline survey 2 (45)	4 (180)	8704	8049
Devil decline survey 3 (13)	20–21 (270)	7080	5203
Devil introduction (Maria Isl. and control over five years)	53–72 (735)	40 684	42 184
Total	1591	76 516	71 666

other species (e.g. quoll responses may in turn affect prey). We also consider that increasing and decreasing trajectories of devil densities may not have symmetrical effects because the costs may be higher for increasing densities (i.e. death) than decreasing densities (i.e. lost foraging opportunity).

Material and methods

Study area and camera trapping

We analysed two independent cases: 1) a space-for-time substitution investigating the disease-induced decline of devils on mainland Tasmania, and 2) a longitudinal study of the introduction of devils to Maria Island, with a control site on Tasmania where devil abundance was low and stable.

Study 1: space-for-time substitution investigating devil declines

Space-for-time substitutions study the relationships between ecological variables at sites at different stages of a response, permitting study of longer time-scales than longitudinal observation would allow (Walker et al. 2010). We combined records from three camera surveys of sites that spanned the gradient of devil population decline, from the disease-free north-west of Tasmania, to the north-east where devils had been exposed to the disease for ~20 yr (Fig. 1A). In total, we surveyed 50 different study sites using 856 remote cameras between 2015 and 2017, for a total of 35 832 camera-nights (Table 1). We sampled three habitat types: wet eucalypt/rainforest, dry eucalypt forest and coastal vegetation. We ensured sites of the same habitat type were environmentally comparable by selecting sites of similar average rainfall/elevation, and ensured that each survey had a similar proportion of sites located in each region and habitat type (Supplementary material Appendix 1 Table A1). To increase detections, we positioned cameras facing animal trails/small clearings and baited them with a general-purpose herbivore and carnivore olfactory lure (Supplementary material Appendix 1 Table A1). The three surveys differed in the number, spacing and duration of camera deployment, but importantly each positioned cameras in the same way and used the same olfactory lure and camera type. Differences in survey effort may influence total detections, but we analysed timing of detections using proportions of detections at a given time of day, not total detections, meaning the three surveys can be analysed together validly.

Study 2: Longitudinal study investigating devil introduction

Devils were first introduced to Maria Island by the Tasmanian government conservation agency in 2012, when 15 animals were released (Thalmann et al. 2016). By 2018 the population had grown to 103, the estimated carrying capacity of the island (Jones and McCallum 2007, DPIPWE 2018). We selected an environmentally comparable control site for Maria Island on the nearby east coast of Tasmania, where the disease arrived and started causing population declines approximately 12 yr prior (Hawkins et al. 2006). Devils remained at consistently low relative density for the duration of our study (Fig. 1B). Camera monitoring at Maria Island and the control site continued from 2013 to 2017, deploying 735 remote cameras over five years for a total of 40 684 camera nights (Table 1). Positioning of cameras and use of lures matched the devil decline survey (details of survey method and site information in Supplementary material Appendix 1 Table A1). Quolls are absent from Maria Island, so we only investigated the response of quolls to devil declines.

Analysis of changes in devil relative density

Camera locations within a study site were not spatially independent. Thus, to reduce the likelihood of double-counting an individual devil on the same or a nearby camera, we first pooled all devil detections at a study site from the first 21 d of a survey, which is the minimum deployment duration recommended for detecting cats, the most cryptic of the carnivores (Robley et al. 2010). We then treated detections as unique if they were separated by > 30 min. This yielded a count of unique devil detections for each survey. We then calculated an index of devil density (termed 'devil relative density') to be used as a predictor variable in subsequent analyses by dividing the number of devil detections by the number of camera nights. This represents a standardized index of relative density and enabled comparison among surveys with different survey effort.

We analysed the predictors of devil detections separately for the declining and increasing devil populations. For devil declines, we modelled the relative density of devils using a generalised additive mixed-effects model (GAMM) with a quasibinomial distribution to prevent negative fitted values ('mgcv' package in R; Wood 2017). We included study site as a random effect to allow for correlations within the sites. The most complex model consisted of an interaction between 'years since disease outbreak' and 'habitat' (coastal, dry eucalypt or wet eucalypt/rainforest). We included a predictor variable for habitat to model habitat-specific differences in devil relative densities or detectability. We assessed whether a smooth term was necessary using the approximate p-values ($\alpha = 0.05$; AIC is not available for this quasi distribution).

For the devil introduction study, we tested whether changes in devil detections through time differed between Maria Island, where devils were introduced, and the control sites by modelling the count of devil detections using a generalised linear model (GLM) with a Poisson distribution in R (R Core Team). The most complex model included predictor variables for 'season' (either summer or winter to account for seasonal differences in behaviour that could influence detectability), and an interaction between 'year' (2013–2017) and 'study site' (Maria Island or control). A mixed-effects model was not necessary because pooling detections for each survey of a site meant there was only a single value for each survey and repeat measures at a site were accounted for using the fixed effect of 'study site'. The GLM contained an offset for the number

