Supplementary Material

Top carnivore decline has cascading effects on scavengers and carrion persistence

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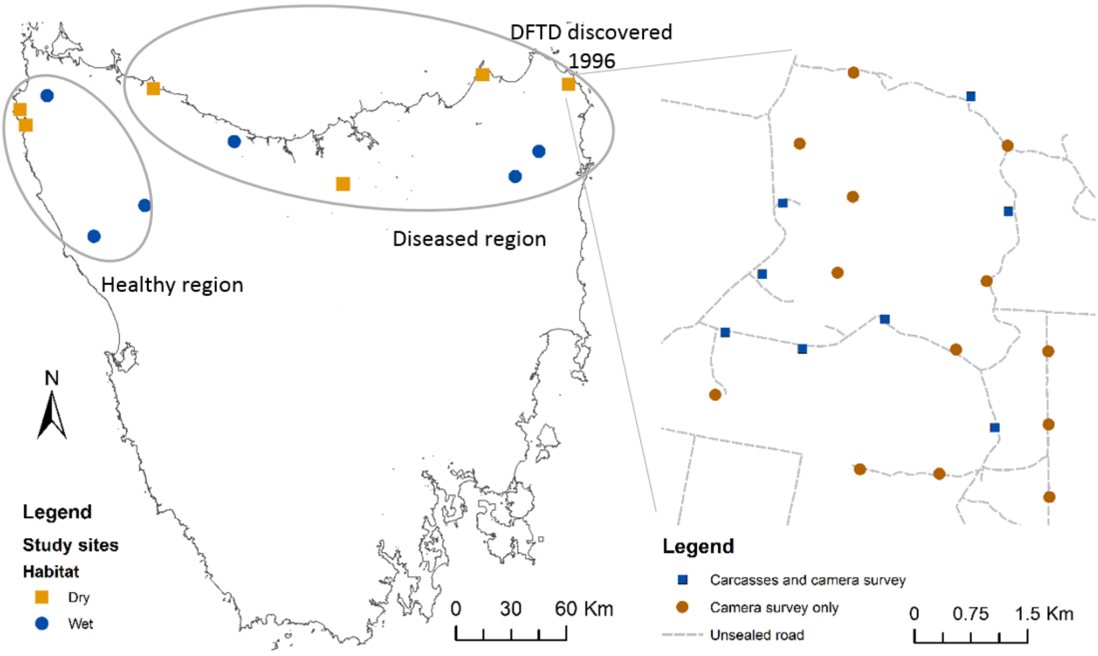

Fig. S1: Map of study sites and example of one camera array used to measure devil activity and conduct a scavenging experiment. We spaced RECONNYX PC-800 passive infrared motion-detector cameras ~1 km apart and attempted to approximate a two-dimensional grid. Each camera was fastened to a tree ca. 1 m above the ground at least 40 m from the road. For the survey of devil activity, we suspended an olfactory and visual lure from a tree 2-3 m in front of the camera. The lure consisted of a perforated PVC canister containing dried beef liver, tuna oil, peanut butter, rolled oats and sardines, with a CD suspended below.

For the scavenging experiment, eight carcasses at each site were deployed randomly at the camera locations used to survey devil activity, excluding locations that were inaccessible in winter. Carcasses were obtained from shooters with crop protection permits, frozen, and then freshly thawed prior to deployment. Two steel stakes through the rib cage and abdomen secured each carcass to the ground. A RECONNYX PC-800 passive infrared motion-detector camera was fastened to a tree ~3 m from each carcass and programmed to take three rapid-fire photos per trigger, with a one second break separating subsequent triggers.

