

## Dynamics, habitat use and extinction risk of a carnivorous desert marsupial

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**Dynamics, habitat use and extinction risk of a carnivorous desert  
marsupial**

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**Short title:** Dynamics and extinction risk of a marsupial.

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# **Dynamics, habitat use and extinction risk of a carnivorous desert marsupial**

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## **Abstract:**

Animals in hot desert environments often show marked fluctuations in population size, persisting in low numbers in refuge habitats during dry periods and expanding after rain when resources increase. Understanding drought-wet cycle dynamics is important for managing arid ecosystems, particularly if populations of threatened species are present. Such species may face increased risks of extinction if all populations decrease synchronously toward zero during low-resource periods, and if key refuge habitats needed during these periods are disturbed or unavailable. Here, we describe the dynamics and habitat requirements of two sub-populations of the kowari, *Dasyuroides byrnei* (Marsupialia: Dasyuridae), during long-term sampling (2000–2015) that encompassed multiple drought-wet cycles. This species is listed currently as Vulnerable on the IUCN Red List. We found that

## Dynamics and extinction risk of a carnivorous marsupial.

1  
2  
3 25 the study region contains favourable habitat, with kowari occurring on hard stony (gibber)  
4  
5 26 pavements in association with coverage of sand that may facilitate construction of burrows.  
6  
7 27 Both sub-populations of kowari declined over the study period irrespective of climatic  
8  
9 28 conditions, despite some evidence that both body condition and reproductive output increased  
10  
11 29 after rain. We suggest that the studied sub-populations are under stress from extrinsic rather  
12  
13 30 than intrinsic factors, with livestock grazing and introduced predators perhaps having the  
14  
15 31 most negative effects. If similar demographic trends are apparent elsewhere in the species'  
16  
17 32 small geographical range, the species would be eligible for listing on the IUCN Red List as  
18  
19 33 Endangered, with a 20% chance of extinction within the next 20 years. Urgent research is  
20  
21 34 required to quantify and mitigate the extrinsic threats to kowari populations. Proactive  
22  
23 35 measures such as captive breeding to act as insurance populations would be prudent.  
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27 36 *Keywords: Extinction, population dynamics, synchrony, arid zone, PVA, MARSS*  
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### 33 **Introduction**

34  
35 39 Desert environments are often characterised by long, dry periods that are punctuated  
36  
37 40 by brief but dramatic rainfall events. The dry periods provide few resources for consumer  
38  
39 41 organisms, but large rainfall events stimulate pulses of primary productivity that may last  
40  
41 42 from a few weeks to many months (Noy-Meir 1973). Wet conditions herald the end of  
42  
43 43 dormancy for the resting stages of many invertebrates, and trigger the temporary ingress of  
44  
45 44 mobile consumers such as birds and flying insects from peri-arid regions (Cloudsley-  
46  
47 45 Thompson 1991, Tischler *et al.* 2013). Populations of small desert-dwelling mammals,  
48  
49 46 especially rodents, increase rapidly, expanding out from dry-season refuges through increased  
50  
51 47 reproduction and survival of young (Milstead *et al.* 2007, Pavey *et al.* 2017). Outbreaks of  
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53 48 rodents are often followed by increases in predator populations, notably mammalian  
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## Dynamics and extinction risk of a carnivorous marsupial.

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2  
3 49 carnivores, owls and diurnal raptors (Jaksic *et al.* 1997, Letnic & Dickman 2010), which can  
4  
5 50 drive prey populations to low levels as conditions begin to dry (Sinclair *et al.* 1998).  
6  
7

8 51 In the central deserts of Australia, drought-wet cycles are driven principally by the El  
9  
10 52 Niño Southern Oscillation, and are particularly intense. Inter-annual variation in rainfall can  
11  
12 53 exceed an order of magnitude (Van Etten 2009), with large rainfalls following long droughts  
13  
14 54 leading to regional-scale irruptions of rodents and their predators (Greenville *et al.* 2013). By  
15  
16 55 contrast, the responses of co-occurring dasyurid marsupials to these climatic events are much  
17  
18 56 less predictable than those of rodents. The same species can respond positively, negatively or  
19  
20 57 not at all to heavy rainfall at the same sites over time, and may show disparate dynamics in  
21  
22 58 response to the same rainfall events across space (Dickman *et al.* 2001, Greenville *et al.*  
23  
24 59 2016). Unlike rodents, it is also not clear whether these marsupials depend on dry-season  
25  
26 60 refuges.  
27  
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29

30 61 In part, the divergent demographic responses to rainfall by arid-dwelling dasyurid  
31  
32 62 marsupials may arise because they are secondary consumers; all species < 100 g feed largely  
33  
34 63 on invertebrates (Fisher & Dickman 1993, Baker & Dickman 2018), which themselves  
35  
36 64 respond variably to drought-wet cycles (Kwok *et al.* 2016). Some studies suggest that  
37  
38 65 dasyurid marsupials > 100 g respond positively and synchronously to heavy rainfall because  
39  
40 66 irruptive rodents, when abundant, form a large part of their diet (Greenville *et al.* 2016, Baker  
41  
42 67 & Dickman 2018). As drought-wet cycles and the impacts of introduced predators on small  
43  
44 68 desert mammals are expected to intensify (Greenville *et al.* 2017), there is an imperative to  
45  
46 69 understand how small marsupials maintain their populations through climatic extremes and  
47  
48 70 how they may fare in future. Dasyurid marsupials form the most species-rich communities of  
49  
50 71 any mammals in central Australia, and also the richest mammalian insectivore-carnivore  
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52 72 assemblages of any arid regions globally (Dickman 2003).  
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## Dynamics and extinction risk of a carnivorous marsupial.

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3 73 Here, we describe the population dynamics of the kowari, *Dasyuroides byrnei*, a  
4  
5 74 carnivorous dasyurid marsupial that occurs in arid Australia. Weighing up to 175 g (males) or  
6  
7 75 140 g (females), this IUCN-listed Vulnerable species lies within the critical weight range  
8  
9 76 (35–5500 g) that, for mammals, has been most susceptible to extinction in Australia  
10  
11 77 (Burbidge & McKenzie 1989). The kowari can breed twice a year between April and  
12  
13 78 December and has a maximum litter size of six (Woolley 1971, Aslin 1974, Canty 2012). It is  
14  
15 79 a nocturnal predator and its diet consists of invertebrates and rodents (Lim 1998). During the  
16  
17 80 day this species shelters in burrows dug into sand mounds that occur infrequently across  
18  
19 81 stony gibber environments (Lim 1998, Canty & Brandle 2008). Its response to climatic  
20  
21 82 conditions is not known; however, the smaller brush-tailed mulgara *D. blythi* (120 g) exhibits  
22  
23 83 large fluctuations in body weight, condition and reproductive performance over drought-wet  
24  
25 84 cycles (Greenville et al. 2016), and it is likely that kowari exhibit similar responses.

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29 85 We use the results from a 16-year monitoring program on kowari to predict that:

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32 86 1. Kowari presence will be associated with key attributes, notably sand mounds, of its  
33  
34 87 stony (gibber) pavement habitat;  
35  
36 88 2. Body and reproductive condition will improve with rainfall-driven increases in  
37  
38 89 productivity; and  
39  
40 90 3. Sub-populations of kowari will respond synchronously to drought-wet cycles.