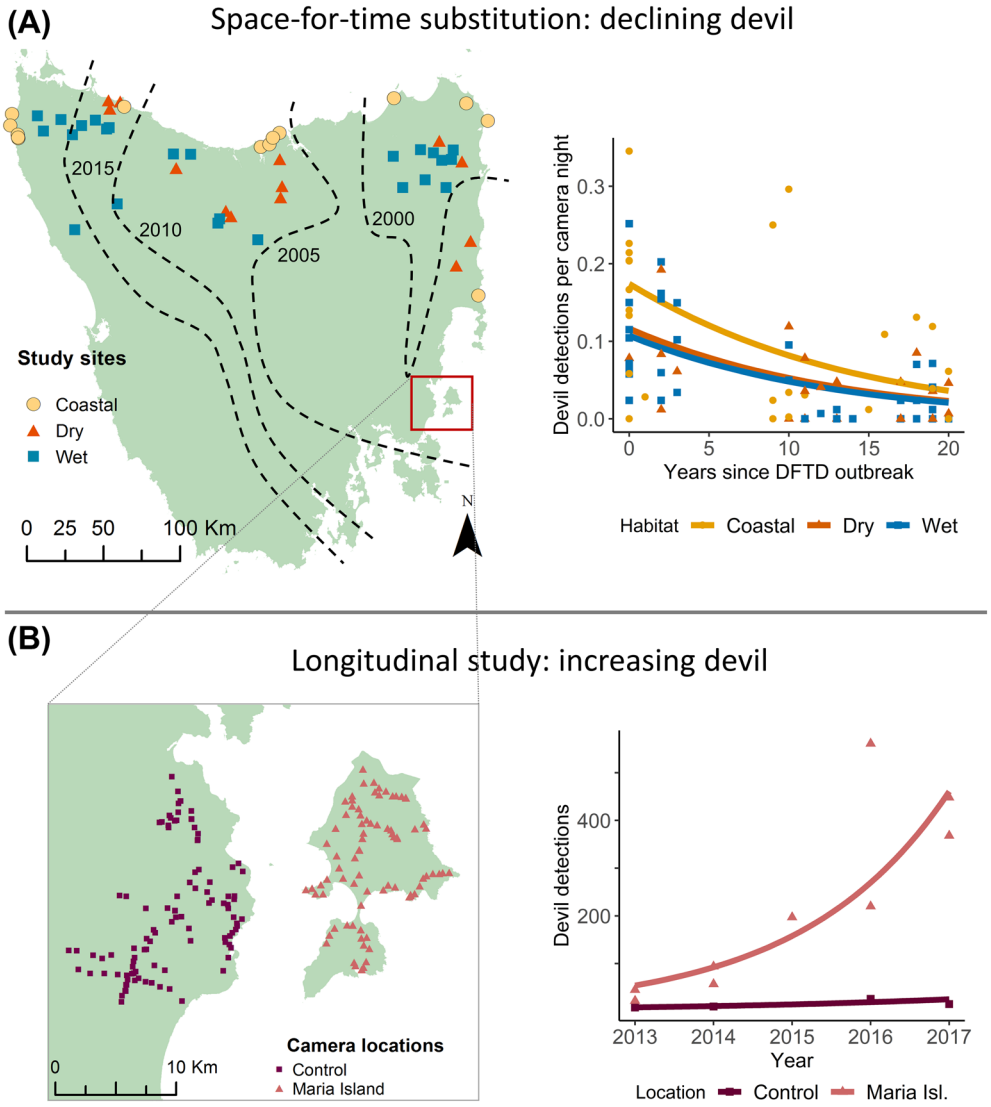

Figure 1. Study design and changes to devil relative density in Tasmania. (A) Map of 50 study sites spanning a gradient of devil population declines, ranging from the north-east of Tasmania where devil facial tumour disease has been present for approximately 20 yr, to the disease-free north-west. Dashed lines represent the estimated disease front. The graph shows that devil detection rates in camera surveys were on average ~80% less at long-diseased (~20 yr) sites than at disease free sites. The lines represent the best-supported GAMM. (B) Camera locations on Maria Island and a control site on mainland Tasmania. The graph shows the best-supported GLM predicting the number of devil detections in a survey. This shows that devil detections on Maria Island rapidly increased following introduction in 2012, while the control site remained stable.

of camera nights, because this varied slightly due to camera malfunctions. We compared the most complex model to all simpler combinations of predictor variables and selected the best model based on small sample corrected Akaike information criterion (AICc) (Burnham and Anderson 2002).

Temporal activity

Data handling

We used the time-stamp on a photo as a record of the time a species was active. Records of the same species at a study site were considered independent if separated by at least 30 min, and assumed to be a random sample from each species' underlying activity distribution, as is common in similar studies (Linkie and Ridout 2011, Brook et al. 2012). Preliminary data exploration when tagging the photos showed that individual animals rarely stayed at a camera for more than ~5 min. Because activity is often organised around circadian events such as sunrise and sunset (Nouvellet et al. 2012), and because our study was conducted across different times of the year, we scaled clock time to sun time, with 06:00 representing sunrise and 18:00 sunset ('sunTime' function, 'overlap' package in R; Ridout and Linkie 2009).

Analysis

We used two approaches to analyse temporal activity: 1) circular overlap, a common technique to compare the diel activity of different groups of animals; and 2) generalised additive models (GAMs), a much less common approach to study temporal activity. The use of GAMs allowed us to model diel activity in response to a continuous predictor variable for devil relative density, rather than comparing grouped records as is necessary in the analysis of overlap.

Circular overlap

We first tested whether a species changed activity patterns by grouping records according to the relative density of devils. We visualised activity profile as a non-parametric kernel density estimate using the 'overlap' package in R and the default smoothing parameters recommended by Ridout and Linkie (2009). We tested for statistical differences in activity using the non-parametric Mardia–Watson–Wheeler test for homogeneity, which tests for differences in the mean angle or variance of two samples (Batschelet 1981), using the 'circular' package in R (Agostinelli and Lund 2017).

