Pacific Conservation Biology https://doi.org/10.1071/PC17030

# Forest connectivity is important for sustaining Admiralty cuscus (*Spilocuscus kraemeri*) in traditional terrestrial no-take areas on Manus Island, Papua New Guinea

John Lamaris<sup>A,B</sup> and Nathan Whitmore<sup>A,C</sup>

<sup>A</sup>Wildlife Conservation Society Papua New Guinea, PO Box 277 Goroka, Eastern Highlands Province, Papua New Guinea.

<sup>B</sup>School of Natural and Physical Sciences, University of Papua New Guinea, Waigani Drive,

Port Moresby, National Capital District, Papua New Guinea.

<sup>C</sup>Corresponding author. Email: nwhitmore@wcs.org

**Abstract.** *Tambu* is a well respected concept in Melanesian societies and represents a periodic cultural restriction on harvesting for the purpose of fulfilling customary obligations and restocking resources. As a result it has been suggested as the basis for conservation and sustainability in Melanesia. One species subject to *tambu* management is the Admiralty cuscus (*Spilocuscus kraemeri*), an arboreal marsupial endemic to Manus Island, Papua New Guinea, where it is a major source of terrestrial protein for forest-dwelling villagers. We investigated the denning home range and movement patterns of 10 cuscus using radio-telemetry in and around a 21-ha forested *tambu* area over a 28-day period. Home-range sizes were estimated using a 95% minimum convex polygon method and possible contributing factors to home-range size were assessed through model selection. Home-range size was highly variable, log-normally distributed (back-transformed mean = 2.9 ha, mean  $\pm 1$  s.d.: 0.6–13.8 ha, n = 8), and was not associated with body mass, age or sex. Additional telemetry data collected from three *S. kraemeri* over 74 days appeared to support the stable nature of the home ranges. Through application of Laplace's extension of the Buffon's needle problem we conclude that, despite potentially high growth rates and short juvenile dispersal distances, *tambu* areas are unlikely to be self-sustaining. We hypothesise that the apparent efficacy of *tambu* areas is a consequence of forest connectivity that allows the immigration of adult founders to offset losses in reproductive stock coming as a result of periodic harvest and juvenile dispersal.

Additional keywords: Buffon's needle, marsupial, Melanesia, minimum convex polygon, Phalangeridae, radio telemetry, taboo, tambu

Received 27 August 2017, accepted 14 January 2018, published online 20 February 2018

#### Introduction

In the tropical rainforest of Papua New Guinea (PNG) and nearby islands forest game remains an important dietary component for the indigenous people (Cuthbert 2010; Pangau-Adam *et al.* 2012). An estimated 0.8–1.6 million people living in rural PNG derive a significant portion of their protein needs from such game (Mack and West 2005). However, access to game species by rural community members is by no means universal, but is often, even today, restricted through a myriad of culturally specific prohibitions predicated on gender roles, initiation rituals, genealogies, totemic associations, and the supernatural (Whitehead 1995; Kagl *et al.* 2015).

Communities in PNG, and elsewhere in Melanesia and Oceania, often intentionally use some cultural prohibitions to control resource use in advance of forthcoming resource need (Ward and Kingdon 1995; Caillaud *et al.* 2004). As a consequence some authors have suggested that such cultural prohibitions may be effective as a basis for local resource management

in developing countries, like PNG, where norms, rather than governmental laws and regulation, determine human behaviour (Colding and Folk 2000). Similarly, other authors have highlighted additional advantages of such cultural prohibitions in terms of low cost and high compliance (e.g. Ward and Kingdon 1995; Caillaud *et al.* 2004; Cinner *et al.* 2005; Jupiter *et al.* 2014). Thus far, while the utility of cultural prohibitions has been demonstrated in regulating marine resource use in Oceania (Jupiter *et al.* 2014), there has been scant investigation of their applicability to terrestrial resource management.

As there are few large animals in PNG forests a large portion of the diet of indigenous forest communities comes from a limited number of relatively small-bodied wild game (Mack and West 2005; Cuthbert 2010). The spotted cuscuses (Phalangeridae: *Spilocuscus*), a genus of nocturnal generalist arboreal frugivore–folivore marsupials endemic to the tropical Australo-Papuan region (Helgen and Flannery 2004), represent one of the larger game species (typically 2–7 kg) and, as a result, are often sought after by hunters (Whitmore *et al.* 2016). However, despite their dietary importance, scientific knowledge regarding most aspects of their biology and ecology remains scant (Tyndale-Biscoe 2005).

