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Research article

Modelling the surprising recolonisation of an understudied aquatic mammal in a highly urbanised area: fortune favoured the smooth-coated otter in Singapore

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Ever-growing human activities present an active and continuing threat to many species throughout the world. Nevertheless, concerted conservation efforts in some regions have balanced these threats and allowed endangered species to recolonise former parts of their original ranges and reverse their decline. This is notably the case of the smooth-coated otter *Lutrogale perspicillata*. In 1998, individuals returned to Singapore after more than a 20-year absence. In 2017, 79 otters were counted throughout the heavily urbanized city. Despite this comeback, the future of the species in Singapore is unclear. By collating information on the species' life history traits, we implemented a spatially explicit individual based model with the aim of first replicating the original recolonisation of the species in Singapore and secondly, trying to predict its future population trend. The model demonstrated that successful establishment of Singapore population from the initial immigrants was highly uncertain. In 43% of cases, stochastic extinction occurred. From the 9% of model replicates that closely reproduced the observed colonisation history, projections showed that the population would reach close to 200 individuals in 50 years. This study successfully demonstrates the use of individual-based modelling to simulate the inherently stochastic recolonisation dynamics of an endangered species and predict its longer-term future. We discuss emerging issues that may arise from increasing negative interactions between otters and humans and the general challenges associated with rewilding highly urbanized environments. We stress the importance of long-term monitoring surveys and education campaigns to mitigate human–wildlife conflicts. With species and natural habitats increasingly threatened by our ever-growing human expansion, understanding the factors that allow human-dominated landscapes to be compatible with biodiversity is of the utmost importance.

Keywords: demography, dispersal, immigration, individual based model, smooth-coated otter, spatial dynamics

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Introduction

Humans have played an undeniable role in the past and current global and regional extinctions of carnivores (Berger 1999, Dalerum et al. 2009). Carnivore populations are diminished or completely eradicated when seen as threatening to either human life and safety or, to crops and livestock (Nyhus 2016). Large carnivores, in particular, have suffered from these real and perceived threats (Di Marco et al. 2014). For example, Chinas' tiger subspecies *Panthera tigris amoyensis*, now considered extinct in the wild, suffered decades of widespread eradication during Mao's war on nature in the 1950s (Tilson et al. 2004, Nyhus 2016). The Eurasian lynx *Lynx lynx*, wolf *Canis lupus* and brown bear *Ursus arctos* were once widespread throughout Europe. The decline of these three species coincided with the expansion of human populations and the associated increase in hunting designed mainly to remove the threat they pose to livestock and game species (Breitenmoser 1998). Other carnivores such as sea otters *Enhydra lutris* were wiped out over much of their range due to the commercial value of their fur during the 18 and 19th century (Larson et al. 2002), leaving remnant scattered populations of only tens to hundreds of individuals at most after their protection in 1911 (Kenyon 1969).

In recent decades, habitat fragmentation and destruction caused by growing human activities have added major and continuing threats for the survival and persistence of many carnivores (Nyhus 2016). Habitat fragmentation is directly linked to long-term negative outcomes, such as decreases in species richness and survivability (Fahrig 2003, Haddad et al. 2015), in the number of large-bodied specialist species (Gibbs and Stanton 2001), and in breeding success, dispersal, predation rates, and foraging success (Bergin et al. 2000, Kurki et al. 2000, Bélisle et al. 2001), as well as in changes in species interactions (Taylor and Merriam 1995). The area of earths' surface occupied by urban areas is around 70 million hectares ca 2001 (Potere et al. 2009) and is expected to triple by 2030 to 0.18 billion hectares (Seto et al. 2012). In the same time, 290 000 km^2 of natural habitat is likely to be turned into urban environment between 2000 and 2030 (McDonald et al. 2019). The increase in urban environments at the global scale challenges effective conservation strategies, in particular, approaches such as the protection and enlargement of suitable habitat areas for wild species, which are now more than ever constrained by the availability of land and hindered by socio-economic issues (Balmford et al. 2001, Lambin and Meyfroidt 2011).

Rewilding, which consists of protecting natural processes and wilderness areas by restoring or conserving and area of land to its natural unmanaged and self-regulated state, is rapidly gaining traction (Hall 2019, Lehmann 2021). While wholescale rewilding of an area may not be compatible with high human densities, there is a considerable interest in how even highly human-populated areas may be rewilded to a considerable extent (Lehmann 2021), with benefits to human health and wellbeing as well as biodiversity. Gaining understanding of how urban areas can be compatible with biodiversity is an increasingly important task given the projected expansion of urbanization around the globe (Knapp et al. 2020). To do so, monitoring surveys, analytical tools, laws and institutions as well as a general growing awareness about the value of biodiversity has contributed to increased and improved conservations efforts in many areas of the world (Nyhus 2016, Sun et al. 2016). These efforts have helped reduce the loss of biodiversity and natural habitats (Treves and Karanth 2003, Chapron et al. 2014), resulting in the increase of certain wildlife populations and allowed many native species to recolonise parts of their former ranges (Nyhus 2016), even in heavily human dominated landscapes.