In the devil decline study, we grouped records based on relative density of devils. In each of the three surveys, we selected records from the 20% of sites with the most devil detections ('high devil') and the 30% of sites with the fewest devil detections ('low devil'). We selected these thresholds because exploration of the data showed that a threshold < 30% would exclude some sites with zero devil detections, clearly undesirable for a group representing low devil densities; sites in the top 20% represent devil detection rates typical of disease-free sites. To include sufficient devil records to allow for reliable kernel estimation of devil activity, we expanded the low category to include the lowest 40% of sites, because otherwise there were few devil records to create a reliable kernel estimate; these lowest 40% of sites represent severe devil population declines. In the devil introduction study, we partitioned records from Maria Island and the control site into two groups: 2013/2014 when devils were at low relative density shortly after release, and 2016/2017 when devils were at high relative density on Maria Island (Fig. 1B).

We additionally investigated whether mesopredators and prey altered their use of the devil's temporal niche in response to changes in the relative density of devils. We did this by first constructing an activity profile that represents the devil's usual temporal niche, which we defined in the devil decline study as records from disease-free areas, and for Maria Island as records from 2016/2017 when devil density was near carrying capacity. We then assessed the overlap of the devil's temporal niche with the temporal activity of mesopredators and prey in areas/periods of high and low devil relative density (as defined in the previous paragraph). We quantified overlap using the coefficient of overlap Δ (with 95% bootstrap confidence intervals), with 0 representing no overlap in activity and 1 representing complete overlap ('overlap' package in R). As recommended by Ridout and Linkie (2009), we used the Δ_4 measure of overlap when the smallest sample size was > 75, and Δ_1 when sample size < 75.

Generalized additive modelling of temporal activity

We further modelled potential non-linear shifts in temporal activity in response to changes in the relative density of devils using GAMs. GAMs have been used to model temporal activity in some previous studies (Bischof et al. 2014); however, we believe they represent an under-used approach to studying the drivers of a species' temporal activity because they are highly flexible, can model circular data (using cyclic regression splines), and can accommodate continuous predictor variables.

We used GAMs to model the four largest shifts in temporal activity revealed in the analysis of overlap: devils in response to declining and increasing relative densities, quolls in response to devil declines, and wallabies in response to devil introduction. For the response variable, we calculated the proportion of activity associated with each hour of the diel cycle (0–23; scaled to sun time), which summed to one for each species in each survey. We modelled proportional activity because we were interested in relative activity throughout the day, not absolute activity. We excluded surveys where a species was detected less than three times because these could lead to biased proportions.

We constructed a varying coefficient model for each species, which allowed the coefficients of a smooth term to interact with a covariate, either a continuous variable (e.g. devil relative density) or a factor (e.g. location) (Wood 2017). We modelled proportional activity using a quasibinomial distribution to prevent negative predicted values, and used a cyclic cubic spline because the diel cycle is circular. For the devil decline study, we modelled proportional activity in response to 'hour' of the day (0–23), and an interaction between 'devil relative density' and 'hour'. For the devil introduction study, we modelled proportional activity in response to 'hour', and an interaction between 'year' (associated with increasing devil densities) and 'hour' by 'location' (Maria Island or control). We used a penalty on the null space of each smooth to select a smooth term out of the model if it was not needed (using the 'select' argument) (Marra and Wood 2011), and used approximate p-values ($\alpha = 0.05$) to judge whether the smooth term should remain in the model. We fitted GAMs using the 'mgcv' package in R (Wood 2017; R Core Team) and visualised results by plotting the interaction term using contour and perspective plots.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.s77dk4v> (Cunningham et al. 2019a).

Results

Changes to devil relative density

Devil detection rates declined with increasing time since disease arrival (Fig. 1A) and increased rapidly on Maria Island following devil introduction (Fig. 1B). In the study

of devil declines, 'years diseased' ($p < 0.0001$, edf = 1.8, deviance explained = 52.2%) was included in the best-supported GAMM (Supplementary material Appendix 1 Table A2). On average, devil detection rates at long-diseased sites (~20 yr) were 80% less than at disease-free sites, similar to other studies (Hawkins et al. 2006, McCallum et al. 2007, Hollings et al. 2014, Lazenby et al. 2018). The best-supported GLM modelling devil detections following devil introduction included an interaction between 'year' and 'study site' (Supplementary material Appendix 1 Table A2), demonstrating markedly different trends between the two sites – devil detections increased rapidly on Maria Island but remained low at the control site (Fig. 1B).

Temporal activity in predators

Devils

Devil decline: temporal activity of devils differed significantly between high- and low-density sites ($p < 0.001$; Fig. 2A). At high relative densities, devils had a defined peak in activity shortly after 18:00 h, whereas at low relative densities, devil activity peaked at ~22:00 h and remained elevated throughout much of the night (Fig. 2A). The GAM predicting the proportional activity of devils contained a significant interaction between hour of the day and the relative density of devils (edf = 2.846, $p = 0.047$, deviance explained = 40.7%). High devil densities were associated with a heightened post-sunset peak and a relative decline in activity during the latter half of the night (Fig. 3A).

