Modelling the Monitoring and Management of Cryptic Threatened Lizard Species in Mauritius

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Covid impact statement

I respectfully request that the impact of the Covid-19 pandemic on the research activity that contributed to this thesis is taken into consideration.

Due to the lockdown periods in the UK and Mauritius during 2020 and 2021, the focal part of the study (the translocation of lesser night gecko to Round Island) was delayed by two years. Field work had been planned for April – November 2020 and January – April 2021 to gain insight into the ecosystem, locate release sites, undertake a translocation and carry out the initial post-release monitoring whilst training an intern to continue collecting data in my absence. All fieldwork was delayed due to Mauritian border closures and instead had to be carried out between October 2021 and Dec 2022, during the 3rd and 4th years of study.

Following the recommendations of the NERC ARIES DTP who funded the project, I sourced an alternative project with my current supervisors that did not require the international travel that was delaying the original project, and I began work on that PhD project in July 2020. The project was examining the potential impact of a planned introduction of Guam kingfisher on the reptiles at the release site. In November 2020, a population of brown tree snakes were discovered at the release site, meaning it was no longer suitable and the project could not be continued. Therefore, we returned to the original project plan and made use of the sparse data available until field work became possible.

The partner organization in Mauritius, the Mauritian Wildlife Foundation, was also negatively impacted by the pandemic due to reduced tourism. This led to reductions in research budgets for the teams I worked with on Round Island and therefore there was less support available than planned during much of the fieldwork.

I am grateful to my supervisors for providing additional support throughout this period and to the NERC ARIES DTP and University of Kent for granting a 6-month extension to this project.

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Author Declaration

All chapters were written by Katie Bickerton, with editorial suggestions provided by supervisors John Ewen, Rachel McCrea, Stefano Canessa, Nik Cole & Jim Groombridge. All data analyses were carried out by Katie Bickerton with guidance from Rachel McCrea and Stefano Canessa. Details regarding additional collaborations and guidance for each chapter are provided below.

Chapter 2: The model described in the chapter was developed with technical support from Fay Frost and Rachel McCrea. The data used in the case study was collected by field teams from the Mauritian Wildlife Foundation, Durrell Wildlife Conservation Trust and the Mauritian National Parks and Conservation Service, led by Nik Cole and Rouben Mootoocurpen. This chapter has been published in *Ecological Applications*, and editorial suggestions from reviewers contributed to the chapter.

Chapter 3: The data used in this chapter were collected by field teams from the Mauritian Wildlife Foundation, Durrell Wildlife Conservation Trust and the Mauritian National Parks and Conservation Service, led by Nik Cole and Rouben Mootoocurpen. Katie Bickerton joined the field teams in collecting data during February & March 2022. Training in photo identification software and help processing images was provided by Rosemary Moorhouse-Gann.

Chapter 4: The data used in this chapter for release site selection and predator removal were collected by Katie Bickerton, with guidance from Nik Cole and Rouben Mootoocurpen, and support from the Mauritian Wildlife Foundation and Durrell Wildlife Conservation Trust. The translocation was a collaborative effort between the Mauritian Wildlife Foundation, Durrell Wildlife Conservation Trust, the Mauritian National Parks and Conservation Service and the Mauritian Forestry Service. The post-release monitoring data in 2022 were collected by Katie Bickerton with support from Ryan Law Yu Kam and field staff from the Mauritian Wildlife Foundation. Post-release monitoring data in 2023 were collected by Alex Ferguson with support from Rouben Mootoocurpen and field staff from the Mauritian Wildlife Foundation. Photo identification was carried out by Katie Bickerton and Alex Ferguson.

Abstract

The use of conservation translocations as a tool for restoration of biodiversity is becoming common practice in the conservation of threatened species. Despite this increase in use, guidance for translocations of reptiles, especially for prey species, is very limited. The cryptic nature of many reptile species further impedes efforts to effectively plan translocations and monitor released populations. This limited information leads to high uncertainty in estimated demographic parameters, which are often used to assess the outcome of translocations and then adaptively manage populations. An incomplete understanding of population dynamics further limits the ability to respond to stochastic events such as extreme weather events or environmental disasters.

Capture-recapture methods are commonly employed to monitor species where individuals can be uniquely identified. The statistical approaches applied to this survey data enable the estimation of demographic parameters such as population size, survival probability and probability of new entrants to a population. However, when working with translocated populations of threatened species, initial population sizes can be very small, leading to high uncertainty in estimated parameters.

In this thesis, I apply statistical methods to increase understanding of threatened reptile population dynamics following conservation management actions. I develop a bespoke capture-recapture model to improve the accuracy of estimates of demographic parameters for translocated populations. I compare the estimates of this model to a standard capture-recapture model (Jolly-Seber/JS model) using a simulation study, and case study of a reintroduced threatened gecko (the lesser night gecko, *Nactus coindemirensis*), in Mauritius. I further examine the demographics of cryptic reptile populations (Bojer’s skink, *Gongylomorphus bojerii* and lesser night gecko) following an environmental disaster in Mauritius, the MV Wakashio oil spill in 2020, using the bespoke capture-recapture model developed for the reintroduced population affected. Finally, I describe the planning process, translocation and initial monitoring for a reintroduction of lesser night gecko to Round

Island, Mauritius, combining existing knowledge with expert elicited recommendations to optimise decisions in an ecosystem where native predators were present.

I demonstrate that the use of standard JS models can lead to overestimates in initial population size of translocated populations where detection probability is below 0.3. The use of the modified JS model developed prevents this overestimation by accounting for translocated individuals, in addition to reducing overall uncertainty in parameter estimates. Results from the analysis of the Bojer’s skink and lesser night gecko populations following the MV Wakashio oil spill indicated limited variation in survival or body condition that could be attributed to the oil spill, due to delays in surveys during the Covid-19 pandemic. Expert recommendations and published literature led to the use of soft-release enclosures for translocation of lesser night geckos to Round Island and highlighted the risks of predation and dispersal. Predator removal, carried out prior to the release, led to population suppression by an estimated 67-75%, assessed using geometric removal models accounting for time-varying detection probability using covariates of survey effort. The analysis of monitoring data from the first seven months after release estimated a monthly survival probability between 0.75-0.92, and by the end of the study juveniles were present in all enclosures.

The findings presented in this thesis emphasize the need for suitable modelling of translocated populations of cryptic species in order to obtain more robust estimates of demographic parameters, better informing management actions and ultimately increasing the likelihood of translocation success. I demonstrate the need for thorough baseline surveys of populations with high risk of extinction, to allow better management following random stochastic events. Further, I highlight the requirement of continued monitoring of translocated populations to allow for accurate measures of success. The evidence I present provides guidance on collection and analysis of monitoring data on cryptic reptile species following conservation management actions.

Keywords: translocation, reintroduction, capture-recapture, reptile, conservation management

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1 Introduction

1.1 Conservation translocations

The use of translocations as a tool for the conservation of threatened species has increased drastically over the last three decades (Armstrong & Seddon 2008; Seddon *et al.* 2012; Seddon & Armstrong 2016; Swan *et al.* 2018; Evans *et al.* 2023). The International Union for the Conservation of Nature (IUCN) defines conservation translocations as the “deliberate movement of organisms from one site for release in another”, to provide “measurable conservation benefit at the levels of a population, species or ecosystem, and not only […] to translocated individuals” (IUCN/SSC, 2013). Despite this increase in use of translocations, failure rates have been high (Morris *et al.* 2021), especially considering that published studies are biased towards success stories (Fischer & Lindenmayer 2000; Bajomi *et al.* 2010).

There is also a taxonomic bias towards mammals and birds (Fischer & Lindenmayer 2000; Bubac *et al.* 2019), which makes understanding patterns of success in underrepresented groups like reptiles more difficult (Germano & Bishop 2009). Furthermore, there is a lack of information about reptile translocations: for many species, small size and highly cryptic behaviour (Bilby & Moseby 2022) make it difficult to track individuals post-release (Towns *et al.* 2016), limiting monitoring and therefore accuracy when evaluating success (Ewen & Armstrong 2008).

Translocations typically have three phases: establishment, growth and regulation (IUCN/SSC 2013). Each has its challenges. In the establishment phase, the highest risks are from immediate mortality and cost of release (Armstrong et al. 2017). Reintroductions in the presence of predators increase the risk of mortality, potentially reducing the size of the population and thus the chance of establishment (Tobajas *et al.* 2020), as smaller populations are less likely to persist due to factors such as Allee effects and genetic drift (Germano & Bishop 2009). A further risk to establishment is the stress associated with the capture and movement of the individuals being translocated, which can be exacerbated by the presence of predators at the release site (Teixeira *et al.* 2007; Dickens *et* *al.* 2010). This can increase dispersal away from the release site, reducing the likelihood of establishment within the selected release habitat and limiting reproduction (Knox & Monks 2014), especially in species with a small home range (Bohm *et al*. 2016). To minimize these risks, managers often use soft-release enclosures, where translocated individuals are held under controlled conditions at the release site, for acclimatisation prior to release (Griffith *et al.* 1989; Armstrong & Seddon 2008). Several studies have demonstrated that this approach can indeed favour anchoring at the release site (Knox *et al.* 2017; Nafus *et al.* 2017; Flynn-Plummer & Monks 2021; Resende *et al.* 2021; Linhoff & Donnelly 2022), but also that it is more costly and not beneficial to all species (de Milliano *et al.* 2016; Bilby & Moseby 2023).

In the growth and regulation phases (in addition to establishment), stochastic events (such as oil spills, extreme weather events and disease outbreaks), can threaten population viability, both directly due to increased mortality, or indirectly through reduction of resources (Bertolero *et al.* 2018). Several studies have demonstrated that environmental stochasticity can limit population growth and substantially increase extinction risk, in both large and small populations (Caughley 1994; Ovaskainen & Meerson 2010; Bertolero *et al.* 2018), and therefore can impact populations in both growth and regulation phases. This impact is particularly apparent in long-lived species, where small declines in adult survival can have greater impacts on population size (Samaranayaka & Fletcher 2010). Demographic stochasticity can also limit growth but is more of a risk when populations are small and therefore at earlier stages of a translocation (Ovaskainen & Meerson 2010). Variation in life-history patterns between species, often referred to as the "fast-slow continuum" (Salguero-Gomez *et al.* 2016), can impact rates of establishment and growth. In slow species, where reproductive output is low and lifespan long, initial survival is generally high following a translocation however growth is slow due to the low reproductive rates (Albrecht *et al.* 2018; Ducatez & Shine 2019). On the other hand, species with fast life history tend to reproduce quickly, therefore grow more quickly but survival is lower reducing success in the establishment phase (Albrecht *et al.* 2018; Ducatez & Shine 2019). The reintroduction literature regularly reports on the establishment of the focal species, however, rarely focuses on long-term growth or community level impacts (Amstrong & Seddon 2008; Taylor *et al.* 2017). This is particularly important as reintroductions are commonly part of restoration projects, and a lack of awareness of community level interactions can have collateral impacts on species already present within the release ecosystem (Baker *et al.* 2019). This could lead to increased competition for resources, especially within heavily altered landscapes, reducing native populations and thereby reducing the chance of successfully restoring the ecosystem (Ferretti *et al.* 2015). Ongoing management is required throughout all phases of translocations, due to the length of time needed to determine success, especially in long-lived species (Germano & Bishop 2009; Canessa *et al.* 2016; Bubac *et al.* 2019). Decisions are required as part of management, either for iterative actions (such as whether and how to reinforce a population), or in response to unexpected events (Armstrong & Seddon 2008). Such decisions should ideally be based on pre-defined indicators of individual or population status, for example, parameters estimated from monitoring, such as survival probability or observed variation in body condition (Ewen *et al.* 2014). Statistical models can be used to inform decisions by estimating demographic parameters from monitoring data, that determine variation in population dynamics (Armstrong & Seddon, 2008). For this reason, monitoring of translocated populations is a vital part of management (Bertolero *et al.* 2018; Bubac *et al.* 2019). However, monitoring presents its own challenges, especially in cryptic species, which can be time consuming to find and capture (Towns *et al.* 2016).

Quantitative measures of successful population establishment following reintroduction are largely related to population growth, survival and reproduction (Morris *et al.* 2021). Obtaining estimates of these parameters from wild populations is challenging and a common survey method is the use of capture-recapture models (Dieterman *et al.* 2010; Dolny *et al.* 2018; Moseby *et al.* 2018; Aguirre *et al.* 2019). These depend on individuals being recaught or resighted and identified individually within a known time period. The data collected from capture-recapture surveys can be used to estimate demographic parameters such as probabilities of survival, new entrants to the population (e.g. recruitment or immigration) and detection, as well as trends in abundance (Lebreton *et al.* 1992;

Pradel 1996). The development of capture-recapture models began with the use of marked animals for estimating survival in the 1930s (Jackson 1933, 1939), however few general models were developed until 1960s (Pollock 2000). When general models were developed, they either focused on open or closed populations (Seber 1986). Closed population models are applicable when populations have been monitored over short time spans therefore impacts of recruitment, mortality and migration are assumed negligible (Seber 1986). The Lincoln-Petersen estimator is the most simple of the general closed population models and assumes that over two capture occasions, where individuals of a population (N) are marked in the first (M) and recaptured (m) in a wider sample (n) in the second, the proportion of marked individuals recaptured in the second sample (m/n) is equal to the proportion marked in the entire population (M/N) (Seber 1982; Pollock 2000). Open population models account for recruitment, mortality and migration, allowing longer time periods to be considered (Pollock 2000). The first general open population model was developed separately by Jolly and Seber (Jolly 1965; Seber 1965), and was designed to estimate abundance, survival probability and number of births by assuming probability of capture and survival did not vary between individuals within the population (Pollock 2000). In the 1990s, interest in estimating survival as opposed to abundance led to a focus on the Cormack-Jolly-Seber model (Cormack 1964; Jolly 1965; Seber 1965), which is conditional on the first capture of each animal but does not assume how newly marked animals are obtained, as is the case in the Jolly-Seber model (Lebreton *et al.* 1992). Development of user-friendly software such as Program MARK (White & Burnham 1999), and the associated R package *RMark* (Laake 2013), has massively increased the use of capture-recapture models in estimating demographic parameters in ecology (Pollock 2000).Jolly-Seber (JS) models (Jolly 1965; Seber 1965) enable estimation of population size. However, when working with translocated populations, initial population size can be very small and remain small during the early establishment phase, prior to reproduction or recruitment of juveniles to the adult population, which can lead to substantial uncertainty in abundance estimates (Hernandez *et al.* 2006). The low detection probabilities associated with cryptic species, especially reptiles, further reduces sample sizes, increasing uncertainty. Technological advances are increasing the quantity and resolution of data available, leading to increasing development of large, complex models (McCrea *et al.* 2023) however these advances are still limited in small cryptic species, leading to need for approaches that make best use of sparse data sets. High uncertainty can limit decision making, and prevent suitable conservation actions from being taken, therefore minimizing uncertainty is a key aim in translocation programmes (Converse *et al.* 2013; Panfylova *et al.* 2019). Expert elicitation is one widely used tool that can be utilised to inform decisions when data is insufficient, and uncertainty is high (Runge *et al.* 2011; Martin *et al.* 2012). This can be particularly useful in scenarios where failure rates have been high, such as with reptile translocations, and due to publication bias, where available information is low (Germano & Bishop 2009). There are a broad variety of elicitation methods to ensure expert judgements can be elicited both efficiently and robustly (Runge *et al.* 2011; Drescher *et al.* 2013). The most common method used in ecological decision making is the Delphi process and its derivatives (Burgman *et al.* 2011). Broadly, the Delphi method consists of gathering input to estimate a parameter by (1) gathering independent input on the parameter in question from each expert, (2) sharing the results and justifications with the group of experts and allow them to adjust their estimates then (3) reshare their estimates and come to a conclusion as a group (Burgman *et al.* 2011; Runge *et al.* 2011; Martin *et al.* 2012). The variation in estimates is often included to account for uncertainty (Runge *et al.* 2011). In group decisions, variation in individual opinion can be lost or overcome by dominant members of a group (Martin *et al.* 2012), estimates can be limited by the ability of an expert to communicate their opinions or by the way their responses are interpreted, and it has been demonstrated that on average, experts exhibit overconfidence in their estimates (Speirs-Bridge *et al.* 2010). Using a structured approach, such as the Delphi method, allows multiple for opinions to be gathered (Martin *et al.* 2012), prevents dominant members of a group from biasing opinions by collecting individual opinions (Burgman *et al.* 2011; Martin *et al.* 2012) and has been shown to reduced bias and error in elicited responses (McBride *et al.* 2012; Drescher *et al.* 2013).