Coordinates of study sites: Arthur River South -41.0704, 144.6900; Arthur River North -41.0012, 144.6474; Bond Tier Forest Reserve -40.9229, 144.8287; Corinna -41.6335, 145.0980; Savage River Regional Reserve -41.4729, 145.4343; Rocky Cape National Park -40.8931, 145.5136; Dial Range -41.1831, 146.0496; Reedy Marsh Forest Reserve -41.3918, 146.7274; Mt Victoria Forest Reserve -41.3449, 147.8448; Blue Tier Forest Reserve -41.2228, 148.0067; Mt William National Park -40.8815, 148.2106; Waterhouse Conservation Area -40.8514, 147.6462)

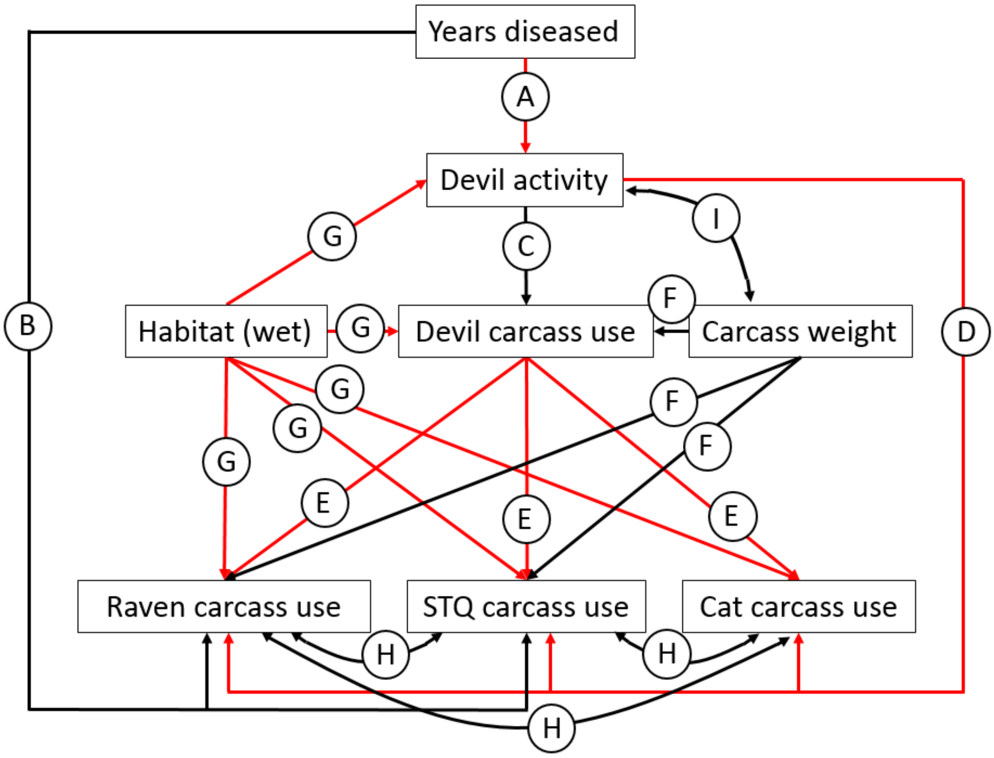

Fig. S2. Justification for hypothesised causal network in the piecewise structural equation model. Red arrows represent hypothesised negative relationship; black arrows represent hypothesised positive relationship; curved double headed arrows represent correlated errors.

We constructed our *a priori* SEM based on theoretical knowledge of the relationships between the species and processes involved in the network. We populated the SEM with data from a remote camera survey of devil activity and with foraging data from experimentally placed carcasses. Below is a theoretical explanation and justification of each path in the network:

A) DFTD has been shown to cause rapid population declines, on average 77% and up to 95% (Hawkins *et al.* 2006; McCallum *et al.* 2007; Hollings *et al.* 2014; Lazenby *et al.* 2018).

B) Time since DFTD onset represents the length of time that mesopredators have had to respond demographically to the decline of the devil, or represents behavioural changes that are time-sensitive.

C) We expected a positive relationship between devil activity and the overall duration that devils fed for because devils in densely populated areas are likely to locate more carcasses.

D) This relates to the size of the devil population, as distinct from the direct effects of consumption by devils, and can be thought of as the effect of the 'landscape of fear' that corresponds to the risk of encountering a devil.