The Wildlife Conservation Society has been undertaking research on the Admiralty cuscus, *Spilocuscus kraemeri* (Cohn 1914), the smallest of the spotted cuscuses (adult weight: 2–4.5 kg), on Manus Island, a 1900-km<sup>2</sup> island to the north of the PNG mainland since 2010 (Whitmore *et al.* 2016). The Admiralty cuscus is the largest native game animal on Manus Island and appears to have been hunted since human colonisation some 11 000 years ago (Williams 1999). Due to overhunting and habitat degradation *S.kraemeri* is currently classified as Near Threatened on the IUCN Red List (Helgen *et al.* 2008).

On Manus Island there appear to be no cultural prohibitions regarding the hunting of S. kraemeri: there are no restrictions on hunting by women, and the species is regarded as a staple protein source. However, some clans have a genealogical and totemic relationship with the species as an ancestor figure, which prohibits their eating of the animal. Owing to the fact that it is a comparatively large game animal S. kraemeri is often expected to be presented as a meal at ceremonial occasions such as 'bride price' celebrations and 1000-day mourning commemorations (Whitmore et al. 2016). The vulnerability of the species to overharvest is recognised by many villagers and, as a result, some clans have reinstigated periodic no-take areas 'tambu' (Tok Pisin: a prohibition) drawing upon traditional cultural prohibitions to manage and restock depleted cuscus populations by closing a parcel of forest to hunting for a specified period (Whitmore et al. 2016). As villagers believe a breach of the tambu area boundary will result in sickness and death, restrictions are generally well abided (Whitmore et al. 2016).

Recent research on *S. kraemeri* and the efficacy of periodic *tambu areas* (Whitmore *et al.* 2016) demonstrated that periodic *tambu* areas may be a sustainable way to manage *S. kraemeri*, given low to medium harvest rates and typical closure durations. However, Whitmore *et al.* (2016) ignored the spatial nature of *S. kraemeri* populations and whether the size of *tambu* areas would allow them to be self-sustaining.

Westbrooke (2007) defined a self-sustaining managed area for a threatened species as the area necessary to allow sufficient recruitment to balance the losses from mortality and natal dispersal, and showed that the minimum size for such an area (modelled as a square cell) could be calculated analytically based on the life history and dispersal characteristics of the species of interest. As periodic *tambu* areas are in many respects akin to a reserve during periods of closure, Westbrooke's (2007) mathematical approach can be applied to identify the minimum size required for a perpetual reserve, thereby setting a minimum size threshold against which periodic *tambu*, by virtue of their non-perpetual nature, must always exceed.

In order to assess the spatial efficacy of periodic *tambu* we: (1) assessed the size and stability of home ranges for *S. kraemeri* in and around a *tambu* area through the radio-tracking of individual animals; and (2) estimated the minimum size of a self-sustaining reserve using the Westbrooke (2007) approach based on vital rates of closely related phalangerid surrogates.

# Materials and methods

#### Study site

This study was conducted on the north coast of Manus Island, PNG (Fig. 1). Manus is the largest island of the Admiralty group of islands with an area of  $\sim 1900 \text{ km}^2$  (Whitmore *et al.* 2016). The study was done in and around a 26-ha *tambu* area, of which 21 ha was forested, owned by the Welei clan of Lehewa village (hereafter referred to as the Welei *tambu*). The forest-free area within the *tambu* area was a mosaic of subsistence gardens, grassy clearings, and a hamlet of seven family homes known as Siloulou. Consent to access land and animals, and to carry out research in the Welei *tambu* area was given by the chief, Charles Chuwek of the Welei clan (and continued upon his death by Terence Chuwek). No specific permits were required for the described study, which complied with all relevant PNG wildlife regulations (as the species is not listed on the schedule of protected species).

The restrictions in Welei *tambu* are specifically geared towards hunting of the Admiralty cuscus and have been described in detail in Whitmore *et al.* (2016). The *tambu*, however, does not restrict members of the clan from entering the area for other purposes such as extracting medicinal plants. The forest at the Welei *tambu* area is a gently sloping ( $<10^\circ$ ) lowland plain forest  $\sim 1$  km from the coast (Fig. 1). The vegetation is best described as a mosaic of older secondary forest growth lacking emergent trees with a canopy  $\sim 20-25$  m high, with localised patches of bracken fern and bamboo indicative of historic disturbance. Tree species characterising advanced regrowth were *Albizia* sp., *Elaeocarpus* spp., *Pometia pinnata*, *Dysoxylum* spp., *Intsia bijuga* and *Calophyllum* spp.