Devil introduction: the diel activity patterns of devils on Maria Island differed significantly between periods of low devil density (2013/2014) and high density (2016/2017; $p < 0.001$; Fig. 2B). When devil density was low, devils had a broad peak in activity that spanned the first half of the night, whereas when devil density was high, activity peaked shortly after sunset before dropping rapidly. The control site, where devil relative density was low and stable, showed no significant differences in temporal overlap between the periods ($p = 0.22$; Fig. 2C). The GAM predicting the proportional activity of devils contained a significant interaction between hour, year and location (edf = 12.54, $p < 0.0001$, deviance explained = 68.5%), showing change in activity pattern as density increased. High devil relative density was associated with a heightened post-sunset peak and a relative decline in activity during the latter half of the night (Fig. 3C).

Spotted-tailed quoll

Devil decline: quolls exhibited markedly different patterns between sites with high and low devil relative densities ($p = 0.04$; Fig. 2D). At sites with high devil relative density, quolls had a pronounced peak in activity shortly before sunrise, whereas the highest peak shifted to shortly after sunset when devil relative density was low, with a much-reduced pre-sunrise peak (Fig. 2D). As devil relative density declined, the activity profile of quolls showed increasing similarity with the devil's high-density profile (Fig. 4), with activity peaking just after sunset, resulting in increased overlap with the devil's temporal niche (Fig. 5). The GAM predicting the temporal activity of quolls contained a significant interaction between hour and devil relative density (edf = 6.6, $p = 0.049$, deviance explained = 11.4%). The pre-sunrise peak in quoll activity at high devil relative densities was more than double the height of this same peak when devils were rare (Fig. 3B).

Feral cats

Devil decline: temporal activity of cats did not differ significantly between sites with high and low devil relative densities ($p = 0.65$; Fig. 2E). Cats were active throughout the diel cycle, irrespective of devil relative density, and showed no change in overlap with the devil's temporal niche (Fig. 5).

Devil introduction: cat temporal activity did not differ significantly on Maria Island between 2013/2014, when devils were at low density, and 2016/2017 when devils were at high density (Fig. 2F; $p = 0.36$), and through time at the control site (Fig. 2G; $p = 0.36$). Like the survey of devil declines, cats were active throughout the entire diel cycle and showed no change in overlap with the devil's temporal niche (Fig. 5).

Temporal activity in key prey species

Tasmanian pademelon

Devil decline: pademelons were highly crepuscular and had slightly higher sunset and sunrise peaks in activity at sites with low devil relative density compared to high relative density, although these were not statistically different ($p = 0.07$; Fig. 2H), and there was no change in overlap with the devil's temporal niche (Fig. 5).

Devil introduction: pademelons had a more pronounced peak at sunset in 2016/2017 when devil density was higher, compared to 2013/2014 ($p = 0.048$; Fig. 2I). The increase in the sunset peak did not reduce the overlap with the devil's temporal niche (Fig. 5).

Bennett's wallaby

Devil decline: the sunrise peak in wallaby activity was slightly higher at sites with high devil relative densities than with low relative densities ($p = 0.005$; Fig. 2K), although this did not change the overlap with the devil's temporal niche (Fig. 5).

Devil introduction: when devils were at low density on Maria Island, activity of wallabies peaked at sunset. With increased devil abundance, nocturnal activity decreased and the highest peak moved to shortly after sunrise ($p < 0.001$; Fig. 2L), resulting in reduced overlap with the devil's temporal niche (Fig. 5). The opposite trend occurred at the control site, where nocturnal activity and the sunset peak both increased in 2016/2017. The GAM predicting the temporal activity of wallabies contained a significant interaction between hour, year and location (edf = 14.11, $p < 0.0001$, deviance explained = 62%). As devil density increased through time, the peak in wallaby activity around sunrise increased and shifted later, while activity in the middle of night declined (Fig. 3D).