1.2 Mauritius as a model system

The majority of tropical islands are part of a biodiversity hotspot, where disproportionately high concentrations of endemic species are found (Myers *et al.* 2000). Island ecosystems have disproportionately high levels of endemism and are highly vulnerable to disturbance (Courchamp *et al.* 2003). The second largest threat to these ecosystems (first being habitat degradation) are invasive species, especially in island ecosystems (Courchamp *et al.* 2003; Emery *et al.* 2020; Cox *et al.* 2022). Mauritius, as part of the Mascarene hotspot, matches this trend, especially with regard to reptiles. The European colonization of Mauritius led to the introduction of a suite of non-native invasive species including rats (*Rattus rattus* and *R. norvegicus*), cats (*Felis domesticus*), mongoose (*Herpestes javanicus*), goats (*Capra aegagrus hircus*), rabbits (*Oryctolagus cuniculus*) and Asian house geckos (*Hemidactylus frenatus*). Non-native species introductions together with large scale habitat loss are thought to have led to the extinction of most reptile species on the main island of Mauritius (Bullock *et al.* 1985; Bullock *et al.* 2002; Cole *et al.* 2005), with the exception of the two species of giant tortoise that were predominantly driven to extinction by overexploitation as a food source (Stoddart *et al.* 1979). The remaining reptile species were restricted to the outlying islands surrounding Mauritius, with several species only found on Round Island which was never invaded by predatory mammals: the Telfair's skink (*Leiolopisma telfairii*), Gunther's gecko (*Phelsuma guentheri*), keel-scaled boa (*Casarea dussumieri*) and Durrell's night gecko (*Nactus durrellorum*).

Round Island has provided source populations for reintroductions of Telfair's skink (Michaelides *et al.* 2015; Cole *et al.* 2018a), Gunther's gecko (Cole *et al.* 2018c) and keel-scaled boa (Cole *et al.* 2018b) to other islands of Mauritius. Additional reintroductions and reinforcements have been carried out on the southeast islets of Mauritius with the Bojer's skink (*Gongylomorphus bojerii;* du Plessis *et al.* 2019) and lesser night gecko (*Nactus coindemirensis;* Bickerton *et al.* 2023). However, at the time this thesis began, there was yet to be a translocation of a prey species to a location where predators were present. The previous experience and long-term monitoring data available from Mauritius provides a suitable model system for trialling a prey species reintroduction which can subsequently be applied to other systems where data is less readily available. The reptile communities on Mauritian islands and use of reintroductions to restore these communities provide an ideal model system to improve understanding of the best management and monitoring practices for cryptic reptiles.

1.3 Aims and objectives

The aim of this thesis is to develop and apply statistical methods to capture the dynamics of translocated reptile populations, under different management actions and environmental variation, and to use this information to plan a reintroduction, and the associated post-release monitoring, of a threatened prey species into a system where native threatened predators are present.

Specifically, I aim to test the suitability of standard capture-recapture models to estimate demographic parameters of translocated populations of a cryptic prey species, the lesser night gecko, in Mauritius, and develop modifications of those models to improve accuracy of predictions (**Chapter 2**). I will then apply the methods developed, along with suitable methods for non-translocated populations, to detect variation in population dynamics of lesser night gecko and Bojer's skink following an environmental disaster, the MV Wakashio oil spill (**Chapter 3**). I will then combine the findings of these studies with expert knowledge to aid the translocation and post-release monitoring of a prey species (lesser night gecko) into a system with threatened endemic predators (**Chapter 4**).

1.4 Thesis structure

In **Chapter 2**, I present a novel modification for the JS model for translocated populations. I demonstrate, using a simulation study, that accuracy of predictions can be improved by accounting for translocated individuals, and that not constraining the standard JS model can lead to overestimates of population size when detection probability is low. I use a case study of a cryptic reptile translocation, the lesser night gecko reintroduction to Ile Marianne, Mauritius, in 2011, to further demonstrate the increased precision in demographic parameter estimates when using the modified JS model in comparison to the standard JS model. This work has been published in *Ecological Applications* along with the associated model code.

In **Chapter 3**, I investigate the impacts of the MV Wakashio oil spill in 2020 on two endemic threatened reptiles, the lesser night gecko and Bojer's skink. Populations, both historical and recently translocated, of both species are present on extremely low-lying islands close to the site of the spill, which due to high winds led to contamination within terrestrial ecosystems. This is the first study to examine the impact of an oil spill on the population dynamics of terrestrial reptiles. I used capture-recapture models to estimate demographic parameters for each reptile population, including the modified JS model described in **Chapter 2**, for previously translocated populations.

In **Chapter 4**, I outline the process of planning a reintroduction of lesser night geckos to Round Island, Mauritius. I describe the factors considered during the planning stages, especially with regard to choosing a release strategy, including previous data from the case study used in **Chapter 2** and semi-structured interviews of herpetofauna experts. Following this, I describe the aims of the reintroduction: to minimize predation and dispersal, and the construction of soft-release enclosures and targeted predator removal surveys. Finally, I explain the translocation process and post-release monitoring that took place over the first seven months following release, providing initial estimates of survival.

Chapter 5 provides an overview of key findings from this thesis and discusses how they interlink to better inform translocations, management and monitoring of cryptic reptile populations. Future directions of study are highlighted for both the study system and the field of reintroduction biology on a broader scale.

2 Avoiding bias in estimates of population size for translocation management

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2.1 Abstract

Mark-recapture surveys are commonly used to monitor translocated populations globally. Data gathered is then used to estimate demographic parameters, such as abundance and survival, using Jolly-Seber (JS) models. However, in translocated populations initial population size is known and failure to account for this may bias parameter estimates which are important for informing conservation decisions during population establishment. Here, we provide methods to account for known initial population size in JS models by incorporating a separate component likelihood for translocated individuals, using a maximum-likelihood estimation, with models that can be fitted using either R or MATLAB. We use simulated data and a case study of a threatened lizard species with low capture probability to demonstrate that unconstrained JS models may overestimate the size of translocated populations, especially in the early stages of post-release monitoring. Our approach corrects this bias; we use our simulations to demonstrate that overestimates of population size between 78-130% can occur in the unconstrained JS models when detection probability is below 0.3, compared to 1-8.9% for our constrained model. Our case study did not show an overestimate; however, accounting for the initial population size greatly reduced error in all parameter estimates and prevented boundary estimates. Adopting the corrected JS model for translocations will help managers obtain more robust estimates of population size of translocated animals, better informing future management including reinforcement decisions, and ultimately improving translocation success.

Key words: capture-recapture; conservation translocation; lesser night gecko; mark-recapture; *Nactus coindemirensis;* reintroduction

2.2 Introduction

Conservation translocations are increasingly used in the conservation of threatened species (Seddon *et al.* 2014) and as part of ecological restoration programmes (Ewen & Armstrong 2008). A conservation translocation is defined as the deliberate movement of organisms from one site to another with beneficial outcomes at population, species or ecosystem level (IUCN/SSC 2013). One of the key aims of a translocation, and a commonly used metric of success, is whether survival of released individuals and their progeny allows the establishment and persistence of a new population (Armstrong & Seddon 2008). Determining this requires intensive post-release monitoring which can be difficult when individuals are hard to detect (Sutherland *et al.* 2010). Low detection hampers distinction between recruitment into a new population versus loss due to post-release dispersal or mortality (Armstrong & Seddon 2008; Converse *et al.* 2013). Additionally, translocated populations are initially small, meaning they can be at risk of Allee effects (Allee 1931; Armstrong & Seddon 2008).

Managers need estimates of population size and other vital rates to make decisions, especially during the early establishment phase, for example whether to stop or continue releases, or to provide additional in-situ management (Armstrong & Seddon 2008). To allow tracking and estimation, animals are usually marked to enable individual identification (e.g. coloured bands, microchips, radio transmitters etc.) or photographed if individuals have unique markings. Individuals can then be surveyed using mark-recapture methodologies, and demographic parameters estimated (Lebreton *et al.* 1992), such as survival and fecundity probabilities, and changes in abundance. One type of mark-recapture model is the Jolly-Seber (JS) model, which can be used to estimate probabilities of survival, capture, new entrants into the population and population size (Jolly 1965; Seber 1965). JS models are commonly used to monitor translocated populations (Dieterman *et al.* 2010; Dolny *et al.* 2018; Moseby *et al.* 2018; Aguirre *et al.* 2019). However, the small size of translocated populations, especially in the initial establishment phase, can create considerable uncertainty in abundance estimates (Hernandez *et al.* 2006). A further potential difficulty is that JS models assume a proportion of the population is caught at each survey occasion. This assumption is violated initially in a translocated population as the first survey is the release, where all individuals in the population are recorded, and capture probability is equal to 1. As far as we are aware, no examination has been made on how failure to account for the known number of individuals at the first occasion biases abundance estimates, nor has it been accounted for when modelling translocated populations.

In this study, we assess whether accounting for known initial population size affects abundance estimates in JS models. We test this by constructing a modified JS model with separate likelihood components for translocated and wild born individuals which we compare to a standard JS model likelihood. We use a simulation study and a translocated population of lesser night gecko (*Nactus coindemirensis*), in Mauritius, to compare the models. Our case study species was chosen due to its low capture probability which can cause high levels of uncertainty in mark-recapture population estimates. Lesser night geckos are small, nocturnal and cryptic, which makes them difficult to capture (Bullock *et al.* 1985; Cole *et al.* 2021). The lesser night gecko reintroduction is a typical example of a translocation within a species known historical range (IUCN/SSC 2013) where long-term mark-recapture studies have been undertaken post-release. We provide methods to modify standard JS models in R (4.3, R Core Team 2023) and MATLAB (MATLAB 2023), to account for known initial population size. We show that not accounting for initial population size within JS models can lead to overestimates in abundance, particularly in species with low detection probability.

2.3 Methods

2.3.1 Translocation Jolly-Seber model

We propose a bespoke mark-recapture model which accounts for translocated individuals, building on the POPAN formulation of the Jolly-Seber (JS) model (Schwarz and Arnason 1996), which we refer to as the translocation JS model. Let h_i denote the encounter history of individual i which is born into the population and let h_i^* denote the encounter history of a translocated individual i. Suppose individual i is first captured on occasion f_i and last captured on occasion δ_i. $x_{ij} = 1$ if individual i is captured at occasion j and $x_{ij} = 0$ otherwise. Let τ denote the occasion that new arrivals start entering the population, let D denote the number of observed individuals (including translocated individuals) and let n_0 denote the number of translocated individuals, and assume that these are ordered as the first n_0 of the D observed individuals.

We define parameters:

N: superpopulation of individuals born into the population (i.e., not including translocated individuals)

ϕ_t: probability an individual who is alive at occasion t remains alive in the study area until occasion $t + 1$ (often referred to as apparent survival probability)

p_t: probability an individual who is alive and in the study area at occasion t is captured on this occasion.

β_{t-1}: proportion of the superpopulation that arrive between occasions $t - 1$ and t, and are first available for capture at occasion t. Note that $\beta_j = 0$ for $t = 1, \dots, \tau - 1$ and $\sum_{j=\tau}^{T} \beta_j = 1$.

The likelihood for the joint model of translocated individuals and individuals hatched post translocation is defined by equations 2.1-2.4:

$$L(\boldsymbol{N},\boldsymbol{\phi},\boldsymbol{p},\boldsymbol{\beta};\boldsymbol{x}) \propto \frac{N!}{(N-D)!}\prod_{i=1}^{n_0}\Pr(h_i^*)\prod_{i=n_0+1}^{D}\Pr(h_i)\times\Pr(h_0)^{N-D} \quad (2.1)$$

where

$$\Pr(h_i) = \sum_{b=\tau}^{f_i}\sum_{d=\delta_i}^{T}\beta_{b-1}\left(\prod_{j=b}^{d-1}\phi_j\right)(1-\phi_d)\left\{\prod_{j=b}^{d}p_j{}^{x_{ij}}(1-p_j)^{1-x_{ij}}\right\} \quad (2.2)$$

$$\Pr(h_i^*) = \sum_{d=\delta_i}^{T}\left(\prod_{j=1}^{d-1}\phi_j\right)(1-\phi_d)\left\{\prod_{j=1}^{d}p_j{}^{x_{ij}}(1-p_j)^{1-x_{ij}}\right\} \quad (2.3)$$

$$\Pr(h_0) = \sum_{b=1}^{T}\sum_{d=b}^{T}\beta_{b-1}\left(\prod_{j=b}^{d-1}\phi_j\right)(1-\phi_d)\left\{\prod_{j=b}^{d}(1-p_j)\right\} \quad (2.4)$$

The likelihood function is then numerically optimised to evaluate the maximum-likelihood estimates of parameters N, ϕ, p and β. The derived estimates of N_t, the number of individuals in the population at occasion N, can be obtained by using the recursion (Equation 2.5):

$$N_{t+1} = N_t\hat{\phi}_t + N\hat{\beta}_t, (2.5)$$

where $N_1 = n_0$.

Confidence intervals for directly estimated and derived parameters are obtained using a non-parametric bootstrap procedure (DiCiccio & Efron 1996). Group-effects can be accommodated within this model, but it should be noted that separate estimates for N, denoted by N_g will be obtained for each group and summed to give the total value of N given in the results (King and McCrea 2019), since the likelihood (Equation 2.6) incorporating group effects will be:

$$L(\boldsymbol{N},\boldsymbol{\phi},\boldsymbol{p},\boldsymbol{\beta};\boldsymbol{x}) \propto \prod_{g=1}^{G}L\left(\boldsymbol{N_g},\boldsymbol{\phi_g},\boldsymbol{p_g},\boldsymbol{\beta_g};\boldsymbol{x_g}\right) \quad (2.6)$$

where x_g denotes the encounter histories for individuals from group g and the parameters with subscript g denote the parameters as defined above but with group-dependence.

The translocation JS model can be fitted through constraining the POPAN JS model, such that the initial value of p and β are set to 1 and 0 respectively until it is biologically feasible for new entrants to have joined the population. In the following analyses, we fitted these models using our bespoke code and a standard unconstrained POPAN formulation of the JS model. We also compared estimates from these models with those from mark-recapture R packages *rMark* (Laake 2013) and *marked* (Laake *et al.* 2013). Parameters can be generalised to include temporal (γ_t) covariates, such that $\text{logit}(\phi_{it}) = \theta_1 + \theta_2\gamma_t$.

2.3.2 Simulation study

To compare our translocation JS model with the unconstrained POPAN formulation of the JS model (hereafter referred to as the standard JS model), we simulated capture histories of translocated populations based upon a standard range of parameter values from the literature. The parameters N, β, ϕ and p can all be estimated from mark-recapture survey data using the POPAN formulation of the Jolly-Seber model (Schwarz & Arnason 1996). By simulating populations, we were able to compare known parameter values with model estimates and assess the accuracy of estimates under different scenarios.

We tested 12 translocation scenarios (Table 2.1) to reflect the variety of situations commonly encountered in conservation translocations. All simulated data were in the form of capture histories across 10 evenly spaced 6-month intervals. We varied N_1 between 15 and 30 and N between 500 and 2000. For all scenarios, we set monthly ϕ to be broadly applicable to all vertebrate species using a random uniform distribution between 0.94-0.99 (bounds are upper and lower quartiles of vertebrates in the DatLife database; DatLife 2021) to allow for stochasticity between surveys. Since the translocation release is counted as the first survey occasion, the initial $p = 1$, as all individuals in the population are detected during this “survey”. The remaining values of p were simulated using a random uniform distribution within intervals specific to the scenario (low = 0.1-0.3; mid = 0.4-0.6; high = 0.7-0.9) as p is highly variable across different animal species. A range was again used to allow for stochasticity. Entry probabilities must sum to 1 within JS models and the first entry β_0 is the proportion of the total population translocated ($\frac{N_1}{N}$). In most translocations, it will be several surveys before new entrants are recorded in the adult population therefore we set $\beta_{1,2} = 0$, the remaining values were generated from a random uniform distribution between 0.1-0.2, then scaled to ensure the values summed to 1 for survey occasions $\beta_{3:K}$. This delay is dependent on the life history of the species being translocated (i.e., gestation period, life stages, recruitment time), the time between surveys and whether non-adult life stages are included as part of the population being estimated.

Table 2.1: Parameter values used for each simulation scenario: total population size (*N*), number of individuals translocated therefore initial population size (N_1), entry probability (β), annual survival probability (ϕ) and capture probability (*p*).

Scenario	**N_1**	**N**	**β***	**ϕ***	**P***
1	15	500	0.1-0.2	0.94-0.99	0.1-0.3
2	15	500	0.1-0.2	0.94-0.99	0.4-0.6
3	15	500	0.1-0.2	0.94-0.99	0.7-0.9
4	30	500	0.1-0.2	0.94-0.99	0.1-0.3
5	30	500	0.1-0.2	0.94-0.99	0.4-0.6
6	30	500	0.1-0.2	0.94-0.99	0.7-0.9
7	15	2000	0.1-0.2	0.94-0.99	0.1-0.3
8	15	2000	0.1-0.2	0.94-0.99	0.4-0.6
9	15	2000	0.1-0.2	0.94-0.99	0.7-0.9
10	30	2000	0.1-0.2	0.94-0.99	0.1-0.3
11	30	2000	0.1-0.2	0.94-0.99	0.4-0.6
12	30	2000	0.1-0.2	0.94-0.99	0.7-0.9

***** Where ranges of values are given, values were selected randomly from a uniform distribution in the interval of these values.