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42  
43 91 Using the demographic results, we also investigate kowari conservation status by estimating  
44  
45 92 the extinction risk of the study populations using IUCN Red List guidelines (IUCN 2012).

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49  
50 94 **Materials and methods**

51  
52  
53 95 *Study site*

## Dynamics and extinction risk of a carnivorous marsupial.

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3 96 The study was conducted at Clifton Hills cattle station in the Sturt Stony Desert,  
4  
5 97 South Australia (Fig. 1). The landscape consists of stony gibber pavements, ephemeral  
6  
7 98 swamps, scattered sand mounds and sand dunes (Canty & Brandle 2008). Vegetation  
8  
9 99 predominantly consists of grasses and sedges: *Astrebla pectinata*, *Tripogon loliiformis* and  
10  
11 100 *Fimbristylis dichotoma* (Canty & Brandle 2008). During summer, temperatures usually  
12  
13 101 exceed 40°C and minima in winter fall below 5°C. Median annual rainfall at Birdsville, near  
14  
15 102 the study site, was 153 mm over the period 1892–2015. The location and habitat in the Sturt  
16  
17 103 Stony Desert is possibly one of the last refuges for the kowari. Rainfall above the median fell  
18  
19 104 in 2000, 2003 and 2011; rainfall in most other years was well below the median (Fig. 2).  
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23 105  
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106 *Animal trapping*

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28 107 Two 4 × 4 km live-trapping grids (WAL and PAN), 30 km apart, were surveyed once  
29  
30 108 a year from 2001 to 2004, then in 2006 (Fig. 1). Uneven and reduced sampling effort  
31  
32 109 occurred on the grids in 2007, 2009, 2011, 2013 and 2015. These two sites were chosen after  
33  
34 110 a preliminary broadscale survey during 1999 (>800 trap-nights per site × 5 sites) spanning the  
35  
36 111 Sturt Stony Desert and 100 km south of the Cooper Creek (R. Barratt & P. Canty  
37  
38 112 unpublished). The preliminary study found that the study sites on Clifton Hills cattle station  
39  
40 113 had the highest trapping rates for the kowari. The distance (30 km) between sites were chosen  
41  
42 114 to ensure independence: no marked animals have been recorded to move between the two  
43  
44 115 sites.  
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47

48 116 At each grid, Elliott traps were spaced 100 m apart on five 4-km lines that were 1-km  
49  
50 117 apart (200 traps per grid). Traps were opened from 1–4 nights depending on weather  
51  
52 118 conditions and available resources, baited with dog biscuits soaked in fish oil, and checked  
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54 119 each morning at first light. The sex of each individual was determined along with  
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## Dynamics and extinction risk of a carnivorous marsupial.

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3 120 measurements of mass, pes length, head length, and indicators of reproductive activity  
4  
5 121 including testis width, pouch condition (developed or not developed) and number of pouch  
6  
7 122 young present. Each animal was marked with a unique microchip from 2000 to 2004 to  
8  
9 123 identify individuals, and with paint marks on the tail during the later, less-frequent visits to  
10  
11 124 identify same-session recaptures.  
12

13  
14 125

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17 126 *Hypothesis 1: habitat assessments*  
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19  
20 127 Habitat data were collected from 25 m × 25 m plots at the 200 trap locations on each  
21  
22 128 grid as visual cover estimates. Six habitat variables were scored; gibber pavement, sand  
23  
24 129 mound (discrete sand lenses comprised of sandy clay loam with distinct convex profiles), thin  
25  
26 130 sand spread (no distinct form and structure), sand dune (deep sands generally taller than 1 m  
27  
28 131 and associated with longitudinal dunes), impermeable drainage depression (bare or pavement  
29  
30 132 but with obvious algal cover from temporary inundation – includes hard pans lake beds), and  
31  
32 133 cracking clay drainage depression (includes temporary swamps and gilgais). These estimates  
33  
34 134 were mutually exclusive and recorded as five cover classes; < 5%, 5–25%, 26–50%, 51–75%,  
35  
36 135 >75%. Related data included gibber size (none, pebbles < 50 mm, cobbles 50–250 mm,  
37  
38 136 boulder > 250 mm) and number of sand mounds.  
39  
40

41  
42 137 To investigate which habitat variables predict kowari presence, a binomial  
43  
44 138 generalized linear model (GLM) was used. The full additive model included site, gibber size,  
45  
46 139 gibber pavement cover, sand mound number, sand mound cover, sand spread cover and hard  
47  
48 140 drainage depression cover. We standardized all factors to have a mean of 0 and standard  
49  
50 141 deviation of 1 so each factor was on the same scale. All models were ranked by the Akaike  
51  
52 142 information criterion adjusted for small sample size (AIC<sub>c</sub>), with the Akaike weight  
53  
54 143 calculated for each model (Burnham & Anderson 2002). We then applied model averaging to  
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## Dynamics and extinction risk of a carnivorous marsupial.

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3 144 account for model uncertainty (Burnham & Anderson 2002), whereby all models within  
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5 145  $\Delta AIC_c < 2$  were considered to have some support. The effect size of each variable was based  
6  
7 146 on the model-averaged parameter estimates, calculated using the average of the coefficient  
8  
9 147 estimates from all models, weighted by the Akaike weight (Burnham & Anderson 2002). We  
10  
11 148 calculated the uncertainty of parameter estimates based on their unconditional standard errors  
12  
13 149 (Burnham & Anderson 2002). To quantify the relative importance of the predictor variables,  
14  
15 150 we summed the Akaike weight from all model combinations where the variable occurred. We  
16  
17 151 then ranked the predictor variables according to their relative importance, with the larger the  
18  
19 152 weight value, the more important the variable is relative to the others. Binomial GLMs were  
20  
21 153 constructed in R version 3.4.0 (R Core Team 2017) and model selection implemented using  
22  
23 154 MuMIn, version 1.15.6 (Barton 2016).  
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156 *Hypothesis 2: body and reproductive condition*

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33 157 To assess whether body condition of male and female kowari differed over time, the  
34  
35 158 average body condition of adults was compared each year (using data from 2000 to 2015) by  
36  
37 159 plotting log-body mass against log-head length, omitting females with pouch young (29  
38  
39 160 females). Residual deviations from the linear regression were averaged each year and used as  
40  
41 161 estimates of body condition. Positive mean residual values indicate above-average body  
42  
43 162 condition and negative values below-average condition. To investigate whether changes in  
44  
45 163 productivity (rainfall, green and non-green fractional cover) influenced body condition for  
46  
47 164 each sex, residuals for each animal were regressed against annual productivity surrogates and,  
48  
49 165 to account for lag effects, productivity surrogates from the year before. Fractional cover  
50  
51 166 estimates obtained from NRM Spatial Hub (2018) are landcover fractions representing the  
52  
53 167 proportions of green and non-green cover derived from Landsat images. For green and non-  
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## Dynamics and extinction risk of a carnivorous marsupial.

