

Home range, habitat suitability and population modelling of feral Indian peafowl (*Pavo cristatus*) on Kangaroo Island, South Australia

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Abstract. The Indian peafowl (*Pavo cristatus*) is a declared alien pest species on Kangaroo Island, South Australia, where it is implicated in a range of social problems and potential ecological impacts. To inform the management of feral peafowl, we aimed to (1) provide an estimate of peafowl distribution and abundance; (2) measure peafowl home ranges; (3) calculate the area of suitable peafowl habitat; and (4) estimate how the population could change under various culling scenarios. Using expert and landholder surveys, we estimated that ~380 individuals (range 330–428) were distributed among 21 separate groups on Kangaroo Island. Habitat suitability modelling identified native vegetation near agriculture as the preferred peafowl habitat and indicated that substantial unoccupied suitable habitat is available. The mean home range of eight peafowl was 52 ha and one dispersal event of 4.5 km demonstrated that unoccupied suitable habitat could feasibly be colonised. Demographic models indicated that, if unmanaged, the peafowl population could exceed 2000 individuals after 10 years, but that culling ~85 individuals annually could maintain the current population size. We therefore suggest that control of the Kangaroo Island peafowl population is warranted while the current distribution of peafowl is well understood.

Additional keywords: invasive species, Maxent, VORTEX.

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Introduction

Alien vertebrate species are a significant component of human-induced global environmental change and native species extinction (Bellard *et al.* 2016). Birds, in particular, have been widely acclimatised, so that today more than 600 species have been introduced worldwide (Cassey *et al.* 2015). Naturalised bird species can negatively affect biodiversity and damage agriculture and human health (Shirley and Kark 2009).

The Indian peafowl (*Pavo cristatus*; hereafter ‘peafowl’) has been popularly spread far beyond its native range through human transport and deliberate acclimatisation activities. Native to the Indian subcontinent, feral peafowl populations now exist in Australia, the USA, Canada, Europe, the West Indies, South Africa and New Zealand (Madge *et al.* 2002; Latham 2011). The Indian peafowl is a large-bodied, brightly coloured pheasant of the Family Phasianidae. In natural environments, peafowl inhabit scrub, jungle and forest edges. In human-modified environments, they commonly inhabit riparian vegetation, crop fields and adjacent scrub, typically roosting in small groups in tall trees at night (Madge *et al.* 2002; Ramesh and McGowan

2009). Peafowl usually emerge from cover in the morning and evening to drink from water bodies and forage for food in clearings and cultivated land. Their diet includes seeds, fruits, flower buds, shoots, invertebrates and small vertebrates (Latham 2011).

The impacts of exotic peafowl are poorly studied, but they are believed to cause a range of ecological and social problems. High peafowl densities on small Japanese islets impact local biota and habitats negatively, potentially driving population declines in one endemic skink, *Eumeces kishinouyei*, and sympatric bird species, such as the Japanese white-eye (*Zosterops japonicas*) (Eguchi and Amano 2004). Feral peafowl in New Zealand consume quality pasture, fruit and crops (Latham 2011) and contaminate silage with faeces, posing health issues for livestock and humans (Hall and Mill 1998). Peafowl are susceptible to approximately 80 infectious diseases and parasites, some of which are harmful to humans, livestock and wildlife (Schwartz 1994, cited in Latham 2011).

At least 17 of Australia’s offshore islands host feral peafowl, including Kangaroo Island (KI) in South Australia (Department

of the Environment 2012). KI is Australia's third largest island and is an important refuge for native flora and fauna, with over half the island still retaining native uncleared vegetation. KI is an Important Bird and Biodiversity Area and is home to several species that have become rare on mainland South Australia. KI has 45 endemic plants and is home to the critically endangered Kangaroo Island dunnart (*Sminthopsis aitkeni*) (BirdLife International 2015). Because of KI's high conservation value, it is important to minimise the spread and ecological impacts of invasive species on the island. Feral peafowl on KI generate considerable public complaint over their potential ecological impacts, and are implicated in causing noise pollution, garden destruction, vehicle collisions, and defaecation on buildings (Natural Resources Kangaroo Island 2012).

The introduction of peafowl on KI dates back to ~1920 when a population existed near Wilson River (Lashmar 1988). The Natural Resource Management Board on KI (NRKI) recorded 10 separate peafowl groups that existed on the island one decade ago (~2000). Historically, a small number of landholders on KI have implemented sporadic peafowl control when groups became very large; for example, one local resident trapped and killed 112 peafowl in less than one year (Natural Resources Kangaroo Island 2012). Control efforts by landholders have been moderately effective in preventing a population explosion, but have not prevented peafowl groups from becoming increasingly widespread across KI. Peafowl management has so far relied on the continued support and goodwill of a few individuals. However, the willingness of landholders to control an increasing peafowl population cannot be guaranteed into the future, warranting the development of a coordinated science-based management plan.

