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 the study region contains favourable habitat, with kowari occurring on hard stony (gibber) pavements in association with coverage of sand that may facilitate construction of burrows. Both sub-populations of kowari declined over the study period irrespective of climatic conditions, despite some evidence that both body condition and reproductive output increased after rain. We suggest that the studied sub-populations are under stress from extrinsic rather than intrinsic factors, with livestock grazing and introduced predators perhaps having the most negative effects. If similar demographic trends are apparent elsewhere in the species' small geographical range, the species would be eligible for listing on the IUCN Red List as Endangered, with a 20% chance of extinction within the next 20 years. Urgent research is required to quantify and mitigate the extrinsic threats to kowari populations. Proactive measures such as captive breeding to act as insurance populations would be prudent.

Introduction

Desert environments are often characterized by long, dry periods that are punctuated by brief but dramatic rainfall events. The dry periods provide few resources for consumer organisms, but large rainfall events stimulate pulses of primary productivity that may last from a few weeks to many months (Noy-Meir, 1973). Wet conditions herald the end of dormancy for the resting stages of many invertebrates, and trigger the temporary ingress of mobile consumers such as birds and flying insects from peri-arid regions (Cloudsley-Thompson, 1991; Tischler, Dickman & Wardle, 2013). Populations of small desert-dwelling mammals, especially rodents, increase rapidly, expanding out from dry-season refuges through increased reproduction and survival of young (Milstead *et al*., 2007; Pavey *et al*., 2017). Outbreaks of rodents are often followed by increases in predator populations, notably mammalian carnivores, owls and diurnal raptors (Jaksic *et al*., 1997; Letnic & Dickman, 2010), which can drive prey populations to low levels as conditions begin to dry (Sinclair *et al*., 1998).

In the central deserts of Australia, drought-wet cycles are driven principally by the El Niño Southern Oscillation, and are particularly intense. Inter-annual variation in rainfall can exceed an order of magnitude (Van Etten, 2009), with large rainfalls following long droughts leading to regional-scale irruptions of rodents and their predators (Greenville, Wardle & Dickman, 2013). By contrast, the responses of co-occurring dasyurid marsupials to these climatic events are much less predictable than those of rodents. The same species can respond positively, negatively or not at all to heavy rainfall at the same sites over time, and may show disparate dynamics in response to the same rainfall events across space (Dickman *et al*., 2001; Greenville *et al*., 2016). Unlike rodents, it is also not clear whether these marsupials depend on dry-season refuges.

In part, the divergent demographic responses to rainfall by arid-dwelling dasyurid marsupials may arise because they are secondary consumers; all species <100 g feed largely on invertebrates (Fisher & Dickman, 1993; Baker & Dickman, 2018), which themselves respond variably to drought-wet cycles (Kwok *et al*., 2016). Some studies suggest that dasyurid marsupials >100 g respond positively and synchronously to heavy rainfall because irruptive rodents, when abundant, form a large part of their diet (Greenville *et al*., 2016; Baker & Dickman, 2018). As drought-wet cycles and the impacts of introduced predators on small desert mammals are expected to intensify (Greenville, Wardle & Dickman, 2017), there is an imperative to understand how small marsupials maintain their populations through climatic extremes and how they may fare in future. Dasyurid marsupials form the most species-rich communities of any mammals in central Australia, and also the richest mammalian insectivore-carnivore assemblages of any arid regions globally (Dickman, 2003).

Here, we describe the population dynamics of the kowari, *Dasyuroides byrnei*, a carnivorous dasyurid marsupial that occurs in arid Australia. Weighing up to 175 g (males) or 140 g (females), this IUCN-listed Vulnerable species lies within the critical weight range (35–5500 g) that, for mammals, has been most susceptible to extinction in Australia (Burbidge & McKenzie, 1989). The kowari can breed twice a year between April and December and has a maximum litter size of six (Woolley, 1971; Aslin, 1974; Canty, 2012). It is a nocturnal predator and its diet consists of invertebrates and rodents (Lim, 1998). During the day this species shelters in burrows dug into sand mounds that occur infrequently across stony gibber environments (Lim, 1998; Canty & Brandle, 2008). Its response to climatic conditions is not known; however, the smaller brush-tailed mulgara *Dasycercus blythi* (120 g) exhibits large fluctuations in body weight, condition and reproductive performance over drought-wet cycles (Greenville *et al*., 2016), and it is likely that kowari exhibit similar responses.