#### Radio-tracking

A team of local hunters, adept in tree climbing, captured S. kraemeri by intercepting animals in the canopy between 5 and 22 May 2013. Once caught, a cuscus was dropped from the canopy into a safety net or carried to the ground, then transferred into a hessian bag and sedated using ketamine (1000 mg mL<sup>-1</sup>) ketamine at a dosage of 0.15 mL kg<sup>-1</sup>). The sex of each cuscus was then determined on the basis of the presence of a pouch and each individual was weighed using a 10-kg pesola scale. For S. kraemeri that weighed  $\geq 0.85$  kg, radio-transmitters (Sirtrack telemetry electronics consultants, New Zealand) were fitted around the neck of the sedated cuscus (model V5C 161, weight 43 g; and model V5C 173A, weight 79 g). All transmitters had 30-cm whip antennas that transmitted signals within the range 160-161 MHz. Transmitters were matched against the weight of the individuals to ensure they did not exceed 5% of the adult weight of the cuscus and were therefore within recommended weight limits (Sikes and Gannon 2011). After collar attachment the cuscus were left to regain consciousness and were released at the capture site  $\sim$ 20–30 min later. Radio-tracking commenced the following day. Ten cuscus (two male and eight female) were radio-tracked daily from 5 May until 1 June 2013.

Radio-tracking was undertaken during the day (between 0600 and 1800 hours) when cuscus were generally inactive, making it easier to locate and record their position. Hence, ours is a denning home range study rather than a foraging home range study and consequently may underestimate the animals' spatial

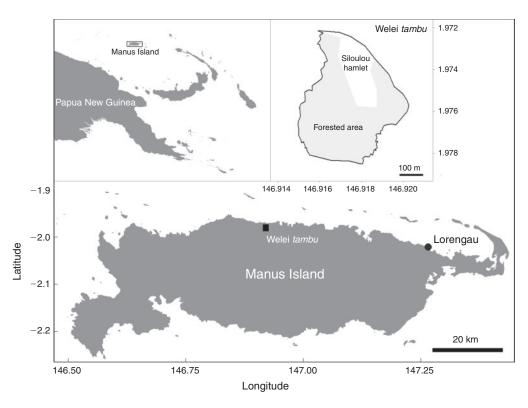


Fig. 1. Map showing study site (Welei *tambu*) in Manus Island, Papua New Guinea, indicating location of *tambu* study site.

requirements. Animals were located using a very-high-frequency receiver (model TR4, frequency 160-164 MHz) and a Sirtrack 3-element folding Yagi antenna (model Sirtrack 5-000094-ANT, frequency 155-165 MHz, Sirtrack Limited, New Zealand). From open hilltops, the transmitter signal could be detected over distances of  $\sim 1$  km. We used the triangulation method to determine the direction of transmitting signal from the animal and then the homing method (White and Garrot 1990) to close in until such time that the radio signal was uniformly strong all around the receiver (both horizontally and directly overhead). The positional fix was recorded with GPS units (Garmin Etrex models 10 and 30). The study concluded on 1 June 2013, just before the opening of the Welei tambu on 2 June 2013 to provide cuscus meat for a customary feast commemorating a 1000-day mourning period. Upon conclusion of the study all animals were recaptured for collar retrieval and released.

A follow-up *ad hoc* radio-tracking study was conducted in the Welei *tambu* over a 74-day period (10 June – 22 August 2014) in order to utilise the remaining battery life of the transmitters. Two females and one male cuscus were captured in the manner described, radio-tagged and intermittently monitored over three periods, each 2–6 days in length. In both the first and the follow-up studies, we recorded one fix per animal per day.

#### Data analysis

Data were analysed in R 3.3.2 (R Core Team 2016) with additional functionality from the package 'adehabitat' (Calenge 2006). Home-range area was estimated using the 95% minimum convex polygon (MCP) method (White and Garrot 1990) based on the capture and recapture locations and the daily positional fixes. MCP (95%) home ranges were calculated for each animal, provided more than five relocations were obtained. The change in estimated home-range against day was plotted for each cuscus. If the home range for a particular animal did not approach a stable horizontal asymptote during the course of the study, the data were discarded on the basis of being an incomplete representation of the animal's home range.

In order to investigate the underlying factors governing home-range size, eight general linear models were constructed that each represented a plausible combination of explanatory variables (weight, sex, and number of GPS fixes obtained). Home range was log-transformed to fit the required assumptions of normality. Each candidate model was tested for its computability. An information theoretic approach was then used whereby these candidate models were compared using Akaike's Information Criterion small sample size adjustment (AICc) and ranked by their model likelihood (*sensu* Burnham and Anderson 2002).