Prior to this study, detailed information was lacking on the spatial ecology of feral peafowl populations, including very limited understanding of peafowl home ranges and dispersal characteristics. On KI, there was no understanding of peafowl habitat requirements, including whether unoccupied suitable habitat existed and how the population was expected to change over time. We aimed to: (1) map the current distribution of peafowl groups using extensive local knowledge; (2) identify peafowl habitat preferences and quantify peafowl home ranges; (3) estimate the area of suitable peafowl habitat on KI using a habitat suitability model; and (4) project the population trajectory under different management scenarios using demographic modelling.

Materials and methods

Current distribution of peafowl on Kangaroo Island

The distribution of peafowl groups was previously mapped on the basis of expert knowledge and from a database of public sightings (Natural Resources Kangaroo Island 2012). We confirmed the accuracy and precision of these estimates by: (1) following up these observations and determining the locations of peafowl groups at a finer scale (see Methods below), and (2) estimating the size of each group. We interviewed 36 residents who had detailed knowledge of peafowl in their areas, or were knowledgeable NRKI employees. Substantial feral goat, deer and pig control has been undertaken by NRKI natural resource managers across much of the conservation

areas, particularly in the west and south of KI. The control and monitoring included camera-trapping, live-trapping and culling from 2006 to the present. The feral animal control officers were also interviewed. Interviewees either gave their best single estimate of group size, or estimated a range for each peafowl group in their location, from which the mid-range was used (mean abundance was calculated when estimates from multiple interviewees differed).

Peafowl are large conspicuous birds that have high site fidelity and form groups that landowners can easily identify. Although individual birds cannot be differentiated, landowners regularly observed patterns in the group size and location of sightings, providing a reasonable ability to estimate group size. Interviewees identified specific patches of vegetation that peafowl were known to frequent, and each group was assigned to a single geographic location based on the site it was believed to frequent the most.

Home range

To quantify peafowl home ranges, we conducted radio-tracking at two study sites: the Dover Farm area (35°38'S, 137°36'E) and the Murray Lagoon area (35°54'S, 137°27'E). The Dover Farm area is located to the north of Kingscote, KI's largest town, in farmland with substantial patches of remnant native vegetation. The Murray Lagoon study site is located just north of Murray Lagoon, on the edge of a farm and the Cape Gantheaume Conservation Park. The farm contains a 20-ha lagoon, which is dominated by various species of tea tree (*Melaleuca* spp.). Murray Lagoon is KI's largest freshwater lagoon (~1000 ha) and is an important nesting site for native waterbirds (McCracken *et al.* 2000).

Eight peafowl (three adult males, four adult females and one subadult of unknown sex [random trapping result]) were trapped in metal pig traps baited with wheat. When peafowl were inside the trap, a rope attached to the open trap door was pulled from an obscured distant location to close the trap. Trapped individuals were fitted with 24-g Sirtrack Ultimate V5N 161 VHF radio-collars around the base of the neck. The collars weighed well below the recommended 3% of bodyweight (Millsbaugh and Marzluff 2001) and had no obvious effect on the peafowl. Radio-tracking was conducted between 1 February 2013 and 16 May 2013, and tracking times were varied between 0530 and 2130 hours so that sampling was not biased to a particular time of day (see Fig. S1, Supplementary Material, for chart of read times). We separated observations on the same individual by at least 1 h to reduce temporal autocorrelation. We note that the interpretation of home ranges should be limited to the radio-tracking period (i.e. late summer to autumn) because home-range characteristics are likely to differ as resource availability changes, and as group dynamics change between breeding and non-breeding seasons (Rands *et al.* 1984; Harikrishnan *et al.* 2010).

Kernel-based methods for home-range calculation are more accurate than alternative methods such as minimum convex polygons or harmonic means (Worton 1995; Swihart and Slade 1997; Seaman *et al.* 1999; Huck *et al.* 2008). We calculated the fixed-kernel home range at the 50% and 95% levels for each individual using the R package *adehabitat* 1.8.12. The default

ad hoc method was used as the smoothing parameter (Worton 1989), as the Least-Squares Cross-Validation smoothing method produced home ranges that were clearly too small and constricted. The minimum sample size recommended for kernel home-range estimation is 50 observations (Seaman *et al.* 1999), which we achieved for six of the eight collared peafowl. This target was not reached for two birds that were shot by local residents before the study ended.

In theory, home-range size estimates should reach an asymptote when sufficient sampling has been performed because additional observations will not affect the estimates (Harris *et al.* 1990; Hansteen *et al.* 1997). We therefore performed asymptote analysis to assess whether sample sizes were sufficient to estimate each individual's home range accurately. We created area-observation plots for each individual by randomly generating 100 subsamples of size x , where x ranged from a minimum of five to the sample size n , and produced home-range estimates for each subsample (Harris *et al.* 1990). We then plotted the mean home-range estimates ($\pm 95\%$ confidence intervals) against the subsample size. We visually inspected the area-observation plot to determine whether the estimated home range for each individual exhibited asymptotic behaviour as the subsample size was increased (Laver and Kelly 2008).