E) Direct effects of devil foraging duration, as a proxy for the amount of the carcass that is consumed by devils. Devils are highly adapted scavengers that are competitively and ecologically dominant in the Tasmanian carnivore community (Jones ME 1995; Jones & Barmuta 1998, 2000; Jones 2003), and we expected them to have a negative effect on carcass consumption by all other species.

F) Carcass weight was included as a covariate to account for its effects on foraging duration (but was not displayed in the final SEM for visual clarity). Total foraging time is likely to be longer at larger carcasses because there is more tissue available for consumption. We were not theoretically interested in this variable, but it was necessary to account for its effects.

G) Habitat type is likely to affect population sizes and resources available to a species, and therefore could affect the carcass consumption by a species.

H) We included a correlation between the carcass consumption of ravens, quolls and cats. We considered that there could be a relationship here that is caused by a shared underlying factor that is not captured in the SEM, and we were additionally unsure of the directionality of the relationship i.e. what the causal relationship is between the species. This correlation has no bearing on model estimates (see (Lefcheck & Duffy 2015) for similar treatment of correlation between variables). We've treated these variables in the same way that the R package 'piecewiseSEM' treats variables assigned as correlated errors: first, omitting these paths from the 'basis set' (used to calculate overall model fit), and then calculating a simple test of significance on the bivariate correlations (Lefcheck 2016).

I) Initial data exploration revealed a small but statistically significant correlation between the variables for 'devil activity' and 'caracass weight'. There is clearly no theoretical link between these variables, however, we included a correlation to account for the shared external driver that is not captured by our SEM. The correlation most likely arose because we received and deployed carcasses in batches that consisted of carcasses of slightly different average sizes. This correlation has no effect on other model estimates.