To simulate capture histories, we first simulated presence histories by randomly assigning when each individual entered the population using a random multinomial distribution with a probability of β_k (k = survey occasion). We then determined whether the individual survived to the next survey occasion using a Bernoulli distribution with a probability of ϕ_k. If the individual does not survive, it is removed and the remainder of the surveys are marked as 0 for absence. From each individual's presence history, we then simulated a capture history. For each occasion where the individual was present, we used a Bernoulli distribution with probability of p_k to determine whether the individual was caught and marked as 1 for seen, and 0 for not seen.

We simulated each scenario 250 times, and estimated values of N, β, ϕ and p using the translocation and standard JS models, with constant N, ϕ and p and time dependent β (from which N_t was calculated by recursion). We calculated the difference between the simulated parameter values and the estimates from the translocation and standard JS models. Both models can be run using R (R Core Team 2023) or MATLAB (MATLAB 2023); we performed our simulations in MATLAB because it allowed faster optimization.

2.3.3 Case study

To demonstrate implementation of the translocation JS model for a real-world case study, we fitted the model to a dataset of the lesser night gecko, one of three endemic *Nactus* species found in Mauritius (Arnold & Jones 1994, Arnold 2000) and currently classified as "Vulnerable" by the IUCN Red List (Cole *et al.* 2021). Lesser night geckos are nocturnal, elusive and the smallest of the Mascarene *Nactus* species with adult snout-to-vent length (SVL) of 30.9mm ± 1.4 (standard error) in males and 33.7mm ± 1.6 in females (Goble & Goetz 2011). Individuals are uniquely identifiable by their dark brown dorsal pattern, making the species a suitable candidate for mark-recapture surveys (2.7.1 Supplementary Information: Figure S2.1). Lesser night geckos were likely widespread across Mauritius prior to European colonisation in the 16th century (Arnold 1980; Cole *et al.* 2005). However, human colonisation resulting in habitat destruction and the introduction of non-native mammal and reptile species, caused the decline and loss of lesser night gecko populations from most of their range (Cole *et al.* 2005). They are now restricted to three offshore islands: Gunner's Quoin (72.9 ha), Ilot Vacoas (1.1 ha) and Pigeon House Rock (1.4 ha) (Cole *et al.* 2021; 2.7.1 Supplementary Information: Table S2.1), as well as a captive population at Durrell Zoo, Jersey, Channel Islands (Figure 2.1).

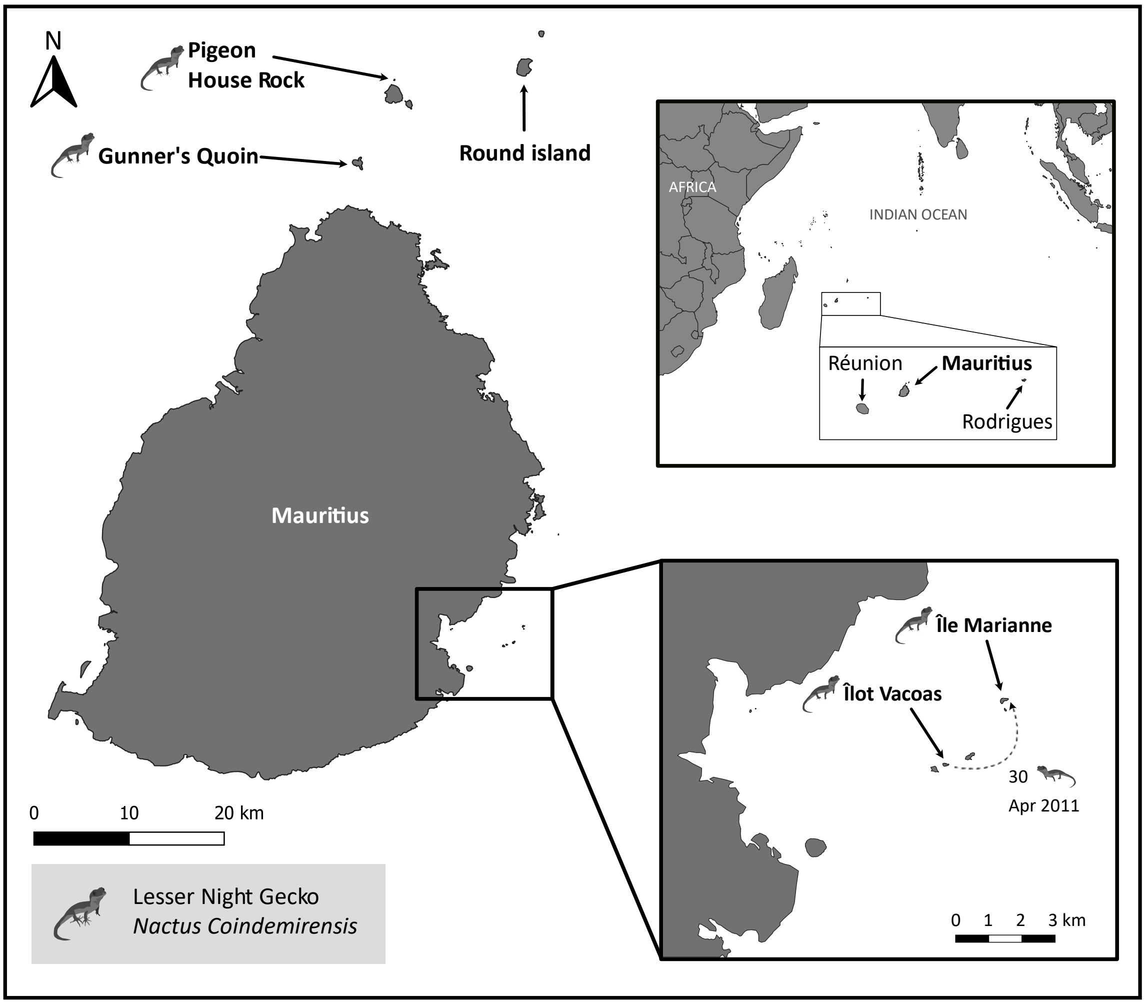

Figure 2.1: Map of Mauritius and outlying Mauritian islands indicating translocations between islands. The dotted line indicates a translocation of lesser night geckos (*Nactus coindemirensis*) with the number of individuals translocated and the month and year of translocation.

A translocation of 75 lesser night geckos was carried out in April 2011 to Ile Marianne, a 2.1 ha island 6.15 km off the SE coast of Mauritius. Wild individuals from nearby Ilot Vacoas (2.4 km southwest of

Ile Marianne) were caught and processed (photographed, weighed, measured and sexed) on 13th of April, then translocated by boat and released upon arrival the same night ($n = 30,\ n_{male} = 15, n_{female} = 15$). Captive bred individuals from Durrell Zoo, Jersey, and 45 eggs were transported via plane from Jersey to Mauritius, arriving on the 14th of April. Individuals were checked before departure and upon arrival by respective government vets. They were held in a biosecure facility until the evening of arrival, processed as above, then transported via boat to Ile Marianne and released immediately ($n = 45, n_{male} = 11, n_{female} = 20, n_{juvenile} = 14$). Eggs were placed in predator-proof nest boxes within suitable habitat at the same time as the captive bred geckos were released.

To monitor population dynamics, 19 mark-recapture surveys have been carried out to date, at least annually since April 2011 (except in 2020, when no surveys could be carried out due to the Covid-19 pandemic). Each survey ran over 2-4 nights. Each night, the same route was walked through the areas of suitable habitat and all lesser night geckos found were caught, processed and checked for injuries. Recaptures across the multiple nights within a survey were combined such that each individual was either seen (1) or not (0) on each survey occasion. Ideally, surveys were carried out on dry nights, at least one hour after the sun had set fully and where possible avoiding a full moon, to maximise capture probability as the species is most active in these conditions. Surveying in ideal conditions is not always possible, therefore temperature and moon phase were recorded at the start of each night. Moon phase and temperature were averaged for each survey (temperatures = mean, moon phase = mode). The same two observers were involved in all 19 surveys. Individual recapture histories were generated by comparing the unique dorsal patterns (between front and hind legs, 2.7.1 Supplementary Information: Figure S2.1) using the photo ID software "Hotspotter" (Crall *et al.* 2013). Only adults were considered in our recapture histories due to low detection probability and high risk of injury during capture of juveniles (no. unique adults = 475). Entrants to the adult population are either those hatched on the island or juveniles released during the translocation that are now of adult size (recruitment occurs at approximately 6 months).

We used the translocation and standard JS models to estimate N, β, ϕ and p for the lesser night gecko population. We also used the *POPAN* model in the R package *rMark* and the *JS* model in the R package *marked*. For all models, N_t was calculated from the estimated parameters. Uneven time intervals between surveys were accounted within the likelihood for ϕ (in months) and by allowing β to be fully time dependent. The release was included as the first survey occasion. We assessed variation in all parameters over time, using a monthly scale as the lifespan of the species is 3-4 years (Goble & Goetz 2011, Cole *et al.* 2021). We also examined whether β, ϕ and p were constant or varied with sex, where individual covariates were modelled as groups. Finally, we looked for variation in p with air temperature, survey effort, substrate temperature and moon phase. Air and substrate temperature are correlated therefore air temperature only was used as more data was available. Survey effort was defined as the number of survey periods for each trip. All covariates were modelled using a *log* link for N, a multinomial *logit* link for β and a *logit* link for ϕ and p. Although each survey consisted of multiple days, a robust design model was not appropriate in this case as there were very few recaptures of individuals within each survey.

We fitted models and completed model selection by optimising the likelihoods of the translocation and standard JS models with all possible combinations of covariates. As model outputs should be the same for the standard JS model and the R packages used, running the selection process in all would have been redundant. Top models were selected using Akaike's Information Criterion (AIC; Akaike 1973, 1974). A comparison of software was carried out using a standard JS model, our translocation JS model, the *POPAN* model in the R package *rMark* and the *JS* model in the R package *marked*. The same model was run in each ($\beta \sim time, \phi \sim time, p \sim 1$) and bootstrap confidence intervals were used.

2.4 Results

2.4.1 Simulation results

The standard Jolly-Seber (JS) model substantially overestimated N_t in the first 2 years when capture probability (p) was below 0.3 whereas, our translocation JS model avoided this by giving estimates much closer to the true value (Figure 2.2: S1, S4, S7 & S10). Both JS models were fitted using time dependent arrival probability (β) and constant population size (N), survival probability (ϕ) and p. In the first two years, the standard JS model has a percentage difference of 78-130% for the low p scenarios, as opposed to 0-8.9% difference in the translocation JS model. After the first two years, estimates were more accurate with percentage differences of 5.2-23% and 0.1-8.9% for standard and translocation models, respectively (2.7.1 Supplementary Information: Table S2.1). This is due to p being constant where initially we know it should be 1, therefore the averaging of values across surveys leads to an initial underestimate, then overestimate in survey occasions following the release. This can be overcome by making parameters fully time dependent; however, this increases the likelihood of boundary estimates and parameter redundancy, especially with small sample sizes as we observed in our preliminary simulations and in our case study.

Accuracy of N_t estimates increased with increasing capture probabilities. In scenarios where p = 0.1-0.3, average percentage difference between true values and estimates were 22.2% and 4.1% for standard JS and translocation JS models respectively. In our medium detection scenarios, where p=0.4-0.6, initial estimates of N_t were slightly inflated and confidence intervals were larger in the standard JS model compared to our translocation JS model (Figure 2.2: S2, S5, S8 & S11) but not on the same scale as with lower p values, as percentage difference between true and estimated values were 6% and 0.2% for standard and translocation JS models respectively. Estimates of N_t were most accurate in scenarios with high p (0.7-0.9) where difference between the standard and translocation JS model were negligible with both models having a percentage difference of 0.5% between true and estimated values (Figure 2.2: S3, S6, S9 & S12; 2.7.2 Supplementary Information: Table S2.2).

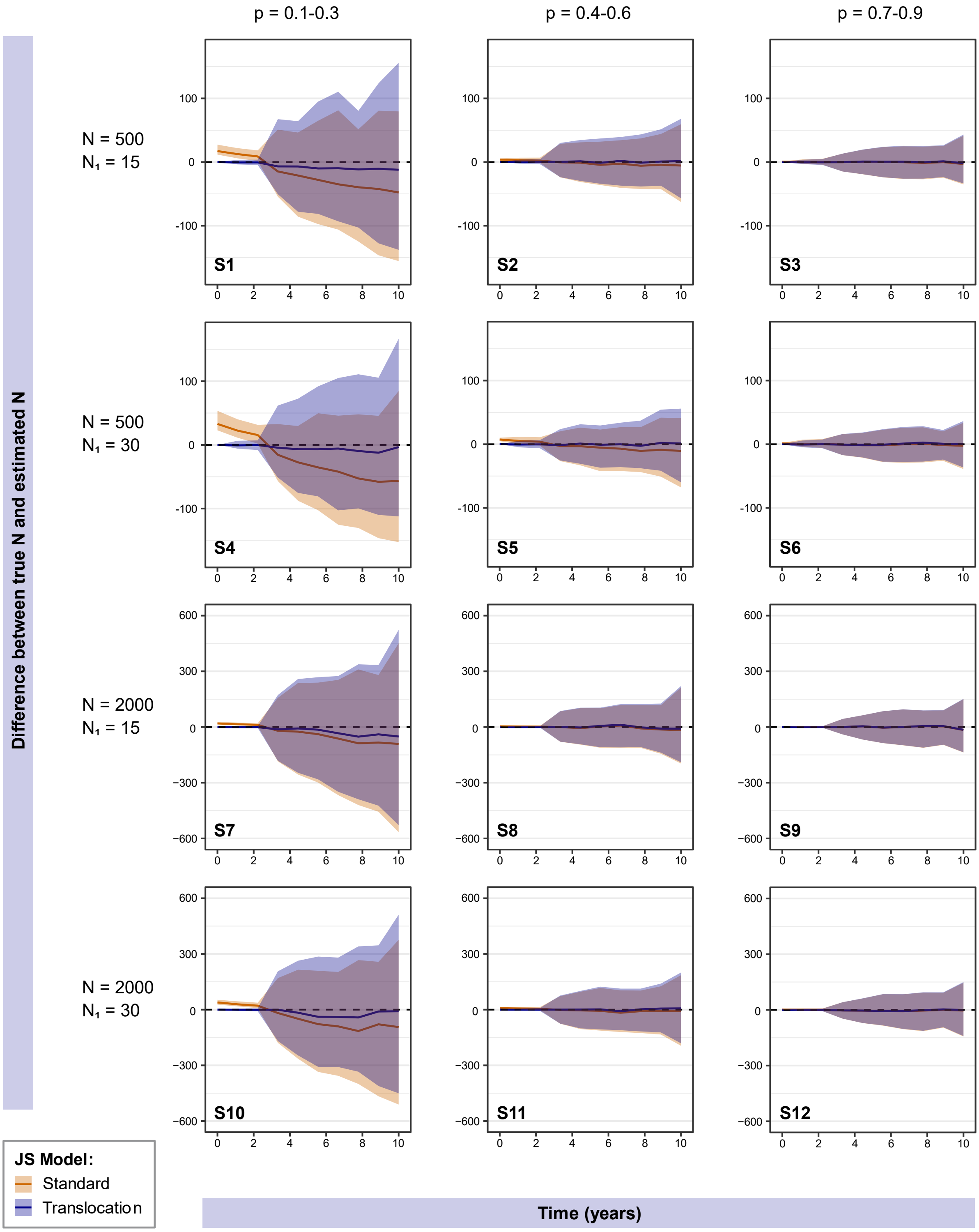

Figure 2.2: Differences between the estimates of population size *Nt* by two models and the true simulated value across 12 scenarios (Table 2.1). Modelled with entry probability as a function of time and survival and capture probabilities as constant. Standard Jolly-Seber model in orange and translocation Jolly-Seber model in blue with 95% confidence intervals.

Larger initial population size increased accuracy of N_t. Simulation scenarios with initial population size of 15 (Figure 2.2: S1-3 & S7-9) had higher average percentage differences in both models (standard JS = 10.4%, translocation JS = 1.7%) compared to scenarios with an initial population size of 30 (standard JS = 8.8%, translocation JS = 1.4%; Figure 2.2: S4-6 & S10-12). Accuracy did not differ between superpopulation sizes.

Estimates of β did not differ significantly between standard and translocation JS models (Figure 2.3). In the simulated data, β was fixed to 0 for the times 2 and 3, to replicate the delay in new entrants to the population post-translocation, which was accounted for in our translocation JS model. In the standard JS model, when β was modelled as time dependent, estimates for times 2 and 3 tended towards 0. As with N_t, uncertainty of estimates was lowest in scenarios with highest p. There was no significant difference in β estimates between high and low superpopulation or initial population scenarios.

In low p scenarios ϕ was underestimated (Figure 2.3: S1,4,7 & 10) by both models. The translocation JS model estimates were more accurate in all scenarios, though this difference was small in medium and high p scenarios (Figure 2.3). In the low p scenarios, percentage difference of the translocation JS models from the true value was between 1.4-3.6% compared to 4.2-8.5% for the standard JS model. Estimates of ϕ from the standard JS model were less accurate in scenarios with lower superpopulation size but did not vary between initial population sizes. The translocation JS model ϕ estimates had similar accuracy with differing superpopulation and initial population size.