Habitat suitability modelling for peafowl on Kangaroo Island

Maxent for habitat suitability modelling

We constructed habitat suitability models for peafowl using *Maxent* 3.3.3k, a general-purpose machine-learning method that is widely used for modelling species' distributions (Phillips *et al.* 2006; Pearson *et al.* 2007) and has been employed to predict the potential distributions of invasive species (Wang *et al.* 2007; Ward 2007; Elith *et al.* 2011). Using presence-only occurrence data, *Maxent* estimates the habitat suitability for a species (i.e. the relative likelihood of a species' occurrence) conditional on a set of environmental variables defined by the environment at locations where the species is known to occur (Phillips *et al.* 2006). *Maxent* consistently performs well even when sample sizes are low and can incorporate both continuous and categorical variables (Elith *et al.* 2006; Hernandez *et al.* 2006; Pearson *et al.* 2007).

Presence data and spatial covariates

The response variable for the habitat suitability modelling consisted of the mapped presence locations (i.e. the locations of peafowl groups) that were identified as previously described. Each group was initially mapped at a singular 20 m \times 20 m pixel in the estimated location that it was observed to frequent most often. Additionally, the locations of two eradicated peafowl groups were also included as presence data. To test whether the model results were sensitive to the fine-scale (single 20-m pixel) placement of each presence location, we additionally modelled suitable habitat using 100 m \times 100 m pixels. We sampled 10 000 background pixels, which were randomly selected from all of KI.

To investigate spatial drivers of peafowl occurrence, we collated the following suite of potentially relevant covariates at two spatial resolutions (20 m \times 20 m and 100 m \times 100 m):

- (1) A categorical habitat variable reflecting the dominant vegetation type or land use (*Habitat*).
- (2) The percentage of pasture (*%Pasture*).
- (3) The Euclidean distance to the nearest pasture, crop or open grass (*Dist2pasture*).
- (4) The percentage of native vegetation (*%Native*).
- (5) The percentage of native vegetation within a moving neighbourhood window (*%NativeNeighbour*), which was used to index the size of vegetation patches, whilst effectively down-weighting contiguous but narrow patches that are unsuitable for peafowl (e.g. vegetation alongside roads or fencelines). This layer was constructed by passing a moving 25-pixel window over the entire island. The percentage of pixels that were native vegetation within the moving window was assigned to the centre pixel of the moving window.

These layers were constructed from spatial datasets provided by the Department of Environment, Water and Natural Resources ('Native Vegetation Floristic – NVIS Statewide' and 'Land Use 2008') and one aerial photograph ('Aerial Photo – Kangaroo Island 2011'). See Table S1 of the Supplementary Material for additional details of the habitat categories and construction of these spatial covariates.

Model fitting, selection and evaluation

Using *Maxent*, we evaluated a candidate set of habitat suitability models that included different combinations of environmental covariates. *Maxent* fits models by optimising the 'gain', a measure of the improvement in the penalised average log-likelihood compared with a null model (Elith *et al.* 2011). *Maxent* iteratively improves model fit (maximises the gain) as it runs an optimisation routine, and also calculates the relative contribution of each covariate to the overall model gain (Phillips *et al.* 2006). Since our primary goal was to develop a predictive model of habitat suitability, we used 10-fold cross-validation (10% of presences were withheld for testing in each of 10 model runs) to compare the performance of candidate models. That is, we evaluated the ability of models to predict the hold-out 'test' presences that were not used during the model training phase, specifically calculating the area under the receiver operating characteristic curve (AUC) and the test gain. The AUC is the probability that a randomly chosen presence site will be ranked above a randomly chosen absence or background site (Phillips and Dudík 2008). An AUC of 0.5 corresponds with a random ranking, while a perfect ranking achieves the best possible AUC of 1 (Phillips and Dudík 2008). The final model was selected because it had the highest test AUC, the highest test gain, and was more parsimonious than other models with similar AUC values.

Given the relatively small number of presence locations, we additionally used the jackknife validation approach developed by Pearson *et al.* (2007) to quantify the selected model's predictive capacity. This approach assesses whether the classification of single, hold-out presences by the model is better than random chance, and generates a *P*-value (Pearson *et al.* 2007). We applied Pearson's jackknife at the minimum training presence threshold. The minimum training presence threshold can be interpreted ecologically as identifying pixels predicted

as being at least as suitable as those where a species' presence has been recorded (Pearson *et al.* 2007).

We used the selected *Maxent* model to generate habitat suitability predictions for peafowl across the whole of KI. Suitability values range from 0 (unsuitable habitat) to 1.0 (highly suitable habitat), with 0.5 representing habitat suitability at typical presence locations (Elith *et al.* 2011).