One excellent case study is provided by the smooth-coated otter *Lutrogale perspicillata* in Singapore. After an absence of three decades, this otter species reappeared in Singapore during the mid-1990s, after the city implemented it's 'Garden City' campaign to green the city in 1967 (Theng and Sivasothi 2016, Khoo and Lee 2020). Through this campaign, pollution was drastically reduced, and nature reserves and parks were created. Waterways and rivers were also cleaned, which allowed aquatic life to return in the late 1980s. Today, despite being the third most densely populated city in the world, Singapore is also one of the greenest (Khoo and Lee 2020). The smooth-coated otter is one of the four species of otters found in Asia, where it is mainly distributed throughout South and South-east Asia (Theng et al. 2016). It is listed as a vulnerable species with a decreasing population trend by the IUCN. The decrease in its population size is due to increasing human populations, habitat destruction, pollution, human–wildlife conflict and lately, illegal wildlife trade (Hussain et al. 2018, Siriwat and Nijman 2018, Wright et al. 2020). As a top predator of wetland habitats, otters act as an indicator species of environmental conditions, and largely depend for their survival on adequate availability of uncontaminated food resources (Theng et al. 2016, Hussain et al. 2018). Thus, their recent disappearance from many wetlands and waterways across Asia is associated with degradation of their habitats by human activity, notably the construction of large-scale hydroelectric projects and the reclamation of land for human settlements and agriculture. Additionally, crucial smooth-coated otter habitats are experiencing increased pollution by pesticides and eutrophication caused by agricultural runoffs (Kruuk 2006, Theng et al. 2016, Hussain et al. 2018). Despite their ecological importance, the smooth-coated otter remains a relatively understudied species compared with other members of the Lutrinae subfamily such as the sea otter *E. lutris* (Estes and Palmisano 1974, Hughes et al. 2019), North American river otter *Lontra canadensis* (Leidy et al. 2000, Ellington et al. 2018), and the Eurasian otter *Lutra lutra* (Carranza et al. 2011, Duplaix and Savage 2018). A lack of baseline data on their ecology and life history traits restricts conservation efforts throughout their range (Khan et al. 2014).

The recolonisation of Singapore by the smooth-coated otter represents a rare opportunity to gain better insight into this elusive species' biology in a highly urbanized environment. In 1998, otters arrived through the Johor straight and settled in the north-western region of Singapore, in the Sungei Buloh Wetland Reserve. Later in 2007, another group of otters settled in the island of Pulau Ubin located on the north-eastern side (Khoo and Lee 2020). These two independent events were subsequently followed by the well-documented expansion of the species throughout Singapore. By 2017, 79 otters were recorded in more than 11 distinct groups (Khoo and Sivasothi 2018), indicating that the species has developed tolerance to human activity and adapted to the urban environment (Khoo and Lee 2020). Good quality data are available on the colonization history of the otters in Singapore, describing the spatial and temporal dynamics of the species as it arrived and spread through the island (Evans et al. 2010, Khoo and Sivasothi 2018, Khoo and Lee 2020).

Using a spatially explicit individual based modelling approach integrating demography and dispersal, we aimed to gain new understanding of the historical recolonisation of the smooth-coated otter observed in Singapore and predict the spatial and temporal population dynamics to assess the future persistence of this re-emerging species.

Material and methods

Modelling software

We used the spatially explicit individual-based model, RangeShifter to implement our study (Bocedi et al. 2014a, b, c, 2021). This model combines demography with a movement model incorporating the three distinct phases of dispersal enabling spatially realistic simulations to be run across complex landscapes. The three key aspects when building and parameterizing the software for a particular set of simulation experiments are the representation of the landscape, the demography and the dispersal. We provide details on each below but in summary we used a 50 m resolution landscape layer for the whole of Singapore, the individualized stage-structured population modelling capability provided as an option with the RangeShifter software, and to represent dispersal we used the stochastic movement simulator (SMS; Palmer et al. 2011) to explicitly model movements of the species throughout Singapore.

Landscape and patches

The landscape representing the different habitats encountered in Singapore was acquired from Gaw et al. (2019). It combined high quality satellite imagery from several sources. The original resolution of 30 cm was changed to 50 m to decrease computing time and match otter home range. Mangroves and freshwater bodies were defined as suitable habitat where the smooth-coated otter is able to reproduce (Theng and Sivasothi 2016). Dispersal costs were assigned according to habitat permeability based on expert opinion.

The patches, representing population spatial units in Rangeshifter, were based on data from Khoo and Sivasothi (2018), in which the distribution of the smooth-coated otter was recorded during field surveys. The minimum linear home ranges calculated for the 11 distinct otter groups identified in the aforementioned study were transformed into polygons representing habitat patches following the home range sizes described by Kruuk (2006) (Fig. 1). All patches followed waterbodies and/or watercourses.