In order to utilise Westbrooke's (2007) model, survival and reproduction rates of juveniles and adults, and estimates of the dispersal distance of juveniles are required. Since no empirical survival estimates exist for *S. kraemeri*, we used the surrogate rates established by Whitmore *et al.* (2016), which were derived from the well studied phalangerid *Trichosurus vulpecula* of Australia, resulting in mean rates of adult survival ( $S_{adult} = 0.82$ ) and juvenile survival ( $S_{juvenile} = 0.65$ ). Reproduction (*rep*) was

Cuscus no.	Study	Age	Sex	Weight (kg)	No. of GPS fixes	Home-range (ha)
1	First	Adult	F	2.2	25	1.0
2	First	Adult	F*	2.6	25	16.2
3	First	Adult	F*	3.7	23	48.3
4	First	Juvenile	F	0.85	21	0.7
5	First	Adult	F	2.5	21	18.3
6	First	Adult	$\mathrm{F}^{\dagger}$	4.4	21	0.7
7	First	Juvenile	F	0.85	21	1.4
8	First	Adult	М	1.8	20	11.1
9	First	Adult	М	2.0	18	0.5
10	First	Adult	F	2.8	10	0.6
11	Second	Adult	М	2.7	12	0.4
12	Second	Adult	$F^{\dagger}$	2.9	12	0.3
13	Second	Adult	F*	3.1	11	1.0

 Table 1. Estimated home-range size for 13 S. kraemeri radio tracked over the initial (first) and follow-up (second) study

  $M = male, F = female without pouch young, F^* = female with furred joey, F^{\dagger} = female with naked joey. Stable home range estimates given in bold,$ 

non-stabilised estimates given in italics

modelled as a sequence of female-only annual reproductive rates between 0.3 and 0.7 at intervals of 0.1 under the assumption of sexual maturity as yearlings (based on anecdotal accounts of the common spotted cuscus, *Spilocuscus maculatus*, a close relative of *S. kraemeri*) (Sinery *et al.* 2013).

The minimum size of a *tambu* area was estimated graphically using Laplace's extension to Buffon's needle problem (*sensu* Westbrooke 2007), through calculation of the *retention rate* (r) (Eqn 1) and the *dispersal ratio* (d; Eqn 2):

$$r = \frac{1 - S_{adult}}{rep \times S_{juvenile}} \tag{1}$$

The *dispersal ratio* (d) (Eqn 2) was calculated for each of the *retention rate* values associated with each of the five reproductive rates.

$$d = 2 - \sqrt{4 - \pi(1 - r)}$$
(2)

The area required (a) (Eqn 3) was calculated for *juvenile* dispersal distances (j) varying from 0 to 1000 m.

$$a = \left(\frac{j}{d}\right)^2 \tag{3}$$

The square root of the mean home range was used as an indicative minimum value for *j* under the assumption that the juvenile cuscus must eventually leave the maternal home range. For comparative context, indicative population growth rates ( $\lambda$ ) were calculated from a two-stage Leslie projection matrix for each of the reproductive rates (*sensu* Caswell 2001).

## Results

#### Home range

During the first study period 10 free-living cuscus were radiotracked, yielding 10–25 daily GPS fixes for each individual. Of the 10 cuscus, two were adult males, two were juvenile females, and six were adult females; three of the adult females carried pouch young (Table 1).

The three cuscus radio-tagged in the follow-up study were all adults (two females, one male), yielding 11 or 12 daily fixes each (Table 1). Both females had pouch young when captured for radio-collar attachment. At the end of the second study period only one female was successfully recaptured for collar retrieval. The other female cuscus managed to lose the collar during the study and it was retrieved from the forest floor. The male cuscus initially avoided recapture but was subsequently recaptured in the study area on 11 April 2016 still wearing the radio-collar and only 25 m from its initial capture site on 10 June 2014 (an interval of 671 days).

The number of daily fixes per animal in both studies (range: 10-25) was above the requirements of five relocation points for MCP calculation. Graphical examination of the home-range estimates through time revealed that most MCP estimates generally had stabilised around 15 fixes (i.e. closely approaching an asymptote of gradient zero) (Fig. 2) or had stabilised by the end of study. In the first study, 15 GPS fixes were not achieved for one cuscus, and the estimate of the MCP did not stabilise by the end of the study for another. As a consequence, both were eliminated from consideration in the home range study (Table 1). The movement pattern of the latter cuscus was not consistent with a home range; instead, the individual appeared to be undertaking directional movement away from the tambu area and was recaptured 1177 m away from its initial capture site. Our follow-up study ended before 15 GPS fixes were obtained for any individual. As a result, the conditions to discern stable home ranges were not met (Table 1). However, the non-stabilised home ranges in the follow-up study were comparable with the initial study for the same number of GPS fixes despite a much longer monitoring period (Fig. 2).