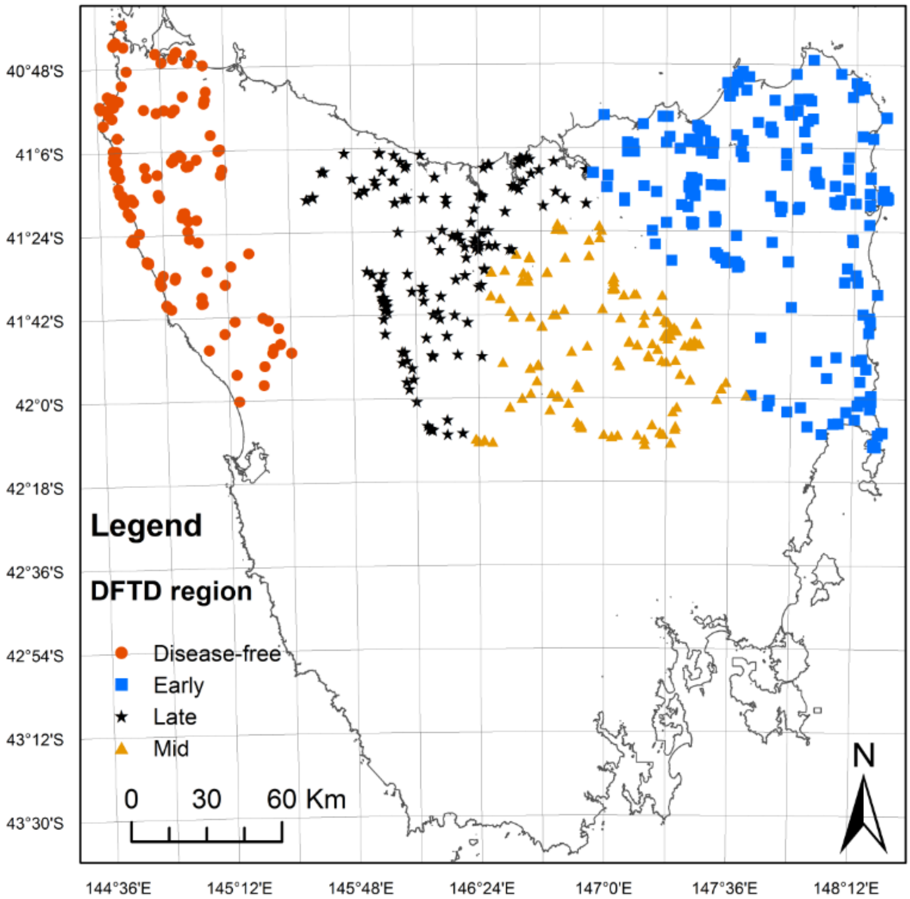

Fig. S3: Map of bird survey sites. We extracted bird survey data from 1998-2017 for northern Tasmania from the BirdLife Australia database. We used the standardized 2-ha 20 min surveys, and removed sites within 2-km of towns, resulting in 1932 surveys. Survey sites were separated into four regions that represent different disease outbreak times (Hollings *et al.* 2014): early outbreak = 1996-1999 (blue squares); mid-term = 2000-2003 (yellow triangles); late-term = 2004-2007 (black stars); disease-free (orange circles). Grid lines represent the cells that were included as a random factor in the generalized linear mixed-effects models to account for spatial autocorrelation between survey sites.

Table S1. Description of the response and predictor variables used in the structural equation model investigating carcass consumption.

Variable	Description
Devil activity	Number of devil detections per 100 camera nights collected from a general-purpose camera trap survey prior to the carcass experiment.
Devil foraging duration	The total duration in minutes that a Tasmanian devil fed at a carcass. - Stage 1 of hurdle model: binary variable (0-1) for whether a devil fed at a carcass - Stage 2 of hurdle model: continuous variable of foraging duration, consisting only of the non-zero data
Quoll foraging duration	The total duration in minutes that a spotted-tailed quoll fed at a carcass. - Stage 1 of hurdle model: binary variable (0-1) for whether a quoll fed at a carcass - Stage 2 of hurdle model: continuous variable of foraging duration, consisting only of the non-zero data
Raven foraging duration	The total duration in minutes that a forest raven fed at a carcass. - Stage 1 of hurdle model: binary variable (0-1) for whether a raven fed at a carcass - Stage 2 of hurdle model: continuous variable of foraging duration, consisting only of the non-zero data
Cat foraging duration	A binary variable of whether a cat fed at a carcass
Years diseased	A numerical variable for the number of years since the estimated year of DFTD onset.
Habitat type	A categorical variable consisting of two broad habitat types: wet Eucalypt / rainforest ('wet') and dry Eucalypt / coastal scrub ('dry')
Initial carcass weight	Initial carcass weight in kg, centred for analysis

Table S2. Overview of model structures that comprise the piecewise structural equation model. We used ordinary least squares regression (OLS) to investigate devil activity because the data from the general-purpose mammal survey had no nested structure and therefore did not require a random effect. We used generalized linear mixed-effects models (GLMM) to investigate carcass use by each species to accommodate a random effect.

Model including fixed effects	Model type	Random effect	Error distribution
Devil activity ~ years since DFTD + habitat	OLS	-	-
Devil carrion ~ devil activity + habitat + carcass weight	GLMM; hurdle	Site	1. Binomial. 2. Gamma
Raven carrion ~ devil activity + devil carrion + habitat + carcass weight + years since DFTD	GLMM; hurdle	Site	1. Binomial. 2. Gamma
S.T. Quoll carrion ~ devil activity + devil carrion + habitat + carcass weight + years since DFTD	GLMM; hurdle	Site	1. Binomial. 2. Gamma
Cat carrion ~ devil activity + devil carrion + habitat	GLMM	Site	Binomial

Table S3: Predictor variables used to model forest raven detections. These variables were used in generalized linear mixed-effects models predicting the presence-absence of forest ravens in standardized bird surveys. All continuous variables were scaled by subtracting the mean and dividing by the standard deviation to help with model convergence.