Species parameters

The species parameters were acquired through a survey of the published literature and unknown parameters were inferred from expert opinion as well as demographic parameters of other otter species, notably, river otters *L. canadensis* and Eurasian otters *L. lutra* (Gorman et al. 2008, Spinola et al. 2008, Brzeski et al. 2013, Lampa et al. 2015). A simple sexual model with no explicit mating system with a proportion of males of 0.5 was implemented, with a stage-structured population (Table 1) and a sex and stage-dependent dispersal (Table 2).

Survival was scheduled between reproductive events, once a year (Hussain 1996, Theng et al. 2016, Khoo and Sivasothi 2018). For both juveniles and adults, in Singapore, survival rates were estimated based on long term surveys recording mortality rates described by Khoo and Sivasothi (2018) and Shivram et al. (2023). Sub-adult survival was kept identical to juvenile survival and the parameters (Table 1) reflected the percentage of individuals becoming adults or staying as sub-adults within one reproductive season. Mortality being relatively low for otters dispersing through Singapore, step mortality was set at 0.0001 per step.

The parameters used for fecundity were also extrapolated from Khoo and Sivasothi (2018) and also corroborated by other studies (Bungum et al. 2022, Shivram et al. 2023). Equilibrium densities of each patch were dependent on habitat type and were estimated from Brzeski et al. (2013) and Lampa et al. (2015). Density dependence acted on female fecundity so that females in patches at carrying capacity would delay reproduction.

For modelling dispersal movement, we used the stochastic movement simulator (SMS), that simulates stepwise nearest-neighbour movements informed by a cost surface (Palmer et al. 2011). Individual movements depend on three parameters: perceptual range (distance at which the individual can evaluate its surroundings), directional persistence (the tendency to which an individual will move in a straight line) and memory size (the number of previous steps used to calculate the directional persistence). As otters are semi-aquatic mammals, travelling is mostly done along water courses and across land to reach new colonizable habitats (Carranza et al. 2011). However, considering the heavily urbanized landscape of Singapore and the many reports of the species using the urban matrix to disperse (Khoo and Sivasothi 2018, Shivram et al. 2023), in this scenario, they are likely to have