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2  
3 168 green fractional cover, both variables were entered into the model, as both contribute to the  
4  
5 169 overall productivity of the system. Linear regression models, with Gaussian error structures,  
6  
7 170 were constructed in R version 3.4.0 (R Core Team 2017); inspection of diagnostic plots  
8  
9 171 indicated that all models met statistical assumptions (Zuur 2009).  
10

11  
12 172 To assess whether the average reproductive condition of males changed over time,  
13  
14 173 residual deviations from the linear regression of log-testis width against log-head length were  
15  
16 174 averaged each year and plotted. As for body condition, data for the linear regression were  
17  
18 175 taken from 2000 to 2015, with positive mean residual values indicating above-average  
19  
20 176 reproductive condition and negative values below-average condition. To test whether  
21  
22 177 productivity (rainfall, green and non-green fractional cover) influenced reproductive  
23  
24 178 condition, residuals for testis length for each animal were regressed against annual  
25  
26 179 productivity surrogates and annual surrogates from the year before. For females, the  
27  
28 180 proportion of animals breeding (i.e. females with pouch young) was calculated for each year.  
29  
30 181 Proportion of breeding females each year and annual rainfall or annual rainfall from the year  
31  
32 182 before were modelled as proportional odds; a quasi-binomial GLM was used, as data were  
33  
34 183 over-dispersed (Zuur 2009). In addition, to investigate whether female fecundity increased  
35  
36 184 with rainfall, the number of pouch young per female each year was regressed against annual  
37  
38 185 rainfall or annual rainfall from the year before; a quasi-Poisson GLM was used due to data  
39  
40 186 over-dispersion (Zuur 2009). As above, both green and non-green fractional cover variables  
41  
42 187 were entered into the model. Generalized linear models were constructed in R version 3.4.0  
43  
44 188 (R Core Team 2017), and inspection of diagnostic plots indicated that all models met  
45  
46 189 statistical assumptions (Zuur 2009).  
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54 191 *Hypothesis 3: long-term spatio-temporal dynamics*  
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## Dynamics and extinction risk of a carnivorous marsupial.

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2  
3 192 To assess whether the two sub-populations of kowari exhibited synchronous or  
4  
5 193 asynchronous dynamics, we used Bayesian multivariate autoregressive state-space (MARSS)  
6  
7 194 models. Live-trapping data were standardized for effort by calculating numbers of captures  
8  
9 195 (excluding recaptures) per year per 100 trap nights and log+1 transformed, as MARSS  
10  
11 196 models use log-space. We based the MARSS models on the Gompertz growth model and  
12  
13 197 assumed that sub-population growth rate varied exponentially with sub-population size and  
14  
15 198 that meta-populations were closed to immigration and emigration (Hinrichsen & Holmes  
16  
17 199 2009). The MARSS framework is hierarchical and allows modelling of different spatial  
18  
19 200 population structures and parameters such as growth rates, while including both process  
20  
21 201 (state) and observation variability (see Supplementary section S1). To select between the  
22  
23 202 synchronous or asynchronous model for the data from the two grids, the best fitting model  
24  
25 203 was considered to be that with the lowest deviance information criterion (DIC).  
26  
27  
28

29 204 To allow model convergence, each model was fitted with three Markov chains, each  
30  
31 205 with 100 000 Markov chain Monte Carlo (MCMC) iterations, thinning of 25 and the first 60  
32  
33 206 000 iterations discarded, leaving 4800 iterations saved (see Supplementary section S1 for  
34  
35 207 description of priors, model formation, and Supplementary section S2 for JAGS code).  
36  
37 208 Inspection of diagnostic plots indicated that all models met statistical assumptions, and all  
38  
39 209 converged. Analyses were conducted in R 3.4.0 (R Core Team 2017) and JAGS 4.2.0  
40  
41 210 (Plummer 2016a), using the R2jags 0.5-7 (Su & Yajima 2015) and rjags 4-6 (Plummer  
42  
43 211 2016b) packages.  
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48  
49 213 *Population viability analysis*

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52 214 We calculated the probability that our combined study sub-populations would hit a  
53  
54 215 threshold (extinction risk metric) based on Dennis *et al.* (1991), but modified to account for  
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## Dynamics and extinction risk of a carnivorous marsupial.

1  
2  
3 216 observation error estimated using the synchronous MARSS model above (Holmes *et al.*  
4  
5 217 2014). We used thresholds set by the IUCN Red List Criterion E, where: critically  
6  
7 218 endangered is a 50% chance of extinction in 10 years; endangered is a 20% chance of  
8  
9 219 extinction in 20 years, and vulnerable is a 10% chance of extinction in 100 years. We defined  
10  
11 220 extinction as a 99% population decline over the time periods for each extinction risk class.  
12  
13 221 We assumed density-independence and based the MARSS models on the Gompertz growth  
14  
15 222 model, as above, and assumed also that 10% of observations were missing due to sites  
16  
17 223 becoming inaccessible after rainfall events or other logistical problems. To test the  
18  
19 224 assumption of density independence, we ran the synchronous MARSS model with and  
20  
21 225 without density dependence. There was no improvement in model fit for the density  
22  
23 226 dependent model (DIC 34.5) versus the density independent model (DIC 33.2) and thus the  
24  
25 227 marginally more parsimonious model was used. Bootstrapping (10 000 simulations) was used  
26  
27 228 to calculate the mean probability of population decline and associated 95% confidence  
28  
29 229 intervals (Holmes *et al.* 2014), with all simulations performed on high performance  
30  
31 230 computers (The University of Sydney HPC Service 2017) in R version 3.3.2 (R Core Team  
32  
33 231 2017) and JAGS version 4.2.0 (Plummer 2016a), using the R2jags 0.5-7 (Su & Yajima 2015)  
34  
35 232 and rjags 4-6 (Plummer 2016b) packages (see Supplementary Data S3 for R code).  
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41

234 **Results**

42  
43  
44  
45 235 In total, 14 250 trapping nights yielded 475 live-captures of 229 individual kowari  
46  
47 236 (3% trap success) from 2000 to 2015. Ninety-one individual males were captured, as well as  
48  
49 237 128 females. Sex was not recorded for 10 captures  
50  
51

238

239 *Habitat assessment*

## Dynamics and extinction risk of a carnivorous marsupial.

1  
2  
3 240 Eight models had  $\Delta AIC_c < 2$  and thus were considered to have support  
4  
5 241 (Supplementary Data S4). Model averaging revealed that gibber pavement cover and sand  
6  
7 242 spread cover were associated positively with kowari presence (Table 1). Site, hard drainage  
8  
9 243 depression cover, number and cover of sand mounds all had large uncertainty around the  
10  
11 244 estimates and thus were not considered useful for predicting kowari presence (Table 1).

245

246 *Body and reproductive condition*

19  
20 247 Body and reproductive condition changed over time for both sexes (Figs 2 and 3), but  
21  
22 248 rainfall was not associated with body condition (Fig. 2; Table 2). There was also no  
23  
24 249 association with green and non-green fractional cover and female body condition (Table 3).  
25  
26 250 However, the interactions of green and non-green fractional cover from the previous year  
27  
28 251 were significant and positively associated with male body condition (Table 3). Rainfall in the  
29  
30 252 previous year was associated positively with the number of pouch young (range 0–6 young),  
31  
32 253 but there was no relationship between rainfall or antecedent rainfall and testis condition (Fig.  
33  
34 254 3; Table 4). There was a significant and positive interaction between green and non-green  
35  
36 255 fractional cover from the previous year and testis condition, but no association between green  
37  
38 256 and non-green fractional cover and the number of pouch young (Table 4).

