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Using a spatial mark-resight model to estimate the parameters of a wild pig (*Sus scrofa*) population in Singapore

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Abstract. The wild pig (*Sus scrofa vittatus*) is the one of the largest mammals in the tropical urban city-state of Singapore, after recolonising the main island in the early 2000s. Currently, little is known about the pig population except that it is not naturally regulated due to the extinction of its natural predators, and the absence of hunting and regular culling practices in Singapore. This study was conducted to estimate the population size and distribution of wild pigs in the Central Catchment Nature Reserve (CCNR) of Singapore (Total area: 32.36 km^2, land area: 24.94 km^2) using a spatial mark-resight model. The CCNR is Singapore's largest reserve and contains the last remaining patches of primary lowland forest scattered within an extensive matrix of secondary forest. From August to September 2016, 40 individuals were tagged and released. From September to November 2016, the 27 camera points setup throughout the CCNR re-captured two tagged individuals and 375 unmarked individuals. The estimated population size was 163.46 pigs and the density was 1.63 pigs/km^2. These estimates were lower than known densities in similar habitats in other countries and may result from the population not having reached its carrying capacity and previous culling events. The density map suggested that resources are clustered on the eastern side of the CCNR. Repeated measures of the population abundance should be carried out to determine if the population is increasing or stable. Given that pigs are omnivorous and can exploit a wide range of food types, dietary studies should be conducted to determine the food types exploited by the pigs in the CCNR.

Key words. abundance, population, spatial mark-resight, *Sus scrofa*, telemetry, urban city state

INTRODUCTION

Rapidly expanding urban landscapes across the globe have increased contact zones between natural habitats and urban areas, with significant implications for ecosystems and wildlife species (Radeloff et al., 2005). Certain generalist wildlife species are able to exploit and even thrive in these contact zones (Cahill et al., 2012), often resulting in conflicts with humans (Loker & Decker, 1998). One such species is the highly adaptable Eurasian wild pig (*Sus scrofa*), which is the most widespread member of the Suidae family (Diong, 1973; Yong et al., 2010). The global population of wild pigs is expanding in both numbers and distribution due to anthropogenic factors such as the loss of predators, supplementary feeding, and the intensification of agricultural practices (Geisser & Reyer, 2005). Conflicts between wild pigs and humans can range in severity, from damaged parks and backyards to traffic accidents and attacks on humans (Kotulski & Konig, 2008).

Singapore is a small (~700 km^2), densely urbanised island city-state, with approximately 5.6 million residents (Singapore Department of Statistics, 2016), located south of the southernmost tip of peninsular Malaysia (1°17′N, 103°0′E). Less than 1 km^2 of the original primary rainforest remains on mainland Singapore (Turner et al., 1997). Although it was formerly extinct in the Central Catchment Nature Reserve (CCNR) (Teo & Rajathurai, 1997), there is firm evidence that the wild pig has re-established itself in the CCNR (Yong et al., 2010). The 32 km^2 CCNR is the largest nature reserve in Singapore and contains the small patches of primary lowland rainforest scattered within an extensive matrix of secondary forest (Corlett, 1992) (Fig. 1). Furthermore, because more than 60% of Singapore's land area is urbanised (Corlett, 1991; Yee et al., 2011), the CCNR is surrounded by urban structures, making the border of the CCNR a contact zone with human activities. Additionally, the secondary forests within the CCNR are varied and can be further classified as old secondary forest, open woodlands, native-dominated young secondary forests and abandoned plantations (Yee et al., 2011).

Due to the extinction of its natural predators such as tigers and leopards (Tan et al., 2015), the wild pig is one of the largest terrestrial mammals in Singapore (Corlett, 1992; Brook et al., 2003) and is not regulated by any natural predation pressure, except possibly by the reticulated python, *Python reticulatus*, which has been reported to consume wild pigs in parts of Indonesia (Auliya, 2003; Fredriksson, 2005). Given the lack of natural predators, little competition from

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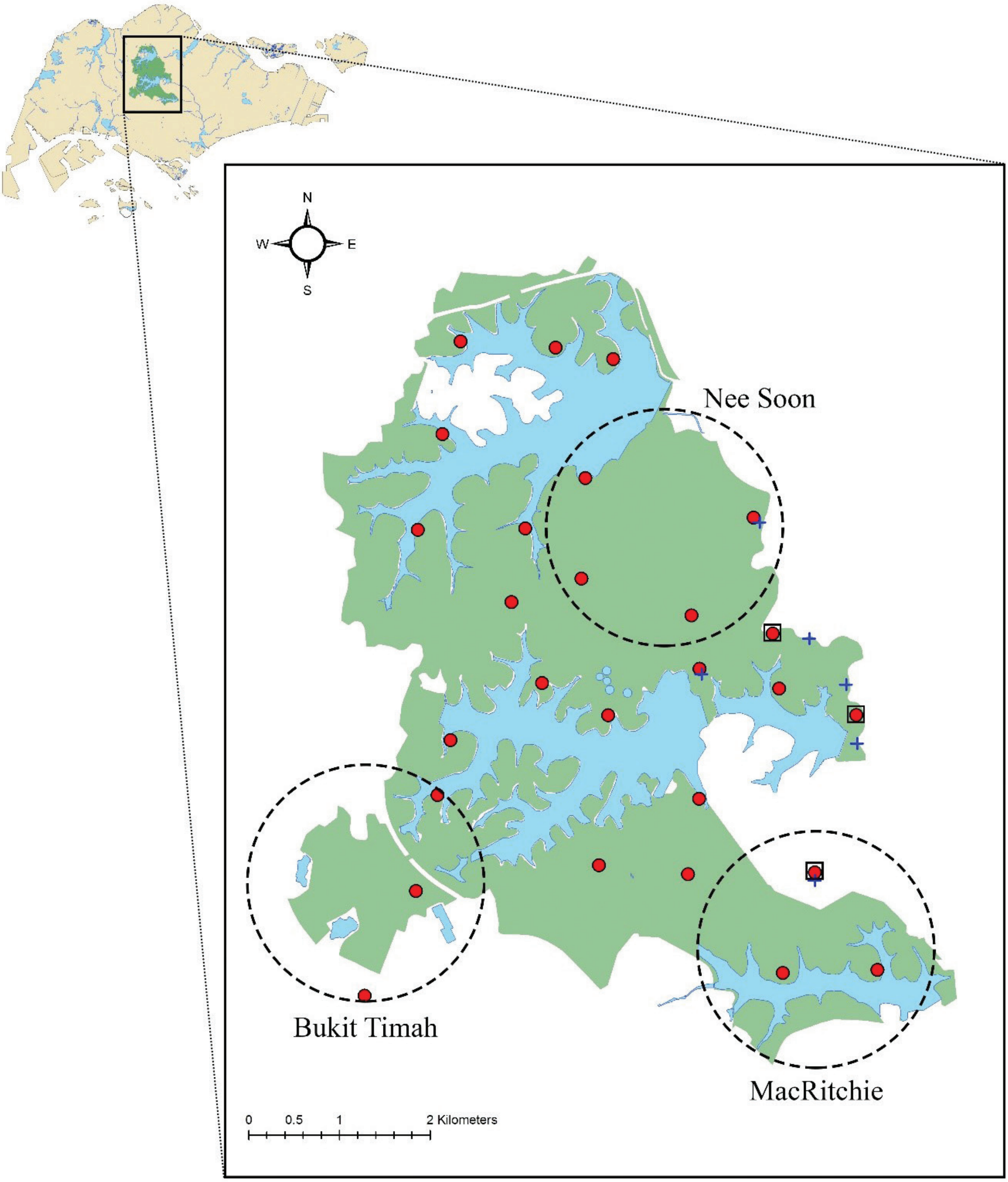