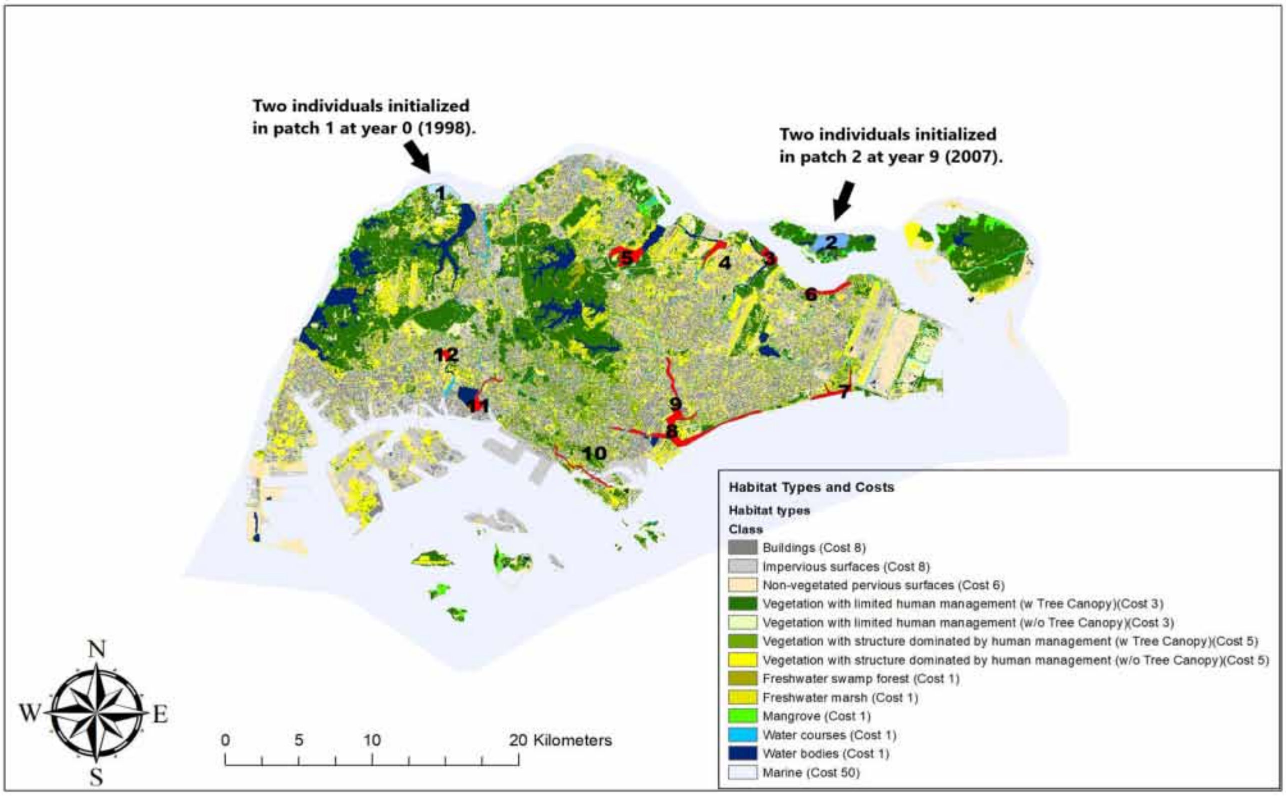

Figure 1. High resolution map of Singapores' habitats. Each habitat type is associated with a dispersal cost. Modelled patches are represented by the red areas and ID number. Patch 1 (light blue) represents the first colonisation event and patch 2 (blue) represents the second event.

a relatively large perceptual range. Furthermore, Khoo and Sivasothi (2018) observed otters travelling up to nearly 9 km in a short time frame, therefore, the perceptual range was set at (7×50 m = 350 m). Simulated trajectories resulting from a range of values of perceptual range and memory size were visualized and plausible combinations were selected by expert judgment.

As our parameters were largely based on evidence from closely related otter species and expert opinion, we undertook a sensitivity analysis to evaluate the robustness of our model to permutations (details in the Supporting information). To assess the model sensitivity, we compared mean population size at year 70 and percentage change relative to the baseline parameters used. The results of the sensitivity analysis showed that by increasing or decreasing survival and fecundity by a few points did not have a drastic impact on the overall population numbers at year 70. Hence giving confidence to the parameters chosen in providing consistent simulations.

Table 1. Transition matrix showing parameters of fecundity, development probability and survival probability for juveniles, sub-adults and adults.

	Juvenile	Sub-Adult	Adult
Juvenile	0	0	$F_A = 4.8$[1,2,5,6]
Sub-adult	$S_J = 0.9$[1,4]	$S_S = 0.23$[1]	0
Adult	0	$S_{SA} = 0.67$[1]	$S_A = 0.95$[1,3,4]

[1]Khoo and Sivasothi 2018.
[2]Feeroz et al. 2011.
[3]Spinola et al. 2008.
[4]Rutter 2018.
[5]Shivram et al. 2023.
[6]Bungum et al. 2022.

Simulations

Simulations were run over the course of 70 years. Results were first analyzed at 20 years (2018) to match the dynamics of the observed colonisation of the smooth-coated otter and then over the next 50 years (up to 2068) to predict the persistence of the population. While we have good information on the time that otters initially arrived and settled at two locations in Singapore, we do not have definitive information on how many arrived. While it is possible that new populations are founded by a group of otters splitting from a larger group and dispersing together, this seems unlikely for a dispersal event across the straight separating Singapore from Malaysia, and there is no observational information to support the arrival of a group. For simplicity, we assume that in each case there were two individuals, enough to enable breeding. Thus, in each simulation, two adult individuals were initialized in patch 1 at simulation year 0 (i.e. 1998) and another two individuals were initialized at simulation year 9 (i.e. 2007) in patch 2 (Fig. 1). 100 replicates were run using the same parameters and initialization procedures. Smooth-coated otter population abundance was counted every year

Table 2. Main parameters used into RangeShifter.

Parameters	Value
Scheduling of survival	between reproductive events
Density dependence in fecundity	yes
1/b, proxy of carrying capacity K (ind. ha^{-1})	mangroves: 0.05[1,2] water course/bodies: 0.05[1,2] other habitats: 0
Stage and sex-dependent emigration probability	density-independent sub-adult females = 0.1 sub-adult males = 0.5 adult females = 0.3 adult males = 0.7
Perceptual range	7 cells
Directional persistence	5
Perceptual range method	1
Memory size	12
Goal type	0
Step mortality	constant 0.0001
Dispersal – Settlement	females and males settle in a new patch if suitable and presence of mate

[1]Lampa et al. 2015.
[2]Brzeski et al. 2013.

before reproduction and thus, before juveniles are produced, hence total population numbers shown account for adults and sub-adults in the population.

Results

Unsurprisingly, for the population dynamics of a species starting out from very low abundances and for which demographic stochasticity is extremely strong, there was a substantial variation between replicate trajectories (Fig. 2). Our simulated results effectively showed a set of possible trajectories (given the model parameters) while our natural population trajectory was just a single realization of what might have happened. Amongst the 100 replicates was a set of simulations that resulted in population extinction (43 out of the 100) and a further set that remained at very low density for an extensive period prior to eventually establishing and growing. For those replicates (57 out of the 100) that did not result in extinction, the mean population size at the year 70 was 184.63 (± 9.23). Then there was a third group that exhibited relatively rapid population growth following the introductions. Our one empirical example of otter population growth (Khoo and Sivasothi 2018) falls within the range of outputs produced by this third set of results.