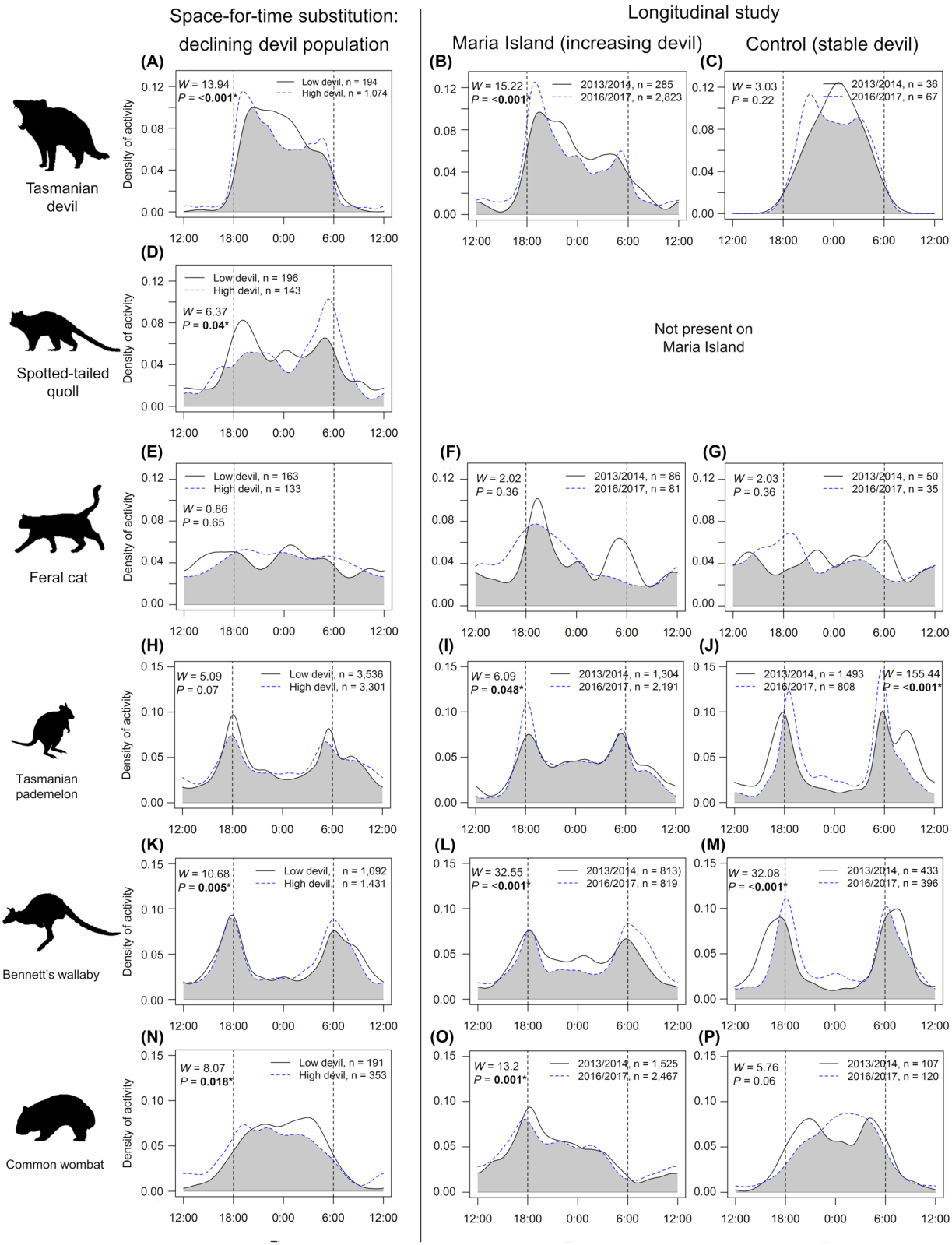

Figure 2. Activity profiles of predators and the major prey species of devils and quolls. The left column compares temporal activity between sites with high relative devil densities against sites where devils have suffered severe disease-induced declines. The right two columns compare Maria Island in 2013/2014, when devils were at low density shortly after their introduction, to 2016/2017 when devils were at high density. The devil population was low and stable at the control site during the study. The plots are centred on midnight and time has been scaled so that sunset occurs at 18:00 and sunrise at 6:00 (vertical lines). p values were calculated using the nonparametric Mardia–Watson–Wheeler test of homogeneity.

Common wombat

Devil decline: wombats were more diurnally active at sites with high devil relative densities, and had a less pronounced nocturnal peak in activity, compared to sites with low devil relative densities ($p = 0.018$; Fig. 2N). This subtle shift did not change the overlap with the devil's temporal niche (Fig. 5).

Devil introduction: a subtle shift in wombat activity occurred on Maria Island as devil densities increased. In 2013/2014, when devils were at low density, wombat activity peaked shortly after sunset. In 2016/2017, when devil density was high, peak activity shifted to shortly before sunset ($p < 0.001$; Fig. 2O), significantly reducing overlap with the devil's temporal niche (Fig. 5).

Discussion

We provide the first investigation of a top predator that is declining in abundance in one area while rapidly increasing in another, providing a novel framework to test the effects on community-wide temporal activity. Devil declines on mainland Tasmania were associated with a strong shift in quoll activity, and statistically significant but subtle shifts in wallabies and wombats. The introduction of devils to Maria Island was associated with larger increases in temporal partitioning by the herbivorous prey species. The invasive feral cat did not shift its temporal activity in response to either decreasing or increasing devil densities. Most previous studies of temporal partitioning between top predators and subordinate species have been non-manipulative, providing support for hypotheses of temporal partitioning but not establishing causal mechanisms (Ramesh et al. 2012, Bischof et al. 2014). However, manipulative or natural experiments provide stronger evidence on causes of patterns. Our study is the largest such study to date.

Carnivore responses and competition

This is the first demonstration, to the best of our knowledge, of density-dependent temporal activity in a top predator: devil activity peaked earlier in the night when relative density was high. Devils are both predators and highly-adapted scavengers, one of the world's few bone-specialist carnivores (Jones 2003). High densities increase competition for carrion (Cunningham et al. 2018), and may force devils to do more hunting, which would require them to match their activity with the crepuscular activity of their primary prey, wallaby and pademelon. Other studies show that predators can time their activity to overlap with peak prey activity. For example, kestrels *Falco tinnunculus* match the regular 2-h peaks in vole *Microtus arvalis* activity (Rijnsdorp et al. 1981, Kronfeld-Schor et al. 2017) and activity patterns of Cooper's hawk *Accipiter cooperii* reflects those of their prey (Roth and Lima 2007).