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

1. Kowari presence will be associated with key attributes, notably sand mounds, of its stony (gibber) pavement habitat;
2. Body and reproductive condition will improve with rainfall-driven increases in productivity; and
3. Sub-populations of kowari will respond synchronously to drought-wet cycles.

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

Materials and methods

Study site

The study was conducted at Clifton Hills cattle station in the Sturt Stony Desert, South Australia (Fig. 1). The landscape consists of stony gibber pavements, ephemeral swamps, scattered sand mounds and sand dunes (Canty & Brandle, 2008). Vegetation predominantly consists of grasses and sedges: *Astrebla pectinata*, *Tripogon loliiformis* and *Fimbristylis dichotoma* (Canty & Brandle, 2008). During summer, temperatures usually exceed 40°C and minima in winter fall below 5°C. Median annual rainfall at Birdsville, near the study site, was 153 mm over the period 1892–2015. The location and habitat in the Sturt Stony Desert is possibly one of the last refuges for the kowari.

Rainfall above the median fell in 2000, 2003 and 2011; rainfall in most other years was well below the median (Fig. 2).

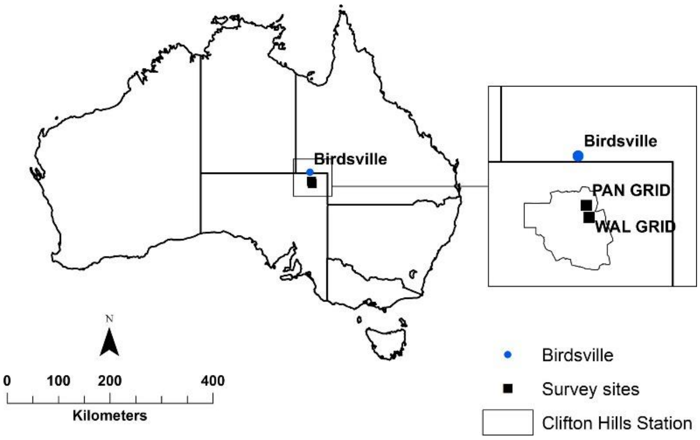

Figure 1: Location of study region, Sturts Stony Desert, South Australia, Australia. Long-term monitoring (2000–2015) was carried out on grids PAN and WAL of two sub-populations of kowari, *Dasyuroides byrnei*, and rainfall data were taken from a weather station at nearby Birdsville (insert).