Population modelling

We projected the stochastic two-sex population dynamics of the KI peafowl population under different management scenarios using *VORTEX* 9.999 software (Lacy and Pollak 2013). *VORTEX* provides a stochastic, individual-based simulation model that tracks the fate of individuals through several stages (e.g. birth, survival, reproduction, death) (Lacy 2000). Although *VORTEX* has typically been used to model small populations from a conservation perspective, it has also been applied to the management of invasive species and can accommodate different culling regimes (Pruett-Jones *et al.* 2007; Ballou *et al.* 2008; Cassey *et al.* 2014). *Vortex* automatically includes demographic stochasticity (i.e. variation in the population growth rate that occurs even if the mean demographic rates remain constant); for example, whether an animal reproduces or dies in a given year is determined by sampling from Bernoulli distributions with means equal to the specified probability of reproducing or mortality rate, respectively. Life-history data specific to the KI peafowl population are not currently available, so a baseline *VORTEX* population model was parameterised using best estimates from an extensive literature survey (key parameters are shown in Table 1; see Table S2 of the Supplementary Material for an extended table of parameters used).

In the absence of detailed information on the structure of the KI peafowl population, we assumed a single island-wide closed population. We ran 100 iterations of the stochastic population model for peafowl over a 10-year management time frame for each of five management scenarios – no peafowl management and fixed annual culls of 50, 85, 100 and 150 individuals. We

assumed that all peafowl age classes and sexes were equally likely to be culled, and we note that this simulated culling represents the total combined off-take by NRKI and landholders. To determine whether model outcomes were robust to uncertainty in the baseline demographic parameters used, we also conducted a sensitivity analysis on three key variables: the percentage of females breeding annually, and the annual (background) mortality rates used for juvenile (0–1 year old) and subadult/adult (>1 year old) peafowl (see Table S2, Supplementary Material).

Results

Current distribution

On the basis of the elicitation of expert local knowledge, we estimated that ~380 peafowl (range = 330–428) were distributed among 21 separate groups across KI (Fig. 1 includes estimates of each group size), up from a reported 10 groups a decade ago (A. McGuire, pers. comm.). The mean estimated group size was 18 individuals (s.d. = 11). Group size varied substantially among sites, ranging from 5 to 45. The regular extensive monitoring of the KI conservation areas by natural resource managers and the strong public support for reporting peafowl sightings provides us confidence that Fig. 1 is an accurate representation of the distribution of the peafowl groups present on KI at the time of the study. This map highlights that peafowl are widely distributed, but are known to occupy only the agricultural regions of the island. Importantly, substantial feral animal control and monitoring in the conservation areas detected no peafowl groups existing solely in these areas. Each peafowl group was observed to use remnant patches of native vegetation for shelter and roosting. Interviewees reported that peafowl often use livestock water troughs as a source of water and will consume spilt grain if available.

Home range

Home ranges were quantified for eight individuals from two study sites. The mean home range was 52.0 ha (s.e. = 9.15 ha),

Table 1. Key parameters used in the baseline *Vortex* population model for feral peafowl

Square brackets indicate the ranges tested during a sensitivity analysis on three key parameters – the percentage of adult females that breed annually, and annual mortality rates for juveniles and adults/subadults. See Table S2, Supplementary Material, for an extended table of the parameters used

Variable	Values	Details and references
No. of years simulated	10	Chosen as a reasonable time-frame for management
Reproductive system	Polygynous	Madge <i>et al.</i> (2002)
Age of first offspring	Females = 2 Males = 3	Coles (2009)
Maximum number of broods per year	1	Although females can double-clutch if their first clutch is destroyed (Latham 2011).
Percentage of adult females breeding	90 [60–100]	In combination with other parameters, an annual breeding probability for adult females of 90% produced a cohort of juveniles in the first simulation year that closely matched the estimated number of juvenile peafowl produced on KI in 2013.
Offspring per female per brood	Mean = 4.5, s.d. = 1, maximum = 8	Madge <i>et al.</i> (2002). Standard deviation (s.d.) is arbitrary.
Mortality for juveniles (age 0–1)	79% [60–100]	Estimated from various sources in the literature. See Table S2, Supplementary Material for details.
Subadult and adult mortality (ages >1 year)	20% [10–50]	Estimated from literature. See Table S2, Supplementary Material for details.
Initial population size	380	Our estimate of the peafowl population size on Kangaroo Island (Fig. 1).