Fig. 1. Map showing the location of the Central Catchment Nature Reserve on mainland Singapore. All 27 camera points are indicated with a red circle. Black squares indicate the three camera points added to the 1 km^2 grid. The six cage traps are marked with a blue cross. Dotted circles indicate areas the last remaining patches of primary forest in Singapore.

other terrestrial herbivores, and the potential food supply from abandoned plantations in the CCNR and nearby city, the population of the highly fecund wild pig in Singapore might have increased substantially since its re-colonisation (Yong et al., 2010).

Wild pigs are considered as ecosystem engineers due to their rooting and nest building behaviors (Crooks, 2002). In areas with high densities of wild pigs, these behaviors can cause the reduction of herbaceous cover by 80-95%, local extinction of certain plant species (Massei & Genov, 2004) and rapidly reduce seedling abundances (Mitchell et al., 2007). Pigs are also well known to consume large quantities of fruit and seeds and contribute significantly to seed mortality for some plant species (Curran & Leighton, 2000). A high density of wild pigs in the CCNR could have negative effects on the remaining patches of primary forest and because the CCNR is surrounded by residential and industrial areas on all sides, it could also increase the risk of human-animal conflicts such as injuring humans and traffic accidents. In response to a number of wild pig attacks and accidents in recent years (Chia, 2012; Kok, 2016; Kok, 2017; Ganesan & Hong, 2018), environmental agencies such as the National Parks Board (NParks) and the Agri-Food and Veterinary Authority of Singapore would, without the knowledge of population abundance, manage wild pig populations with occasional, but irregular culling.

Managing a wild pig population requires the ability to monitor pig abundance. Globally, most abundance estimates of pig populations were made with either traditional capture-recapture (CR) models (Caley, 1993; Sweitzer et al., 2000; Hebeisen et al., 2008), or removal data from hunting practices (Sáez-Royuela & TellerÍIa, 1986; Cahill & Llimona, 2004; Fonseca et al., 2004). However, removal methods cannot be implemented because of the prohibition of hunting in Singapore, and traditional CR models assume that the capture probability is the same for every individual in the population (Krebs, 1999); which is easily violated due to spatial heterogeneity and trap response (Royle et al., 2014a). Spatial Capture-Recapture (SCR) models are a recent development that overcome the assumptions of equal capture probability by including spatial information. Chandler & Royle (2013) introduced an extension of the SCR model, called the Spatial Mark-Resight (SMR) model, which supplements an observed encounter history of marked individuals with trap- and occasion- specific counts of unmarked individuals, and concluded that the SMR was capable of producing accurate estimates of population abundance regardless of the size of the population. Additionally, SMR models, unlike traditional CR models that require at least 50% of the population to be marked (Krebs, 1999), only need approximately 30% of the population to be marked to obtain precise estimates (Chandler & Royle, 2013). Therefore, the primary aim of this study was to estimate the absolute abundance, density and distribution of wild pigs in the CCNR using the SMR model. This would aid wild pig management in the CCNR by providing the first population estimate of wild pigs in the CCNR and developing a feasible protocol for future monitoring programs.

MATERIAL AND METHODS

Camera trap setup. In May 2016, a total of 27 camera points were setup (Fig. 1). Twenty-four of those camera points were laid out uniformly in a grid consisting of 1 km^2 squares throughout the CCNR. Within each 1 km^2, the exact location of the camera point was selected based on the presence of pig signs such as wallowing and rooting. In areas where pig signs were not present, camera points were setup with a clear view of trails or clearings that may be used by pigs. During the pilot study conducted in January 2015, these 24 camera points failed to capture sufficient pictures of both marked and unmarked individuals for a reliable population estimate. Therefore, for the 2016 study, three camera points were added to the grid in forested areas with signs of extensive pig damage (Fig. 1). Only three additional camera points were added because there were not enough camera traps to tighten the entire grid.

At each camera point, to increase the area of detection, two camera traps, one Reconyx© HC550 Hyperfire and one Cuddeback© C123. Both camera traps were secured on separate trees, spaced 2 m apart, and directed at a point 3 m away from both camera traps and 30 cm above the ground. A laser distance measurer with a bubble leveler was used to measure the distances, while a PVC pipe was used to measure the point 30 cm above the ground. The camera traps were checked once a month, to have their batteries and SD cards replaced, for six months.