Detection probability p was overestimated by both models in low p scenarios (Figure 2.3: S1,4,7 & 10) but only the standard JS model in medium p scenarios (Figure 2.3: S2,5,8 & 11) and overestimations were higher in scenarios with smaller superpopulation size. For low p and low superpopulation scenarios, percentage difference between true and estimated values was between 9.8-16% for the standard JS and 3.3-5.1% for the translocation JS model, compared to 0.9-1.2%

(standard) and 1.6-3.1% (translocation) for the low p and high superpopulation models. Initial population size did not affect estimates of p.

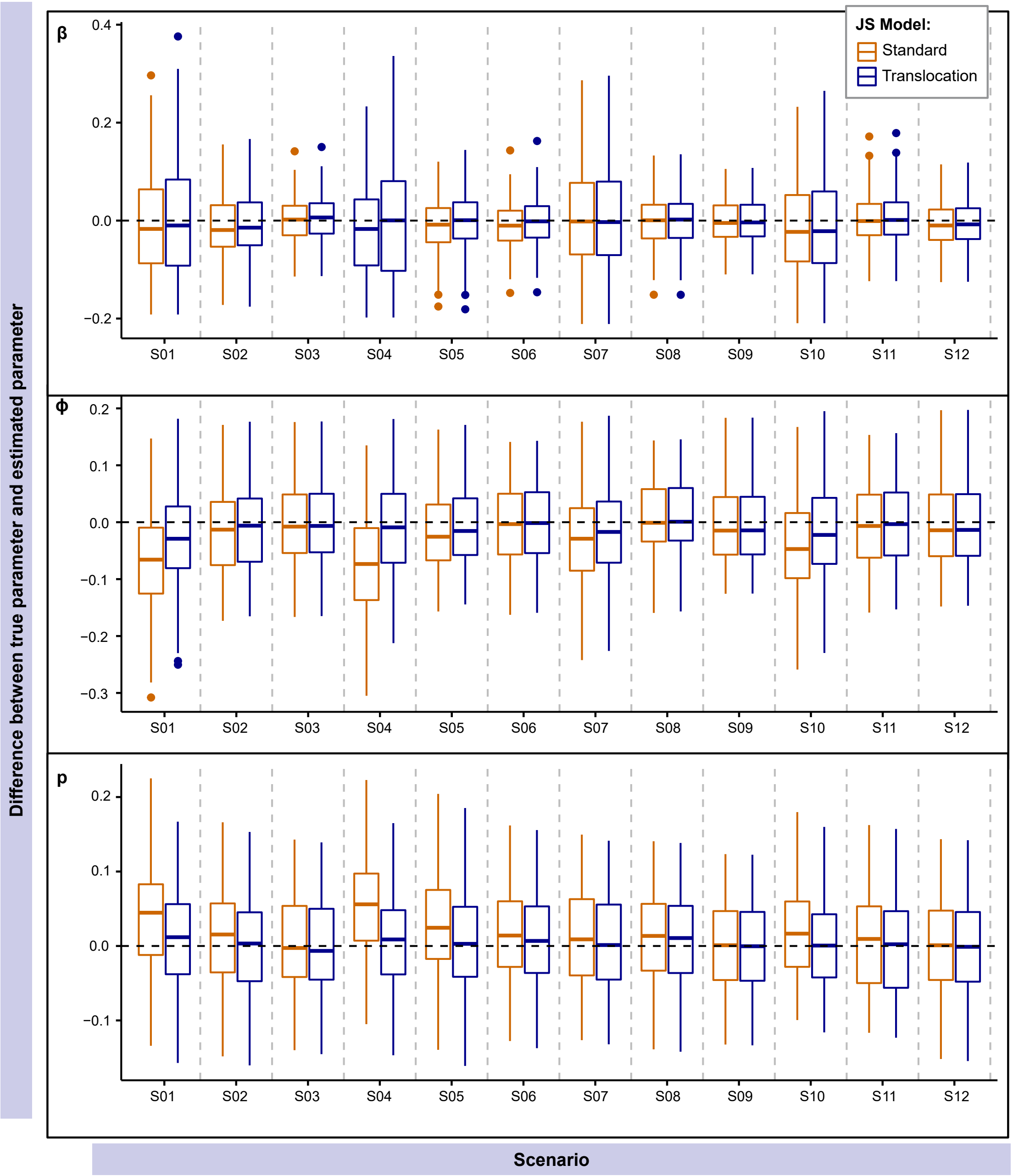

Figure 2.3: Difference between estimates and true simulated values of entry probability β, survival probability ϕ and capture probability p from standard Jolly-Seber model (orange) and translocation Jolly-Seber model (blue) across 12 scenarios (Table 2.1). Modelled with entry probability as a function of time and survival and capture probabilities as constant. Boxplots show median, upper and lower quartiles, and range.

2.4.2 Case study results

The model with the lowest value of AIC, and thus the most favoured model for our translocation JS formulation, had time dependent β, constant ϕ, and capture that varied with survey effort, moon phase and air temperature (see 2.7.3 Supplementary Information: Table S2.3 for full model selection). The lowest AIC for our standard JS formulation resulted from β, ϕ and p all being time dependent (see 2.7.3 Supplementary Information: Table S2.4 for full model selection). In the period prior to new entrants joining the population ($\beta = 0$), estimates of N_t were lower for the standard JS compared to the translocation JS (Figure 2.4). The lack of the overestimates that were observed in our simulation study is due to the time dependence in β, ϕ and p, preventing the overestimation of the initial population size. Once new entrants started joining the population, the standard JS model estimated a sudden increase and a highly variable population size. The translocation JS model estimated a similar average population size to the standard JS model with a more gradual increase and lower uncertainty.

Estimates of β, ϕ and p from the standard and translocation JS models are similar, however the translocation JS model consistently has lower uncertainty and more gradual variations in estimated values than the standard JS model (Figure 2.4). Estimated values of β were similar for both models and despite only the translocation model accounting for the period of no new entrants initially, both models estimated initial $\beta = 0$ then increased over time. Estimates of ϕ followed a similar trend in both models with high survival of translocated individuals initially, then variation across time. The standard JS model, which was fully time dependent, gives boundary estimates ($\phi = 1$) for 7 of the survey periods, and confidence intervals are consistently very broad. This does not occur in the translocation JS model where annual ϕ was constant ($\phi = 0.514\ (0.452 - 0.575)$). In the translocation JS model, p was fixed to 1 initially to account for the translocation, the standard JS model, although not fixed, also estimated the value of $p_1 = 1$. The translocation JS model estimated that p increased linearly with survey effort and air temperature and was highest when the moon phase was between crescent and gibbous, and lowest close to new and full moons.

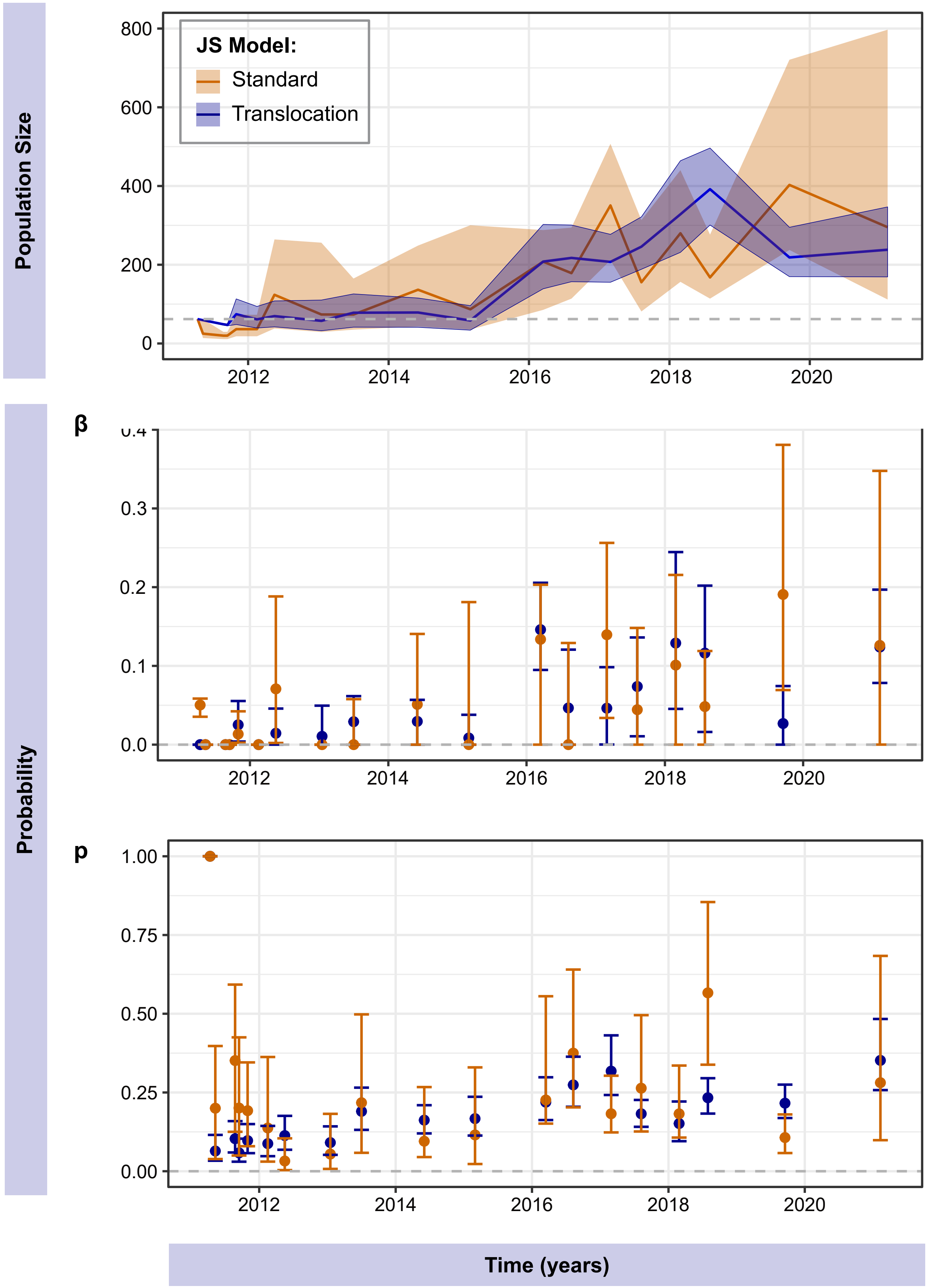

Figure 2.4: Comparison of parameter estimates for population size *Nt*, entry probability β and capture probability *p* from top fitting models (lowest AIC value) for the standard Jolly-Seber model (orange) and the translocation Jolly-Seber model (blue) for the lesser night gecko (*Nactus*

coindemirensis) population on Ile Marianne, Mauritius. Estimates from translocation in April 2011 until most recent survey in June 2021. Initial population size (n = 62) is indicated in top panel (grey dashed line). Both top models had sex dependent superpopulation N and time dependent β, the standard JS model had time dependent ϕ and p, the translocation JS model had constant ϕ and p dependent on survey effort, air temperature and moon phase.

A comparison of models was carried out using a standard JS model, our translocation JS model (both run using MATLAB), the *POPAN* model in the R package *rMark* and the *JS* model in the R package *marked* (2.7.3 Supplementary Information: Figures S2.2-S2.4). We encountered optimisation issues with both R packages with and without fixed parameters, especially when attempting to fix initial capture probability to 1, leading to boundary estimates. Abundance estimates from *rMark* and *marked* both dropped below 1 individual in the first year post release (2.7.3 Supplementary Information: Figure S2.2). The parameter estimates and confidence intervals from *rMark* were very similar to the standard JS model and translocation JS model, with similar final estimates of abundance, and greater variance in estimates of β and ϕ although following the same pattern (2.7.3 Supplementary Information: Figures S2.3 & S2.4). The final abundance estimate from *marked* was much lower in comparison with broader confidence intervals (2.7.3 Supplementary Information: Figure S2.2) and there were more boundary estimates of β and ϕ (2.7.3 Supplementary Information: Figures S2.3 & S2.4) indicating issues with optimisation.

2.5 Discussion

Our results demonstrate that the standard POPAN formulation of the Jolly-Seber (JS) model is likely to overestimate population size when fitted to translocated populations, especially in challenging translocations with small numbers of founders and low detection probabilities. Unfortunately, low detection and few founders are common features of many conservation translocations, which then frequently need ongoing management to support population establishment. To our knowledge, although JS models are commonly used to estimate abundance of translocated populations, accounting for known initial population size in JS models for translocated populations is not standard practise. However, overestimating population size can have serious implications for conservation management decisions that rely on accurate estimates. In both our simulations and case study, accounting for initial population size within JS models through a translocation-specific likelihood substantially improved estimates. Our case study demonstrated that separating the translocated individuals can allow covariates to explain the trends in the data as opposed to purely time dependence, reducing the number of parameters and therefore the likelihood of parameter redundancy.

In the case of the lesser night gecko (*Nactus coindemirensis*), a cryptic threatened species with low detectability, we were able to avoid overestimation even with the standard JS model, by fitting a fully time dependent model (i.e., one where β, ϕ and p varied by time). However, a fully time dependent formulation has a high number of parameters ($k = 60$) and so is more likely to encounter parameter redundancy, as we saw with the boundary estimates in survival (Figure 2.4). More parameters increase the chance of estimates with high uncertainty and low accuracy. In contrast, when we fitted our translocation JS model, the AIC supported simpler models, and the top-ranked model had fewer parameters ($k = 22$). This was achieved through being able to use covariates to explain patterns in capture, allowing optimisation of future surveys (Broder *et al.* 2020). The reduced uncertainty and lack of boundary estimates produce realistic estimates of population size from this model.

On one hand, overestimated population size can generate unfounded optimism in reintroduction success. In such cases, if managers believe the population is larger than it really is, they might miss a crucial window of opportunity to reinforce it, thereby leading to possible establishment failure (Armstrong & Seddon 2008; Panfylova *et al.* 2019) driven by stochastic demographic processes (Griffith *et al.* 1989; Clark *et al.* 2002; Converse *et al.* 2013; Bubac *et al.* 2019), dispersal (Moseby *et al.* 2014; Resende *et al.* 2021) or Allee effects (Allee 1931; Courchamp *et al.* 1999; Armstrong & Wittmer 2011). Even if the population persists without reinforcement, it may be at increased risk of longer-term inbreeding depression and reduced adaptive potential driven by this and genetic drift (Frankel 1970; Frankham 2005; Balestrieri *et al.* 2021).

On the other hand, underestimating population size might lead to programmes either prematurely giving up on supporting the establishing population or investing in added but unnecessary management (Armstrong & Wittmer 2011). For example, if managers mistakenly believe a population to be at risk, they might undertake reinforcements that impact source populations (Dimond & Armstrong 2007; Earnhardt *et al.* 2014; Turko *et al.* 2021) and incur additional resource commitments (Crimmins *et al.* 2009; Bubac *et al.* 2019; Berger-Tal *et al.* 2020). Individuals released in reinforcement translocations may face unexpected resistance to recruitment into the reintroduced population due to territorial aggression from residents from earlier releases.

Accurate estimates of population size and the parameters from which they are derived are therefore important for good state dependent management decisions, as growth or decline of populations are key metrics in guiding future management actions (Seddon *et al.* 2007; Armstrong & Seddon 2008). Additionally, if planned in accordance with the IUCN guidelines, most translocations are likely to have specific demographic targets or trigger points at which specific management actions are taken (Armstrong & Ewen 2001; Chadès *et al.* 2008). Minimizing uncertainty is important to ensure management actions are timely (Converse *et al.* 2013; Panfylova *et al.* 2019).

We note a simple constrain to the initial population size could be easily implemented in a Bayesian framework. However, our model goes beyond simply constraining the model, instead allowing a separate likelihood component for translocated individuals that can be used in for single or multiple translocation events, for example in the event of subsequent reinforcements. These likelihood components do not directly contribute to the estimation of population size as the model is derived by conditioning on these known releases. Moreover, Bayesian inference is still not necessarily accessible to all ecologists, and much management inference relies on maximum-likelihood based software like program MARK or the related R packages we considered in our analysis.

When estimating abundance of translocated populations with low capture probability, especially in the early stages of the translocation, uncertainty can be high and models less informative, which can result in poor decisions. In such situations, we recommend accounting for known initial population size by use of our translocation Jolly-Seber model, to increase accuracy of parameter estimates, better inform future management decisions, and increase the chance of successful establishment and persistence.

2.6 Acknowledgements

We thank the Durrell Wildlife conservation trust, Mauritian Wildlife Foundation and the Mauritian Government’s Forestry Service and National Parks and Conservation Service for supporting this project. We thank Nik Cole and Rouben Mootoocurpen for lesser night gecko data collection and Rose Moorhouse-Gann for assistance with image processing. Katherine Bickerton is supported by a Natural Environment Research Council studentship, as part of the ARIES DTP. Fay Frost and Rachel McCrea are supported by EPSRC grant EP/S020470/1.

2.6.1 Data & code availability

The formatted data set and R code used in this chapter are available in Zenodo at: https://doi.org/10.5281/zenodo.8215314.

2.7 Supplementary Information

2.7.1 Case study additional information

Table S2.1: Geographical information about the study system islands.