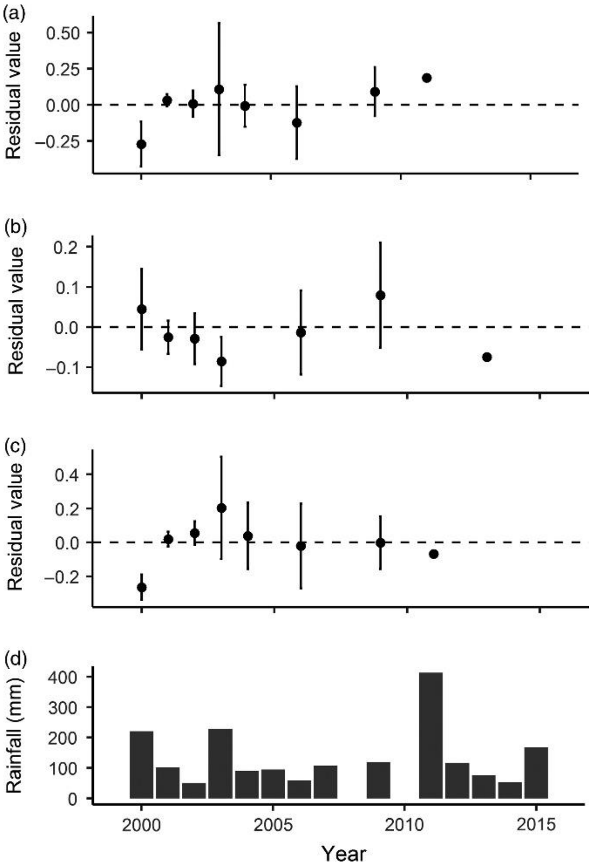

Figure 2: Mean body condition of (a) male and (b) female kowari *Dasyuroides byrnei*, (c) male testis condition, and (d) total annual rainfall at Birdsville for each survey year (2000–2015) in Sturts Stony Desert, South Australia. Points (±se) above the dashed line represent body or testis condition 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.

Animal trapping

Two 4 × 4 km live-trapping grids (WAL and PAN), 30 km apart, were surveyed once a year from 2001 to 2004, then in 2006 (Fig. 1). Uneven and reduced sampling effort occurred on the grids in 2007, 2009, 2011, 2013 and 2015. These two sites were chosen after a preliminary broadscale survey during 1999 (>800 trap-nights per site × 5 sites) spanning the Sturt Stony Desert and 100 km south of the Cooper Creek (R. Barratt & P. Canty unpublished). The preliminary study found that the study sites on Clifton Hills cattle station had the highest trapping rates for the kowari. The distance (30 km) between sites were chosen to ensure independence: no marked animals have been recorded to move between the two sites.

At each grid, Elliott traps were spaced 100 m apart on five 4-km lines that were 1-km apart (200 traps per grid). Traps were opened from 1 to 4 nights depending on weather conditions and available resources, baited with dog biscuits soaked in fish oil, and checked each morning at first light. The sex of each individual was determined along with measurements of mass, pes length, head length, and indicators of reproductive activity including testis width, pouch condition (developed or not developed) and number of pouch young present. Each animal was marked with a unique microchip from 2000 to 2004 to identify individuals, and with paint marks on the tail during the later, less-frequent visits to identify same-session recaptures.

Hypothesis 1: habitat assessments

Habitat data were collected from 25 m × 25 m plots at the 200 trap locations on each grid as visual cover estimates. Six habitat variables were scored; gibber pavement, sand mound (discrete sand lenses comprised of sandy clay loam with distinct convex profiles), thin sand spread (no distinct form and structure), sand dune (deep sands generally taller than 1 m and associated with longitudinal dunes), impermeable drainage depression (bare or pavement but with obvious algal cover from temporary inundation – includes hard pans and lake beds), and cracking clay drainage depression (includes temporary swamps and gilgais). These estimates were mutually exclusive and recorded as five cover classes; <5%, 5–25%, 26–50%, 51–75%, >75%. Related data included gibber size (none, pebbles <50 mm, cobbles 50–250 mm, boulder >250 mm) and number of sand mounds.

To investigate which habitat variables predict kowari presence, a binomial generalized linear model (GLM) was used. The full additive model included site, gibber size, gibber pavement cover, sand mound number, sand mound cover, sand spread cover and hard drainage depression cover. We standardized all factors to have a mean of 0 and standard deviation of 1 so each factor was on the same scale. All models were ranked by the Akaike information criterion adjusted for small sample size (AIC_c), with the Akaike weight calculated for each model (Burnham & Anderson, 2002). We then applied model averaging to account for model uncertainty (Burnham & Anderson, 2002), whereby all models within $\Delta AIC_c < 2$ were considered to have some support. The effect size of each variable was based on the model-averaged parameter estimates, calculated using the average of the coefficient estimates from all models, weighted by the Akaike weight (Burnham & Anderson, 2002). We calculated the uncertainty of parameter estimates based on their unconditional standard errors (Burnham & Anderson, 2002). To quantify the relative importance of the predictor variables, we summed the Akaike weight from all model combinations where the variable occurred. We then ranked the predictor variables according to their relative importance, with the larger the weight value, the more important the variable is relative to the others. Binomial GLMs were constructed in r version 3.4.0 (R Core Team 2017) and model selection implemented using MuMIn, version 1.15.6 (Barton, 2016).