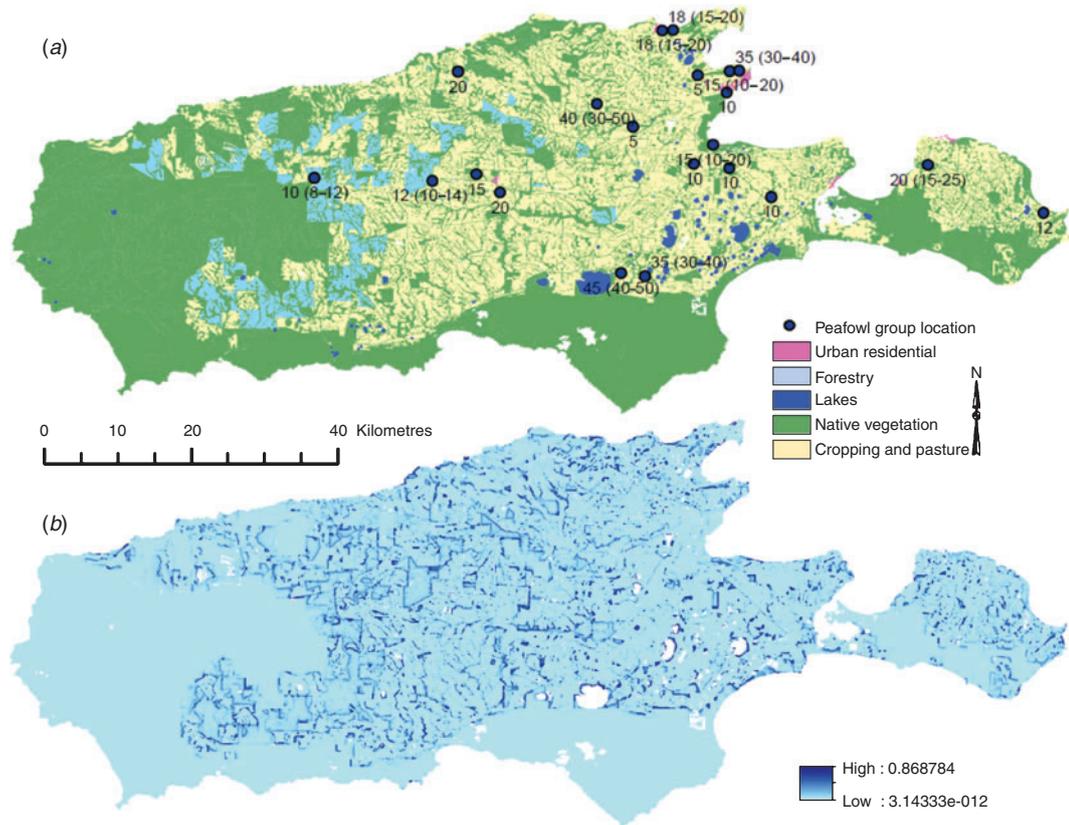


Fig. 1. Estimated distribution of peafowl groups and suitable habitat on Kangaroo Island. (a) Peafowl groups are indicated by blue dots and the adjacent number indicates the estimated size of that group (the range is given in parentheses when interviewees estimated a range). This distribution was estimated from expert knowledge, a database of public sightings and interviews with local residents. The map is believed to contain all peafowl groups on Kangaroo Island at the time of the study. (b) Map of predicted habitat suitability generated using the selected *Maxent* model.

Table 2. Peafowl radio-tracking information

Radio-tracking was conducted on eight peafowl from two broad study sites (DF, Dover Farm; ML, Murray Lagoon). 'DF-5' and 'DF-6' were shot by local residents prior to the end of the study. The mean group size was calculated from all sightings of a collared individual. The largest group size is the greatest number of peafowl a collared individual was sighted with

ID	Sex	95% fixed-kernel home range (ha)	Observations (parentheses indicate unsuccessful reads)	Days tracked	Mean number of peafowl in group (s.d.)	Median group size	Largest group size (no. of peafowl)
DF-1	Male	46.2	60	44	16.1 (7.4)	16	30
DF-2	Male	80.0	96	97	5.3 (8.6)	1.5	28
DF-3	Female	35.1	57 (5)	45	4.0 (1.8)	4	9
DF-4	Female	60.5	51	29	6.2 (1.3)	6	9
DF-5	Subadult	55.7	18	11	4.9 (2.2)	4	9
DF-6	Female	91.9	29	47	7.8 (4)	9	11
ML-1	Female	11.7	51	19	13.4 (7.2)	11	30
ML-2	Male	35.2	51	19	11.5 (7.2)	10	30

but ranged from 11.7 ha to 91.9 ha (Table 2). Home ranges were highly localised, with 50% cores near the centre of each home range (Fig. 2 shows an example of two overlapping peafowl home ranges). All the home ranges were broadly centred over patches of native vegetation, or on the edge of a patch of native vegetation and pasture. Peafowl demonstrated strong

site fidelity over the tracking period and were generally active across much of their home ranges for the duration of radio-tracking (see Fig. S2, Supplementary Material, for each peafowl's home range with individual relocations separated into time periods). Visual examination of area-observation plots indicated that sampling was sufficient to stabilise the home-range estimates