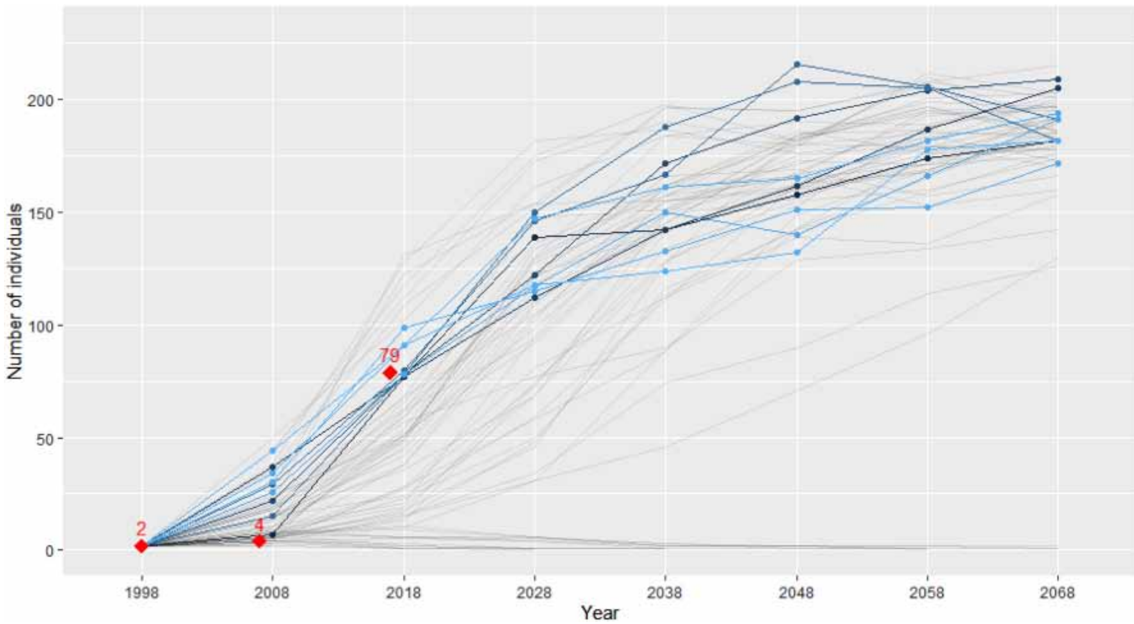

Figure 2. Modelled number of individuals over 70 years for each replicate. The coloured lines represent the replicates that reproduced the actual number of individuals (red diamonds) in the observed population in Singapore. The faded lines represent replicates that did not.

Out of the 100 simulation replicates, nine produced a population of 70–90 individuals in 2018, which is close to the 79 individuals actually counted in 2017 in Singapore (Fig. 2). Within those replicates, four came within one individual (78 n = 3, 80 n = 1). While the population was founded with two individuals in 1998 and two more in 2007, the mean simulated number of individuals from the nine replicates closest to our empirical results was 83.2 ± 5.1 in 2018. The settlement of an additional two otters in 2007 seemed to have a drastic effect on the overall population growth in those nine replicates, as the mean growth rate was 2.5 ± 0.7 between 1998 to 2008 and 5.6 ± 0.5 between 2008 to 2018. Finally, when looking at the future projections for population growth shown by the nine replicates, there was a stable increase until 2048, after which the population stabilized by 2068 with a mean number of individuals in the population of 189.7 ± 7.3 (Fig. 2).

The mean number of individuals per patch (sub-adults and adults) was calculated from the nine replicates that were closest to the empirical trajectory (Fig. 3). When comparing the characteristics of the otter populations in individual patches, in some cases there are close matches between the simulation outputs and the single natural patterns of observations. Specifically, patch 9 had the highest number of individuals in the observed distribution (13 individuals in 2017) and this was well reflected in the simulation (17 ± 3.4 individuals in 2018). Moreover, patches 10 and 12 had identical distributions between what was observed (seven and two individual otters respectively) and simulated (7 ± 2.6 and 2 ± 1.3 respectively).