Hypothesis 2: body and reproductive condition

To assess whether body condition of male and female kowari differed over time, the average body condition of adults was compared each year (using data from 2000 to 2015) by plotting log-body mass against log-head length, omitting females with pouch young (29 females). Residual deviations from the linear regression were averaged each year and used as estimates of body condition. Positive mean residual values indicate above-average body condition and negative values below-average condition. To investigate whether changes in productivity (rainfall, green and non-green fractional cover) influenced body condition for each sex, residuals for each animal were regressed against annual productivity surrogates and, to account for lag effects, productivity surrogates from the year before. Fractional cover estimates obtained from NRM Spatial Hub (2018) are landcover fractions representing the proportions of green and non-green cover derived from Landsat images. For green and non-green fractional cover, both variables were entered into the model, as both contribute to the overall productivity of the system. Linear regression models, with Gaussian error structures, were constructed in r version 3.4.0 (R Core Team 2017); inspection of diagnostic plots indicated that all models met statistical assumptions (Zuur, 2009).

To assess whether the average reproductive condition of males changed over time, residual deviations from the linear regression of log-testis width against log-head length were averaged each year and plotted. As for body condition, data for the linear regression were taken from 2000 to 2015, with positive mean residual values indicating above-average reproductive condition and negative values below-average condition. To test whether productivity (rainfall, green and non-green fractional cover) influenced reproductive condition, residuals for testis length for each animal were regressed against annual productivity surrogates and annual surrogates from the year before. For females, the proportion of animals breeding (i.e. females with pouch young) was calculated for each year. Proportion of breeding females each year and annual rainfall or annual rainfall from the year before were modelled as proportional odds; a quasi-binomial GLM was used, as data were over-dispersed (Zuur, 2009). In addition, to investigate whether female fecundity increased with rainfall, the number of pouch young per female each year was regressed against annual rainfall or annual rainfall from the year before; a quasi-Poisson GLM was used due to data over-dispersion (Zuur, 2009). As above, both green and non-green fractional cover variables were entered into the model. Generalized linear models were constructed in r version 3.4.0 (R Core Team 2017), and inspection of diagnostic plots indicated that all models met statistical assumptions (Zuur, 2009).

Hypothesis 3: long-term spatio-temporal dynamics

To assess whether the two sub-populations of kowari exhibited synchronous or asynchronous dynamics, we used Bayesian multivariate autoregressive state-space (MARSS) models. Live-trapping data were standardized for effort by calculating numbers of captures (excluding recaptures) per year per 100 trap nights and log + 1 transformed, as MARSS models use log-space. We based the MARSS models on the Gompertz growth model and assumed that sub-population growth rate varied exponentially with sub-population size and that meta-populations were closed to immigration and emigration (Hinrichsen & Holmes, 2009). The MARSS framework is hierarchical and allows modelling of different spatial population structures and parameters such as growth rates, while including both process (state) and observation variability (see Appendix S1). To select between the synchronous or asynchronous model for the data from the two grids, the best fitting model was considered to be that with the lowest deviance information criterion (DIC).

To allow model convergence, each model was fitted with three Markov chains, each with 100 000 Markov chain Monte Carlo (MCMC) iterations, thinning of 25 and the first 60 000 iterations discarded, leaving 4800 iterations saved (see Appendix S1 for description of priors, model formation, and Data S1 for JAGS code). Inspection of diagnostic plots indicated that all models met statistical assumptions, and all converged. Analyses were conducted in r 3.4.0 (R Core Team 2017) and jags 4.2.0 (Plummer, 2016a), using the R2jags 0.5–7 (Su & Yajima, 2015) and rjags 4–6 (Plummer, 2016b) packages.