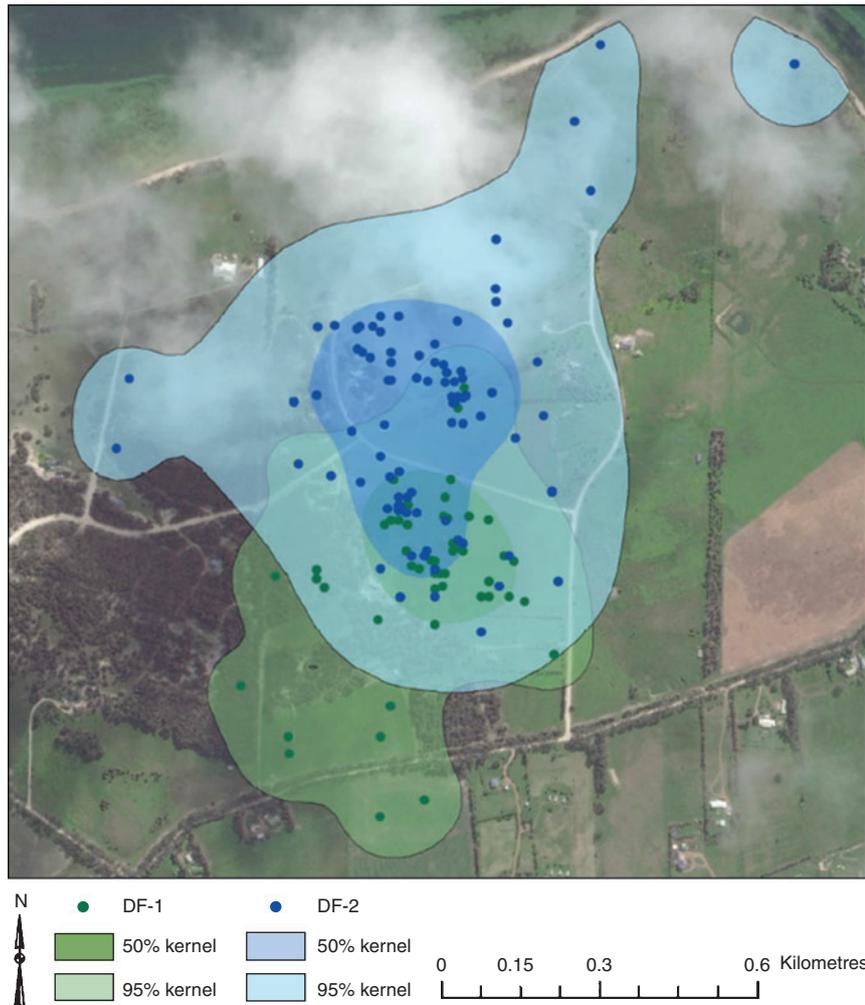


Fig. 2. Two overlapping peafowl home ranges on Kangaroo Island. Radio-tracking locations, 50% and 95% fixed-kernel home ranges are shown for two radio-collared peafowl in the Dover Farm area.

for six of eight tracked individuals, and confirmed that peafowl did establish home ranges (Fig. S3, Supplementary Material).

One particularly interesting observation was the long-distance dispersal of one female ('DF-3') (Table 2), who could not be tracked for five days because she had moved out of range. This female was located 4.5 km away with a separate group of ~30 peafowl. She established a new home range and remained at this new site for the remainder of the study.

Habitat suitability modelling for peafowl on Kangaroo Island

On the basis of the cross-validation performance of candidate habitat suitability models, using a 20-m resolution, we selected a model formulation that included three environmental covariates – the dominant habitat type (*Habitat*), the distance to pasture (*Dist2pasture*), and the percentage of native vegetation (*%Native*) (Table 3). This selected model had a mean AUC on hold-out data of 0.965 (s.d. = 0.018), demonstrating high discrimination

between occurrences and background points (values close to 1 indicate high performance: Phillips *et al.* 2006). Using the jackknife technique developed by Pearson *et al.* (2007) for small sample sizes, the successful classification rate of the selected model was 82.6% ($P < 0.001$) at the minimum training presence threshold. The same model formulation was selected when a 100-m resolution was used, indicating that the model selection procedure was resilient to the scale at which peafowl presence locations were mapped. We therefore focussed subsequent interpretation on the model at 20-m resolution.