Stabilised home-range areas from the first study varied from 0.5 ha to 18.3 ha, and appeared to follow a log-normal distribution. There were both intra- and intersex home range overlaps present (Fig. 3). The mean normalised home range after

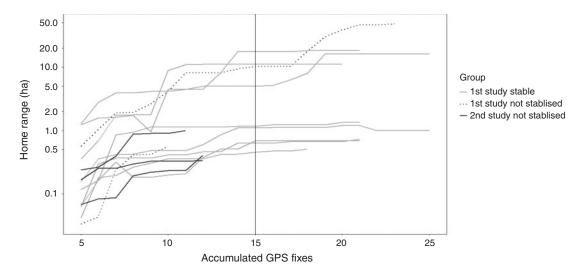
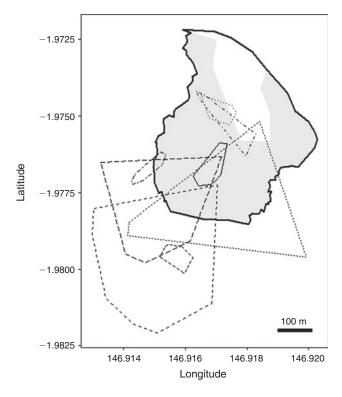


Fig. 2. Graph indicating the stabilisation of home ranges estimated from 95% minimum convex polygons with increasing number of accumulated GPS fixes for each of the radio-tracked *S. kraemeri*.



**Fig. 3.** Map showing the eight stabilised home ranges estimated from 95% minimum convex polygons (all from the initial study). Key: shaded area represents the forested area of Welei *tambu* area, borderline indicates the customary boundary of the entire *tambu* area.

back-transformation was 2.9 ha (mean  $\pm$  1 s.d.: 0.6–13.8 ha, n = 8). The most parsimonious model describing home range was an uninformative simple mean (Table 2). There was only marginal support for associations with weight, sex, and number of GPS fixes (Table 2).

# Table 2. Candidate models explaining the underlining cause of home range size ranked by Akaike Information Criterion (AICc)

K = number of parameters,  $\Delta AICc$  = difference between the AICc of the current model and the top model, Model Weight = the relative likelihood of the model, LL = maximised value of the log-likelihood function

Model	Κ	AICc	$\Delta AICc$	Model weight	LL
Simple intercept	2	34.94	0	0.75	-14.27
Weight		38.41	3.47	0.13	-13.20
GPS fixes	3	39.78	4.84	0.07	-13.89
Sex	3	40.54	5.6	0.05	-14.27
GPS fixes + weight	4	45.97	11.03	0	-12.32
Sex + weight	4	46.74	11.79	0	-12.70
GPS fixes + sex	4	48.48	13.53	0	-13.57
GPS fixes + weight + sex	5	64.61	29.67	0	-12.30

#### Minimum size of a tambu area

Using the forested area of the Welei tambu (21 ha) area as a baseline, if juvenile dispersal exceeded 252 m there is little possibility that an area of such a size could be self-sustaining (Fig. 4). At high reproductive rates (0.6–0.7) a juvenile dispersal distance equivalent to the square root of one home range (170 m) could allow for a self-sustaining population in a 21-ha tambu area (if it was permanently closed to harvest). A reproductive rate <0.5, however, would likely preclude an area of such a size from being self-sustaining. If a precautionary approach is taken using a juvenile dispersal distance equivalent to the square root of the maximum recorded home range (427 m), and a conservative reproductive rate (0.4) then a *tambu* area >250 ha would be required. Additionally, our analysis also revealed that a reproductive rate of 0.3 is much too low to be ecologically plausible, as the S. kraemeri population under natural circumstances (without harvesting) would only just be marginally better than stable ( $\lambda = 1.01$ ). At such a rate, the species (as a

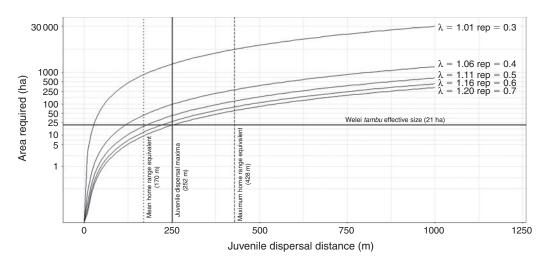


Fig. 4. An assessment of whether a 21-ha *tambu* area can adequately protect a population of *S. kraemeri* at differing reproductive rates (rep) indexed as population growth rate ( $\lambda$ ) equivalents. Key: vertical dotted line represents juvenile dispersal distance if equivalent to mean home range; solid vertical line represents dispersal maxima for Welei *tambu* area; dashed vertical line represents juvenile dispersal distance if equivalent to maximum home range; horizontal solid line represents Welei *tambu* area size (ha).

whole) would have had no capacity to survive the 11 000 years of harvesting inferred by Williams (1999).