Population viability analysis

We calculated the probability that our combined study sub-populations would hit a threshold (extinction risk metric) based on Dennis, Munholland & Scott (1991), but modified to account for observation error estimated using the synchronous MARSS model above (Holmes, Ward & Scheuerell, 2014). We used thresholds set by the IUCN Red List Criterion *E*, where: critically endangered is a 50% chance of extinction in 10 years; endangered is a 20% chance of extinction in 20 years, and vulnerable is a 10% chance of extinction in 100 years. We defined extinction as a 99% population decline over the time periods for each extinction risk class. We assumed density-independence and based the MARSS models on the Gompertz growth model, as above, and assumed also that 10% of observations were missing due to sites becoming inaccessible after rainfall events or other logistical problems. To test the assumption of density independence, we ran the synchronous MARSS model with and without density dependence. There was no improvement in model fit for the density dependent model (DIC 34.5) vs. the density independent model (DIC 33.2) and thus the marginally more parsimonious model was used. Bootstrapping (10 000 simulations) was used to calculate the mean probability of population decline and associated 95% confidence intervals (Holmes *et al*., 2014), with all simulations performed on high performance computers (The University of Sydney HPC Service 2017) in r version 3.3.2 (R Core Team 2017) and jags version 4.2.0 (Plummer, 2016a), using the R2jags 0.5–7 (Su & Yajima, 2015) and rjags 4–6 (Plummer, 2016b) packages (see Data S2 for r code).

Results

In total, 14 250 trapping nights yielded 475 live-captures of 229 individual kowari (3% trap success) from 2000 to 2015. Ninety-one individual males were captured, as well as 128 females. Sex was not recorded for 10 captures.

Habitat assessment

Eight models had ΔAIC_c <2 and thus were considered to have support (Table S1). Model averaging revealed that gibber pavement cover and sand spread cover were associated positively with kowari presence (Table 1). Site, hard drainage depression cover, number and cover of sand mounds all had large uncertainty around the estimates and thus were not considered useful for predicting kowari presence (Table 1).

Table 1. Model averaged estimates from the top eight binominal generalized linear models investigating which combinations of habitat variables successfully predict the presence of kowari, *Dasyuroides byrnei*

Variable	Estimate	se	*z*-value	Relative importance
Intercept	1.37	0.22	6.35	

Variable	Estimate	se	*z*-value	Relative importance
Gibber pavement cover	0.47	0.18	2.63	1
Sand spread cover	0.34	0.15	2.23	1
Site$_{\text{Wal grid}}$	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

Surveys were conducted from 2000 to 2015, Sturts Stony Desert, South Australia.

Body and reproductive condition

Body and reproductive condition changed over time for both sexes (Figs 2 and 3), but rainfall was not associated with body condition (Fig. 2; Table 2). There was also no association with green and non-green fractional cover and female body condition (Table 3). However, the interactions of green and non-green fractional cover from the previous year were significant and positively associated with male body condition (Table 3). Rainfall in the previous year was associated positively with the number of pouch young (range: 0–6 young), but there was no relationship between rainfall or antecedent rainfall and testis condition (Fig. 3; Table 4). There was a significant and positive interaction between green and non-green fractional cover from the previous year and testis condition, but no association between green and non-green fractional cover and the number of pouch young (Table 4).