257

258 *Long-term spatio-temporal dynamics*

46  
47 259 The synchronous MARSS population model provided a better fit (DIC 34.6) than the  
48  
49 260 asynchronous MARSS model (DIC 71.3), indicating the two sub-populations fluctuated in  
50  
51 261 synch. Long-term monitoring of kowari revealed that the mean population growth rate was  
52  
53 262 negative (Table 5; Fig. 3), with the modelling showing that process (environmental; Q) and  
54  
55 263 observation (R) errors were similar (Table 5).

## Dynamics and extinction risk of a carnivorous marsupial.

264

265 *Population viability analysis*

266 Population viability analysis showed that the studied kowari population has a 20%  
267 chance of extinction (99% population decline) in the next 20 years. This meets the criteria  
268 (for this population) for 'Endangered' status under IUCN Red List criterion E (Fig. 4).

269

270 **Discussion**

271 The results provide partial support for our first two predictions and strong support for  
272 our third. Taken together, the results also suggest that kowari populations in our study region  
273 are declining and face an appreciable risk of extinction in the short term. We interpret these  
274 findings and propose further research below.

275 Habitat selectivity by kowari was demonstrated by the positive association of capture  
276 data with two habitat variables; gibber pavement and sand cover. The importance of these  
277 variables probably arises both from their high coverage within the study area, and the fact  
278 that kowari forage on the open gibber but use sandy areas for burrows (Canty 2012). We had  
279 expected that sand mounds, in particular, would emerge as important habitat components as  
280 burrows are frequently found in these structures (Canty 2012). However, it is possible that  
281 our 25 m × 25 m habitat plots were too small to reliably sample these sparsely scattered  
282 structures. Kowari are probably highly mobile and would have encountered our traps while  
283 they were active at night; hence, associations between captured animals and habitat  
284 components may simply reflect where they forage rather than where they burrow by day.  
285 Alternatively, heavy grazing by cattle occurs in part of the study area (PAN site) and may  
286 lead to declines in habitat quality, particularly to deflation of the sand patches in which the  
287 majority of kowari burrow (Canty 2012, Woinarski *et al.* 2014, Read & Moseby 2015). We

## Dynamics and extinction risk of a carnivorous marsupial.

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2  
3 288 suggest that further research identifying refuges and investigating links with kowari  
4  
5 289 population health and habitat quality is urgently required.  
6

7  
8 290 Arid-dwelling dasyurids show complex relationships with rainfall-driven pulses of  
9  
10 291 productivity, with populations and the body and reproductive condition of individuals often  
11  
12 292 fluctuating idiosyncratically (Baker & Dickman 2018). For example, Dickman *et al.* (2001)  
13  
14 293 used body condition as a surrogate for available food resources for small and medium-sized  
15  
16 294 dasyurids, and found that capture rates did not increase with increasing body condition. This  
17  
18 295 suggested a weak link between body condition and rainfall, in contrast to patterns found in  
19  
20 296 other desert-dwelling mammals in Africa and North America (Marshall *et al.* 2008, Turner *et*  
21  
22 297 *al.* 2012). However, the body condition of male kowari did increase with fractional  
23  
24 298 vegetation cover, suggesting that these individuals took advantage of increased productivity.  
25  
26 299 Females did not. Possibly, as males are larger than females they have greater mobility and  
27  
28 300 thus propensity than females to access sites of locally high productivity. Alternatively, as we  
29  
30 301 excluded females with pouch young from assessments of body condition, females exploited  
31  
32 302 productivity by channelling resources into reproduction rather than somatic growth. In  
33  
34 303 addition, sites surveyed in this study may act as refuges and thus buffer animals from  
35  
36 304 environmental extremes (Pavey *et al.* 2017).  
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40  
41 305 Male testis condition was below average in 2000 but stable from 2001–2015 and not  
42  
43 306 influenced by rainfall. However, testis condition improved with green and non-green  
44  
45 307 fractional cover, suggesting that on-site increases in productivity did influence male  
46  
47 308 reproductive condition. The proportion of females breeding (with pouch young) also changed  
48  
49 309 over time. This may reflect the variable sampling times during this study, thus limiting our  
50  
51 310 ability to quantify the effects of rainfall and primary productivity on reproduction. However,  
52  
53 311 litter size (number of pouch young) did increase with rainfall in the previous year. Maximum  
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## Dynamics and extinction risk of a carnivorous marsupial.

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3 312 litter size was six, as in captive animals maintained under optimal conditions (Woolley 1971,  
4  
5 313 Aslin 1974), suggesting that increased productivity improved female fecundity.  
6  
7

8 314 The two sub-populations of kowari exhibited synchronous dynamics over the study  
9  
10 315 period. The similar-sized brush-tailed mulgara, *Dasyercus blythi*, also showed synchronous  
11  
12 316 dynamics across an 8000 km<sup>2</sup> area of the Simpson Desert, perhaps suggesting that dasyurids  
13  
14 317 > 100 g often show synchronous responses to environmental conditions, whereas smaller  
15  
16 318 species respond more locally (Greenville et al. 2016). Understanding the scale of species'  
17  
18 319 responses has practical importance for conservation. For example, if populations of kowari  
19  
20 320 fluctuate synchronously, the risk of extinction will be high if all populations decrease towards  
21  
22 321 zero at the same time and rescue through colonization is prohibited (Heino *et al.* 1997,  
23  
24 322 Greenville et al. 2016). Alarmingly, our findings suggest that the two sub-populations of  
25  
26 323 kowari we studied have declined synchronously over the last 16 years, and are continuing to  
27  
28 324 fall despite recent and exceptional rainfalls during 2010-11 (Brandle & Canty 2011, Read &  
29  
30 325 Moseby 2015).  
31  
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33

34 326 This study confirms that the study region contains favourable habitat for kowari; we  
35  
36 327 identified habitat preferences for open gibber pavement with some surface sand and, in-part,  
37  
38 328 showed that body condition and reproductive output increased with improvements in  
39  
40 329 environmental productivity. However, population viability analysis suggests that kowari sub-  
41  
42 330 populations are at risk of local extinction in the near to medium future. Given that the study  
43  
44 331 area was chosen because of its high capture rates during earlier studies (Lim 1998) and  
45  
46 332 subsequent sampling (Canty & Brandle 2008, Brandle & Canty 2011, Read & Moseby 2015),  
47  
48 333 as well as evidently low recruitment of juveniles into the current population, we suggest that  
49  
50 334 the population is under stress from extrinsic rather than intrinsic factors. The most likely  
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52 335 factors are discussed below.  
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## Dynamics and extinction risk of a carnivorous marsupial.

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3 336           Grazing or trampling from stock can flatten sand mounds and degrade habitat for  
4  
5 337   breeding burrows (Canty & Brandle 2008, Canty 2012, Woinarski et al. 2014, Read &  
6  
7 338   Moseby 2015). Protecting breeding habitat by excluding stock using fencing or reduced  
8  
9 339   stocking rates could aid recovery. Secondly, predation from introduced predators, such as  
10  
11 340   feral cats and foxes, may limit recruitment to the population. The open gibber habitat of  
12  
13 341   kowari provides little cover and shelter opportunities from avian and introduced predators,  
14  
15 342   and reduction in burrowing opportunities may increase predation risk. The kowari is at  
16  
17 343   particularly high risk from feral cat predation (Dickman 1996). Lastly, the synergistic and  
18  
19 344   additive effects of predation, grazing and predicted range declines from climate change  
20  
21 345   (Chapman & Milne 1998, Doherty *et al.* 2015) may further amplify extinction risk for the  
22  
23 346   kowari. If other populations of kowari are declining in a manner similar to those in South  
24  
25 347   Australia, the species would meet the criteria for listing as Endangered (IUCN 2012).  
26  
27 348   Monitoring needs to continue and be expanded to encompass other populations within the  
28  
29 349   tiny current range of the kowari, urgent research is required to elucidate the impacts of  
30  
31 350   grazing and introduced predators, and insurance populations need to be established by captive  
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33 351   breeding programs.  
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Dynamics and extinction risk of a carnivorous marsupial.