Island	**Area (ha)**	**Area (km^2)**	**Latitude**	**Longitude**
Gunner's Quoin	72.9	0.73	-19.94133	57.61998
Île Marianne	2.1	0.02	-20.38019	57.78723
Ilot Vacoas	1.1	0.01	-20.39776	57.77053
Pigeon House Rock (Rocher aux Pigeons)	1.4	0.01	-19.86271	57.65740

Figure S2.1: Example photo from mark-recapture surveys of lesser night gecko (*Nactus coindemirensis*). The region used in photo identification is indicated by the brown rectangle and unique individuals are identified using *Hotspotter* (Crall *et al.* 2013), which allocated a unique reference code to each individual, as shown. Photo credit Nik Cole.

2.7.2 Simulation results

Table S2.2: Simulated and estimated average values of population size over time Nt. Simulated values are labelled as true, estimates from the standard Jolly-Seber model as JS and estimates from the translocation Jolly-Seber model as T. Percentage differences were calculated between simulated and estimated values for standard and translocation Jolly-Seber models, indicated as % Diff.

Scenario	Time	True Nt	Nt T	Nt JS	% Diff T	% Diff JS
S1	1	15	15	32	0.000	1.150
	2	13	12	25	-0.080	0.902
	3	10	10	19	-0.046	0.877
	4	80	73	65	-0.079	-0.180
	5	135	130	116	-0.037	-0.139
	6	181	168	149	-0.073	-0.175
	7	221	203	181	-0.077	-0.178
	8	248	236	211	-0.045	-0.146
	9	267	252	223	-0.057	-0.164
	10	290	276	243	-0.048	-0.160
S2	1	15	15	19	0.000	0.253
	2	12	12	15	0.028	0.278
	3	10	10	13	0.015	0.251
	4	79	79	78	-0.004	-0.013
	5	137	138	135	0.004	-0.013
	6	181	180	178	-0.006	-0.018
	7	217	216	212	-0.002	-0.021
	8	247	247	242	0.000	-0.020
	9	268	273	267	0.018	-0.004
	10	290	291	284	0.003	-0.021
S3	1	15	15	16	0.000	0.047

	2	13	12	13	-0.051	-0.009
	3	11	10	11	-0.078	-0.038
	4	77	76	76	-0.007	-0.008
	5	132	131	131	-0.006	-0.008
	6	179	181	180	0.013	0.010
	7	215	212	212	-0.010	-0.013
	8	246	245	244	-0.003	-0.007
	9	271	271	270	0.004	-0.002
	10	294	292	290	-0.007	-0.013
S4	1	30	30	63	0.000	1.097
	2	25	24	47	-0.025	0.890
	3	20	20	36	-0.010	0.780
	4	85	77	67	-0.089	-0.216
	5	137	129	105	-0.055	-0.231
	6	181	174	145	-0.038	-0.199
	7	215	208	170	-0.035	-0.212
	8	241	234	197	-0.027	-0.183
	9	266	255	211	-0.041	-0.208
	10	282	281	231	-0.002	-0.181
S5	1	30	30	37	0.000	0.247
	2	25	25	30	-0.014	0.216
	3	21	20	25	-0.012	0.199
	4	85	83	81	-0.028	-0.047
	5	134	134	130	0.000	-0.026
	6	177	176	171	-0.005	-0.035
	7	213	213	207	0.000	-0.029
	8	245	244	236	-0.003	-0.036
	9	269	271	262	0.007	-0.027

	10	291	287	276	-0.011	-0.052
S6	1	30	30	31	0.000	0.044
	2	25	25	26	-0.016	0.027
	3	20	20	21	0.009	0.050
	4	82	79	79	-0.031	-0.032
	5	136	133	133	-0.015	-0.018
	6	177	175	174	-0.011	-0.016
	7	212	214	212	0.007	0.001
	8	239	241	239	0.008	0.001
	9	265	267	265	0.010	0.001
	10	286	286	284	0.003	-0.007
S7	1	15	15	35	0.000	1.304
	2	13	12	28	-0.069	1.117
	3	10	10	22	-0.023	1.187
	4	287	271	261	-0.056	-0.091
	5	517	495	476	-0.042	-0.079
	6	705	695	668	-0.014	-0.052
	7	870	836	806	-0.039	-0.073
	8	1007	957	924	-0.049	-0.083
	9	1120	1076	1033	-0.039	-0.078
	10	1209	1131	1088	-0.064	-0.100
S8	1	15	15	19	0.000	0.261
	2	13	12	15	-0.056	0.192
	3	10	10	13	0.005	0.265
	4	297	293	292	-0.011	-0.015
	5	520	523	521	0.007	0.003
	6	700	702	699	0.003	0.000
	7	864	872	867	0.010	0.003
	8	997	997	991	0.000	-0.006

	9	1114	1094	1087	-0.018	-0.024
	10	1192	1181	1174	-0.009	-0.015
S9	1	15	15	16	0.000	0.047
	2	12	12	13	0.031	0.079
	3	10	10	11	0.021	0.066
	4	299	289	289	-0.032	-0.032
	5	521	529	529	0.017	0.016
	6	717	715	715	-0.002	-0.003
	7	875	877	876	0.002	0.002
	8	1001	1000	999	-0.001	-0.002
	9	1119	1112	1110	-0.007	-0.008
	10	1208	1196	1194	-0.010	-0.011
S10	1	30	30	69	0.000	1.295
	2	25	24	53	-0.032	1.132
	3	21	20	42	-0.070	0.994
	4	303	292	276	-0.037	-0.089
	5	528	514	485	-0.027	-0.082
	6	716	675	632	-0.058	-0.118
	7	868	811	757	-0.065	-0.127
	8	988	935	876	-0.054	-0.113
	9	1085	1065	1003	-0.018	-0.075
	10	1175	1145	1065	-0.025	-0.093
S11	1	30	30	38	0.000	0.264
	2	25	25	31	-0.010	0.242
	3	20	20	25	0.021	0.273
	4	290	280	278	-0.033	-0.039
	5	511	507	502	-0.007	-0.016
	6	702	700	694	-0.002	-0.011
	7	858	856	847	-0.002	-0.012

	8	991	994	983	0.004	-0.008
	9	1104	1104	1092	0.000	-0.011
	10	1174	1196	1181	0.019	0.006
S12	1	30	30	31	0.000	0.047
	2	25	25	26	-0.019	0.029
	3	21	20	21	-0.022	0.023
	4	289	282	282	-0.023	-0.023
	5	526	529	529	0.007	0.005
	6	715	709	708	-0.009	-0.010
	7	878	867	866	-0.012	-0.013
	8	997	1003	1002	0.007	0.005
	9	1097	1094	1092	-0.003	-0.004
	10	1171	1173	1171	0.002	0.000

2.7.3 Case study results

Table S2.3: Model selection table for translocation likelihood model, indicating formulas for each parameter: population size *N*, entry probability β, survival probability ϕ and capture probability *p*. Log likelihood *LogL*, number of parameters *k*, Akaike's Information Criterion *AIC*, and difference between top ranked model (by AIC) and all other models *ΔAIC*, is given for each model. The top 10 best fitting models (by AIC) are given as well as the models where either ϕ or *p* are constant or time dependent (where these were not within the 10 best models).

N	***β***	***ϕ***	***p***	***LogL***	***k***	***AICc***	***ΔAICc***
Sex	Time	1	Temp + Moon + Effort	-422.85	22	-801.69	0
Sex	Time	Sex	Temp + Moon + Effort	-423.20	23	-800.39	1.30
Sex	Time	1	Sex + Temp + Moon + Effort	-425.54	26	-799.08	2.61
Sex	Time	Time	Temp + Effort	-437.19	39	-796.37	5.32
Sex	Time	Time	Effort	-436.07	38	-796.14	5.55
Sex	Time	Time	Temp	-435.75	38	-795.49	6.20
Sex	Time	Time	1	-434.38	37	-794.76	6.93
Sex	Time	Time	Temp + Moon + Effort	-437.26	40	-794.53	7.16
Sex	Time	Time	Moon + Effort	-436.07	39	-794.14	7.55
Sex	Time	Time	Temp + Moon	-435.76	39	-793.53	8.16
Sex	Time	Time	Time	-451.60	55	-793.19	8.50
Sex	Time	1	Time	-432.24	37	-790.49	11.20
Sex	Time	1	1	-405.94	19	-773.89	27.80

Table S2.4: Model selection table for standard Jolly-Seber model, indicating formulas for each parameter: population size *N*, entry probability β, survival probability *ϕ* and capture probability *p*. Log likelihood *LogL*, number of parameters *k*, Akaike's Information Criterion *AIC*, and difference between top ranked model (by AIC) and all other models *ΔAIC*, is given for each model. The top 10 best fitting models (by AIC) are given as well as the models where either *ϕ* or *p* are constant or time dependent (where these were not within the 10 best models).

N	***β***	***ϕ***	***p***	***LogL***	***k***	***AICc***	***ΔAICc***
Sex	Time	Time	Time	-602.82	60	-1085.64	0
Sex	Time	1	Time	-583.48	42	-1082.96	2.68
Sex	Time	Sex	Time	-583.62	43	-1081.23	4.41
Sex	Time	Time	1	-565.31	41	-1048.63	37.01
Sex	Time	Time	Moon	-566.24	42	-1048.48	37.16
Sex	Time	Time	Sex	-565.66	42	-1047.32	38.32
Sex	Time	Time	Effort	-565.46	42	-1046.92	38.72
Sex	Time	Time	Moon + Effort	-566.17	43	-1046.33	39.31
Sex	Time	Time	Sex + Moon	-566.76	44	-1045.52	40.12
Sex	Time	Time	Temp	-564.71	42	-1045.43	40.21
Sex	Time	1	1	-493.13	23	-940.26	145.38

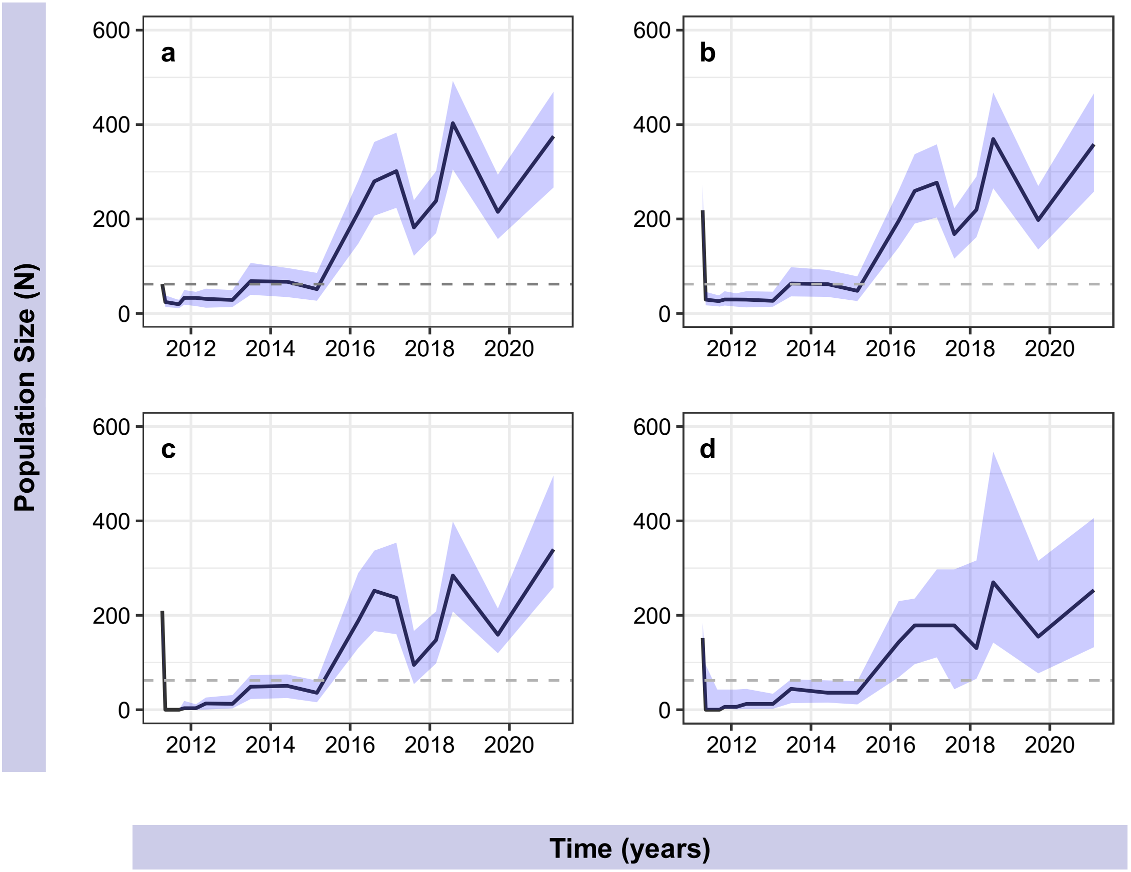

Figure S2.2: Comparison of abundance estimates from four formulations of the Jolly-Seber model: a) our translocation model which accounts for known initial population size; b) the standard POPAN formulation of the Jolly-Seber model; c) the *POPAN* model provided in the R package *Rmark* (Laake 2013); d) the *JS* model provided in the R package *marked* (Laake *et al.* 2013). Abundance estimates are for the population of lesser night gecko (*Nactus coindemirensis)* on Ile Marianne, between the translocation of 62 adults in April 2011 (indicated by the grey dashed line) and June 2021. The model had time dependent β and ϕ and constant p.

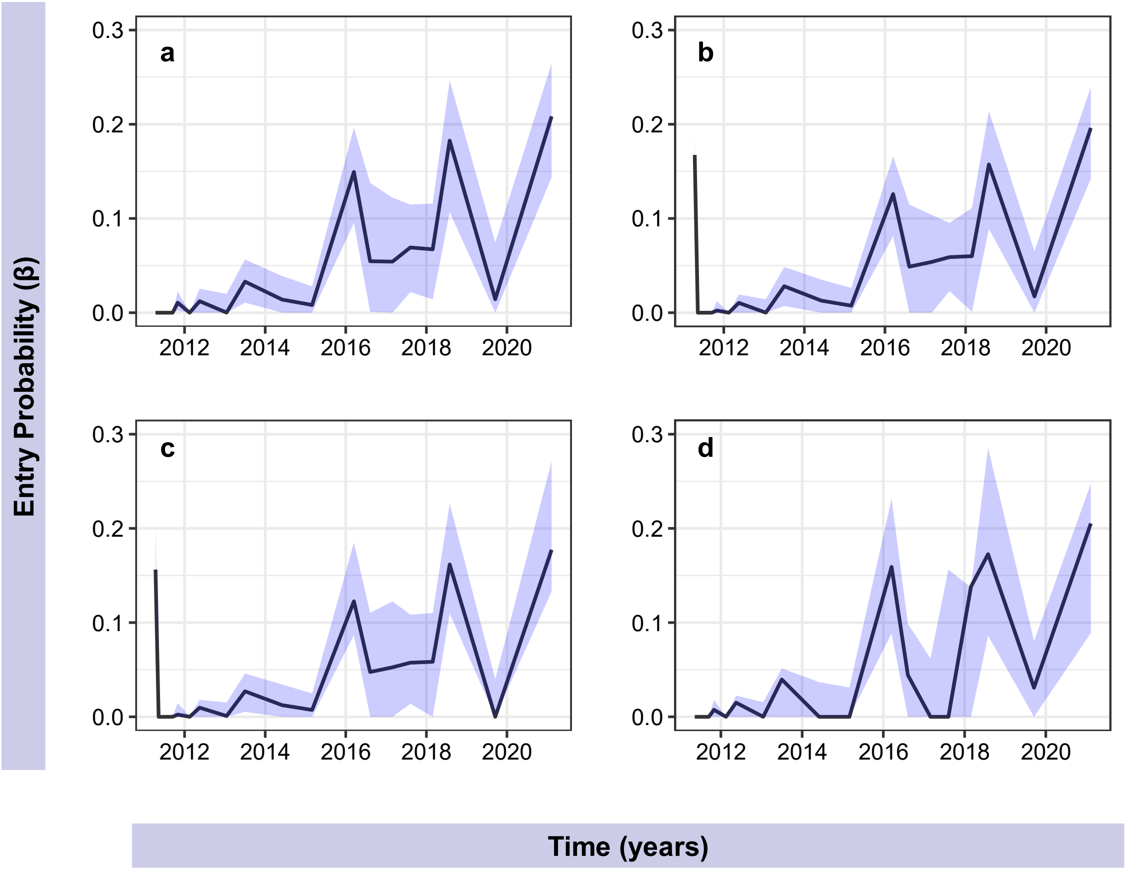

Figure S2.3: Comparison of entry probability β estimates from four formulations of the Jolly-Seber model: a) our translocation model which accounts for known initial population size; b) the standard POPAN formulation of the Jolly-Seber model; c) the *POPAN* model provided in the R package *Rmark* (Laake 2013); d) the *JS* model provided in the R package *marked* (Laake *et al.* 2013). Estimates are for the population of lesser night gecko (*Nactus coindemirensis)* on Ile Marianne, between the translocation of 62 adults in April 2011 and June 2021. The model had time dependent β and ϕ and constant *p*.