Quolls, the species with greatest dietary overlap with devils (Jones and Barmuta 1998, Andersen et al. 2017), showed a pronounced shift in activity in response to declining devil densities, suggesting active temporal avoidance to reduce encounters with a devil. Quolls shifted their activity peak from dawn, when devils are abundant, to dusk, when devils were rare, strongly suggesting competitive release. At low devil densities, quoll temporal activity

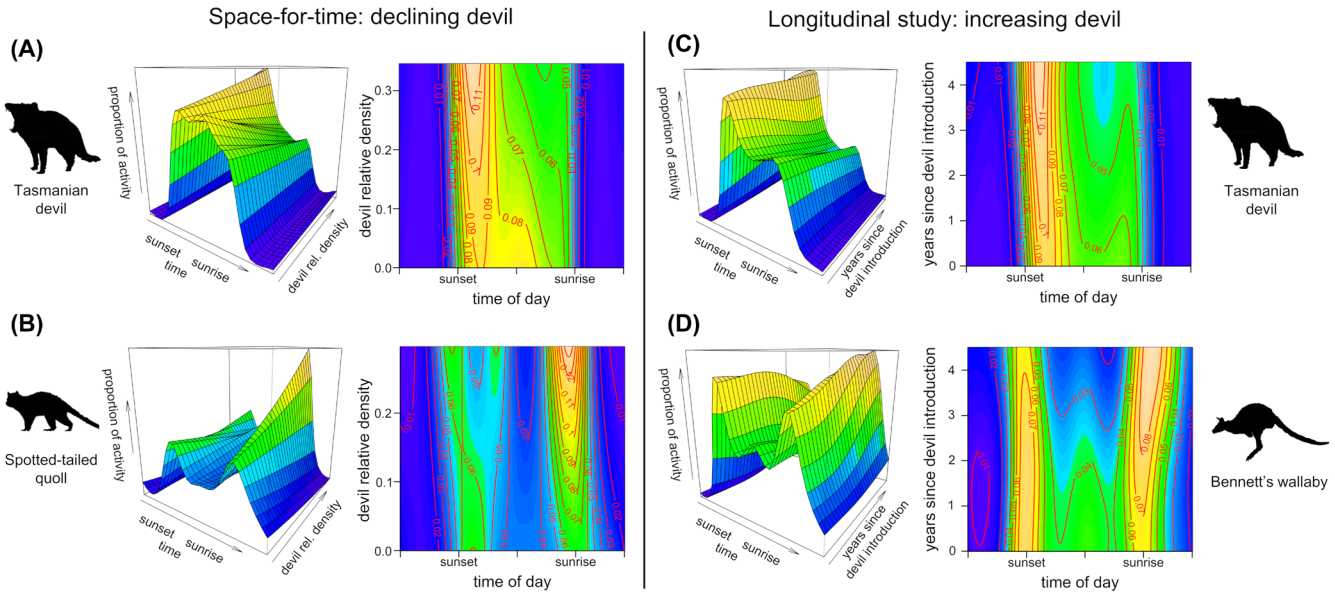

Figure 3. Interaction plots from GAMs predicting the temporal activity of a species based on changes in the devil population. Devil relative density refers to the number of devil detections per camera night. In the devil introduction study, increasing years since devil introduction is correlated with rapid increases in devil density. Perspective plots (left panel for each species) show the proportional activity of a species on the vertical axis, with time of day and devil relative abundance on the horizontal axes. The contour plots (right panel for each species) are a different visualisation of the same information, with contours showing the proportional activity of a species at a given time of the day.