1  
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## Dynamics and extinction risk of a carnivorous marsupial.

475 **Tables**

476 Table 1: Model averaged estimates from the top eight binominal generalized linear models  
 477 investigating which combinations of habitat variables successfully predict the presence of  
 478 kowari, *Dasyuroides byrnei*. Surveys were conducted from 2000–2015, Sturts Stony Desert,  
 479 South Australia.

Variable	Estimate	SE	z-value	Relative importance
Intercept	1.37	0.22	6.35	
Gibber pavement cover	0.47	0.18	2.63	1
Sand spread cover	0.34	0.15	2.23	1
Site <sub>wal grid</sub>	0.27	0.37	0.75	0.52
Hard drainage depression cover	-0.04	0.09	0.42	0.3
Sand mound cover	0.04	0.10	0.37	0.28
Sand mound number	-0.003	0.04	0.07	0.08

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## Dynamics and extinction risk of a carnivorous marsupial.

482 Table 2: The influence of rainfall on body condition of each sex of the kowari, *Dasyuroides*  
 483 *byrnei*. Results from the linear regression of residuals for each animal were regressed against  
 484 annual rainfall and annual rainfall from the year before. Residuals for body condition were  
 485 calculated by plotting log-body mass against log-head length of adults, omitting females with  
 486 pouch young. Surveys were conducted from 2000–2015, Sturts Stony Desert, South  
 487 Australia.

Variable	Estimate	SE	<i>t</i> -value	<i>P</i>
<i>Females</i>				
Intercept	-0.01	0.04	-0.26	0.79
Rainfall	0.00008	0.0003	0.30	0.77
Intercept	-0.05	0.04	-1.35	0.18
Rainfall previous year	0.0002	0.0003	0.94	0.35
<i>Males</i>				
Intercept	0.06	0.05	1.07	0.29
Rainfall	-0.0005	0.0004	-1.21	0.23
Intercept	-0.05	0.08	-0.69	0.49
Rainfall previous year	0.0002	0.0004	0.50	0.62

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## Dynamics and extinction risk of a carnivorous marsupial.

490 Table 3: The influence of green and non-green fractional cover on body condition of each sex  
 491 of the kowari, *Dasyuroides byrnei*. Results from the linear regression of residuals for each  
 492 animal were regressed against annual rainfall and annual rainfall from the year before.  
 493 Residuals for body condition were calculated by plotting log-body mass against log-head  
 494 length of adults, omitting females with pouch young. Surveys were conducted from 2000–  
 495 2015, Sturts Stony Desert, South Australia.

Variable	Estimate	SE	<i>t</i> -value	<i>P</i>
<i>Females</i>				
Intercept	0.53	0.54	0.99	0.32
Green	-0.12	0.18	-0.64	0.32
Non-green	-0.02	0.02	-1.30	0.53
Green × Non-green	0.005	0.006	0.92	0.20
Intercept	0.18	0.42	0.44	0.66
Green previous year	0.01	0.12	0.09	0.93
Non-green previous year	-0.01	0.02	-0.63	0.53
Green × Non-green previous year	0.0005	0.004	0.11	0.91
<i>Males</i>				
Intercept	0.81	0.62	1.31	0.19
Green	-0.19	0.20	-0.93	0.36
Non-green	-0.02	0.02	-1.10	0.27
Green × Non-green	0.004	0.006	0.71	0.48

## Dynamics and extinction risk of a carnivorous marsupial.

Intercept	1.15	0.40	2.91	0.005
Green previous year	-0.36	0.13	-2.86	0.005
Non-green previous year	-0.03	0.01	-2.58	0.01
Green $\times$ Non-green previous year	0.01	0.004	2.99	0.004

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## Dynamics and extinction risk of a carnivorous marsupial.

498 Table 4: The influence of rainfall on testis condition, proportion of females breeding (with  
 499 pouch young) and number of pouch young for the kowari, *Dasyuroides byrnei*. Also shown is  
 500 the influence of green and non-green fractional cover on testis condition and number of  
 501 pouch young. Residuals for testis condition were calculated by plotting log-testis length  
 502 against log-head length of adults. Surveys were conducted from 2000–2015, Sturts Stony  
 503 Desert, South Australia.

Variable	Estimate	SE	t-value	P
<i>Testes condition</i>				
<i>Rainfall</i>				
Intercept	0.07	0.04	1.67	0.10
Rainfall	-0.0006	0.0003	-1.89	0.06
Intercept	0.05	0.06	0.85	0.40
Rainfall previous year	-0.0003	0.0004	-0.89	0.38
<i>Fractional cover</i>				
Intercept	0.37	0.51	0.74	0.46
Green	-0.10	0.17	-0.59	0.55
Non-green	-0.004	0.02	-0.23	0.82
Green × Non-green	0.0004	0.005	0.09	0.93
Intercept	0.79	0.33	2.39	0.02
Green previous year	-0.33	0.11	-3.16	0.002
Non-green previous year	-0.02	0.01	-1.41	0.16
Green × Non-green previous year	0.008	0.003	2.76	0.007
<i>Proportion females breeding</i>				
<i>Rainfall</i>				
Intercept	-1.23	1.64	-0.75	0.48
Rainfall	0.003	0.01	0.24	0.82

## Dynamics and extinction risk of a carnivorous marsupial.

Intercept	-1.91	1.92	-0.99	0.36
Rainfall previous year	0.009	0.01	0.71	0.50
<i>Number of pouch young</i>				
<i>Rainfall</i>				
Intercept	-0.12	0.37	-0.33	0.74
Rainfall	-0.002	0.003	-0.68	0.50
Intercept	-2.85	1.02	-2.80	0.006
Rainfall previous year	0.01	0.005	2.97	0.004
<i>Fractional cover</i>				
Intercept	-6.20	6.28	-0.99	0.33
Green	0.38	2.29	0.17	0.87
Non-green	0.32	0.20	1.58	0.12
Green × Non-green	-0.04	0.07	-0.64	0.53
Intercept	-8.57	6.72	-1.28	0.20
Green previous year	1.18	1.69	0.70	0.49
Non-green previous year	0.26	0.25	1.05	0.30
Green × Non-green previous year	-0.03	0.06	-0.59	0.56

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## Dynamics and extinction risk of a carnivorous marsupial.

506 Table 5: Population parameter estimates from Bayesian multivariate autoregressive state-  
 507 space models. Live-trapping data on kowari, *Dasyuroides byrnei* (2000–2015) were  
 508 standardized for effort by calculating numbers of captures per year per 100 trap nights on two  
 509 live-trapping grids, PAN and WAL. The synchronous model was the best fit to the data,  
 510 suggesting the two sub-populations in Sturts Stony Desert, South Australia, have similar  
 511 trajectories over time. Mean population growth rate (U), mean site bias (A), process error (Q)  
 512 and observation error (R) are shown.