# Discussion

While it is straight-forward to radio-track an animal, it is somewhat more difficult to determine whether or not the resulting information represents a true home range. Our study showed that the estimation of home range through MCP rapidly increased with the initial accumulation of GPS fixes but generally levelled off after ~15 fixes. This suggests that to accurately estimate home-range area for *S. kraemeri* at least 15 GPS fixes will be required. Our follow-up study, while failing to obtain sufficient GPS fixes, appeared to reinforce the outcome of our original study, despite the much longer monitoring period, and suggests that most *S. kraemeri* will tend to have home ranges that are stable and overlapping.

We found that the mean denning home-range size for S. kraemeri was 2.9 ha (back-transformed, mean  $1 \pm$  s.d.: 0.6– 13.8), which is broadly comparable with the tropical foraging home ranges recorded for T. vulpecula (males 3.9  $\pm$  1.4 ha, females  $2.1 \pm 1.2$  ha, calculated using 90% MCP: DeGabriel et al. 2014). However, the individual home ranges of S. kraemeri in our analysis were much more variable than those recorded for T. vulpecula (DeGabriel et al. 2014). Three S. kraemeri had home ranges exceeding 10 ha and extending well beyond the borders of the *tambu* area and into the hunting area. It is conceivable that these larger home ranges are an edge effect of the tambu area brought on by lower S. kraemeri densities at the edge of the tambu area due to hunting mortality. If such a phenomenon exists, S. kraemeri bordering or outside the tambu area might be expected to occupy larger home ranges than those in the centre of the tambu area. Such a 'vacuum effect' has also been observed for T. vulpecula (Efford et al. 2000; Ji et al. 2001). Notwithstanding, our linear modelling analysis failed to reveal any individual characteristics that were associated with home-range size.

As such, factors influencing home range remain unknown and would suggest that a much larger sample would be required to develop a basic predictive model based on physical characteristics, let alone investigate potential density-dependent edge effects.

Westbrooke (2007) identified that the required size and shape of a managed area that allows threatened species to have a stable population has been a central issue for conservation management. Our results suggest that the current Welei tambu size would be appropriate if juveniles were dispersing only small distances (roughly equivalent of one home range from their mother), female adults possessed a reproductive rate  $\geq 0.5$ , and the area was permanently closed to harvest. As the Welei tambu would achieve a self-sustaining population only under these restrictive circumstances if the area was a perpetual reserve, we postulate that any similar-sized tambu area (or smaller) that is subject to periodic harvest and open to migration is unlikely to be self-sustaining. We hypothesise that the apparent efficacy of tambu areas as a sustainable harvest management technique is actually a consequence of forest connectivity, which allows the immigration of adult founders to offset losses in reproductive stock coming as a result of periodic harvest and juvenile dispersal.

Given the lack of empirical survival, reproductive, and harvest rates as well as juvenile dispersal distances, a precautionary approach might suggest that a *tambu* area >250 ha would be appropriate. However, a *tambu* area of such size will likely be impractical on Manus Island given the high rate of land disputes and the entrenched practice of shifting cultivation.

Determination of the empirical survival and reproductive rates is currently underway by the authors, with 163 *S. kraemeri* tagged with microtransponders at multiple *tambu* locations as of June 2017. We are hopeful that ongoing mark–recapture data collection will provide an opportunity for robust estimation of vital rates and allow a reanalysis of the required reserve area, using empirical data, within the next five years.

Forest connectivity important for Admiralty cuscus

A synthesis of our analysis and that of Whitmore *et al.* (2016) suggests that while the growth rate of the *S. kraemeri* population is likely sufficient for periodic harvest within *tambu* areas, the maintenance of such a population would be dependent on immigration of adult founders from adjacent forest areas in order to replace deficits caused by juvenile dispersal and losses of adults through periodic harvest. The ramification of such a dynamic is that *tambu* areas will variously serve roles as localised population sources and sinks at different stages of their closure cycle.