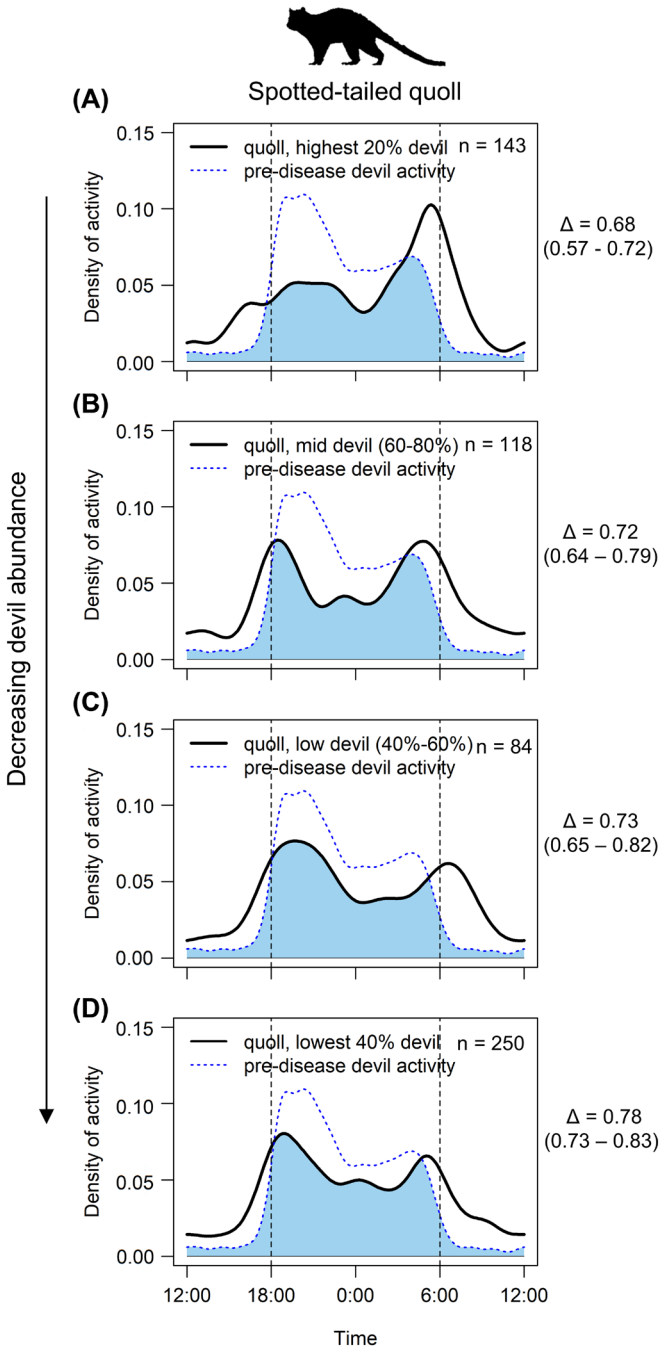

Figure 4. Temporal activity of spotted-tailed quolls (solid line) compared with the devil's temporal niche (blue dashed line; pre-disease temporal activity). We separated quoll activity according to the relative density of devils, which shows a shift in peak activity from sunrise when devils were abundant to sunset when devils were rare. The coefficient of overlap Δ (95% bootstrapped CI) shows that as devil relative densities decline, quolls increased their overlap with the devil's increasingly vacant temporal niche. (A) Sites in the top 20% reflect pre-disease devil densities. (B) Sites with intermediate devil abundance. (C) Low devil abundance sites (40–60%) represent substantial population declines. (D) Very low devil sites (lowest 40%) correspond to severe devil declines.

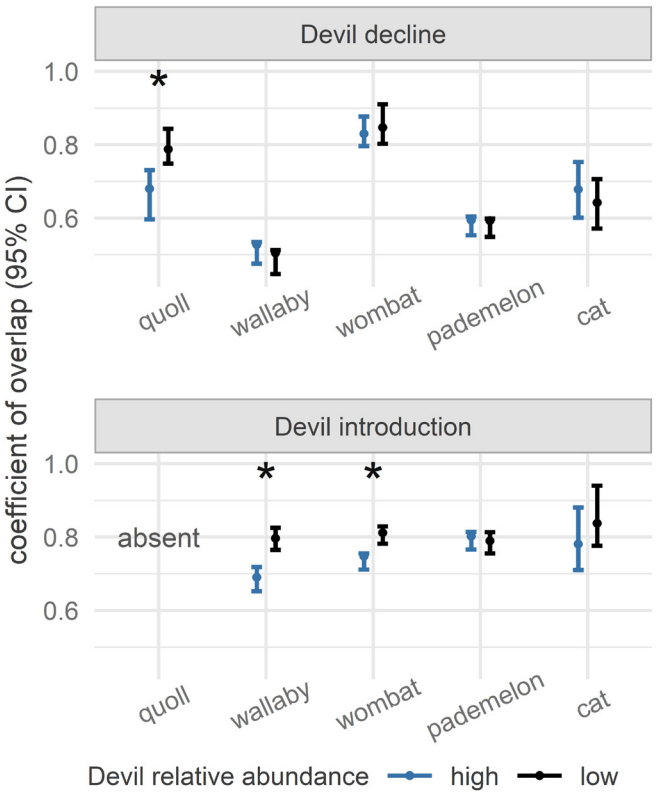

Figure 5. Change in overlap of the devil's temporal niche with mesopredators and major prey species. The coefficient of overlap ranges from 1, representing total temporal overlap, to zero, representing no overlap. The top panel shows the study of a declining devil population, and the bottom panel shows the study of an increasing devil population following their introduction to Maria Island. Quolls increased their use of the devil's temporal niche following devil declines (top panel). Quolls, however, were not present on Maria Island, where wallaby and wombats both reduced their use of the devil's niche following rapid increases in devil density (bottom panel). Error bars show the bootstrapped 95% confidence interval and * highlights non-overlapping confidence intervals.

resembled that of devils at high density, which suggests that quolls may be attracted to the early period of the night for the same reasons as devils – to hunt when prey are most active and exploit newly-available carrion. Carrion is a resource that is largely unavailable to quolls where devils are abundant, but is used by them where devils have declined (Cunningham et al. 2018). The best examples of competition-induced temporal shifts in mammals include two species that shift to the opposite part of the diel cycle. Invasive American mink *Neovison vison* in the UK shifted from nocturnal to diurnal activity following the recovery of a native carnivore (Harrington et al. 2009). Golden spiny mice *Acomys russatus* in the Judean desert are diurnal in the presence of their less arid-adapted competitor, *A. cahirinus*, but increase nocturnal activity in their absence (Kronfeld-Schor and Dayan 2003). In general, however, such extreme competition-induced shifts in activity are rare (Kronfeld-Schor and Dayan 2003).

Activity of cats did not respond to changes in devil density, helping to resolve a debate about the nature of mesopredator release of cats in Tasmania. Long-term, island-wide nocturnal spotlight surveys revealed an increase in cat detections following devil declines (Hollings et al. 2014), which was interpreted as increased density. However, in a separate study using cameras only in areas where the disease was present, Fancourt et al. (2015) claimed that cats are more nocturnal in the long-term disease region, instead suggesting that shifts in diel activity explain the increase in detections. Unlike Fancourt et al. (2015), we measured cat activity across the full range of devil densities, including a time series of increasing density on Maria Island, and found no shifts in cat activity due to devil density. This suggests that increased cat detections following devil decline (Hollings et al. 2014) are not caused by changes in temporal activity and may reflect increased cat abundance.