Pig tagging and trapping. Pigs were tagged with small, circular ear studs with diameters of 1.6 cm and a piece of reflective tape pasted on the face of the ear stud. Although small, the colors of the reflective tape could be clearly seen up to 5 m away when flashed upon with white light. Five different colors of reflective tape were used, and each tagged individual had a unique color combination assigned to it. Depending on the size of the caught individual, two to three ear studs were attached to each ear with the use of a hollow ear-piercing needle. Albedo100© reflective spray paint for horses and pets was also used to mark each individual with a unique pattern sprayed on both sides of the body. Individuals over 50 kg also had an Iridium 3-D satellite collar fastened around their necks. The satellite collars were programmed to take a GPS fix every 45 minutes.

Six cage traps were then set up throughout the months of June and July 2016 (Fig. 1). Cage trap locations were based on areas where there was an abundance of pig signs. Although there were many suitable cage trap sites on the western side of the CCNR, all of them fell in areas that were too exposed to the public or located in restricted military areas. Cage traps typically consisted of five to six modular steel panels and one trap door. Each steel panel was about 1.5 m tall and 2 m wide. The trap door would fall when an animal enters the cage trap and triggers the release mechanism by pulling on the mesh box filled with bait. Modifications, such as lining the interior of the cage trap with plastic barrels and adding an opaque shroud on the exterior, were also made to the cage trap to prevent injury to the animals.

Following the setup of the cage traps, the trap doors were locked open and the traps were conditioned for two weeks. Trapping started on 15 August 2016 and ended on 9 September 2016. Cage traps were checked every morning at 0630 hours. Trapped individuals were sexed, weighed, had their measurements taken, tagged and finally released. Individuals that weighed more than 25 kg were sedated by a licensed veterinarian on-site for safety reasons. Following which, the cage traps were re-activated, and the bait inside the cage traps was replenished. At the end of trapping, 40 individuals were successfully marked and released. Three of the tagged individuals had satellite collars fastened around their necks.

Data analyses: Absolute abundance and density. The SMR model, as described in Royle et al. (2014b) and Rutledge et al. (2015), was used to analyse the camera trapping data and estimate the absolute abundance and density. Because it could not be confirmed if a marked individual was still alive or still retained its ear studs, the number of marked individuals was treated as an unknown parameter and estimated as part of the model. This introduced a data augmentation parameter (Ψ_m) and an auxiliary alive-state variable (zm_i) for marked individuals. Additionally, there were instances when a recaptured individual was marked but could not be identified because one or two ear studs had dislodged from its ear. Therefore, the sum of all correctly identified recaptured marked individuals was divided by the total number of recaptured marked individuals to obtain a correction factor (c) for the baseline encounter rate (λ_0) of marked individuals. Therefore, the full SMR model used in this paper can be described as:

Prior distributions:

$$c \sim Beta(1,1)$$
$$\lambda_0 \sim Uniform(0,5)$$
$$\Psi_m \sim Uniform(1,1)$$
$$\Psi \sim Uniform(1,1)$$
$$\sigma \sim Uniform(0,100)$$
$$(S_i \ldots S_m, S_u \ldots S_M) \sim Uniform(S)$$

Marked individuals:

$$zm_i \sim Bernoulli(\Psi_m)$$
$$y_{ijk} \sim Poisson(\lambda_{ij} cz\ m_i)$$
$$\lambda_{ij} = \lambda_0 \exp\left(-\frac{\|x_j - s_i\|^2}{2\sigma^2}\right) zm_i$$

Unmarked individuals:

$$z_u \sim Bernoulli(\Psi)$$
$$y_{ujk} \sim Multinomial(n_{jk}, \pi_{uj})$$
$$\pi_{uj} = \lambda_0 \exp\left(-\frac{\|x_j - s_u\|^2}{2\sigma^2}\right) z_u$$

where ψ is the data augmentation parameter for unmarked individuals, σ is the scale parameter which determined the rate of decay in encounter probability with distance from an individual's activity centre, S_i is the coordinates of marked individual i's activity centre, m is the number of data augmented marked individuals, S_u is the coordinates of unmarked individual u's activity centre, M is the number of data augmented marked and unmarked individuals, S is the state-space, y_{ilk} is the observed capture frequency of marked individual i at trap j on sampling occasion k, λ_{ij} is the expected encounter probability of marked individual i at trap j, x_j is the coordinates of trap j, Z_u is the auxiliary alive-state variable for unmarked individual u, y_{ujk} is the number of unmarked individuals observed at trap j on sampling occasion k, n_{jk} is the sum of all latent (unobserved) detections of unique unmarked individuals at trap j on sampling occasion k, and π_{uj} is the expected encounter probability of all unmarked individuals at trap j scaled to 1.

To provide more precise estimates of the scale parameter σ, which determines the rate of decay in encounter probability with distance from an individual's activity centre, telemetry data collected from the collared individual was implemented into the SMR model as described in Sollmann et al. (2013). An activity centre is a latent variable that is defined as the centre of the space a particular individual occupied during the period in which the traps were active (Royle et al., 2014a). It should be noted that the activity centre of an individual does not equate to the area where the individual spent most of its time and, depending on the length of the study, may or may not be equivalent to the home range centre (Royle et al., 2014a). To ensure that the activity centre of every individual in the population was included, the state-space was defined as a large area (10 km × 10 km) encompassing the CCNR. Additionally, because pigs have been reported to cross man-made structures (Mata et al., 2008; Corlatti et al., 2009; Frantz et al. 2012) and swim across 13 km of sea (Rawlinson et al., 1992), no habitat mask was applied to the state-space to exclude the surrounding urban areas and reservoirs within the CCNR; as plausible locations for activity centres should not be excluded from the SMR model (Royle et al., 2014a). Only the last nine weeks of camera trapping data, which occurred after trapping and tagging, was used in the analysis to estimate the abundance of pigs.