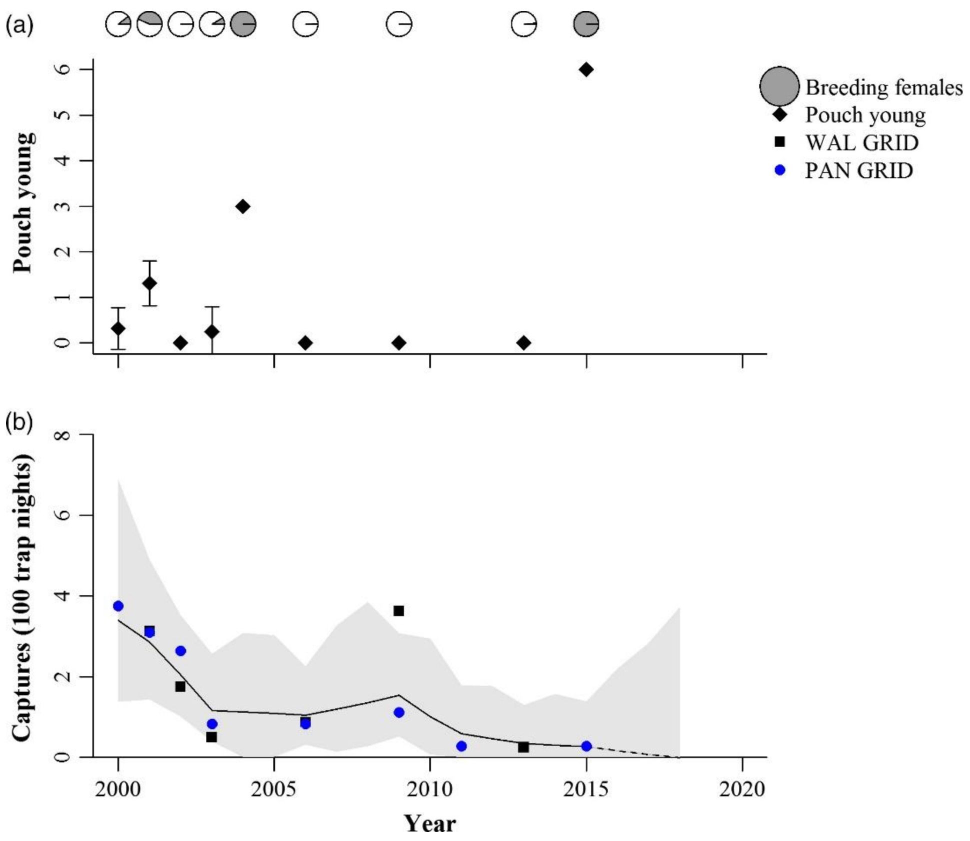

Figure 3: Long-term (2000–2015) dynamics of two sub-populations of kowari, *Dasyuroides byrnei*, on PAN and WAL grids, Sturts Stony Desert, South Australia. (a) Mean number of pouch young female per year (±se) and proportion of reproductive females pooled across the two sub-populations (N = 2, 17, 0, 1, 8, 0,0, 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.

Table 2. The influence of rainfall on body condition of each sex of the kowari, *Dasyuroides byrnei*

Variable	**Estimate**	**se**	***t*-value**	***P***
Females				
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

Variable	Estimate	se	*t*-value	*P*
Males				
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

Results from the linear regression of residuals for each animal were regressed against annual rainfall and annual rainfall from the year before. Residuals for body condition were calculated by plotting log-body mass against log-head length of adults, omitting females with pouch young. Surveys were conducted from 2000 to 2015, Sturts Stony Desert, South Australia.

Table 3. The influence of green and non-green fractional cover on body condition of each sex of the kowari, *Dasyuroides byrnei*

Variable	Estimate	se	*t*-value	*P*
Females				
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
Males				
Intercept	0.81	0.62	1.31	0.19

Variable	Estimate	se	*t*-value	*P*
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
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 × Non-green previous year	0.01	0.004	2.99	0.004

Results from the linear regression of residuals for each animal were regressed against annual rainfall and annual rainfall from the year before. Residuals for body condition were calculated by plotting log-body mass against log-head length of adults, omitting females with pouch young. Surveys were conducted from 2000 to 2015, Sturts Stony Desert, South Australia.

Long-term spatio-temporal dynamics

The synchronous MARSS population model provided a better fit (DIC 34.6) than the asynchronous MARSS model (DIC 71.3), indicating the two sub-populations fluctuated in synch. Long-term monitoring of kowari revealed that the mean population growth rate was negative (Table 5; Fig. 3), with the modelling showing that process (environmental; *Q*) and observation (*R*) errors were similar (Table 5).