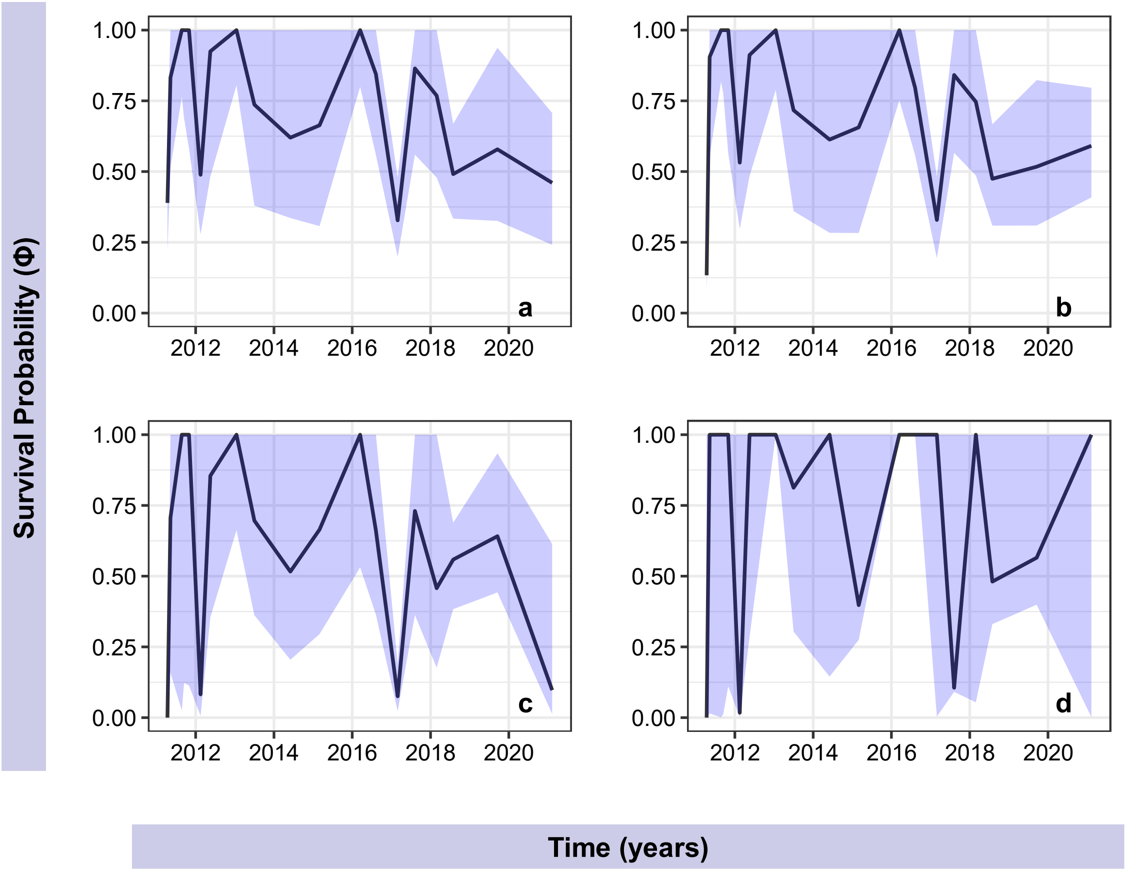

Figure S2.4: Comparison of survival probability ϕ estimates from four formulations of the Jolly-Seber model: a) our translocation model which accounts for known initial population size; b) the standard POPAN formulation of the Jolly-Seber model; c) the *POPAN* model provided in the R package *Rmark* (Laake 2013); d) the *JS* model provided in the R package *marked* (Laake *et al.* 2013). Estimates are for the population of lesser night gecko (*Nactus coindemirensis)* on Ile Marianne, between the translocation of 62 adults in April 2011 and June 2021. The model had time dependent β and ϕ and constant p.

3 Population dynamics and condition variation of two threatened lizard species following the 2020 Wakashio oil spill in Mauritius

Authors & Affiliation

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3.1 Abstract

Oil spills pose a huge risk to biodiversity but are mainly viewed from a marine perspective despite oil coming into contact with terrestrial systems. In July 2020, the MV Wakashio, a Japanese freighter, carrying approximately 3900 tonnes of fuel oil ran aground on a reef 1.1 km from the coast of Mauritius in the Indian Ocean. An estimated 1000 tonnes of the oil leaked into the surrounding reef system and was observed on several of the low-lying islands within the reef. These islands are one of the last refuges for two threatened terrestrial reptile species, the Bojer's skink *Gongylomorphus bojerii* and the lesser night gecko *Nactus coindemirensis*, both of which are endemic to Mauritius. Furthermore, the populations found in the southeast are genetically distinct from populations elsewhere in Mauritius. Here, we examine the variation in population dynamics and body condition before and after the MV Wakashio oil spill, using mark-recapture models to estimate population size and survival, and scaled body mass index as a proxy for body condition within generalised linear mixed models, across 3 populations of Bojer's skink and 2 populations of lesser night gecko. We saw a small decrease in survival and body condition in one population of lesser night gecko following the oil spill; the second lesser night gecko population and all three Bojer's skink populations showed very little variation and high uncertainty in survival and population size estimates. Two of the Bojer's skink populations had lower body condition directly following the oil spill: however, this cannot be differentiated from seasonal variation in body condition. The population where effects of the oil spill were detected had over 3 times as many surveys prior to the oil spill compared to the other populations, highlighting the importance of good baseline surveys. However, we appreciate that funding for baseline surveys is limited and surveying locations directly following an environmental disaster can be hazardous, limiting the data available to examine these effects. We recommend prioritising baseline surveys for areas at high risk of an environmental disaster or populations that are particularly vulnerable to environmental change, to enable better understanding and mitigate effects of future events.

Key words: oil spill; population dynamics; terrestrial reptiles; Mauritius; capture-recapture

3.2 Introduction

Pollution is one of the five greatest risks to biodiversity (IPBES 2019) and pollutants released during oil spills, especially polycyclic aromatic hydrocarbons (PAHs), are some of the most commonly occurring contaminants in the environment (Fernandes *et al.* 2022). PAHs are known to be toxic and mutagenic to wildlife and can persist within environments causing long-term damage (Burns *et al.* 2014; Asif *et al.* 2022). These effects can be seen throughout the food chain, with growing literature on bioaccumulation of PAHs in invertebrate communities, leading to loss of species diversity and reduced population sizes, as seen in Louisiana following the Deepwater Horizon oil spill in 2010 (Beyer *et al.* 2016; Bam *et al.* 2018) and in ants 12 years after oil pollution in Kuwait (Al-Hashem *et al.* 2007). The majority of literature on the effects oil spills on vertebrates focuses on marine species and as only 100 of the known 12000 species and subspecies of reptiles are found in marine environments, there is a lack of knowledge surrounding the impact of oil spills on reptiles (Rasmussen *et al.* 2011). Evidence of adverse effects of oil in reptiles has been recorded in marine iguanas following the Jessica oil tanker spill in the Galapagos, where the main food source for the iguanas, an algae species, became contaminated leading to a 62% population decline (Wikelski *et al.* 2002), and in marine turtles following the Deepwater Horizon spill, where increased mortality and record numbers of strandings were observed (Beyer *et al.* 2016). Additional evidence suggests that marine turtle eggs exposed to petroleum have lower rates of hatching success and higher rates of deformity in those that do hatch (Fritts & McGehee 1982). Bioaccumulation of PAHs has also been recorded in several terrestrial lizard species, but impacts on physiology, health or population dynamics were not investigated (Al-Hashem *et al.* 2007; Zychowski & Godard-Codding 2017).

On 25 July 2020, the bulk carrier MV Wakashio ran aground on a coral reef approximately 1.1 km from Point d'Esny, southeast Mauritius, carrying approximately 3900 tonnes of fuel oil, 1000 tonnes of which leaked into the area surrounding the ship (Lewis 2020; Scarlett *et al.* 2021; Figure 3.1), including an internationally important biodiversity hotspot identified under the Ramsar Convention. On 9 August, oil was detected on low-lying islands (Ilot Vacoas and Ile aux Fouquets) up to 4.8 km northwest of the ship, all of which are home to threatened endemic species of flora and fauna. These include two terrestrial, threatened, endemic reptiles with differing natural histories, the lesser night gecko *Nactus coindemirensis* and Bojer's skink *Gongylomorphus bojerii* which are classified on the IUCN red list as Vulnerable (Cole *et al.* 2021) and Critically Endangered (Cole & Payne 2022) respectively. Both species are restricted to outlying islands to the north and southeast of Mauritius, however the genetically distinct populations in the southeast are much smaller than the northern ones, putting them at greater risk of stochastic events (Armstrong & Seddon 2008). The diet of both species predominantly consists of invertebrates (Cole *et al.* 2009), which are one of the groups most at risk of long-term bioaccumulation of contaminants. This can both cause decline in the invertebrate communities, reducing food availability for both reptiles, and lead to direct transfer of pollutants to reptiles, potentially leading to bioaccumulation (Fernandes *et al.* 2022). Additionally, the islets in the southeast are formed of porous coralline rock, increasing the risk that oil from the spill will permeate the rock, and potentially be redispersed during heavy rainfall or storms.

In this study, we aim to identify the impact of the MV Wakashio oil spill in Mauritius on populations of Bojer's skink and lesser night gecko. We used capture-recapture models to compare population size and survival probability, and generalized linear mixed models and general linear models to examine body condition (scaled mass index) of 5 reptile populations across 4 of the affected islets in the southeast of Mauritius prior to and in the two years following the oil spill. The two species have differing ecologies, with the Bojer's skink being a diurnal generalist predator of invertebrates and the lesser night gecko being a nocturnal micromoth specialist. To our knowledge, this is the first study to assess differences in population size, survival and body condition of terrestrial reptile species in the tropics following an oil spill.

3.3 Methods

3.3.1 Study sites & species

Prior to the introduction of invasive predators/competitors such as the wolf snake (*Lycodon capucinus),* musk shrew (*Suncus murinus)*, and Asian house gecko (*Hemidactylus frenatus)*, the Bojer's skink (*Gongylomorphus bojerii*) and the lesser night gecko (*Nactus coindemirensis)* were thought to be widespread across Mauritius (Jones 1993; Cole *et al.* 2005; Michaelides *et al.* 2015). By the 1970s, the Bojer's skink was restricted to only seven outlying islands (Michaelides *et al.* 2015), and the lesser night gecko (discovered in 1982; Bullock *et al.* 1985) to four, all of which were to the north of the main island, apart from one: Ilot Vacoas (IV; 1.1ha) to the south-east. It has since been demonstrated that the south-eastern populations of both species are genetically distinct from those in the north and have much lower population sizes due to the small size of the islands in the southeast. Eradication of non-native predators on the neighbouring southeast islets of Ile aux Fouquets (IAF; 2.6ha), Ile de la Passe (IDLP; 2.4ha) and Ile Marianne (IM; 2.1ha) led to them becoming suitable candidates for reintroductions (3.6. Supplementary Information: Table S3.1). Between 2007-2009, 60 Bojer's skink were reintroduced to IAF from IV. In 2009, a small population of Bojer's skinks were found on IDLP and reinforcement translocations of 20 and 16 individuals carried out in 2013 from IAF and IV respectively (du Plessis *et al.* 2019). In 2011, 75 lesser night geckos were reintroduced to IM, 30 from IV and 45 captive bred from Jersey Zoo (Bickerton *et al.* 2023).

The Bojer's skink populations were surveyed using capture-recapture surveys between 2013 and 2019 on an approximately annual basis (full details in 3.6 Supplementary Information: Table S3.2) to monitor population dynamics. The IV lesser night gecko population was also surveyed approximately annually and the IM population twice a year between 2011-2019 (with the exception of 2011 where they were surveyed 4 times, and 2014, 2015 and 2019 where they were only surveyed once) using the same methodology (Bickerton *et al.* 2023; 3.6 Supplementary Information: Table S3.2). Standard surveys were not carried out in 2020 due to the Covid-19 pandemic. Both species are small and cryptic in behaviour, leading to low capture probabilities, especially during the wet season when vegetation is dense.

Following the MV Wakashio oil spill in July 2020, initial monitoring of the southeast islets was carried out on 9th August 2020. The islets are all formed of porous coralline rock and are situated on the edge of the coral reef, with each having a beach facing the mainland and lagoon to the northwest, and a rocky coast on the south-eastern oceanic side (Figure 3.1). Oil was found on IV (4.83 km from spill site) and IAF (5.46 km), predominantly on the oceanic side. Oil droplets were also observed being carried over the islands by sea spray. No oil was detected on IM (7.44km) or IDLP (4.55 km) however it is likely oil would have been carried over by sea spray. At the site of the oil spill, the predominant current direction is southwest and wind direction was predominantly from the southeast during the period two weeks following the spill (Gurumoorthi *et al.* 2021).

After the oil spill, capture-recapture surveys were carried out twice a year in 2021 and 2022. These are the only populations of either species present in the area affected by the oil spill. All surveys were conducted over a period of 2-4 days during which all suitable habitat was surveyed every day for each species during the day for Bojer's skink (surveys between 8-11am and 2-5pm) and at night for lesser night geckos. The same survey route was walked each day and all animals found were caught. For the Bojer's skinks, all animals were caught and held in cloth reptile bags until the survey was complete, and then processed. For lesser night geckos, animals were caught and processed immediately due to their higher sensitivity to stress. During processing, animals were weighed, measured, visually inspected for scars, tail and toe losses and any other injuries, then photographed.

Both species have unique dorsal patterns between their fore and hind legs which allows for individuals to be identified. Identification was carried out using the photo identification software "Hotspotter" (Crall *et al.* 2013). Air temperature and substrate temperature were also recorded, and in surveys after 2017, rainfall, wind and sun or moon visibility. Binary capture histories were constructed for each skink and gecko population for each survey, using a 1 to represent a capture, and 0 to represent no capture. Multiple captures of the same individual within a single survey were grouped.

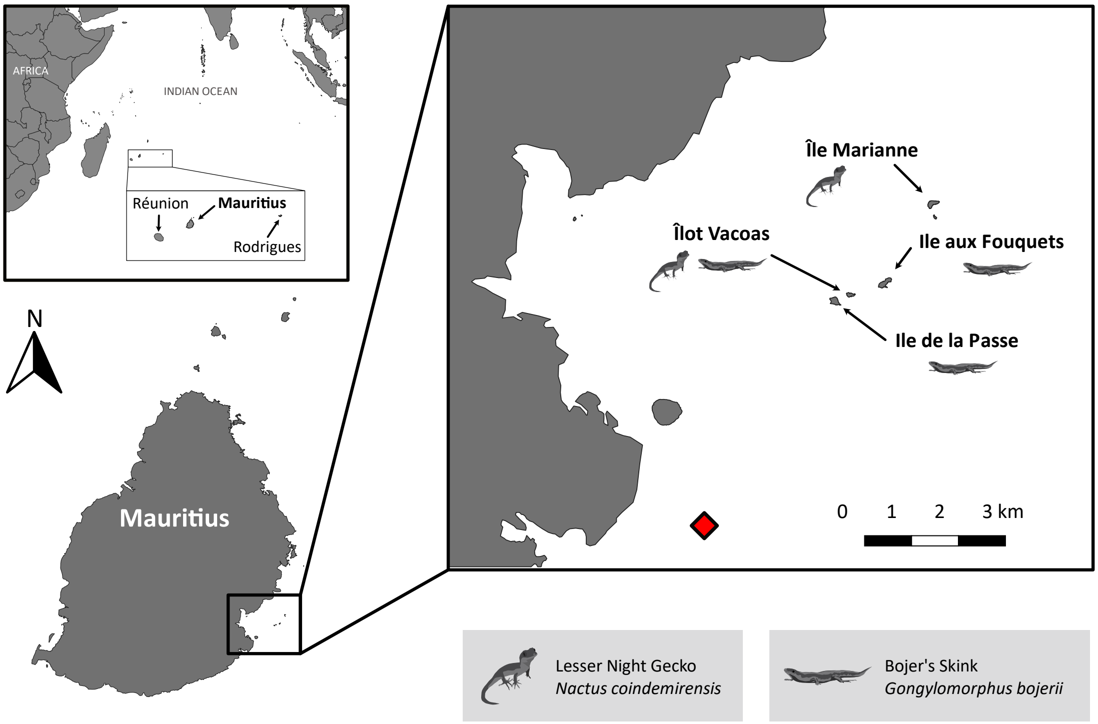

Figure 3.1: Map of Mauritius, showing the southeast islets and the five reptile populations, three populations of Bojer's skink (*Gongylomorphus bojerii*) and two populations of lesser night gecko (*Nactus coindemirensis*). The location where the MV Wakashio grounded and began leaking fuel is shown by the red point.