The data was augmented to 340 individuals and the model was implemented in the software R 3.2.2 (R Development Core Team, 2016). The model ran four Markov Chain Monte Carlo (MCMC) chains, each with 800,000 iterations, and discarded the first 50,000 iterations as burn-in. Convergence of the chains was checked by calculating the Gelman-Rubin convergence statistic (Gelman et al., 2013) with the R package coda, and by visually inspecting the time series and density plots (Fig. S1). A visualisation of the data required for the SMR model is also shown in the attached Appendix (Fig. S2). Values of below 1.1 indicated convergence. The convergence statistic, posterior means (± standard deviation) and 95% Bayesian credible intervals (BCI) were reported for all parameters. To calculate density, the abundance estimate was divided by the area of the state-space (100 km^2) (Royle et al., 2014a).

To investigate the distribution of the population of pigs, a density map was created. This was done by extracting the locations of the activity centres from the model output and plotting them throughout the state-space, along with the boundary of the CCNR and locations of the 27 camera points. The full code of the SMR model can be found in the Appendix.

Data analyses: Home range and movement. The analysis of the collared pigs' activity range was carried out in the program ArcGIS (ESRI® version 10.5). The home range area was calculated as the 95% kernel density estimate (KDE) using Home Range Tools (Rodgers et al., 2015). For this study, because Home Range Tools (HRT) uses a standard bivariate normal probability density function to estimate the utilization distribution, a reference bandwidth (h_{ref}) was calculated as:

$$h_{ref} = \mathrm{n}^{-\frac{1}{6}} \sqrt{\frac{\mathrm{var}_x + \mathrm{var}_y}{2}}$$

Where var_x is the mean variance of the x coordinates, var_y is the mean variance of the y coordinates and n is the number of points (Worton, 1995).

The GPS fixes were separated into Day (0700 to 1900 hours) and Night (1900 to 0700 hours) fixes, and for both categories the 95% KDE was calculated for four periods to illustrate the changes in the home range over the six months of data collection. The four periods were: 1) the first month, 2) the second, third and fourth months, 3) the fifth month and 4) the sixth month. The KDEs from each period were plotted on a map together to show the movement of the collared pig over the six-month period. To determine the area of an aggregate home range, an outermost isopleth (99% KDE), which enclosed all other isopleths, was calculated.

Data analyses: Age class structure. Individuals caught in the cage traps during the pilot and 2016 study were used to investigate the age class structure. Because it was difficult to age live individuals by dentition for this study, a simpler method of aging individuals which still adhered closely to the age classification laid out by Diong (1973) was adopted. The method involved the use of the presence of stripes and weight to group individuals into an age class.

1. Juvenile (0 – months) – striped individuals
2. Sub-adults (5 – 20 months) – Females: non-striped individuals below 22 kg

Males: non-striped individuals with a scrotum that was not distinctly
bulbous and narrower than 5 cm

3. Adults (>20 months) – Females: non-striped individuals above 22kg

Males: non-striped individuals with distinctly bulbous scrotum and wider than 5 cm.

Because most of the trapped females did not have a swollen/loose vulva, weight was used to distinguish between adult and sub-adult females. The body weight of 22 kg was observed in the lightest adult female with a swollen vulva, indicating that it was sexually mature and was in heat. Therefore, non-striped females that weighed more than 22 kg were defined as adult females. Sexual maturity in males was determined by measuring scrotal width. Individuals with a scrotum that was not distinctly bulbous and narrower than 5 cm were defined as sub-adult males.

Data analyses: Mean group size. The photos taken by the camera traps throughout the six months were used to estimate the mean group size. Because the camera traps took a sequence of three photos each time they were triggered, the photos were separated according to their respective sequences. Sequences separated by more than half an hour were assumed to be photos of different groups of pigs. A total of 167 observations were obtained from the camera trap photos. The number of individuals in each observation was counted and tabulated with the number of individuals caught in each cage trap. The mean was calculated by totaling the number of individuals seen and dividing it by the total number of observations.

Data analyses: Identifying group types. The observed pig groups were broken down into the number of adult males, adult females, sub-adults and juveniles found in each observation. To differentiate between sub-adults and adults in the photos, the average shoulder height of sub-adults caught during trapping and tagging was calculated to be 35 cm. Hence, a shoulder height of 35 cm was used to differentiate between adults and sub-adult pigs in the photos. Reference photographs were taken with a 35 cm long PVC pipe placed at four different distances (1 m, 2 m, 3 m and 4 m) from the camera traps. The reference photographs were used to differentiate sub-adults and adults seen in the photographs and individuals above the PVC pipe were considered to be adults. Each observation was then simplified to binary data, which only indicated the presence or absence of each age-sex class. Because it was impossible to determine the sex of some of the adult pigs seen in the pictures, of the 167 observations used for calculating the mean group size, only 108 were eligible for the cluster analysis.

A cluster analysis, namely Clustering Large Applications (CLARA), was used to assign each observation into a group and identify the main group types present in the CCNR. To determine the best-fit model, 19 different CLARA analyses were carried out; each with a different number of medoids defined (). Cluster validation was performed by constructing silhouette plots of each analysis and selecting the analysis with the highest silhouette coefficient. The silhouette coefficient is a dimensionless number that has a maximum value of one and is based on the maximum average silhouette width (Kaufman & Rousseeuw, 2008b). Silhouette coefficients with values closer to one correspond to stronger clustering structures (Kaufman & Rousseeuw, 2008a). To ensure the performance of each CLARA analysis, 10,700 samples were drawn from the dataset for each CLARA analysis. The cluster analysis was carried out in the software R 3.2.2 (R Development Core Team, 2016) with the package 'cluster'. The code used to run the cluster analysis can be found in the Appendix. Following the cluster analysis, the average number of individuals per observation was calculated for each age-sex class within each group type.

Table 1. Summary of the analysis by the Spatial Mark-Resight model showing the posterior mean, standard deviation and 95% Bayesian Credible Interval and Gelman-Rubin convergence statistic ($\hat{R}$) of the various parameters. The parameters estimated were the scale parameter of the rate of decay in encounter probability (σ), the baseline encounter probability (λ_0), the correction factor of λ_0 for imperfect identification (c), the prior for the auxiliary "alive state" variable for both unmarked (ψ) and marked (ψ_m) individuals, the estimated number of marked individuals (m), the total abundance of marked and unmarked individuals (N), and the overall density (D, individuals per km^2).