Predictor variable	Description
Years diseased	The duration in years that a site had been diseased for at the time of a survey, with surveys conducted prior to disease onset given a value of zero. Estimated year of DFTD onset was based on a previous study (Hollings *et al.* 2014). We excluded a band of sites near the disease front because there was no reliable data available to accurately estimate the year of disease outbreak. Before inclusion in the global model, we investigated lag-times from zero to five years. To do this, we ran GLMMs (raven presence/absence predicted by years diseased with 0-5 years lag) and compared models using AICc to see which lag-time was a better predictor of raven detections. Zero years lag had the lowest AICc, so this was included in subsequent models.
Survey year	Year that the survey was conducted in.
DFTD region	We categorised four disease regions based on the disease regions used in a previous study(Hollings *et al.* 2014): - Early outbreak: DFTD outbreak 1996-1999 - Mid-term: DFTD outbreak 2000-2003 - Late-term: DFTD outbreak 2004-2007 - Disease-free We also included a 'survey year' by 'DFTD region' interaction to investigate whether temporal effects depended on DFTD region.
Average rainfall	We obtained gridded estimates of mean rainfall from the Australian Bureau of Meteorology.
Percent agriculture	Using the TASVEG 3.0 shapefile in ArcGIS, we rasterized the 'Agricultural land' category at a 50 m resolution. We then used the 'focal statistics' tool to calculate the percentage of agricultural cells within a 5 km search radius and extracted this percentage value for each survey location.

Percent dry Eucalypt	Using the same approach as ‘percent agriculture’, instead using the category ‘dry Eucalypt forest and woodland’ within a 2 km search radius.
Percent wet forest / rainforest	Using the same approach as ‘percent agriculture’, instead using categories ‘wet Eucalypt forest and woodland’ and ‘rainforest and related scrub’. This variable was moderately correlated with average rainfall (r = 0.66), so we excluded it from inclusion in the model.
Public road density	Using the ‘road centrelines’ shapefile (LISTmap), we used the ‘line density’ tool in ArcGIS with a 2 km search radius to create a raster of the density of ‘public’ roads. We extracted public road densities for each survey location. We hypothesised that road density may influence raven density through the regular provisioning of roadkill subsidies.
Elevation	Elevation was extracted from a state-wide digital elevation model in ArcGIS.
Cell	Each survey was assigned to the 0.3 x 0.3 degree grid cell that it was located within (see Supplementary Figure 2), and this was included as a random effect to account for spatial autocorrelation.

Table S4. Results of survival analysis investigating carcass persistence and discovery. The sets of Cox proportional hazards models within 2 ΔAICc of the top model for the number of days that experimentally placed carcasses persist in the environment, and the number of hours until carcass discovery, across a gradient of devil population declines. The table shows the model rank based on change in AICc (ΔAICc), model weights (w_i) and model coefficient estimates ± s.e. for each predictor variable. The relative importance of variables was calculated by summing the weights of all candidate models containing the variable. Not all models are shown.