Variable	Estimate	Lower CI	Upper CI
<i>Synchronous</i>			
U	-0.08	-0.28	0.10
A <sub>Wal grid</sub>	-0.04	-0.43	0.38
Q	0.30	0.16	0.69
R	0.24	0.13	0.42
<i>Asynchronous</i>			
U <sub>Pan grid</sub>	-0.08	-0.43	0.30
U <sub>Wal grid</sub>	-0.09	-0.23	0.06
Q <sub>Pan grid</sub>	0.55	0.12	1.35
Q <sub>Wal grid</sub>	0.23	0.07	0.58
R	0.20	0.08	0.25

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515

## Dynamics and extinction risk of a carnivorous marsupial.

516 **Figures**

517 Figure 1: Location of study region, Sturts Stony Desert, South Australia, Australia. Long-  
518 term monitoring (2000–2015) was carried out on grids PAN and WAL of two sub-  
519 populations of kowari, *Dasyuroides byrnei*, and rainfall data were taken from a weather  
520 station at nearby Birdsville (insert).

521

522 Figure 2: Mean body condition of (a) male and (b) female kowari *Dasyuroides byrnei*, (c)  
523 male testis condition, and (d) total annual rainfall at Birdsville for each survey year (2000–  
524 2015) in Sturts Stony Desert, South Australia. Points ( $\pm$  SE) above the dashed line represent  
525 body or testis condition greater than the long-term mean and points below the dashed line  
526 represent body or testis condition below the long-term mean. Surveys were conducted in  
527 2000–2004, 2006–2007, 2009, 2011, 2013 and 2015.

528

529 Figure 3: Long-term (2000–2015) dynamics of two sub-populations of kowari, *Dasyuroides*  
530 *byrnei*, on PAN and WAL grids, Sturts Stony Desert, South Australia. (a) Mean number of  
531 pouch young per year ( $\pm$  SE) and proportion of reproductive females pooled across the two  
532 sub-populations (N = 2, 17, 0, 1, 8, 0,0, 0,0, 0, 1, in 2000–2004, 2006–2007, 2009, 2011,  
533 2013 and 2015, respectively. There were no surveys in other years). (b) Size of the population  
534 as estimated by the synchronous MARSS model (sub-populations combined), expressed as  
535 captures per 100 trap nights per year (black line), and forecast population (dashed line). Grey  
536 shaded area represents 95% credible intervals. Points indicate captures for WAL (black  
537 square) and PAN (blue circle) grids. Years without points indicate no survey occurred.

538

## Dynamics and extinction risk of a carnivorous marsupial.

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3 539 Figure 4: Population viability analysis of kowari, *Dasyuroides byrnei*, Sturts Stony Desert,  
4  
5 540 South Australia. The IUCN Red List criterion E was used to assess the conservation status of  
6  
7 541 this threatened species, where: (a) critically endangered populations are projected to  
8  
9 542 experience a 50% chance of extinction in 10 years, (b) endangered populations are projected  
10  
11 543 to experience a 20% chance of extinction in 20 years, and (c) vulnerable populations are  
12  
13 544 projected to experience a 10% chance of extinction in 100 years. Extinction was defined as a  
14  
15 545 99% population decline. Dashed black lines are the 95% credible intervals and dashed red  
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17 546 line represents the extinction risk threshold defined by the IUCN (2012) (i.e. 50, 20 or 10%).  
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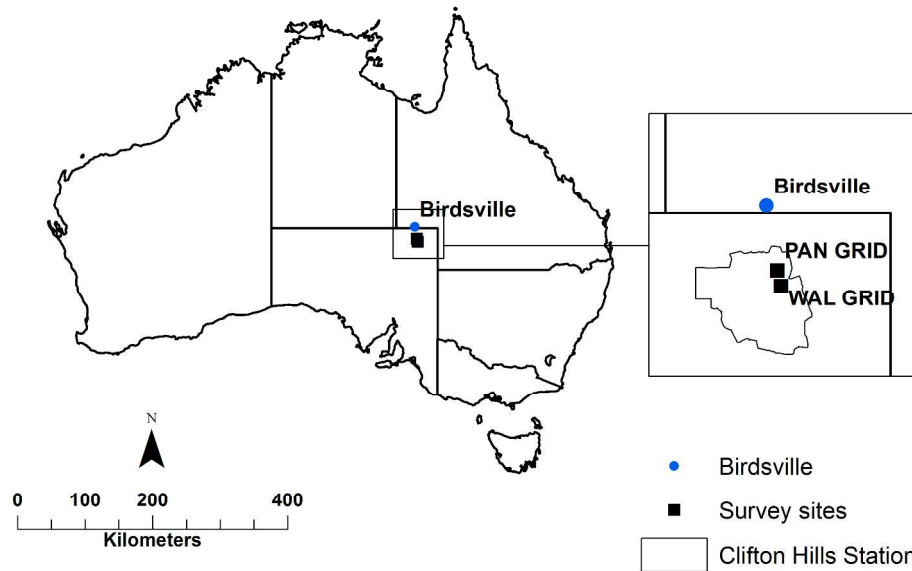


Figure 1: Location of study region, Sturts Stony Desert, South Australia, Australia. Long-term monitoring (2000–2015) was carried out on grids PAN and WAL of two sub-populations of kowari, *Dasyuroides byrnei*, and rainfall data were taken from a weather station at nearby Birdsville (insert).

296x210mm (300 x 300 DPI)

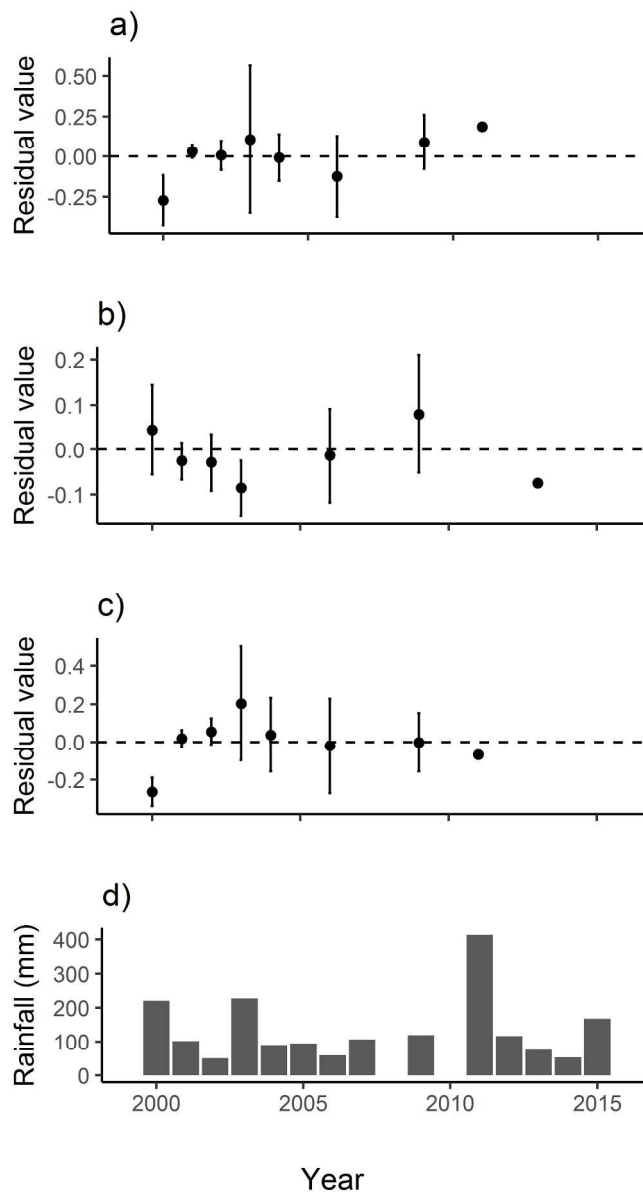


Figure 2: Mean body condition of (a) male and (b) female kowari *Dasyuroides byrnei*, (c) male testis condition, and (d) total annual rainfall at Birdsville for each survey year (2000–2015) in Sturts Stony Desert, South Australia. Points ( $\pm$  SE) above the dashed line represent body or testis condition greater than the long-term mean and points below the dashed line represent body or testis condition below the long-term mean. Surveys were conducted in 2000–2004, 2006–2007, 2009, 2011, 2013 and 2015.