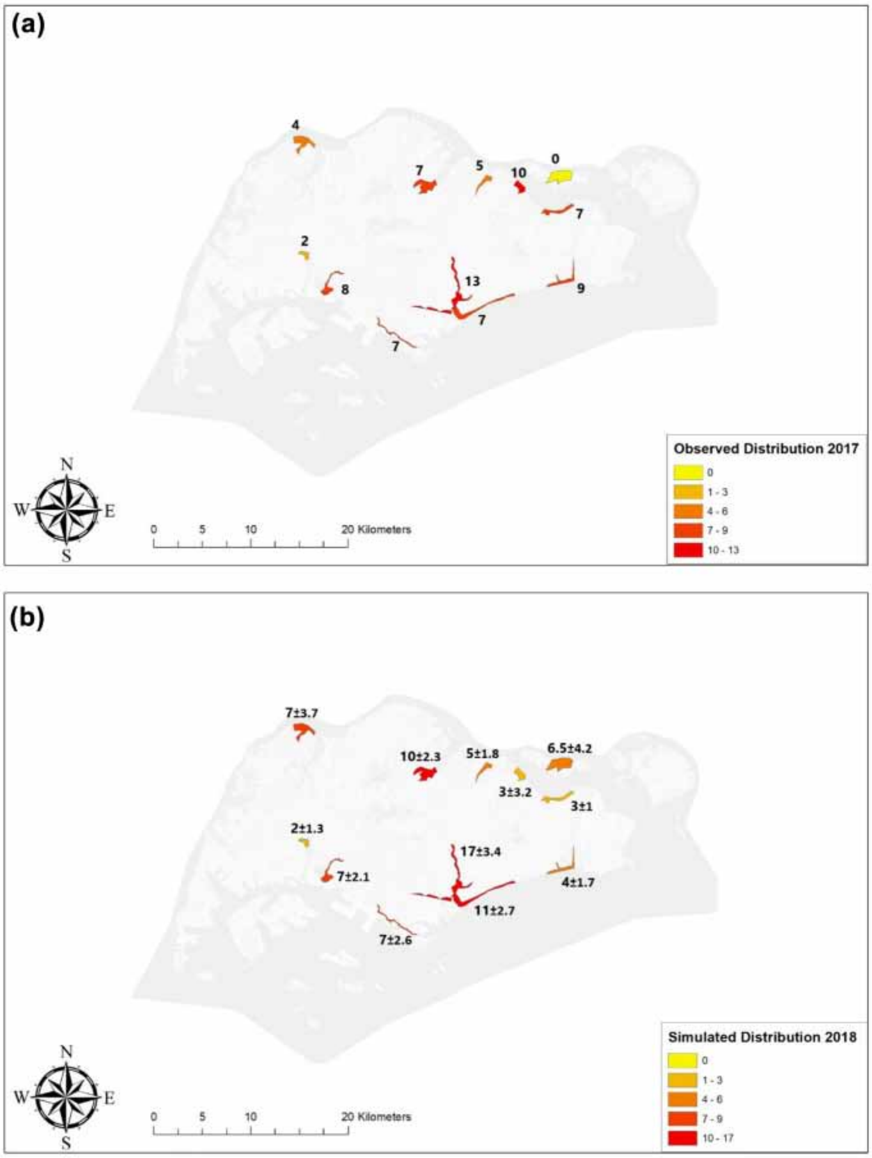

Figure 3. (a) Observed (2017) versus (b) simulated distribution (2018) of the smooth-coated otter in Singapore.

The simulated distribution however did not replicate as well the observed one in other patches (Fig. 3). Patch 2 had no individuals observed whereas the simulation resulted in 6.5 ± 4.2 individuals, nevertheless, three out of the nine successful replicates had 0 individuals in patch 2. Additionally, patches 4, 6 and 7 had considerably more individual otters in the observed distribution (10, 7 and 9 individuals respectively) compared to the simulated one (3 ± 3.2, 3 ± 1 and 4 ± 1.7 individuals respectively). More importantly, the simulated ratio of adults to sub-adults was not matched in any of the patches compared to what was observed in Singapore (Fig. 4). The number of sub-adults in the observed distribution was higher than in the simulation. Furthermore, some patches held sub-adults in the simulated distribution but not in the observed distribution and vice versa (Fig. 3–4).

Discussion

We used a spatially explicit individual-based model to provide understanding of the recent recolonisation of the smooth-coated otter in Singapore and forecast its future. Based on recent population numbers obtained from the literature, we examined whether the model was performant at reproducing the actual temporal and spatial dynamics of this newly formed population and predicting its future dynamics. Only 9% of the replicates accurately reproduced the observed number of individuals after 20 years. This result does not imply that the model is performing poorly. Rather it serves to emphasize how the stochasticity inherent in populations at small sizes can drastically affect the fate of the population. In this case, the model suggests that fortune favoured the otter, indicating that from the same starting conditions the population would, simply by chance, have been expected to become extinct 40% of the time. Further, when comparing the one natural population growth trajectory against the simulated trajectories that persisted, the natural trajectory falls into the group that grew in size relatively quickly – a further set had a much longer lag with the population remaining at lower abundance before the growth took off.

Compared to the latest census on the smooth-coated otter in Singapore in 2021, with a recorded number of 170 individuals (Shivram et al. 2023), our model underperformed, with a mean number of 99 ± 3.1 otters. However, it did predict what researchers are now seeing. There is a saturation of colonizable habitats, hence, the otter population has reached a plateau. This is evidenced by increased inter-specific competition between otter families, resulting in conflict and death of pups; the increased rate of mortality due to road kills because of dispersal along roads, and the lower rate of dispersal in juveniles and sub-adults otters, delayed by the aforementioned habitat saturation (Shivram et al. 2023). Another reason why our model underperformed compared to the observed situation in Singapore is that our model exclusively modelled appropriate habitats for otters as waterways and mangrove habitats but as the population has grown across Singapore, otters are now moving to occupy reservoir and watershed habitats (Shivram et al. 2023).