	Posterior Mean	S.D.	2.50%	97.50%	$\hat{R}$
σ	0.182	0.003	0.176	0.188	1.00
λ_0	9.426	3.840	4.264	18.682	1.07
c	0.500	0.189	0.147	0.853	1.00
ψ	0.4122	0.113	0.229	0.671	1.00
ψ_m	0.975	0.024	0.911	0.999	1.00
m	39.968	0.176	39.000	40.000	1.00
N	163.456	33.187	111.000	240.000	1.00
D	1.635	0.332	1.11	2.40	1.00

RESULTS

Absolute abundance and density. A total of four resightings of marked pigs and 375 sightings of unmarked pigs were accumulated across nine consecutive sampling weeks. Of the four resightings of marked pigs, only two were confidently identified. Of the three pigs that were collared, only one adult male pig remained collared during and after the study and a total of 3,202 GPS fixes were obtained within a six-month period. However, of the 3,202 GPS fixes, 748 GPS fixes failed to obtain a stable satellite connection and did not provide coordinates. Additionally, another 92 fixes had a Dilution of Precision (DOP) of more than eight and were rejected to ensure the precision of the fixes. Only 856 fixes, of the remaining 2,362 GPS fixes obtained from the collared individual, were implemented into the SMR model because the other fixes did not coincide with the time of the camera trapping. All the model parameters had a value lower than 1.1 indicating convergence. The density plot of N showed that the state-space was large enough to include the activity centres of all the individuals and that the data was sufficiently augmented (Fig. S1). The SMR model estimated that 163.46 ± 33.19 (standard deviation of mean) pigs were present in the CCNR at an average density of 1.63 ± 0.33 pigs/km^2 (Table 1). The estimate of σ, was found to be 0.18 ± 0.003 (Table 1).

The population of pigs was not uniformly distributed throughout the CCNR and was absent from most of the CCNR, with the exception of the eastern side of the CCNR where densities reached 3.72 individuals/km^2 (Fig. 2). Additionally, the pigs were not confined to the boundary of the CCNR and would move out of it but not beyond the boundary of the state-space (Fig. 2). This was also corroborated by the GPS points of the collared pig.

Home range and movement. During the first month, after being caught and collared, the pig moved north, out of the CCNR, and into a small patch of forest, which was in between

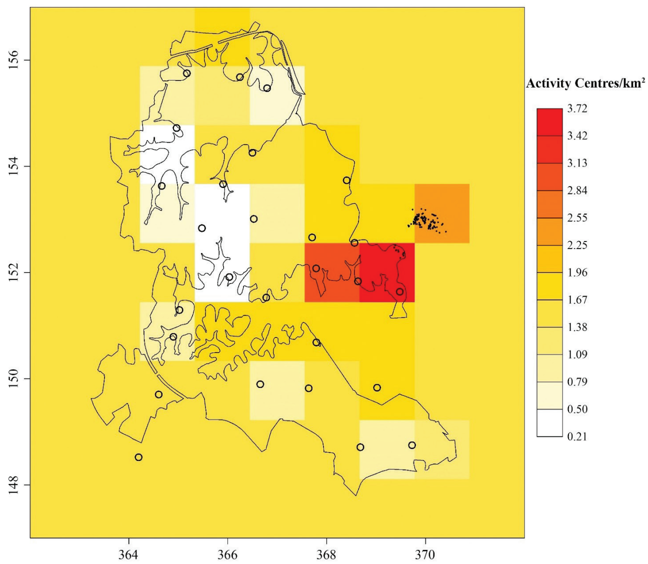

Fig. 2. The density map showing the number of activity centres per kilometer square, the locations of the camera points (circles), 143 out of 856 GPS locations from the collared pig (black dots) and the boundary of the Central Catchment Nature Reserve. Only a fraction of the GPS locations was plotted to prevent the colored pixels from being obscured. Each pixel is 1 km^2. X and Y coordinates are in kilometers.

a residential area and an industrial area, where it remained in that small patch of forest for the next three months (Fig. 3). The collared pig was most active during the fifth month (3 January 2017 to 2 February 2017) and moved back and forth between the areas north and south of the Seletar Expressway (SLE) (Fig. 3). The pig crossed the SLE at least 11 times in the fifth and sixth month; of which the collar captured the exact time period of six of the crossings.

Three crossings occurred during the day:

1. 9 January 2017 between 0901 and 0946 hours, from the north to the south of the SLE
2. 10 March 2017 between 0930 and 1015 hours, from the north to the south of the SLE