All three covariates in the selected model contributed substantially to the selected model's performance (see Fig. S4, Supplementary Material, for partial effects plots):

- (1) *Dist2pasture* contributed 52.5% to the model gain. Presence locations for peafowl had a mean distance to pasture of 91 m and modelled habitat suitability rapidly declined as the distance to pasture increased.
- (2) *%Native* contributed 32.8% to model gain. The 1-km² grid cells surrounding the presence locations had a mean of 29.6% native vegetation cover, and habitat suitability

Table 3. Habitat suitability models for peafowl on Kangaroo Island

This table illustrates the performance of the candidate habitat suitability models (i.e. *Maxent* models that include different spatial covariates) at 20-m and 100-m spatial resolution. Models are ordered by the mean test AUC and the test gain (derived through 10-fold cross-validation), which compare the ability of candidate models to correctly predict the presence locations that were left out of the model training phase. The selected habitat suitability model is shown in bold

Model	20-m spatial resolution			100-m spatial resolution		
	Test AUC (s.d.)	Training gain	Test gain	Test AUC (s.d.)	Training gain	Test gain
Dist2pasture + Habitat + %Native	0.965 (0.018)	2.19	2.27	0.943 (0.047)	1.78	1.75
Dist2pasture + %Native	0.95 (0.03)	1.83	1.93	0.889 (0.095)	1.27	1.23
Dist2pasture + Habitat + %Pasture	0.95 (0.026)	1.94	1.89	0.874 (0.116)	1.41	1.24
Dist2pasture	0.945 (0.033)	1.65	1.82	0.883 (0.097)	1.13	1.15
Dist2pasture + %Pasture	0.942 (0.026)	1.76	1.77	0.886 (0.095)	1.26	1.17
Dist2pasture + Habitat + %Native + %NativeNeighbour + %Pasture	0.939 (0.093)	2.44	2.07	0.916 (0.077)	1.91	1.53
Dist2pasture + Habitat + %Native + %NativeNeighbour	0.937 (0.1)	2.38	2.08	0.924 (0.079)	1.70	1.58
Dist2pasture + Habitat + %Pasture + %NativeNeighbour	0.918 (0.123)	2.07	1.61	0.888 (0.110)	1.45	1.05
%Pasture	0.773 (0.060)	0.52	0.61	0.772 (0.090)	0.50	0.61
%NativeNeighbour	0.769 (0.132)	0.53	0.43	0.682 (0.154)	0.34	0.22
Habitat	0.766 (0.064)	0.46	0.47	0.679 (0.118)	0.28	0.26
%Native	0.717 (0.113)	0.37	0.38	0.710 (0.108)	0.38	0.34

decreased as native vegetation cover increased, indicating that peafowl have a preference for access to open habitats.

- (3) *Habitat* contributed 14.7% to model gain. Melaleuca shrubland and mallee/stringybark were the preferred habitats for peafowl.

We used the selected (20-m resolution) model to generate habitat suitability predictions for peafowl across the whole of KI and, using the minimum training presence threshold, classified each grid cell as suitable or unsuitable habitat. The selected model classified 9% of KI as suitable habitat for peafowl (Fig. 1), which equates to an area of ~396 km². Most suitable habitat identified was characterised by small patches of remnant native vegetation within the broadly agricultural area. Of the ~640 km² of native vegetation within KI's agricultural region, ~60% was classified as suitable for peafowl inhabitation. The model classified the interior of large patches of native vegetation as unsuitable, largely because the distance to pasture was too great (Fig. 1).

Population modelling

The stochastic population model indicated that substantial population growth is plausible over a 10-year management window (Fig. 3). The baseline demographic parameterisation produced a positive population growth rate, with a deterministic exponential rate of increase (r) of 0.16. Under a zero-cull regime, therefore, the simulated population grew to ~2400 individuals after 10 years. An annual harvest of 150 peafowl was required to drive the simulated population to extinction within 10 years; mean time to extinction was six years under this management scenario. Culling 85 individuals each year was sufficient to produce a stable simulated population over the 10-year time frame. Sensitivity analysis on key model parameters revealed that the simulation results were particularly susceptible to our assumptions regarding juvenile survival (Fig. S5, Supplementary Material). Importantly, however, some culling was required to

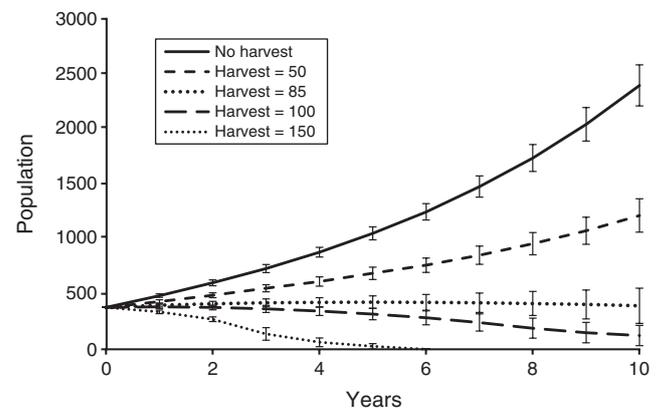


Fig. 3. Peafowl population projections assuming the baseline demographic model. This stochastic population model was initiated with a starting population size of 380 peafowl. Mean (\pm s.d.) peafowl population size is plotted over a 10-year management window for different management scenarios.

maintain population stability for all the parameterisations we tested.