One hypothesis for the contrasting responses of quolls and cats is that interference competition from devils is mediated through food resources, causing quolls and cats to experience interference differently. Interference competition in carnivores, involving aggressive exclusion from a resource (Linnell and Strand 2000), is probably a stronger driver of temporal partitioning than exploitation competition (Carothers and Jaksić 1984). Quolls and devils have high dietary overlap (Jones and Barmuta 1998, Andersen et al. 2017), whereas cats typically consume smaller fauna (Doherty et al. 2015). Devils additionally pose a strong risk of kleptoparasitism for quolls, but less so for cats due to their smaller prey size. If devils exclude mesopredators from the early period of the night to monopolise food resources, quolls should show the strongest response. Devils aggressively protect carcasses and exclude other species from feeding (Cunningham et al. 2018), but there is only anecdotal information about devils killing or actively persecuting mesopredators (Jones 2003), as some other top predators do (Palomares and Caro 1999). For example, dingoes *Canis lupus dingo* kill cats, and cats avoid dingoes temporally (Brook et al. 2012). Similarly, wolves *Canis lupus* kill coyotes *Canis latrans*, which show temporal avoidance of wolves during winter (Arjo and Pletscher 1999). A better understanding of the mechanisms by which devils interfere with mesopredators, whether active persecution or resource-mediated aggression, may help explain the contrasting behavioural responses of the two mesopredators.

Subtle and variable responses by prey

The major prey species of devils (and quolls) showed stronger shifts in their overlap with the devil's temporal niche in response to rising than to falling devil densities. Specifically, wombat and wallaby reduced their use of the devil's temporal niche following increases in devil density, and pademelon showed a more pronounced peak at sunset. Responses were subtler for declining devil densities; wallaby and wombat showed statistically significant but small differences in their temporal activity, which did not reduce their overlap with the devil's niche (and pademelon showed no change).

We offer two non-exclusive hypotheses for the differing strengths of prey responses. First, the costs associated with increasing top-predator densities (death or injury) are probably much higher than the costs associated with decreasing predator densities (small potential foraging loss). Declining predator densities may therefore elicit a more gradual response because persistence of low-cost behaviours can be adaptive even when selection is relaxed (Flecker 1992, Kronfeld-Schor et al. 2017). Second, the multi-predator hypothesis suggests that the presence of one predator species can maintain anti-predator behaviours that relate to another extinct predator (Blumstein 2006). Thus, the presence of quolls on the Tasmanian mainland, but not on Maria Island, could possibly maintain behaviours in these shared prey species in the absence of devils. Further, quolls responded to devil declines by increasing their use of the devil's temporal niche, which could in turn maintain avoidance behaviours in prey because of continued predation pressure. The near-absence of nocturnal predators of wallaby and wombat before the introduction of devils means they were shifting from a predator-free baseline, which could explain their initially higher nocturnal activity and the larger temporal shift.

Habitat differences may further explain the stronger response of pademelon on Maria Island than the Tasmanian mainland. Pademelon activity at sunset increased on Maria Island when devils were at high densities, whereas there was no significant change in response to devil decline on the Tasmanian mainland. These different patterns may reflect diel migrations by pademelon that vary in response to habitat; specifically, open grasslands are found only on Maria Island. Diel migrations – cyclical back and forth diel movements along a spatial or ecological gradient – are employed by prey to reduce the risk of encountering predators (Courbin et al. 2018). Zebras, for example, forage during the day in grassland near waterholes, the preferred habitat for lions, but move further from waterholes at night when lions become active (Courbin et al. 2018). Pademelons exhibit similar behaviour; they typically move from forest to grasslands to feed, and where devils are abundant they emerge from the forest earlier in the evening and forage further from the forest edge (Nielsen 2009), possibly to minimize risk at the edge where devils hunt (Baynes 2007). Although the increase in sunset activity by pademelons did not reduce their overlap with the devil's temporal niche, the increase in sunset activity may reflect spatio-temporal avoidance of risky areas.

The subtle responses of wallaby and pademelon to rapid changes in predator density suggest either that they are constrained by circadian rhythms or that they make greater use of other anti-predator behaviours (Kronfeld-Schor and Dayan 2003). Circadian rhythms evolve to ensure animals are active at the most beneficial time of the diel cycle, and can have low short-term plasticity (Flecker 1992, Kronfeld-Schor et al. 2017). The Tasmanian night now has vastly lower predation risk following the extinction of the thylacine in the mid-20th century and the recent decline of the devil. If current predation is the major driver of temporal activity, we would expect substantial increases in nocturnal activity of

pademelon and wallaby when devils are rare, rather than the subtle responses reported here. Instead, it is likely that wallaby and pademelon use fine-scale spatio-temporal avoidance behaviours to avoid predation by devils rather than temporal avoidance alone (Nielsen 2009).

Conclusions

This study demonstrates that rising or falling abundance of a top predator can have far-reaching effects on the behaviour of other carnivore and prey species. While there is much evidence of the cascading effects that often follow top-predator removal, there is less evidence about the reversal of effects following predator recovery (Alston et al. 2019). Our study provides valuable evidence that top predator recoveries can reinstate anti-predator behaviours in other species (Berger et al. 2001, Estes et al. 2011, Cunningham et al. 2019b). The effects we show are distinct from the direct demographic impacts of predation on population size or distribution, but they may compound those direct impacts. Moreover, these behavioural changes operate over short timescales, as shown by the rapid responses that we observed on Maria Island. The density-dependence of devil temporal activity highlights the need for recovery efforts to focus on restoring predator populations to functional densities if we wish to maintain the full spectrum of adaptive behaviours in predators themselves and the species they influence.

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Supplementary material (available online as Appendix ecog-04485 at <www.ecography.org/appendix/ecog-04485>). Appendix 1.

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