Table 5. Population parameter estimates from Bayesian multivariate autoregressive state-space models

Variable	Estimate	Lower CI	Upper CI
Synchronous			
U	−0.08	−0.28	0.10
$A_{\text{Wal grid}}$	−0.04	−0.43	0.38
Q	0.30	0.16	0.69
R	0.24	0.13	0.42

Variable	Estimate	Lower CI	Upper CI
Asynchronous			
$U_{\text{Pan grid}}$	−0.08	−0.43	0.30
$U_{\text{Wal grid}}$	−0.09	−0.23	0.06
$Q_{\text{Pan grid}}$	0.55	0.12	1.35
$Q_{\text{Wal grid}}$	0.23	0.07	0.58
R	0.20	0.08	0.25

Live-trapping data on kowari, *Dasyuroides byrnei* (2000–2015) were standardized for effort by calculating numbers of captures per year per 100 trap nights on two live-trapping grids, PAN and WAL. The synchronous model was the best fit to the data, suggesting the two sub-populations in Sturts Stony Desert, South Australia, have similar trajectories over time. Mean population growth rate (U), mean site bias (A), process error (Q) and observation error (R) are shown.

Population viability analysis

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

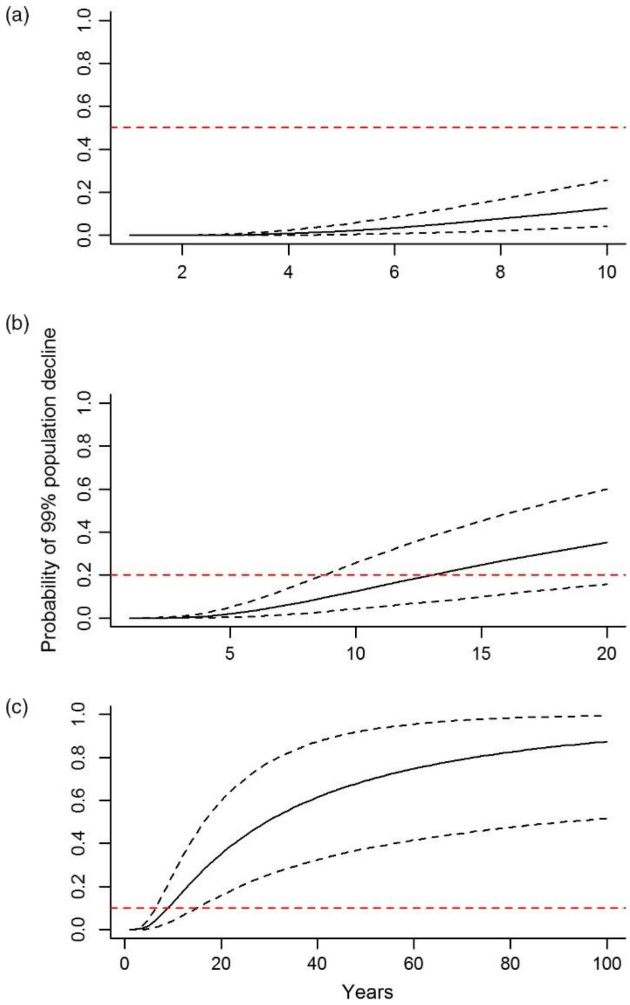

Figure 4: Population viability analysis of kowari, *Dasyuroides byrnei*, Sturts Stony Desert, South Australia. The IUCN Red List criterion *E* was used to assess the conservation status of this threatened species, where: (a) critically endangered populations are projected to experience a 50% chance of 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 horizontal line represents the extinction risk threshold defined by the IUCN (2012) (i.e. 50%, 20% or 10%).