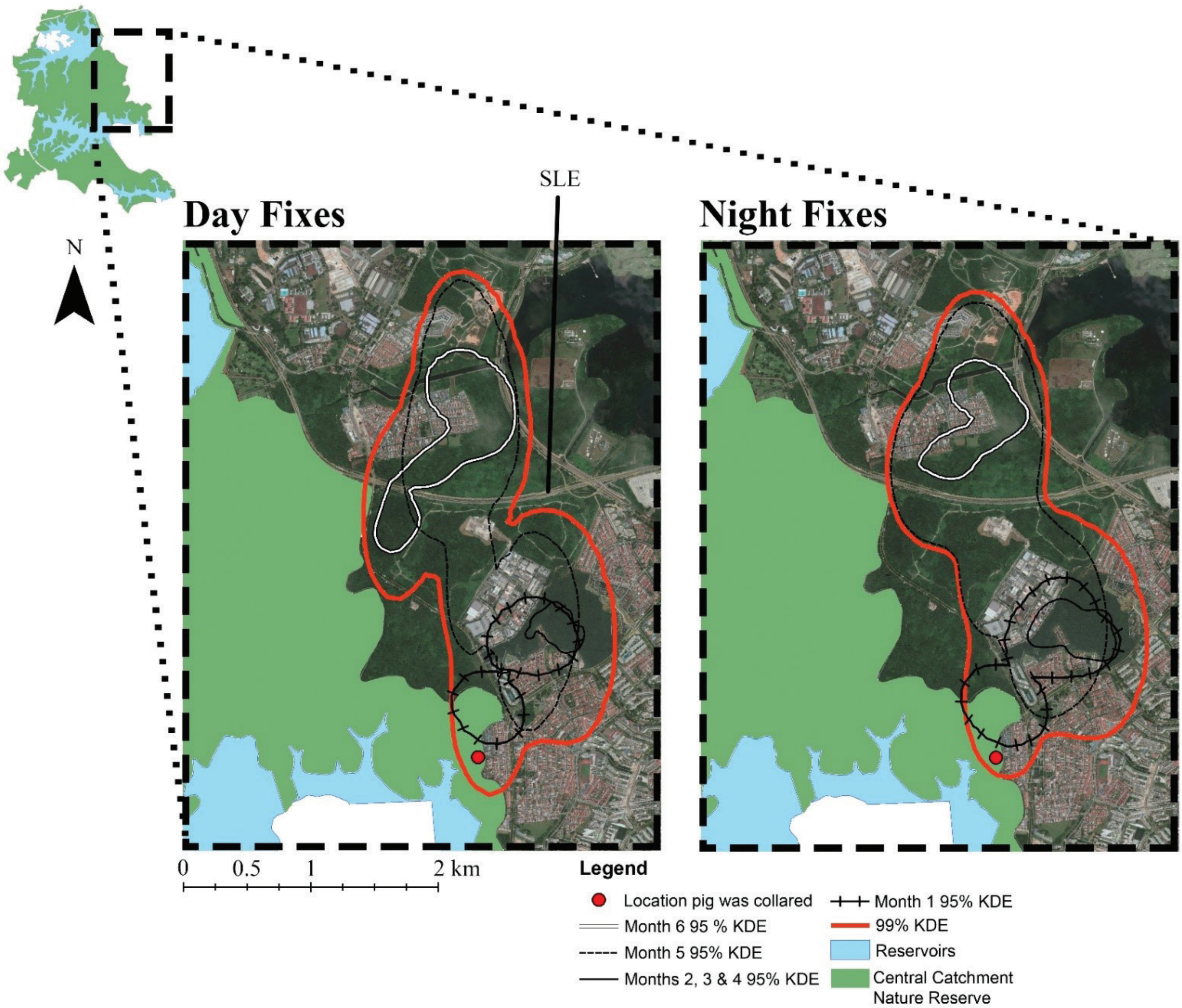

Fig. 3. Map of the Central Catchment Nature Reserve showing the day and night fixes of the collared pig. The home ranges are calculated from the monthly 95% Kernel Density Estimate (KDE), while the aggregate home range was calculated from the 99% KDE from all six months. The Seletar Expressway (SLE) is pointed out on the map and the satellite overlay was adapted from Google Earth.

3. 13 March 2017 between 0800 and 0845 hours, from the north to the south of the SLE

The other three captured crossings occurred at night:

1. 15 January 2017 between 2018 and 2145 hours, from the north to the south of the SLE
2. 17 January 2017 between 2145 and 2316 hours, from the south to the north of the SLE
3. 19 January 2017 0000 and 0046 hours, from the north to the south of the SLE

The remaining crossings occurred before 9 January 2017, in between the ninth and 15 January 2017, in between 19 January 2017 and 10 March 2017, and in between 10 March 2017 and 13 January 2017. These crossings were not recorded because the collar lost its satellite connection during that time period. For the Day fixes, the average monthly home range size was 0.69 km^2 and the individual home range sizes were 0.59 km^2, 0.11 km^2, 2.51 km^2, and 0.69 km^2 for the first, second, third, fourth time periods respectively. For the Night fixes, the average home range size was 0.82 km^2 and the individual home range sizes were 0.86 km^2, 0.23 km^2, 2.97 km^2, and 0.42 km^2 for the first, second, third, fourth time periods respectively.

When calculating the aggregate home range of the collared pig for the six-month period, only the 99% KDE produced a continuous outer isopleth (Fig. 3). The calculated area of this 99% KDE was 4.46 km^2 and 4.25km^2 for the Day and Night fixes respectively.

Sex ratio and age class structure. A total of 83 individuals (40 males and 43 females) were caught in the pilot and 2016 study. This gave an overall M:F ratio of 1: 1.075. Of the 83 individuals trapped, 13 were adult females, and 11 were adult males which gave an adult M:F ratio of 1: 1.18. Of the 83 individuals caught, 13% were juveniles, 58% sub-adults and 29% adults.

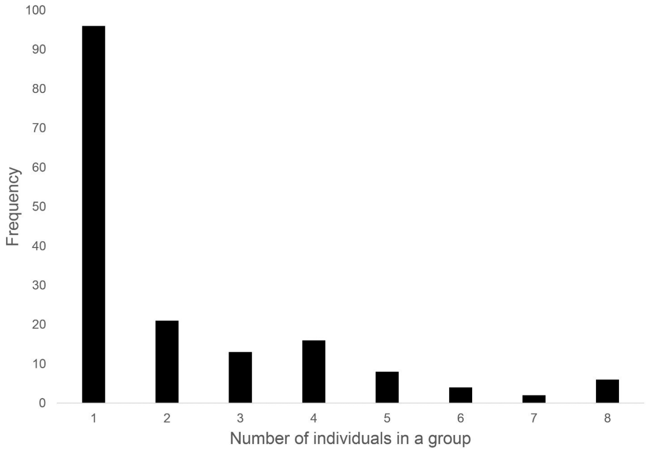

Fig. 4. Frequency of Sus scrofa group sizes observed in 167 unique camera trap observations from May 2016 to August 2016.

Mean group size. Of the 167 observations from the camera trap photos, the most commonly observed group sizes were one individual (n = 96 observations), two individuals (n = 21), and four individuals (n = 16) (Fig. 4). Groups consisting of more than eight individuals were not observed.