Model rank	ΔAICc	w_i	df	Years diseased	Habitat	Devil activity	Carcass weight
Carcass persistence							
1	0.00	0.283	3	-0.0593 ± 0.0171	-0.357 ± 0.266 (W)		
2	0.80	0.190	4	-0.0609 ± 0.0184			
3	1.73	0.115	4	-0.0570 ± 0.0226	-0.382 ± 0.314 (W)	0.0044 ± 0.03	
4	1.79	0.119	4	-0.0680 ± 0.0226		-0.015 ± 0.0279	
11 (null)	7.75	0.006	7				
Relative importance of variables				0.96	0.57	0.34	0.26
Carcass discovery							
All vertebrates							
1	0.00	0.281	2		-1.0099 ± 0.245 (W)		0.1096 ± 0.077
2	0.36	0.234	1		-0.9112 ± 0.238 (W)		
3	1.87	0.110	3		-0.9831 ± 0.25 (W)	-0.0096 ± 0.019	0.1199 ± 0.08
4	1.98	0.104	3	0.0048 ± 0.013	-1.0187 ± 0.246 (W)		0.1068 ± 0.078
5	2.00	0.103	2	0.0067 ± 0.013	-0.9285 ± 0.24 (W)		
10 (null)	12.56	0.001	6				
Relative importance of variables				0.29	1.00	0.28	0.53
Tasmanian devil							
1	0.00	0.373	5		-0.9336 ± 0.317 (W)	0.06342 ± 0.025	
2	1.47	0.179	5	0.0031 ± 0.022	-0.9473 ± 0.332 (W)	0.0663 ± 0.032	
8 (null)	5.49	0.024	7				
Relative importance of variables				0.37	0.88	0.79	0.25
Forest raven							
1	0.00	0.266	4		-1.5341 ± 0.41 (W)	-0.0733 ± 0.038	
2	0.51	0.206	4		-1.6127 ± 0.41 (W)	-0.0824 ± 0.038	0.1423 ± 0.118
3	0.99	0.162	4	0.0183 ± 0.026	-1.6105 ± 0.42 (W)	-0.0568 ± 0.043	

4	1.28	0.140	3	0.0366 ± 0.022	-1.795 ± 0.399 (W)		
14 (null)	12.09	0.001	8				
Relative importance of variables				0.44	0.99	0.73	0.37
Spotted-tailed quoll							
1	0.00	0.173	6			-0.1264 ± 0.061	
2	0.35	0.145	7		-0.5587 ± 0.647 (W)	-0.113 ± 0.06	
3	0.54	0.132	7	-0.0307 ± 0.046		-0.152 ± 0.071	
4	1.18	0.096	7	-0.0205 ± 0.047	-0.4723 ± 0.674 (W)	-0.132 ± 0.074	
6 (null)	2.19	0.058	8				
Relative importance of variables				0.42	0.46	0.72	0.24

Table S5. Species observed feeding on experimentally-placed Tasmanian pademelon (*Thylogale billardierii*) carcasses.

Common name	**Scientific name**	**Number of carcasses observed feeding at**
Black rat	*Rattus rattus*	*12*
Brown falcon	*Falco berigora*	*1*
Brown goshawk	*Accipiter fasciatus*	*3*
Grey butcherbird	*Cracticus torquatus*	*1*
Common brushtail possum	*Trichosurus vulpecula*	*5*
Dog	*Canis lupus familiaris*	*2*
Eastern quoll	*Dasyurus viverrinus*	*2*
Feral cat	*Felis catus*	*12*
Forest raven	*Corvus tasmanicus*	*45*
Spotted-tailed quoll	*Dasyurus maculatus*	*32*
Swamp harrier	*Circus approximans*	*2*
Tasmanian devil	*Sarcophilus harrisii*	*76*
Wedge-tailed eagle	*Aquila audax*	*2*

Table S6. Raw results of the regressions that comprise the piecewise structural equation model. Bivariate correlations from variables relate to variables that we included as having 'correlated errors' (see description for pathways (H) and (I) in Supplementary Figure 1). Bold values indicate statistically significant pathways at alpha = 0.05.