## Management implications

Results from our study suggest that most periodically harvested tambu areas will be insufficiently large to maintain a selfsustaining population of S. kraemeri without immigration. As the required reserve area is proportional to the square of the juvenile dispersal distance, marginal increases in the *tambu* area will not substantially improve the likelihood of an area being self-sustaining. Given the ubiquitous nature of land disputes in Manus, coupled with growing human population pressures, the prospects of increasing tambu areas sufficiently to have a high probability of being self-sustaining (i.e. >250 ha) appears impractical. An alternative strategy to adequately conserve local populations of S. kraemeri could involve the development of a network of tambu areas within contiguous forest habitat to act as a proxy for a larger reserve area that would otherwise be unobtainable (i.e. in a manner not dissimilar to locally managed marine areas sensu Ward and Kingdon 1995; Cinner et al. 2012; Jupiter et al. 2014). To this end, two practical options could be: (1) to guide the landowners and local communities through the process of land-use planning where they are encouraged to designate certain portions of their clan land for tambu areas and as a collective community agree to maintain forest corridors, or (2) ostensibly arrive at the same point through an indirect process of fostering pride in traditional land management techniques and promoting these methods in a way to foster social contagion.

#### Conclusion

Our analysis suggests that typically sized *tambu* areas, operating for the management of *S. kraemeri* and periodically harvested, are unlikely to be self-sustaining. We postulate that the apparent efficacy of *tambu* areas as a sustainable management technique is a result of the innate characteristic of the species for stable home ranges and high population growth rates, in combination with adult immigration via contiguous forest corridors. As a consequence, the sustainability of a particular *tambu* area will be dependent on the wider extent of forest connectivity. As *tambu* areas are widely used across the Pacific region our findings may be broadly applicable to the management of other arboreal animals across the region, and suggest that forest fragmentation could pose a major threat to this form of indigenous management.

#### Conflicts of interest

The authors declare no conflicts of interest.

## Acknowledgements

We thank the Welei clan of Lehewa village Manus and in particular the late chief, Charles Chuwek, and Terence Chuwek for allowing access to the study site. We acknowledge the assistance in the field provided by the Welei hunters: Greg, Kora and Tony. We deeply appreciate the logistic support provided by the Wildlife Conservation Society staff: Benson Lian, Arison Arihafa, Nixon Komboli, and the late David Posa. We are deeply indebted to Richard Cuthbert, Sven Frijlink, John Genolagani, Stacy Jupiter, and Ian Westbrooke for constructive comments that greatly improved this manuscript. This work was funded through two successive Australian Aid grants from the Australian Government Department for Foreign Affairs and Trade: 'Strengthening the capacity of vulnerable coastal and inland communities in Papua New Guinea to adapt to climate change' and 'Building climate change resilience and conservation management in Manus Province, Papua New Guinea'.

## References

- Burnham, K. P., and Anderson, D. R. (2002). 'Model Selection and Inference: a Practical Information- theoretic Approach.' 2nd edn. (Springer-Verlag: New York.)
- Caillaud, A., Boengkih, S., Evans-Illidge, E., Genolagani, J., Havemann, P., Henao, D., Kwa, E., Llewell, D., Ridep-Morris, A., Rose, J., and Nari, R. (2004). Tabus or not taboos. How to use traditional environmental knowledge to support sustainable development of marine resources in Melanesia. SPC Traditional Marine Resource Management and Knowledge Information Bulletin 17, 14–35.
- Calenge, C. (2006). The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* **197**, 516–519. doi:10.1016/J.ECOLMODEL.2006.03.017
- Caswell, H. (2001). 'Matrix Population Models.' 2nd edn. (Sinauer Associates: Sunderland, MA.)
- Cinner, J. E., Marnane, M. J., and Mcclanahan, T. R. (2005). Conservation and community benefits from traditional coral reef management at Ahus Island, Papua New Guinea. *Conservation Biology* **19**, 1714–1723. doi:10.1111/J.1523-1739.2005.00209.X-11
- Cinner, J. E., Basurto, X. B., Fidelman, P. A., Kuange, J., Lahari, R., and Mukminin, A. (2012). Institutional designs of customary fisheries management arrangements in Indonesia, Papua New Guinea, and Mexico. *Marine Policy* **36**, 278–285. doi:10.1016/J.MARPOL.2011.06.005
- Cohn, L. (1914). Eine neue Varietät von Phalanger maculatus. Zoologischer Anzeiger 44, 507–516.
- Colding, J., and Folk, C. (2000). Social taboos: 'invisible' systems of local resource management and biological conservation. *Ecological Applications* 11, 584–600.
- Cuthbert, R. (2010). Sustainability of hunting, population densities, intrinsic rates of increase and conservation of Papua New Guinean mammals: a quantitative review. *Biological Conservation* **143**, 1850–1859. doi:10.1016/J.BIOCON.2010.04.005
- DeGabriel, J. L., Moore, B. D., Foley, W. J., and Johnson, C. N. (2014). Male-biased predation and its effect on paternity skew and life history in a population of common brushtail possums (*Trichosurus vulpecula*). *PLoS One* 9, e111746. doi:10.1371/JOURNAL.PONE.0111746
- Efford, M., Warburton, B., and Spencer, N. (2000). Home-range changes by brushtail possums in response to control. *Wildlife Research* 27, 117–127. doi:10.1071/WR99005
- Helgen, K. M., and Flannery, T. (2004). Notes on the phalangerid marsupial genus *Spilocuscus*, with description of a new species from Papua. *Journal of Mammalogy* 85, 825–833. doi:10.1644/BER-110
- Helgen, K., Leary, T., Singadan, R., Menzies, J., and Wright, D. (2008). *Spilocuscus kraemeri*. The IUCN Red List of Threatened Species. Available at: http://dx.doi.org/10.2305/IUCN.UK.2008. RLTS.T20637A9216570.en [accessed 18 August 2017].
- Ji, W., Sarre, S. D., Aitken, N., Hankin, R. K. S., and Clout, M. N. (2001). Sex-biased dispersal and a density-independent mating system in the Australian brushtail possum, as revealed by minisatellite DNA profiling. *Molecular Ecology* **10**, 1527–1537. doi:10.1046/J.1365-294X.2001. 01287.X