Discussion

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

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

Arid-dwelling dasyurids show complex relationships with rainfall-driven pulses of productivity, with populations and the body and reproductive condition of individuals often fluctuating idiosyncratically (Baker & Dickman, 2018). For example, Dickman *et al.* (2001) used body condition as a surrogate for available food resources for small and medium-sized dasyurids, and found that capture rates did not increase with increasing body condition. This suggested a weak link between body condition and rainfall, in contrast to patterns found in other desert-dwelling mammals in Africa and North America (Marshal, Krausman & Bleich, 2008; Turner *et al*., 2012). However, the body condition of male kowari did increase with fractional vegetation cover, suggesting that these individuals took advantage of increased productivity. Females did not. Possibly, as males are larger than females they have greater mobility and thus propensity than females to access sites of locally high productivity. Alternatively, as we excluded females with pouch young from assessments of body condition, females exploited productivity by channelling resources into reproduction rather than somatic growth. In addition, sites surveyed in this study may act as refuges and thus buffer animals from environmental extremes (Pavey *et al*., 2017).

Male testis condition was below average in 2000 but stable from 2001 to 2015 and not influenced by rainfall. However, testis condition improved with green and non-green fractional cover, suggesting that on-site increases in productivity did influence male reproductive condition. The proportion of females breeding (with pouch young) also changed over time. This may reflect the variable sampling times during this study, thus limiting our ability to quantify the effects of rainfall and primary productivity on reproduction. However, litter size (number of pouch young) did increase with rainfall in the previous year. Maximum litter size was six, as in captive animals maintained under optimal conditions (Woolley, 1971; Aslin, 1974), suggesting that increased productivity improved female fecundity.

The two sub-populations of kowari exhibited synchronous dynamics over the study period. The similar-sized brush-tailed mulgara, *D. blythi*, also showed synchronous dynamics across an 8000 km^2 area of the Simpson Desert, perhaps suggesting that dasyurids >100 g often show synchronous responses to environmental conditions, whereas smaller species respond more locally (Greenville *et al*., 2016). Understanding the scale of species' responses has practical importance for conservation. For example, if populations of kowari fluctuate synchronously, the risk of extinction will be high if all populations decrease towards zero at the same time and rescue through colonization is prohibited (Heino *et al*., 1997; Greenville *et al*., 2016). Alarmingly, our findings suggest that the two sub-populations of kowari we studied have declined synchronously over the last 16 years, and are continuing to fall despite recent and exceptional rainfalls during 2010–2011 (Brandle & Canty, 2011; Read & Moseby, 2015).

This study confirms that the study region contains favourable habitat for kowari; we identified habitat preferences for open gibber pavement with some surface sand and, in-part, showed that body condition and reproductive output increased with improvements in environmental productivity. However, population viability analysis suggests that kowari sub-populations are at risk of local extinction in the near to medium future. Given that the study area was chosen because of its high capture rates during earlier studies (Lim, 1998) and subsequent sampling (Canty & Brandle, 2008; Brandle & Canty, 2011; Read & Moseby, 2015), as well as evidently low recruitment of juveniles into the current population, we suggest that the population is under stress from extrinsic rather than intrinsic factors. The most likely factors are discussed below.

Grazing or trampling from stock can flatten sand mounds and degrade habitat for breeding burrows (Canty & Brandle, 2008; Canty, 2012; Woinarski *et al*., 2014; Read & Moseby, 2015). Protecting breeding habitat by excluding stock using fencing or reduced stocking rates could aid recovery. Secondly, predation from introduced predators, such as feral cats and foxes, may limit recruitment to the population. The open gibber habitat of kowari provides little cover and shelter opportunities from avian and introduced predators, and reduction in burrowing opportunities may increase predation risk. The kowari is at particularly high risk from feral cat predation (Dickman, 1996). Lastly, the synergistic and additive effects of predation, grazing and predicted range declines from climate change (Chapman & Milne, 1998; Doherty *et al*., 2015) may further amplify extinction risk for the kowari. If other populations of kowari are declining in a manner similar to those in South Australia, the species would meet the criteria for listing as Endangered (IUCN 2012). Monitoring needs to continue and be expanded to encompass other populations within the tiny current range of the kowari, urgent research is required to elucidate the impacts of grazing and introduced predators, and insurance populations need to be established by captive breeding programs.

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