The mean number of individuals in a group was 2.23 ± 0.14 (S.E) individuals with the approximate 95% confidence interval being 1.95 to 2.51 individuals. Approximately 57% of the observations were of lone individuals. Of the 96 observations of solitary individuals, the sex could be identified for 46 observations. Of these 46 observations, 29 were individual males. Only five observations were made for adult males traveling in groups with more than two individuals. For groups that had more than two individuals, the average group size was 3.89 ± 0.22 (S.E) individuals. Larger groups that had more than five individuals consisted of the group types A, D, E, F, G, H, and I (see section below). The largest groups observed consisted of eight individuals and belonged to either group types D, G or I.

Identifying group types. The CLARA analysis when , had the highest silhouette coefficient value of 0.97 and was selected as the best-fit model. After assigning each observation to its respective cluster, the chi-squared goodness-of-fit tests identified the clusters as nine group types:

A. Groups that consists only of juveniles (6 observations)
B. Groups that consists only of adult males (33 observations)
C. Groups that consists only of adult females (22 observations)
D. Groups that consist of adult females and juveniles (17 observations)
E. Groups that consist of adult females and sub-adults (7 observations)
F. Groups that consists only of sub-adults (17 observations)
G. Groups that consist of adult females, sub-adults, and juveniles (2 observations)
H. Groups that consist of sub-adults and juveniles (3 observations)
I. Groups that consist of adult males, adult females, sub-adults and juveniles (1 observation)

These group types differed from the group types reported by Fernández-Llario et al. (1996). These authors identified ten group types, most of which were the same as the nine group types identified by the cluster analysis (Table 2). However, their study did not include groups A and H, but did include:

J. Groups that consist of adult males and adult females
K. Groups that consist of adult males, adult females, and sub-adults
L. Groups that consist of adult males, adult females, and juveniles

There was no significant difference in the average number of individuals for each age-sex classes between the present study and the study by Fernández-Llario et al. (1996) for each group type.

DISCUSSION

The low number of recaptures was most likely due to the ear tags dropping off marked individuals. Further studies should be conducted to develop more robust methods of tagging pigs. Additionally, due to permit limitations, the trapping and tagging of individuals was spatially biased. Despite that and the high levels of habitat heterogeneity in the CCNR, the SMR model performed well. The estimated density of 1.63 ± 0.33 individuals/km^2 was much lower than the density of wild pigs previously reported by Yong et al. (2010). However, the estimates in Yong et al. (2010), 23.6 to 45.4 individuals/km^2, were not obtained from empirical field data from the CCNR, but from density estimates from the Pasoh Forest Reserve and Peucang Island. The estimated density of 1.63 ± 0.33 individuals/km^2 in the CCNR was much lower than the density wild pigs found in other forests where pigs are native and predation and hunting were absent. For example, the density of wild pigs was 47 individuals/km^2 in Pasoh Forest Reserve, Peninsular Malaysia (Ickes, 2001), 10.6 individuals/km^2 in the Canton of Geneva, Switzerland (Hebeisen et al., 2008), and 3–18 individuals/km^2 in Maremma Natural Park, Central Italy (Massei et al., 1997b). Unlike the CCNR, large areas of cultivated land surrounded the study sites used by Ickes (2001) and Hebeisen et al. (2008). The abundant supply of crops and fruits might have artificially inflated the carrying capacity and densities of wild pigs at these study sites. However, the estimated wild pig density in the CCNR was still lower than the pig density in Massei et al. (1997b), which was not surrounded by cultivated areas.

The low pig density in the CCNR may have been a result of culling. The last culling event in the CCNR occurred at the end of 2014, two years before this study (personal communication), where NParks reportedly removed 80 individuals from the CCNR (Feng, 2014). However, because wild pigs are omnivorous (Diong, 1973; Ickes et al., 2001) and have a high reproductive rate (Massei & Genov, 2004), wild pig densities can increase drastically in short periods of time; especially when food is abundant. Massei et al. (1997b) reported that the density of wild pigs was driven by food availability and could increase by six times in one year

Table 2. Table showing the average number of each age-sex class found in each group type. Capitalised group letters indicate values taken from this study. Lower case group letters indicate values taken from a study conducted in Doñana National Park, Italy (Fernández-Llario et al., 1996). Group type letters found in the same row indicate that both studies identified that particular group type. Underlined letters indicate group types only found in this study. Italicised letters indicate group types only found in Fernández-Llario et al. (1996). ** Indicates that the group only had one observation.

	Average number of individuals			
Group Type	**Adult Males**	**Adult Females**	**Sub-adults**	**Juveniles**
A	0	0	0	3.17
B	1.06	0.03	0	0
b	1.08	0	0.09	0.01
C	0	1.18	0	0
c	0.02	1.64	0.13	0.36
D	0.06	1.41	0	2.41
d	0	1.16	0.13	3.64
E	0	1.57	2	0
e	0	1.12	2.03	0.07
F	0	0	3.29	0
f	0	0	1.84	0
G	0	2	1	3
g	0	1.26	2.47	2.65
H	0.33	0	2	3
I**	1	1	5	1
i	1.04	1.5	2.64	3
j	1.06	1.09	0.36	0.04
k	1.06	1.2	2.8	0.06
l	1.07	1.14	0.5	2.64

when native food sources were abundant. Similarly, Luskin et al. (2017) reported that in peninsular Malaysia, adjacent oil palm farmlands increased wild pig densities by 100 times in five years. Therefore, it is more likely that the low density of pigs was caused by the limitation of resources. Singapore has undergone rapid and large-scale habitat modification for urbanisation since 1959 (Yee et al., 2011). By 1990, more than 99% of the original forest had been cleared and most of the plantations had been abandoned (Corlett, 1991, 1992). The remaining original forest form less than 1 km^2 and are scattered in small patches of primary lowland tropical rainforest fragments in a large matrix of secondary forest (Corlett, 1992; Turner et al., 1997). The surrounding secondary forest, now consisting mostly of a wide variety of cultivated and naturalised invasive plant species, have lost most of their plant diversity and are both floristically and structurally much simpler (Corlett, 1992; Teo et al., 2003). Forest fragmentation and the lack of agricultural land and original forest could have reduced breeding and feeding sites; resulting in low pig densities. Given that pigs were previously extinct in the CCNR (Teo & Rajathurai, 1997), it is probable that the pig population in the CCNR has not reached its carrying capacity and, likely to continue to increase if left unmanaged.