169x288mm (300 x 300 DPI)

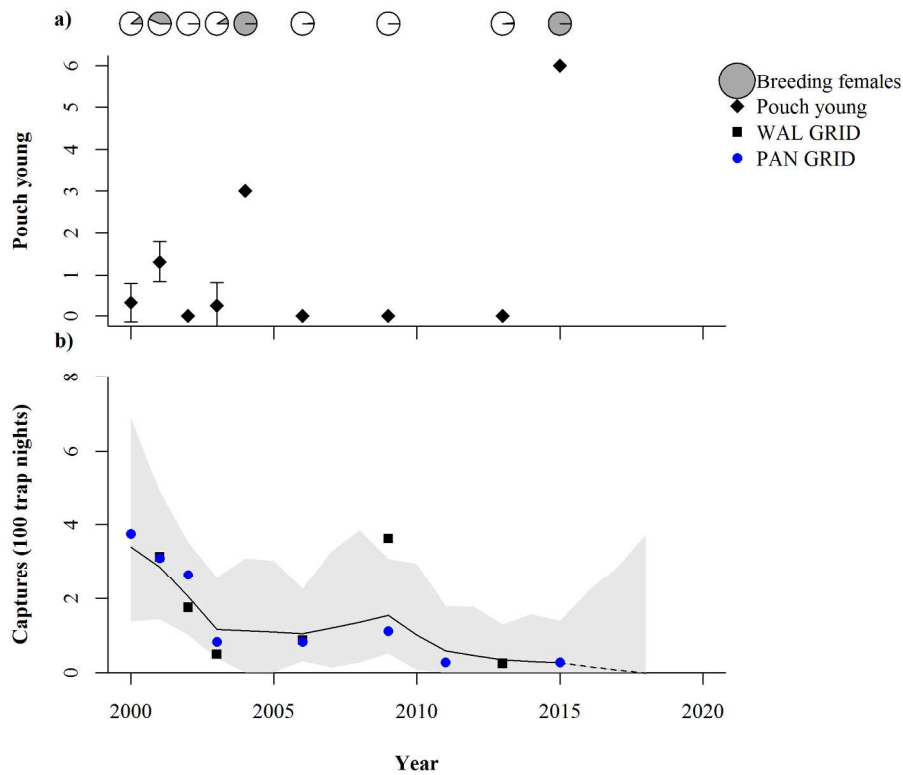


Figure 3: Long-term (2000–2015) dynamics of two sub-populations of kowari, *Dasyuroides byrnei*, on PAN and WAL grids, Sturts Stony Desert, South Australia. (a) Mean number of pouch young per year ( $\pm$  SE) and proportion of reproductive females pooled across the two sub-populations ( $N = 2, 17, 0, 1, 8, 0, 0, 0, 0, 1,$  in 2000–2004, 2006–2007, 2009, 2011, 2013 and 2015, respectively). There were no surveys in other years). (b) Size of the population as estimated by the synchronous MARSS model (sub-populations combined), expressed as captures per 100 trap nights per year (black line), and forecast population (dashed line). Grey shaded area represents 95% credible intervals. Points indicate captures for WAL (black square) and PAN (blue circle) grids. Years without points indicate no survey occurred.

199x159mm (300 x 300 DPI)

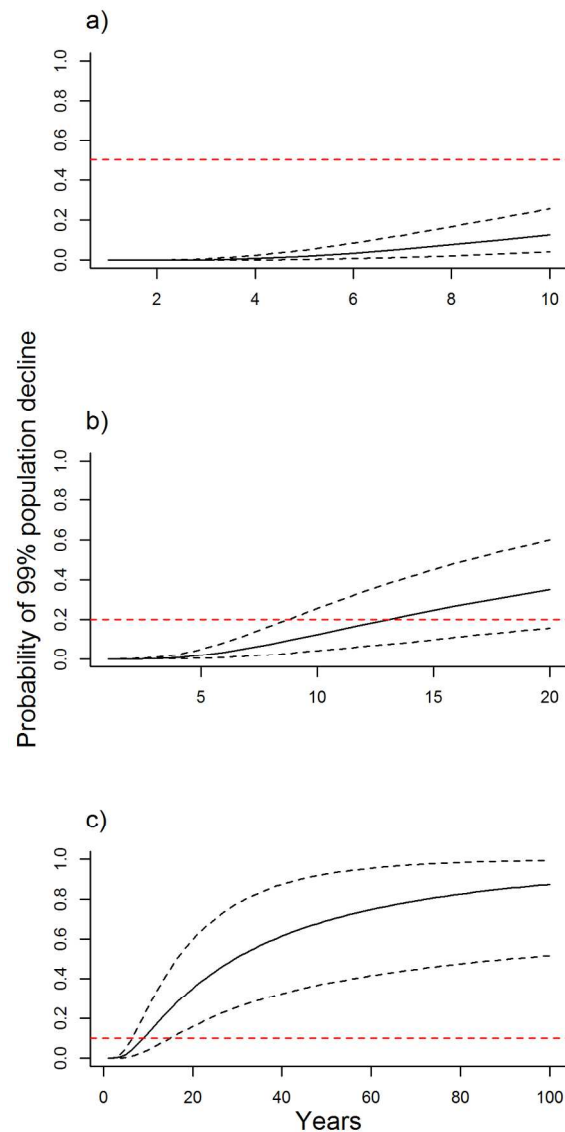


Figure 4: Population viability analysis of kowari, *Dasyuroides byrnei*, Sturts Stony Desert, South Australia. The IUCN Red List criterion E was used to assess the conservation status of this threatened species, where: (a) critically endangered populations are projected to experience a 50% chance of extinction in 10 years, (b) endangered populations are projected to experience a 20% chance of extinction in 20 years, and (c) vulnerable populations are projected to experience a 10% chance of extinction in 100 years. Extinction was defined as a 99% population decline. Dashed black lines are the 95% credible intervals and dashed red line represents the extinction risk threshold defined by the IUCN (2012) (i.e. 50, 20 or 10%).

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## Supplementary Section: Greenville et al.