Undoubtedly, and as in the case in almost all ecological modelling exercises, the parameter values used in our model are not perfect. Some parameters, for which we could find no estimates for smooth-coated otter, had to be taken from

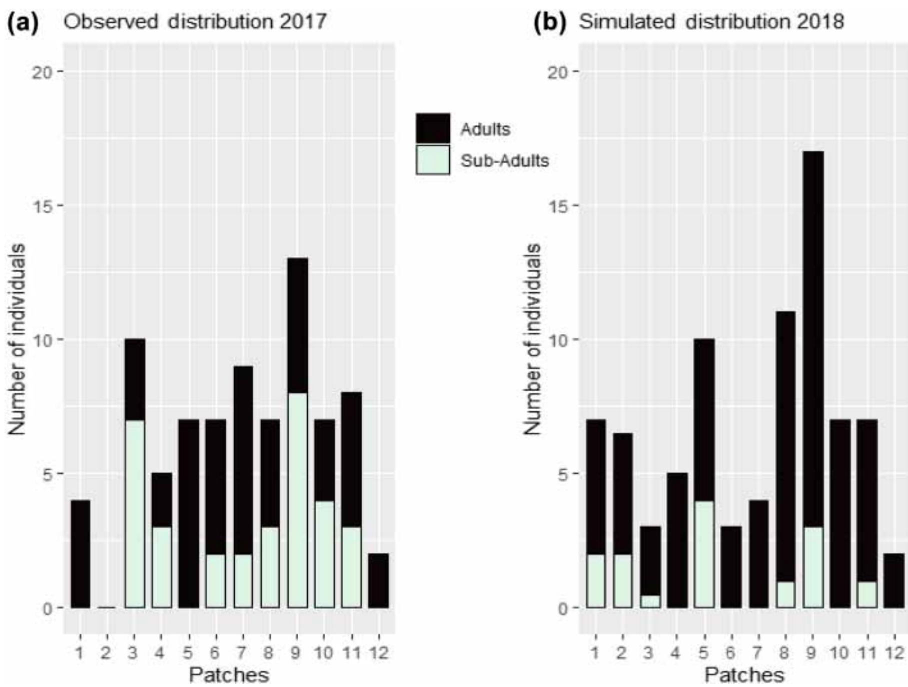

Figure 4. (a) Observed (2017) versus (b) simulated distribution (2018) of adult and sub-adults smooth-coated otter in Singapore (The simulated distribution is acquired from the mean number of individuals for all nine successful replicates).

closely related species (Table 1–2), notably parameters related to densities in the different habitats (1/b), which were inferred from river otters *L. canadensis*. As no information was available for smooth-coated otter on the emigration probability as well as the way individuals settle in a new patch (males and females may not need the presence of mates to settle into a new suitable patch), the parameter inputs into RangeShifter might have been under or overestimated. But despite those less precise parameter estimates, the model still provided reasonable population trajectories. This suggests that the values used were reasonable. Ideally, we might have used a pattern-oriented modelling approach (Gallagher et al. 2021), or even formal inverse fitting (Dominguez Almela et al. 2020), to improve parameter estimates of the model. However, given the inherent stochasticity present in the dynamics and given that a set of our replicates match well the observed dynamics it is unclear how this would provide additional value at this stage. In this case, for now it is better to retain our a priori estimates for the parameters.

Importantly, when the simulation was run without the addition of two individuals in 2007, the population either went extinct or struggled to reach high numbers of otters. The high extinction rate is most likely due to the small number of initial colonizers. For replicates where populations went extinct, they suffered from demographic stochasticity in the environment and the inability to colonize new patches as well as reproduce in sufficient numbers to sustain their population before the addition of new individuals in 2008. This reaffirms the importance of additional immigrants at the early stages of population development, allowing to rapidly increase population size and improve future persistence (Oro and Ruxton 2001, Santoro et al. 2016, Lee et al. 2018). By the end of the simulations, each patch contained 15–23 otters, which is well within the range of the largest recorded group of 16 individual in the Corbet Tiger Reserve in India (Nawab and Hussain 2012), and more recently, perfectly in range with the numbers recorded in Singapore, with group sizes between 17 to 24 otters (Shivram et al. 2023). This suggests that our density estimates, inferred from river otters and implemented in the model, are realistic and that density-dependence acts the same as in other less urbanized areas.