Discussion

Feral alien peafowl are a declared pest species and public nuisance on KI, and other Australian offshore islands. We estimated that a few hundred peafowl (~380) were distributed among 21 separate groups on KI in 2013, up from approximately 10 groups a decade before. This is potentially problematic given that a more widespread peafowl population could become increasingly difficult to control via current practices of *ad hoc* landholder management.

Our habitat suitability model indicated that, based on the current and historical locations of peafowl groups, there is abundant unexploited suitable habitat available for peafowl on

KI. We predicted that much of the remnant native vegetation within the agricultural area is suitable, specifically the fringes of *Melaleuca*, mallee, and tall eucalypt habitats. Our modelling revealed that the large sections of interior native vegetation are less suitable for peafowl, lying too far from the beneficial resources associated with open human-modified habitats. Peafowl on KI are regularly observed feeding in pasture, normally at the edges of cover-providing vegetation, which is consistent with peafowl behaviour in their native range (Ramesh and McGowan 2009). Water troughs and dams for livestock, which are abundant on grazed properties, are used by peafowl (C. Cunningham, pers. obs.) and are likely to be important for sustaining peafowl populations throughout KI's dry, temperate summer.

Our study is, to the best of our knowledge, the first to confirm using telemetry that peafowl establish localised home ranges, which ranged from 11.7 ha to 91.9 ha. Yasmin (1995) estimated peafowl home ranges in India based on sightings of eight identifiable individuals to be between 0.9 and 15.5 ha. All peafowl home ranges on KI were centred over patches of native vegetation, and the maximum distance from vegetation of any located peafowl was 230 m, suggesting that peafowl are wary of straying far from cover. It was unclear how groups were socially structured; however, there was considerable variability in group structure between sightings. Specifically, variation existed between the maximum and average number of peafowl that radio-tracked individuals were observed to associate with (Table 2). One 4.5-km dispersal event along a linear stretch of remnant vegetation suggests that dispersal may be facilitated by continuous stretches of remnant vegetation, which is known to facilitate dispersal in other species (Bennett 1990; Machtans *et al.* 1996; Haddad *et al.* 2003). In general, however, we found that peafowl establish small and highly localised home ranges, which provides confidence that peafowl sightings several kilometres apart actually represented individuals from different groups.

Although our habitat suitability modelling classified conservation areas beyond KI's agricultural zone as unsuitable for peafowl (Fig. 1), we cannot rule out the possibility of the species colonising these regions. Population density affects habitat occupancy in other bird species (O'Connor 1981), and if the KI peafowl population were to increase, then dispersal away from high-density suitable regions to less suitable unoccupied regions might occur. Very little is known about peafowl dispersal abilities on KI or what role humans have played in their dispersal. However, our radio-tracking showed that one individual ('DF-3') travelled 4.5 km from her initial location, demonstrating that peafowl on KI are capable of freely dispersing over long distances.

There is some anecdotal evidence that the future dispersal of peafowl into conservation areas is unlikely. The Murray Lagoon peafowl group has been free-roaming since they were released there in 1927 (G. Brooksby, pers. comm.). Individuals have subsequently been sighted throughout much of the surrounding agricultural land but never far beyond the margins of an adjacent conservation park. Given almost a century of occupation around Murray Lagoon, there has been ample time for peafowl to disperse into the adjacent conservation park if that provided suitable habitat. Considerable monitoring and control for other

feral animals has also failed to find any peafowl existing solely within a conservation area. We suggest that feral peafowl are too reliant on the water and food provided by agricultural practices to disperse and persist in these vegetation-dense conservation areas. Similar observations have been made in an area bordering the Flinders Chase National Park (A. McGuire, pers. comm.).

Given that the number of discrete peafowl groups on KI has approximately doubled over the past decade, and that there is abundant suitable but unoccupied habitat available, it is important to consider what level of management is required to maintain a stable or declining peafowl population. Using demographic rates sourced from the literature, we estimated an exponential rate of increase for peafowl equivalent to a 17% population increase each year. The baseline population model required an annual harvest of 150 peafowl to completely eradicate them within six years (i.e. a total of 900 individuals culled), while removing 85 peafowl each year was sufficient to produce a stable population (Fig. 3). These results are conditional on the baseline demographic rates used for the population model; however, our sensitivity analysis indicated that substantial culling is required to produce a declining peafowl population, even if key demographic rates are less favourable on KI than expected.

In summary, we have predicted that population growth can be expected in the absence of culling, and there is abundant suitable unoccupied habitat for range expansion. Dispersal characteristics of peafowl are poorly understood, but one long-range dispersal event suggested that dispersal is possible through remnant vegetation. We suggest that control is warranted while the KI peafowl population remains relatively small and that managers should exercise caution when managing populations in areas that are well connected by remnant vegetation to ensure that dispersal is not triggered.

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