3.3.2 Survival & population size

We modelled population size N and survival probability ϕ using the POPAN formulation of the Jolly-Seber model (Schwarz & Arnason 1996) to assess potential demographic impacts of the oil spill. This model also allows estimation of entry probability β and detection probability p. For the IM population, we used a modified Jolly-Seber model that accounts for translocated individuals and estimates the same parameters (Bickerton *et al.* 2023), as this was the only population where our mark-recapture surveys included the translocated individuals and not accounting for translocated individuals can lead to overestimates in population size as demonstrated in Chapter 2. We used estimated parameters to calculate derived estimates of population size at each survey occasion N_t. Each population of geckos and skinks were modelled separately due to availability of photos varying between islands (for a summary of surveys used see 3.6 Supplementary Information: Table S3.3), and we accounted for differing time intervals between surveys. For all populations, we assessed variation in parameters over time and variation between sexes (only adults were used in this analysis due to unknown consistency in body markings between juveniles and adults). We also looked for variation in ϕ following the oil spill, which we modelled as a binary covariate in two ways, (1) using 0 to denote the time prior to the oil spill and 1 to denote the time after the oil spill and (2) using 0 to denote the times before and after the oil spill and 1 for the time interval in which the oil spill occurred. These covariate structures correspond to long-term and short-term effects. Due to small sample sizes, we were unable to use a formulation that had three separate phases accounting for long- and short-term effects within the same model. We assessed whether p varied with air temperature, survey effort and moon phase (only for lesser night geckos). We defined survey effort as the number of nights surveyed per trip for lesser night gecko, and the total number of morning and afternoon surveys per trip for Bojer's skinks (3.6 Supplementary Information: Table S3.2). All covariates were modelled using a *log* link for N, a multinomial *logit* link for β and a *logit* link for ϕ and p. We completed model selection using all possible combinations of covariates and compared these using Akaike's Information Criterion (AIC; Akaike 1973, 1974) and the corrected AIC for small sample sizes AICc (Hurvich & Tsai 1989). Confidence intervals were obtained for all parameters using a non-parametric bootstrap procedure (DiCiccio & Efron 1996).

3.3.3 Body condition

To assess potential impacts of the oil spill on reptile fitness, we calculated a body condition score for each individual. There are a variety of body condition indices that aim to account for the size of individuals energy reserves and thereby fitness (Peig & Green 2009; Falk *et al*. 2017) from mass and length measurements that were taken during surveys. Here, we use the scaled mass index (SMI):

$$\widehat{M}_i = M_i \left[\frac{L_0}{L_i}\right]^b$$

where $\widehat{M}_i$ is the scaled mass index for an individual, M_i is the individuals recorded mass, L_i is the individuals' snout-to-vent length, L_0 is the mean snout-to-vent length (svl) of the population and b is the scaling exponent from the regression of M on L for the entire population (Peig & Green 2009). We chose to use SMI as it has been shown to predict body condition more accurately in reptiles (Peig & Green 2009; Falk *et al.* 2017), across multiple age and sex classes (Peig & Green 2010) when compared to other condition indices. In addition, both lesser night geckos and Bojer's skinks are sexually dimorphic, with females being slightly larger in lesser night geckos (Bullock *et al.* 1985) and males being significantly larger in Bojer's skinks (Cole & Payne 2022). Our preliminary analysis demonstrated that a simple ratio of mass:svl was skewed by sex whereas SMI was more consistent between sexes, allowing us to identify trends in body condition without further splitting of sparse datasets. Variation in body condition was modelled separately for the two species, using generalized linear mixed models (GLMMs). For both species, we used fixed effects of time (modelled discretely per survey trip), sex, season and island, and individual ID as a random effect to test the impact of individual variation on body condition. Seasons were defined as follows: Summer 1 (November – January), start of summer after a dry winter where resources are very limited; Summer 2 (February – April) end of summer where greater rainfall has increased resources and temperatures are still high; Winter 1 (May – July) where temperatures are cooling and resources are readily available after the rains; Winter 2 (August – September) end of winter during which temperatures are lower and there is less rainfall. For models where random effects were not significant, a generalised linear mixed model was run (GLM) using the same fixed effects, giving very similar estimates. Significance was assessed by comparing the marginal and conditional R^2 values which correspond to the proportions of the data explained by the fixed effects (without random effects) and the whole model (with random effects) respectively. We also modelled body condition using GLMs with an extended dataset including surveys carried out between 2013 and 2022 (additional surveys shown in 3.6

Supplementary Information: Table S3.3) without individual IDs due to photos not being available. The models most supported by the data for each dataset were selected using AIC.

3.4 Results

3.4.1 Survival & population size

Population size and survival were estimated using Jolly-Seber models (modified Jolly-Seber model for Ile Marianne (IM); Bickerton *et al.* 2023), with each reptile population modelled separately. The models with lowest AIC (3.6 Supplementary Information: Table S3.4) for the IM population of lesser night geckos was: $N{\sim}sex, \beta{\sim}time, \phi{\sim}oil\ spill\ (1), p{\sim}survey\ effort + moon\ phase$ and for the Ilot Vacoas (IV) population: $N{\sim}sex, \beta{\sim}time, \phi{\sim}1, p{\sim}1$ (model selection tables 3.6 Supplementary Information: Tables S3.4-3.5). On IM, the population size grew following the translocation and appears to decline before the oil spill (Figure 3.2) and increases following the oil spill, demonstrating limited long-term effects. The same is seen in the Ilot Vacoas population however due to a very limited number of surveys and recaptures, error is very high for the population estimates therefore no clear pattern can be shown (Figure 3.2). Survival of the IM population directly related to our oil covariate with annual survival before the oil spill being 0.539 (95% CI: 0.462-0.603) and after 0.393 (95% CI: 0.262-0.512). Annual survival of the IV population was 0.574 (95% CI: 0.083-0.747), similar to the pre-oil survival probability of the IM population however, as with the population estimates, has very high uncertainty.

The Jolly-Seber models for the populations of Bojer's skink on Ile aux Fouquets (IAF), Ile de la Passe (IDLP) and IV with the lowest AICs were as follows: IAF $N{\sim}sex, \beta{\sim}time, \phi{\sim}sex, p{\sim}sex + survey\ effort + temperature$; IDLP $N{\sim}sex, \beta{\sim}time, \phi{\sim}time, p{\sim}sex + temperature$; IV $N{\sim}sex, \beta{\sim}time, \phi{\sim}1, p{\sim}sex + time$ (3.6 Supplementary Information: Tables S3.6-3.8). The estimates of population size for the three populations of Bojer's skink do not indicate any decline following the oil spill and all have large confidence intervals, likely due to large time gaps between surveys and low numbers of recaptures in the surveys before the oil spill (Figure 3.3). This is especially apparent for the IDLP population, where survival is estimated at 0 between 2015 and 2021 due to a lack of recaptures, which can be common when working with elusive threatened species with life spans in the range of 3-4 years (Cole & Payne 2022). Survival on IAF, the largest of the populations, did not vary with time, only sex, with males having an annual survival probability of 0.177 (95% CI: 0.062-0.361) compared to 0.413 (95% CI: 0.204-0.595) for females, however these values are likely due to the time interval between surveys relative to the life span which reduces the numbers of individuals available to be recaptured. Survival on IV was constant, at 0.408 (95% CI: 0.324-0.481), again showing relatively high uncertainty but comparable to the IAF population.

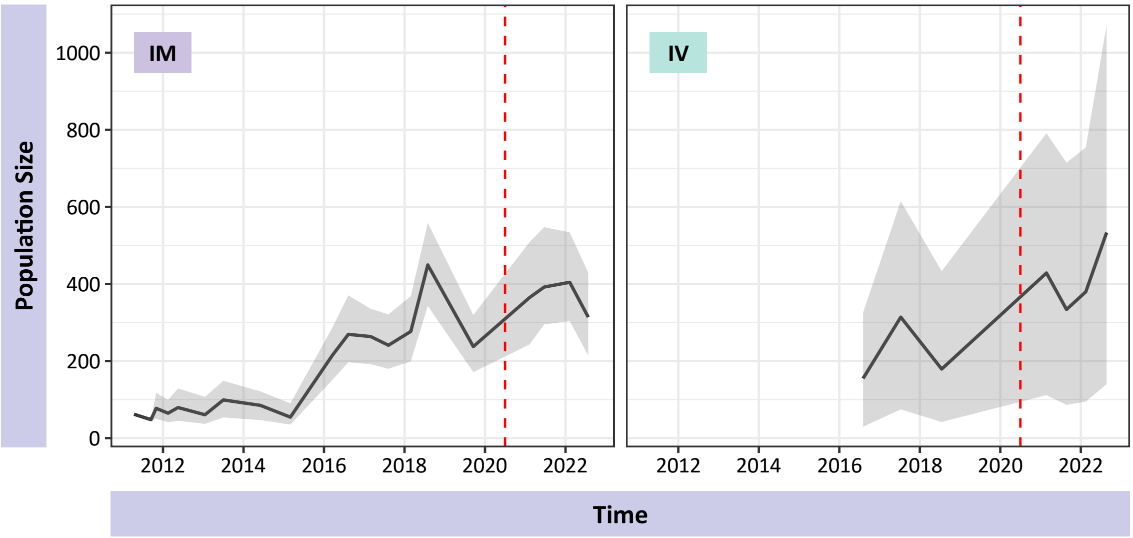

Figure 3.2: Variation in population size of lesser night gecko populations on Ile Marianne (IM) and Ilot Vacoas (IV) from capture-mark-recapture surveys. Red dashed line indicates the MV Wakashio oil spill in July 2020. Grey area around the line gives 95% confidence intervals. Both populations were modelled using Jolly-Seber models have sex dependent population size and time dependent entry probability. IM has survival dependent on our first oil covariate and detection dependent on survey effort and moon phase. IV has constant survival and detection probabilities.

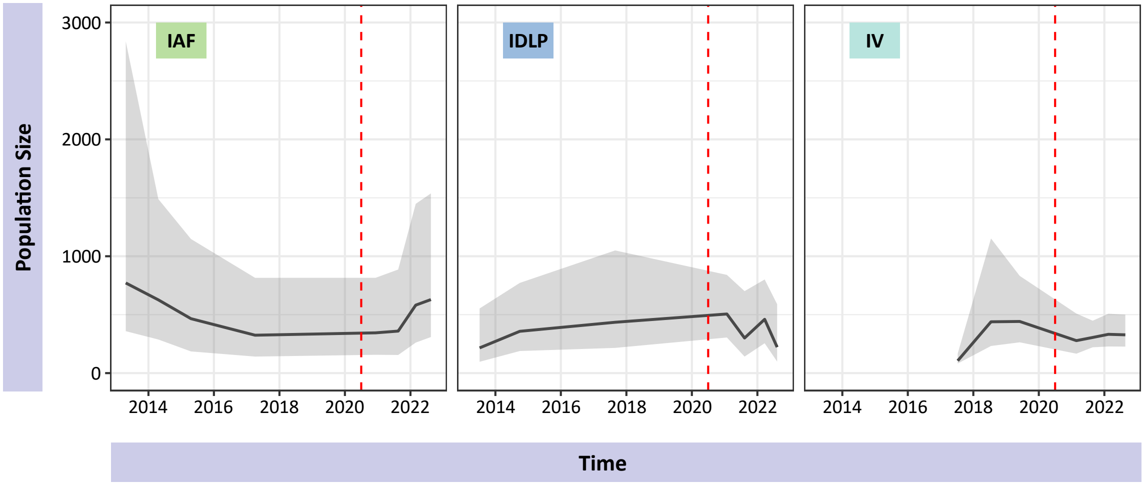

Figure 3.3*:* Variation in population size of Bojer's skink populations on Ile aux Fouquet (IAF), Ile de la Passe (IDLP) and Ilot Vacoas (IV) from capture-mark-recapture surveys. Red dashed line indicates the MV Wakashio oil spill in July 2020. Grey area around the line gives 95% confidence intervals. All populations used Jolly-Seber models which had sex dependent population size and time dependent entry probability. Survival probability is dependent on sex for IAF, time for IDLP and constant for IV. Detection probability is dependent on sex, survey effort and temperature for IAF, sex and temperature for IDLP and sex and time for IV.

3.4.2 Body condition

The most important factor for determining body condition in lesser night gecko was time with the lowest AIC value of our GLMMs ($SMI \sim Time + (1|ID)$; 3.6 Supplementary Information: Table S3.9). SMI scores were generally highest between 2016 and 2018 then slightly lower from 2019. There was very little seasonal variation, however no surveys were carried out in the driest season and there was little variation between islands. In our model with lowest AIC, the marginal $R^2 = 0.220$ and condition $R^2 = 0.278$ indicating a lower impact of individual variation on overall body condition compared to the Bojer's skink. The top model is significantly different from the null (ANOVA: χ^2 = 213.2, df = 7, $p < 0.005$). There is no strong evidence of the oil spill impacting body condition of lesser night geckos as there is little variation in SMI in the surveys before and after the oil spill (Figure

3.4). Gravid females within the dataset have led to outlying SMI values (Figure 3.4), due to the large mass gain relative to their body size when gravid. These are more evident before the oil spill due to the timing of the surveys.

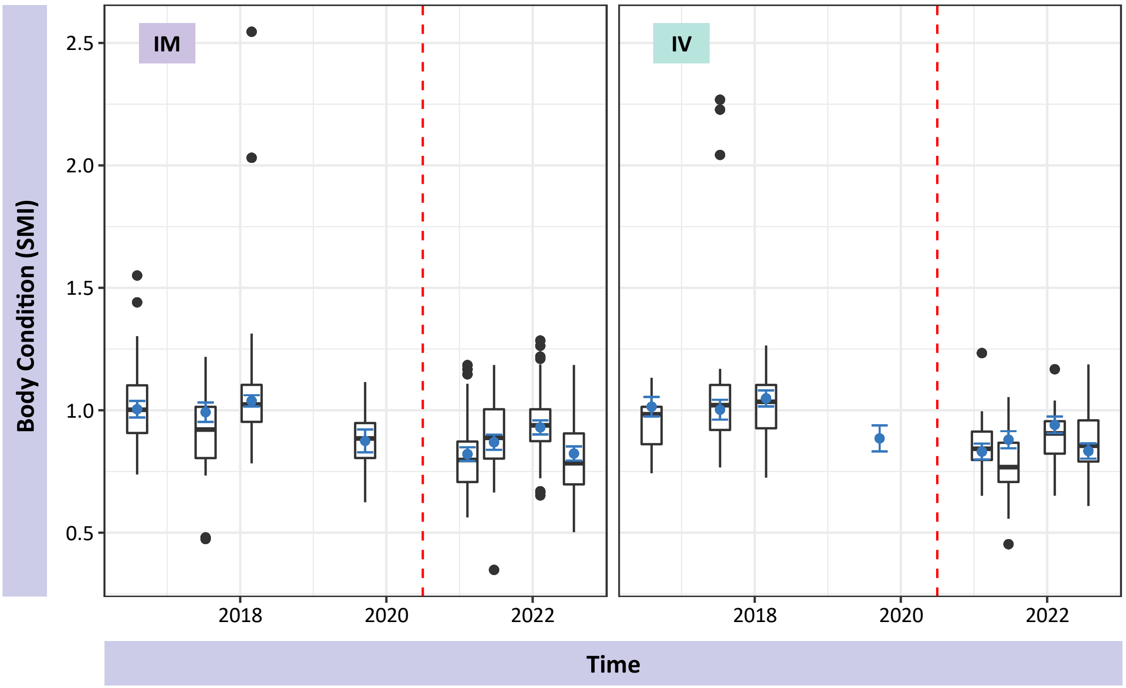

Figure 3.4: Variation in scaled mass index as a proxy for body condition for the lesser night gecko between 2016 and 2022, with predicted values from our highest ranked model $SMI \sim Time + (1|ID)$ given in blue with 95% confidence intervals, split by island (IM: Ile Marianne; IV: Ilot Vacoas). Red dashed line indicates the date of the oil spill.

The most important features in determining body condition in Bojer's skinks, from our GLMM models using scaled mass index (SMI), were island, sex and season (model with lowest AIC: $SMI \sim Island + Sex + Season + (1|ID)$; 3.6 Supplementary Information: Table S3.10). The Ile aux Fouquet population had a significantly lower SMI score compared to Ile de la Passe and Ilot Vacoas which were very similar. Males had a higher SMI than females on all islands. SMI peaks in the period we defined as Summer 2, February – April, where resources are highest due to rainfall and peak hatching season for reptiles and seabirds, and lowest at the start of summer (Summer 1), where resources are very limited after the winter and rainfall is typically low. SMI is similar for both winter periods and is lower than the end of summer but a lot higher than the start of summer (3.6 Supplementary Information: Figure S3.1). In our model with the lowest AIC, the marginal $R^2 = 0.137$ and condition $R^2 = 0.507$, which are the proportions of the data explained by the fixed effects and the whole model respectively. The difference in these values highlights the large effect of variation between individuals and therefore the importance of including a random effect in the model. The top model is significantly different from the null (ANOVA: $\chi^2 = 290.3$, df = 6, $p < 0.005$). There is no evidence of body condition changing due to either oil spill metric (Figure 3.5). There is a decrease in body condition on Ile aux Fouquet and Ile de la Passe between the final survey before the oil spill (IAF: April 2017; IDLP: August 2017) and the first survey after the oil spill (IAF: December 2020; IDLP: January 2021), however given the length of time between surveys and the seasonal differences between the surveys (i.e. after the oil spill being the driest time of year where resources are least available), we cannot be certain that this is due to impacts of the oil spill.