Response variable	Model type	Predictor variable	Estimate	SE	p-value
Devil activity	Linear regression	**Intercept**	**9.171**	**2.540**	**0.00565****
		DFTD	**-0.411**	**0.171**	**0.03933***
		Habitat (W)	3.947	2.863	0.20128
Devil carcass	1. Hurdle GLMM: binomial	Intercept	0.605	0.590	0.30517
		Devil activity	**0.338**	**0.105**	**0.0012****
		Habitat (W)	-1.220	0.694	0.0789
		Carcass weight	0.043	0.276	0.8775
	2. Hurdle GLMM: gamma	**Intercept**	**4.474**	**0.177**	**< 2e-16*****
		Devil activity	**0.0408**	**0.019**	**0.0295***
		Habitat (W)	-0.084	0.223	0.7057
		Carcass weight	**0.303**	**0.052**	**5.1e-09*****
Raven carcass	1. Hurdle GLMM: binomial	**Intercept**	**2.998**	**1.068**	**0.005004****
		Devil carcass	**-0.016**	**0.005**	**0.000491*****
		Devil activity	-0.083	0.074	0.262305
		Habitat (W)	**-1.841**	**0.655**	**0.004936****
		Carcass weight	**0.660**	**0.327**	**0.043883***
		Years diseased	0.027	0.046	0.560189
	2. Hurdle GLMM: gamma	**Intercept**	**5.724**	**0.428**	**< 2e-16*****
		Devil carcass	**-0.006**	**0.002**	**0.00157****
		Devil activity	0.011	0.042	0.79604
		Habitat (W)	-0.009	0.401	0.98266
		Carcass weight	0.107	0.120	0.37174
		Years diseased	0.031	0.024	0.20208
Quoll carcass	1. Hurdle GLMM: binomial	Intercept	0.731	0.972	0.4525
		Devil carcass	**-0.010**	**0.004**	**0.0135***
		Devil activity	-0.113	0.086	0.1917
		Habitat (W)	0.514	0.712	0.4699
		Carcass weight	0.207	0.240	0.3892

		Years diseased	0.015	0.050	0.7643
	2. Hurdle GLMM: gamma	**Intercept**	**4.224**	**0.910**	**3.42e-06*** **
		Devil carcass	-0.005	0.003	0.0999
		Devil activity	-0.021	0.075	0.7835
		Habitat (W)	-0.193	0.570	0.7354
		Carcass weight	0.277	0.170	0.1037
		Years diseased	**0.106**	**0.044**	**0.0163***
Cat carcass	GLMM: binomial	**Intercept**	**-1.752**	**0.598**	**0.00341****
		Devil carcass	0.002	0.003	0.59093
		Devil activity	**-0.172**	**0.087**	**0.04708***
		Habitat (W)	1.364	0.704	0.05285

Bivariate correlations (analogous to 'correlated errors')	**Pearson's r**	**P**
Quoll, raven	0.07	0.51
Quoll, cat	0.10	0.34
Cat, raven	-0.09	0.39
Devil activity, carcass weight	**0.29**	**0.006****

Table S7: Model selection table and coefficient values for the analysis of population trends in forest ravens from 1998 to 2017. The sets of generalized linear mixed-effects models predicting the odds of detecting a raven through time and across a gradient of devil population declines. The best model estimated a 2.2-fold increase in the odds of detecting a forest raven from 1998-2017. Table shows the model rank based on change in AICc (ΔAICc), model weights (w_i) and model coefficient estimates for each predictor variable. Standard error is shown italicized for parameter estimates for the highest ranked model. The coefficients for DFTD region are contrasted with the early disease region; D=disease-free, L=late-term diseased, M=mid-term diseased.

	Environmental covariates held constant						Variables of primary interest						
	(Int)	%ag	%dry	elev	avg rain	road density	DFTD region	survey year	years diseased	DFTD region * survey year	df	ΔAICc	*wi*
1	-0.43	0.39	0.26	0.25	-0.49	0.18	D 1.56; L 0.69; M 0.35	0.23			11	0.00	0.79
s.e.	*± 0.2*	*± 0.1*	*± 0.07*	*± 0.25*	*± 0.13*	*± 0.07*	*D ± 0.38; L ± 0.32; M ± 0.31*	*± 0.06*					
2	-0.57	0.40	0.27	0.25	-0.50	0.19	+		0.20		11	4.30	0.09
3	-0.41	0.38	0.26	0.24	-0.48	0.18	+	0.27		+	14	5.17	0.06
4	-0.41	0.38	0.26	0.24	-0.48	0.18	+			+	14	5.17	0.06
5	-0.52	0.36	0.26	0.23	-0.51	0.22	+				10	13.24	0.00
env	0.09	0.40	0.23	0.12	-0.27	0.17					7	24.70	0.00
null	-0.12										2	68.15	0.00

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