The density map (Fig. 2) showed high densities of pigs clustered on the eastern side of the CCNR. The most plausible explanation for this is greater availability of food and other resources in this location. Spitz & Janeau (1995) reported that both male and female pigs selected habitats based on food abundance. It is unlikely that the clustering of pigs was a result of the small activity range diameter (0.89 km) found in this study. This is because despite their large home ranges, 95% of the time, wild pigs would not move more than a mean distance of one kilometer from the centre of their calculated home ranges (Caley, 1997; Mitchell et al., 2009). Considering that pigs are highly adaptable and consume a broad range of food types, such as tapioca, padi, coconut, molluscs, arthropods, worms and plant roots (Diong, 1973), a dietary study should be carried out to examine the food types consumed by the pigs found in the CCNR, and the availability and distribution of these resources in the CCNR. Mapping the availability of food in the CCNR could be useful for developing strategies for managing pig movement and distribution.

Because only one pig retained its collar for the duration of the study, its movements and aggregate home range cannot be considered to be representative of the population. In general, wild pigs have shown to shift their home ranges in response to spatio-temporal variance in food abundance (Mitchell et al., 2009). The shifting of home range can be seen in Fig. 3 where the pig, despite the presence of man-made structures in between forest patches, moved its home range after the first month and then in the fifth month. The ability to move between forest patches in a fragmented landscape is not unique to the collared pig in this study and has been reported in other studies (Gabor et al., 2001; Virgos, 2002). Throughout the six months, the collared pig ranged outside of the CCNR and suggests that future camera trapping should

Table 3. Comparison of sex ratios and percentage of individuals below 20 months between this study and a study in Tuscany, Italy (Boitani et al., 1995) and in Perak and Johor, Malaysia (Diong, 1973).

	This Study	**Boitani et al. (1995)**	**Diong (1973)**
Sex Ratio (M:F)	1: 1.075	1: 0.85	1: 0.71
Percentage of individuals < 20 months old	71%	70%	76.7%

be expanded to forest patches on the border of the CCNR. The average monthly home range sizes of the collared pig (Day – 0.69 km^2, Night – 0.82 km^2) were small when compared to the average monthly home range sizes of 2.85 km^2 in Central Italy (Massei et al., 1997a) and 33.5 km^2 in the Northern Territory of Australia (Caley, 1997). Three factors could account for the small home range:

1. The abundance of food in the area may have resulted in the small home range of the pig, as the home range of wild pigs has been reported to vary inversely with resource abundance (Singer et al., 1981; Diong, 1982; Caley, 1997).
2. Conversely, Massei et al. (1997a) reported that when food is scarce, wild pigs reduce the size of their home range while increasing the amount of foraging activity in a smaller area.
3. The fence surrounding the area limited the movement of the collared pig during the second, third and fourth month (Fig. 11).

However, because the fence did not prevent the collared pig from moving in and out of the area during the fifth month, it is more likely that the small home range was caused by food availability and distribution. The environmental conditions and settings of this study were also dissimilar to the study in Massei et al. (1997a); where food was so scarce a large number of pigs starved to death. Therefore, it is most likely that the small home range of the collared pig was a result of an abundance of food in the areas frequented by the pig.

For the most part, the population of pigs in the CCNR had similar demographic structures as other wild pig populations (Diong, 1973; Boitani et al., 1995) (Table 3). However, the mean group size found in this study (2.23 ± 0.14 individuals per group) was relatively smaller than the mean group sizes found in other studies. For example, Fernández-Llario et al. (1996) reported a mean group size of 3.21 ± 0.69 individuals and Gabor et al. (1999) had a mean group size of 3.9 ± 0.5 individuals. According to Estevez et al. (2007), the group size of a natural population is self-regulating and considered to be a byproduct of habitat suitability. In areas where predation/hunting risk high, there is an advantage in forming larger groups to increase the chances of detecting predators/hunters (Roberts, 1996; Krause & Ruxton, 2002; Beauchamp, 2003). However, there are costs to group living, such as the intensity of intra-group competition for food or access to other necessary resources. In environments where resources are plentiful, intra-group competition is low and large groups can be sustained (Estevez et al., 2007). Conversely, when resources are clustered or limited, intra-group competition will be high, and the resulting social groups will be smaller (Estevez et al., 2007). Therefore, the smaller mean group size found in the CCNR may be a result of an increase of intra-group competition, which may have been caused the clustering of resources in the eastern side of the CCNR (Fig. 2). An increase in the level of competition between individuals may also explain why group types that consist of only juveniles and sub-adults were observed in the CCNR and not in other studies. It should be noted that juvenile pigs are weaned and can move independent of a sow before reaching sub-adulthood and losing their striped pelage (Diong, 1973). In conclusion, this study provides the first population estimate of *Sus scrofa* in the CCNR obtained from empirical data. The population of wild pigs in the CCNR is demographically similar to other pig populations in terms of sex ratios and age structure. However, despite the lack of predation and hunting, pig abundance was lower than expected and is likely caused by the recent re-establishment of the population in the CCNR. The density map and the small home range of the collared pig suggested that resources may be clustered in the eastern side of the CCNR. Intraspecific competition for food within the CCNR may also explain why we observed smaller group sizes and groups consisting only of sub-adults and juveniles compared to pigs in Italy.

We also note that the SMR model can be a useful monitoring tool when circumstances and environmental conditions do not suit traditional methods of estimating abundance, such as when the animals are not uniquely identifiable. To improve on the SMR approach, we suggest a more robust methods of tagging and repeated measures of the population, with a greater coverage of cage traps and camera traps. Studies examining the diet of the pigs should also be conducted to identify the resources exploited by the pigs and, by extension, determine the availability of these resources in the CCNR and neighboring urban areas where pigs also forage. Future studies should also determine if the CCNR pig population has reached its carrying capacity.

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