When looking more specifically at the distribution of individuals on occupied patches and the detailed number of adults and sub-adults per patch, successful replicates produced mixed results. The model generated the right number of individuals per patch but did not accurately produce the right ratio of adults and sub-adults with generally a lower number of simulated sub-adults compared to the observed ones. This discrepancy may be attributed to the fact that direct observations in the field often grouped juveniles and sub-adults because the two ages classes cannot be discriminated. On the contrary, simulations counted juveniles and sub-adults separately and thus, the number of sub-adults was lower. In the field, each count is meant as a snapshot as a few areas could not be sampled due to logistics and some areas were restricted. The amount of family groups and individuals throughout Singapore may be higher than what has been counted (MacKenzie 2005) and this might explain why our simulations have more individuals than observations. Nevertheless, those limitations should be reduced with an improvement of the knowledge of the smooth-coated otter in Singapore but also throughout its range. Because the population in Singapore is relatively accessible, some capture–recaptures should be possible and would be particularly useful to gain more insights into the local demographic parameters of the smooth-coated otter and determine whether this population living in a highly urbanized environment differs from other populations.

Otters being semi-aquatic carnivores, increased urbanization in most of their range presents challenges to their survival as it threatens key requirements for their subsistence, notably, access to suitable habitats, unpolluted water and sufficient food resources. For this reason, the smooth-coated otter was not considered to be able to persist in urban environments (Kamjing et al. 2017). Nevertheless, what has been observed in Singapore has proven the contrary. Due to the stable population increase both observed and simulated in Singapore, strains and threats to their subsistence are already appearing and will likely increase (Khoo and Sivasothi 2018, Khoo and Lee 2020). One of the reasons for the successful recolonisation of otters in Singapore was the positive perception of the species by the public (Khoo and Lee 2020). Indeed, the smooth-coated otter has become a flagship species for Singapore, symbolizing the incredible successful transformation the city has undergone. However, some recent trends have shown this positivity might be at risk, as isolated incidents of people being bitten or otters raiding private fishponds have been increasingly reported (Khoo and Sivasothi 2018). And the smooth-coated otter is not an isolated case in this regard. Many species, such as parrots in the Caribbean (Wiley et al. 2004) or mountain lions in North America (Clifford 1998) were hailed as flagship species after their populations rebounded to highlight successful recolonisation. But those successes also highlighted increasing conflict with people living in proximity to these animals. Much of the literature on human–wildlife conflict agrees that damage to property and attacks on humans result in a detrimental perception of wildlife, and these negative reactions often remain even after solutions have been found, causing increased hurdles for the persistence of the species (Messmer 2000, Karanth et al. 2013, Nyhus 2016). Therefore, in the longer-term, the successful recolonisation of smooth-coated otter might be jeopardized if conflicts with humans become too frequent.

Private organization and NGO's play a big role in continuing to educate and inform the citizens of Singapore and owners of private property about the species (Khoo and Lee 2020). However, potential human–otter conflicts resulting from issues like those mentioned above are not the only areas of concern. As modelled in this study, the species will likely reach carrying capacity in the next 40 years. Habitat space would then become clearly limiting, and future intraspecific competition for space and resources will likely become an issue, resulting in increased mortality from aggression between groups. Aggressivity might become a more common behaviour, worsening the negative interactions with humans. Road kills might also become a serious concern, as otters may disperse further and more frequently to find more suitable habitats (Khoo and Sivasothi 2018).

If the situation in Singapore remains stable and efforts to protect the smooth-coated otter through habitat management and public education continue, the current population should continue to increase in the next decades to finally reach carrying capacity. Our individual-based model should prove to be an effective tool if used alongside the ongoing monitoring of the species in Singapore and iterative improvement of the parameterization. It can provide a better insight into the future dispersal events of the smooth-coated otter in this urban environment and also aid in effective targeting of management strategies and allocation of resources, such as improving connectivity between suitable habitat patches and possibly creating new suitable areas for otter settlement. This study also has implications for the protection and management of the species in other parts of its range. In areas where smooth-coated otter populations are present but not monitored, this modelling approach could provide clarifications of local population status and pin-point areas where survey efforts should concentrate to help gather data on presence and abundance of the species. Where the smooth-coated otter persists in semi-urban or human-modified landscapes, replicating some of the environmental changes seen in Singapore coupled with a modelling approach would point out which areas could be managed to increase the survival of the species, what the impacts of different habitat types have and what effects some management strategies would have on the survival of the smooth-coated otter. Lastly, the restructuration of the Singapore has proven that it is possible to have viable populations of wildlife living in heavily urbanized environments. Many lessons should and could be taken by governments around the world to rewild their urban centers to improve biodiversity and allow charismatic species to recolonise their landscapes while educating local people to mitigate human–wildlife conflicts.

Highlights

Urbanisation is accelerating worldwide with drastic consequences for wildlife species and natural habitats. Re-colonisations of highly urbanised landscapes by mammals are rare events and highly stochastic in nature. Using individual-based models incorporating demography and dispersal can help reconstitute such re-colonisation events and predict the persistence of the population in the future. Understanding how species can subsist in urban landscapes is key to limit future loss of biodiversity.

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Author contributions

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Supporting information

The Supporting information associated with this article is available with the online version.

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