### Supplementary S1: Bayesian multivariate autoregressive state-space models

The multivariate autoregressive state-space models (MARSS) framework has proven useful for modelling population data in the present study system, particularly for incorporating process and observation error in long-term monitoring data (Nguyen *et al.* 2015, Greenville *et al.* 2016). Process variability represents temporal variability in population size due to environmental and demographic stochasticity (Ward *et al.* 2010). Observation variability includes sampling error (e.g. temporal changes in detectability or error resulting in only a sub-sample of the population being counted). The process component is a multivariate first-order autoregressive process and is written in log-space (2012, Holmes *et al.* 2014) as:

$$\mathbf{X}_t = \mathbf{X}_{t-1} + \mathbf{u} + \mathbf{w}_t; \quad \mathbf{w}_t \sim MVN(0, \mathbf{Q}) \quad (1)$$

where  $\mathbf{X}_t$  represents a vector of all  $m$  sub-populations (up to nine sub-populations for each species) at time  $t$  (year), and  $\mathbf{u}$  is a vector of length  $m$ .  $\mathbf{Q}$  is a matrix that denotes process parameters. The parameter  $\mathbf{u}$  describes the trend of the population.  $\mathbf{w}_t$  denotes process errors, which we assumed to be independent and to follow a multivariate normal distribution with a mean of zero and variance-covariance matrix  $\mathbf{Q}$  (i.e.  $\mathbf{Q}$  diagonals represent process variance and off-diagonals represent how the populations are correlated to one another). We allowed  $\mathbf{Q}$  to have different variances across the two sites (diagonals,  $q_{iis}^2$ , were allowed to vary, while off-diagonals were set to zero), as process variation was assumed to differ across space.

The observation component, written in log-space (2012, Holmes *et al.* 2014), is:

$$\mathbf{Y}_t = \mathbf{Z}\mathbf{X}_t + \mathbf{a} + \mathbf{v}_t; \quad \mathbf{v}_t \sim MVN(0, \mathbf{R}) \quad (2)$$

where  $\mathbf{Y}_t$  represents a vector of all observations at  $n$  sites at time  $t$ ,  $\mathbf{a}$  denotes the mean bias between sites, and  $\mathbf{Z}$  is an  $n \times m$  matrix of 0s and 1s that assigns observations to a population

1  
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3 structure. The number of sites ( $n$ ) may be different from the number of populations ( $m$ ) at  
4  
5 time  $t$  (Ward et al. 2010). Observation errors,  $\mathbf{v}_t$ , are assumed to be uncorrelated and follow a  
6  
7 multivariate normal distribution, with a mean of zero and a variance-covariance matrix  $\mathbf{R}$ .  
8  
9 We set the diagonals in  $\mathbf{R}$  ( $r^2_{i,i}$ ) to have equal variance across sites, as the same trapping  
10  
11 methods were employed throughout the study, and to avoid over-parameterising the models.  
12  
13 The  $\mathbf{R}$  off-diagonals were set to zero. Equations (1) and (2) comprise the MARSS model.  
14  
15

### 16 Expanded matrix model form

#### 17 Synchronous population model:

18 Process model:

$$19 [X_{kowari,t}] = [X_{kowari,t-1}] + [U_{kowari}] + [W_{Reptile,t}]; \quad \mathbf{w}_t \sim MVN(0, \mathbf{Q})$$

$$20 \mathbf{Q} = [q^2_{kowari}]$$

$$21 q^2 \sim Gamma(0.01, 0.01)$$

$$22 \mathbf{U} \sim Normal(0, 0.1)$$

23 Note: Kowari captures per 100 trap nights (log+1 transformed).  
24  
25

26 Observation model:

$$27 \begin{bmatrix} Y_{Pop_1,t} \\ Y_{Pop_2,t} \end{bmatrix} = \begin{bmatrix} 1 \\ 1 \end{bmatrix} [X_{Reptile,t}] + \begin{bmatrix} 0 \\ A_{Pop_2} \end{bmatrix} + \begin{bmatrix} v_{Pop_1,t} \\ v_{Pop_2,t} \end{bmatrix}; \quad \mathbf{v}_t \sim MVN(0, \mathbf{R})$$

28 Note that subscripts below Pop represent each population (sites).  
29  
30

$$31 \mathbf{R} = \begin{bmatrix} r^2 & 0 \\ 0 & r^2 \end{bmatrix}$$

$$32 r^2 \sim Gamma(0.01, 0.01)$$

$$33 A_{Pop_2} \sim Normal(0, 1)$$

34 Note Observation error was assumed to be the same within each species and the diagonals ( $r^2_{i,i}$ ).  
35  
36

**Asynchronous model:**

Process model:

$$\begin{bmatrix} X_{Pop_1,t} \\ X_{Pop_2,t} \end{bmatrix} = \begin{bmatrix} X_{Pop_1,t-1} \\ X_{Pop_2,t-1} \end{bmatrix} + \begin{bmatrix} U_{Pop_1} \\ U_{Pop_2} \end{bmatrix} + \begin{bmatrix} W_{Pop_1,t} \\ W_{Pop_2,t} \end{bmatrix}; \quad \mathbf{w}_t \sim MVN(\mathbf{0}, \mathbf{Q})$$

$$\mathbf{Q} = \begin{bmatrix} q_{pop_1}^2 & 0 \\ 0 & q_{pop_2}^2 \end{bmatrix}$$

$$q^2 \sim Gamma(0.01, 0.01)$$

$$\mathbf{U} \sim Normal(0, 0.1)$$

Note: Captures per 100 trap nights (log+1 transformed). Pop is population number.

Process errors ( $q_{i,i}^2$ ) are diagonal and unequal to allow process variation to differ for each population.

Observation model:

$$\begin{bmatrix} Y_{Pop_1,t} \\ Y_{Pop_2,t} \end{bmatrix} = \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix} \begin{bmatrix} X_{Pop_1,t} \\ X_{Pop_2,t} \end{bmatrix} + \begin{bmatrix} 0 \\ 0 \end{bmatrix} + \begin{bmatrix} v_{Pop_1,t} \\ v_{Pop_2,t} \end{bmatrix}; \quad \mathbf{v}_t \sim MVN(\mathbf{0}, \mathbf{R})$$

$$\mathbf{R} = \begin{bmatrix} r^2 & 0 \\ 0 & r^2 \end{bmatrix}$$

$$r^2 \sim Gamma(0.01, 0.01)$$

Note: Observation error was assumed to be the same within each species and the diagonals ( $r_{i,i}^2$ ) for the same species were set to be equal.

**References:**

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**Supplementary Section: Greenville et al.**

**Supplementary S4:** Top ranked binomial Generalised Linear Models (GLM) for habitat variables that could successfully predict kowari presence. All models within Delta AICc < 2 were considered to have support from the data.

Model	Intercept	Gibber pavement cover	Hard drainage depression cover	Sand mound cover	Sand mound number	Sand spread cover	Site	df	logLik	AICc	delta	Weight
1	1.26	0.55				0.34	+	4	-187.73	383.6	0	0.22
2	1.50	0.39				0.35		3	-188.90	383.9	0.29	0.19
3	1.24	0.56	-0.12			0.33	+	5	-187.26	384.7	1.11	0.13
4	1.50	0.36		0.13		0.32		4	-188.45	385.0	1.4	0.11
5	1.50	0.40	-0.16			0.35		4	-187.59	385.3	1.71	0.09
6	1.28	0.51		0.07		0.32	+	5	-187.60	385.3	1.78	0.09
7	1.51	0.35	-0.16	0.20		0.31		5	-187.69	385.5	1.96	0.08
8	1.24	0.56			-0.04	0.34	+	5	-187.70	385.6	1.99	0.08