#### H Pacific Conservation Biology

- Jupiter, S. D., Cohen, P. J., Weeks, R., Tawake, A., and Govan, H. (2014). Locally-managed marine areas: multiple objectives and diverse strategies. *Pacific Conservation Biology* 20, 165–179. doi:10.1071/ PC140165
- Kagl, J. P., Whitmore, N., and Aplin, K. P. (2015). Traditional & local ecological knowledge. In 'A Rapid Biodiversity Assessment of Papua New Guinea's Hindenburg Wall Region'. (Eds S. J. Richards, and N. Whitmore.) Chapter 1, pp. 3–13. (Wildlife Conservation Society Papua New Guinea Program: Goroka, PNG.)
- Mack, A. L., and West, P. (2005). Ten thousand tonnes of small animals: wildlife consumption in Papua New Guinea. Resource Management in Asia-Pacific Working Paper No. 61. Resource Management in Asia-Pacific Program, the Australian National University, Canberra.
- Pangau-Adam, M., Noske, R., and Muehlenberg, M. (2012). Wildmeat or bushmeat? Subsistence hunting and commercial harvesting in Papua (West New Guinea), Indonesia. *Human Ecology* 40, 611–621. doi:10.1007/S10745-012-9492-5
- R Core Team (2016). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: www.R-project.org/
- Sikes, R. S., and Gannon, W. L. (2011). Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 92, 235–253. doi:10.1644/10-MAMM-F-355.1

- Sinery, A. S., Boer, C., and Farida, W. R. (2013). The dynamics of cuscus in tourist island of Ahe, District of Nabire, Papua. *Biodiversitas* (*Surakarta*) 14, 95–100. doi:10.13057/BIODIV/D140207
- Tyndale-Biscoe, H. (2005). 'Life of Marsupials.' (CSIRO Publishing: Melbourne.)
- Ward, R. G., and Kingdon, E. (Eds) (1995). 'Land, Custom and Practice in the South Pacific.' (Cambridge University Press: Cambridge.)
- Westbrooke, I. (2007). How large a managed area is needed to protect a threatened animal species? Combining simple dispersal and population models. *New Zealand Journal of Ecology* **31**, 154–159.
- White, G. C., and Garrot, R. A. (1990). 'Analysis of Wildlife Radio-tracking Data.' (Academic Press, Inc.: San Diego.)
- Whitehead, H. (1995). Identifying game species with the aid of pictures in Papua New Guinea. *Pacific Studies* 18, 1–38.
- Whitmore, N., Lamaris, J., Takendu, W., Charles, D., Chuwek, T., Mohe, B., Kanau, L., and Pe-eu, S. (2016). The context and potential sustainability of traditional terrestrial periodic *tambu* areas: insights from Manus Island, Papua New Guinea. *Pacific Conservation Biology* 22, 151–158. doi:10.1071/PC15036
- Williams, C. (1999). Faunal composition of Pamwak site, Manus Island, PNG. In 'Le Pacific de 5000 à 2000 avant le Present'. (Eds J.-C. Galipaud and I. Lilley.) pp. 241–249. (Institut de Recherche pour le Développement: Paris.)