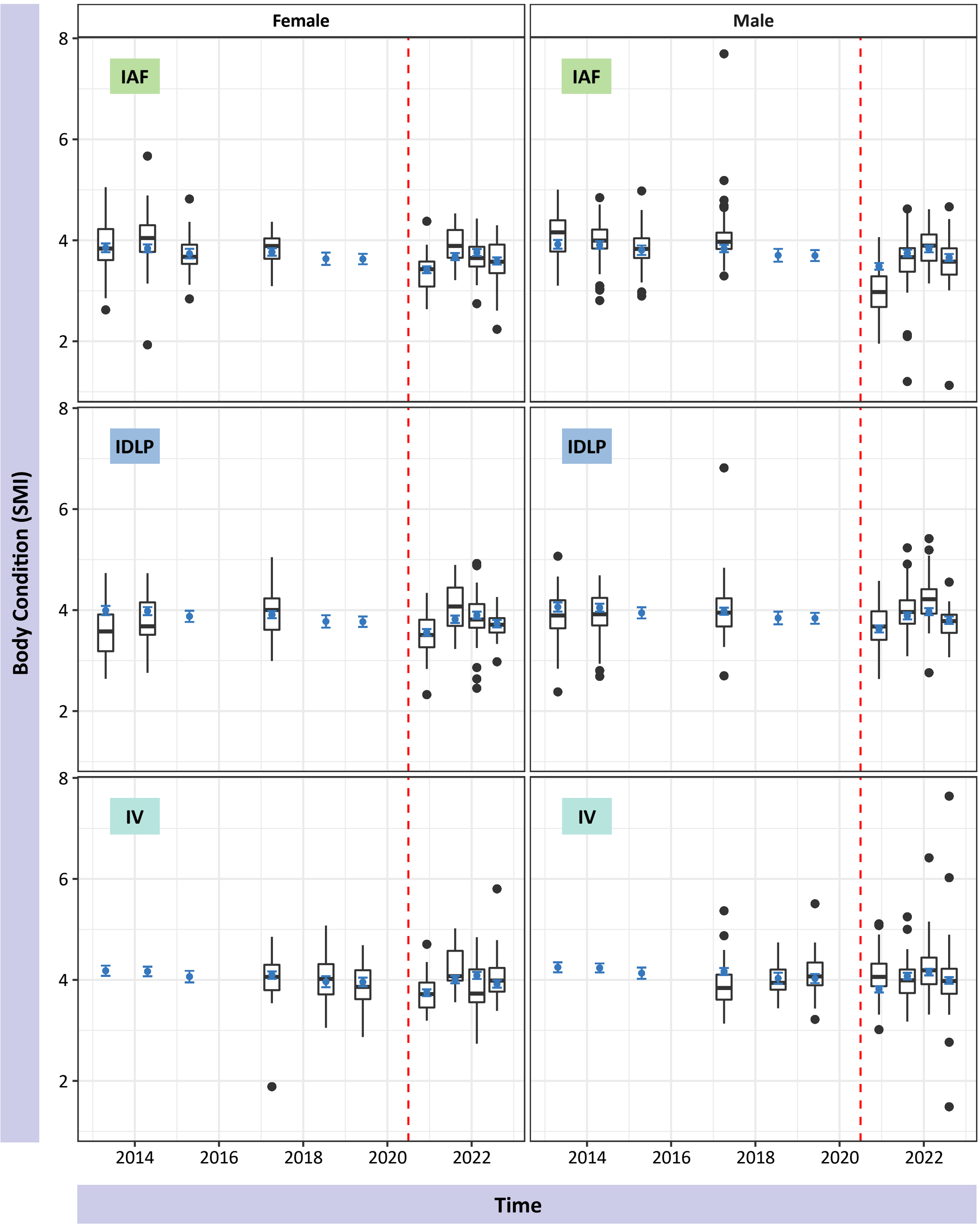

Figure 3.5: Variation in scaled mass index as a proxy for body condition for the Bojer's skink between 2013 and 2022, with predicted values from our highest ranked model $SMI \sim Island + Sex + Season + (1|ID)$ given in blue with 95% confidence intervals, split by sex and island (IAF: Ile aux Fouquets; IDLP: Ile de la Passe; IV: Ilot Vacoas). Red dashed line indicates the date of the oil spill. Blue values where no black boxplot is present represent model estimates for years with no available data, where surveys were carried out on other islands.

3.5 Discussion

We assessed whether there was a change in population size, survival probability or body condition of two threatened terrestrial lizard species following the MV Wakashio oil spill in Mauritius. We detected no significant changes in population size following the oil spill in any of the 5 populations. The Ile Marianne population of lesser night gecko had a lower estimated survival following the oil spill, but none of the other populations showed any change in survival relating to the spill. We detected declines in body condition immediately following the oil spill in two of the Bojer's skink populations, but those declines could also be due to resource shortages as the surveys occurred at the time of year when resources are most limited.

Of the five reptile populations studied, only the Ile Marianne lesser night gecko population had any parameters that correlated with the oil spill. Survival was estimated to be lower after the oil spill and population was predicted to decrease. However, Ile Marianne is the furthest island from the site of the oil spill, with no oil detected during visual inspections of the island. Furthermore, the population size started to decrease in 2019, before the oil spill, indicating the decline may not be linked to the spill. It is possible, as the Ile Marianne population was reintroduced in 2011, that the population is nearing carrying capacity and the decline is due to density dependence as opposed to oil, and this may also link to the decreased survival. The decrease in survival may also be a combination of the two processes, and further surveys will be needed before any longer-term effects can be detected. Additionally, the slight decrease in body condition following the oil spill could support both increased population density with the resulting competition for resources and impacts of the oil spill. Estimates of population size and survival from this population are surrounded by less uncertainty as the population was surveyed more regularly prior to the oil spill. In contrast, the Ilot Vacoas population had fewer surveys and, on average, a lower detection probability with fewer individuals caught, reducing our power to detect spill-related impacts. On one hand, we can be confident that the Ilot Vacoas population has not been severely impacted; on the other hand, we cannot say with confidence whether there have been any smaller scale or short-term impacts, especially as oil was detected on the island during initial surveys. We may be able to use the survival estimates from the IM population to predict changes in abundance, however the fluctuation as the population reaches carrying capacity may lead to complexity that is difficult to account for without further modifications to the capture-recapture model formulations. The uncertainty surrounding the survival estimates of the Bojer's skink populations and the IV lesser night gecko population greatly limit our ability make reliable future predictions.

Although most oil spills occur in marine ecosystems, terrestrial species still regularly come into contact with oil or derived contaminants in a variety of ecosystems across the planet (Chilvers *et al.* 2021). Of all reported spills between 1970 and 2018, 7% were classified as terrestrial and of these, only 15% reported that they had investigated the impacts on wildlife (Chilvers *et al.* 2021). Additionally, reptiles are underrepresented in ecotoxicology literature (Zychowski & Godard-Codding 2017). The lack of research in this area highlights a need for both better monitoring and better reporting systems, which would allow comparisons to be drawn and effective mitigation to be put in place.

In the immediate aftermath of oil spills, most damaging effects are due to direct contact between organisms and oil (Burns *et al.* 2014). However, our study was unlikely to detect short-term effects, as surveys of population and body condition were not started until at least 4 months after the spill, due to special permissions required to access the islands during the Covid-19 pandemic. On the other hand, given the observed stability of population sizes following the oil spill, it is unlikely any direct contact with oil had long-term impacts. Ideally, following an oil spill, surveys of populations with existing baseline data should be carried out as soon as possible, so short-term impacts can be quantified and impacts better understood, allowing for more efficient mitigation in the future. However, we appreciate that access to a site following an environmental disaster can be limited due to safety resources. For example, this limitation was recognized following the large 2020 wildfires in Australia: like oil spills, wildfires are often unpredictable and surveying effectively requires long-term planning which is not always possible under the financial constraints of conservation as well as the safety implications for those carrying out the survey (Southwell *et al.* 2021). In our study area in Mauritius, delays also occurred partly due to a lack of protective equipment to protect against oil fumes.

In the short-term, especially in coastal ecosystems, reptile species may be affected by decline of invertebrate prey following oil spills, a common theme in terrestrial studies (Couceiro *et al.* 2007; Bam *et al.* 2018). Both our study species are insectivorous; however, the lesser night gecko is less likely to be affected by this prey loss as its main food source are micromoths which are mostly airborne and feed from terrestrial plant species that are less likely to be found near to the coast, in addition to the IM population being further from the spill relative to the other islets. The Bojer's skinks could be impacted as they scavenge in addition to hunting and their prey is terrestrial therefore had a higher chance of being directly in contact with oil.

Longer term impacts may occur if contaminants accumulate within the food chain. Although our estimates show no evidence of this, it may take longer for a population-level impact to become apparent, again highlighting the need for continued monitoring. Although there is great variation between the impact of oil on terrestrial vertebrates, it has been suggested that shorter lived species are less likely to be impacted by the carcinogenic effects of oil as tumours can take time to develop so may not affect the fitness of a short-lived species within its lifespan, compared to longer-lived species (Malcolm & Shore 2003; Esler *et al.* 2018). As both species examined here are relatively short-lived, this could explain the general lack of significant differences in survival probability following the oil spill. Additionally, the coastlines of the SE islets are coralline rock with very little sediment, potentially reducing accumulation in comparison to sediment-rich areas such as salt marshes (in the case of the Deep Water Horizon spill; Burns *et al.* 2014), beaches (in the case of the Exxon Valdez spill; Short *et al.* 2007) and deserts (such as the Kuwait oil fields; Al-Hashem *et al.* 2007) where evidence of long-term persistence and exposure of vertebrates to contaminants was observed, including the presence of PAHs in *Acanthodactylus scutellatus* lizards and their ant prey in Kuwait (Al-Hashem *et al.* 2007), one of the few studies published on terrestrial reptiles.

The observed patterns or lack thereof may of course be equally affected by the monitoring protocol pre- and post-spill, with important implications for evaluation and management. The lack of available data on juvenile animals, due to the difficulty of capture and previous surveys being focused primarily on adult animals due to the stress caused when capturing juveniles, may have led to our results underestimating the impact of the spill, as juvenile animals are often more vulnerable to the effects of oil (Asif et al. 2022). Due to generation time, it is also unlikely any population level effects on the adult population due to a decline in juveniles would be apparent within the scope of the surveys carried out. If we had been able to monitor juvenile survival, it may have given a more of an indication of mortality and a greater ability to predict future declines in recruitment. We would therefore recommend continued monitoring of these populations, especially of juveniles, and comparisons of juvenile body condition to be carried out where possible, to enable understanding of potential long-term effects.

Both species examined in this study have low detection probabilities (less than 0.20) which can greatly impact our ability to capture and recapture individuals during surveys (Sutherland *et al.* 2010). Jolly-Seber models rely on recaptures to produce accurate estimates of demographic parameters, which in turn are needed to identify impacts of natural disasters such as oil spills and separate them from other environmental and demographic factors, such as the seasonality in the Bojer’s skink body conditions. Where possible, timing surveys to be consistent with known environmental factors, such as season and moon phase, for baseline surveys can help to simplify modelling of data and allow for better understanding of population dynamics following stochastic events. For example, if the surveys for the Bojer’s skinks had all been carried out in the same season, we would be able to determine with greater confidence whether the oil spill affected body condition.

The Covid-19 pandemic might also have affected our study system and estimates in different ways. On one hand, the pandemic could potentially explain the increase in population size of the IAF Bojer population as the island, which is normally open to tourists, was closed during the pandemic and reopened at the end of 2021. Tourists have previously been noted as a food source for the Bojer's skink, which often scavenge as well as hunting (Cole *et al.* 2009; du Plessis *et al.* 2019). The return of tourists could have increased resources on the island, helping the population growth we observed in 2022. On the other hand, pandemic-related restrictions prevented routine surveys of the islands creating a 2-3 year gap in surveys before and after the oil spill. As the life span of lesser night geckos and Bojer's skinks is 3-4 years, a time gap of this size can prevent recaptures and generate spurious estimates of declines in survival or population size. This effect might influence our models for the IDLP Bojer's skink population, as recaptures were scarce before the oil spill, where gaps between surveys are over a year. This population also has a lower density in comparison to other islands, further decreasing the chance of recaptures, biasing estimates of survival and increasing uncertainty around population size.

To conclude, our study found very limited impacts of the MV Wakashio oil spill on two threatened terrestrial reptile species, with no indication of long-term population-level effects. This is encouraging, but we recognize our data were inadequate to detect several sources of short- and longer-term effects that might reasonably be expected based on known ecotoxicology and species ecology, including physical damage from oil and longer-term bioaccumulation. To improve the ability to conserve terrestrial species that come into contact with oil, we recommend that consistent baseline data is collected for those species that inhabit terrestrial habitats at risk of oil spills, such as coastal systems or small islands near to shipping lanes. We appreciate that funding for baseline surveys is limited, and therefore stress the need for consistency in any surveys that are carried out and the importance of surveys of multiple species at lower levels in the food chain.

3.6 Supplementary Information

***Table S3.1**: Location of South-Eastern Islets and species present.*

Island	**Latitude**	**Longitude**	**Species**
Ile aux Fouquets	-20.395391	57.777716	Bojer’s Skink
Ile de la Passe	-20.399050	57.767440	Bojer’s Skink
Ile Marianne	-20.380190	57.787217	Lesser Night Gecko
Ilot Vacoas	-20.397788	57.770578	Both

***Table S3.2*: Survey effort for each population where photos were available.**

Island	Survey	Survey Length (days)	No. Bojer’s skink surveys	No. lesser night gecko surveys
Ile aux Fouquets	Apr 2013	3	6	
	Apr 2014	4	7	
	Apr 2015	5	8	
	Apr 2017	4	7	
	Dec 2020	4	8	
	Aug 2021	4	7	
	Mar 2022	4	8	
	Aug 2022	3	6	
Ile de la Passe	Jul 2013	3	6	
	Oct 2014	4	8	
	Aug 2017	4	8	
	Jan 2021	4	8	
	Aug 2021	3	6	
	Mar 2022	3	6	
	Aug 2022	4	6	
Ilot Vacoas	Aug 2016	2		2
	Jul 2017	4	8	2
	Jul 2018	4	7	1
	Jun 2019	4	8	
	Feb 2021	4	8	4
	Aug 2021	3	6	3
	Feb 2022	3	5	2
	Aug 2022	4	8	4
Ile Marianne	Apr 2011	2		2
	May 2011	2		2
	Aug 2011	2		2
	Sep 2011	2		2
	Nov 2011	2		2
	Feb 2012	2		2
	May 2012	2		2
	Jan 2013	2		2
	Jul 2013	3		3
	Jun 2014	3		3
	Mar 2015	4		4

	Mar 2016	4		4
	Aug 2016	4		4
	Mar 2017	4		4
	Aug 2017	4		4
	Mar 2018	4		4
	Jul 2018	4		4
	Sep 2019	4		4
	Feb 2021	4		4
	Jun 2021	4		4
	Feb 2022	4		4
	Jul 2022	4		4

Table S3.3: Summary of the data used in analysis for each island population and each species, where CMR represents capture-mark-recapture analysis where photos were available and individuals were identified, and BC represents body condition analysis, where unknown individuals were also included in the analysis.

Year	Ile aux Fouquets	Ile de la Passe	Ilot Vacoas		Ile Marianne
	Bojer's Skink	Bojer's Skink	Bojer's Skink	Lesser Night Gecko	Lesser Night Gecko
2013	CMR & BC	CMR & BC	BC	BC	CMR & BC
2014	CMR & BC	CMR & BC	BC	BC	CMR & BC
2015	CMR & BC	BC	BC	BC	CMR & BC
2016	BC	BC	BC	CMR & BC	CMR & BC
2017	CMR & BC	CMR & BC	CMR & BC	CMR & BC	CMR & BC
2018	BC	BC	CMR & BC	CMR & BC	CMR & BC
2019	BC	BC	CMR & BC	None	CMR & BC
2020/2021 (Dec/Jan/Feb)	CMR & BC	CMR & BC	CMR & BC	CMR & BC	CMR & BC
2021 (Aug)	CMR & BC	CMR & BC	CMR & BC	CMR & BC	CMR & BC
2022 (Feb/Mar)	CMR & BC	CMR & BC	CMR & BC	CMR & BC	CMR & BC
2022 (Jul/Aug)	CMR & BC	CMR & BC	CMR & BC	CMR & BC	CMR & BC

Table S3.4: Model selection for the Ile Marianne Lesser Night Gecko CMR, 10 models with lowest AIC shown. Oil (1) denotes where the oil spill covariate was split into one value for surveys before and one value for all surveys after the oil spill, for oil (2) the covariate was one values for all surveys apart from the one directly following the oil spill.

N	***β***	***ϕ***	***P***	***k***	***AIC***	***ΔAIC***	**AICc**	***ΔAICc***
sex	time	oil (1)	effort + moon	24	-1253.50	0.00	-1251.63	0.122
sex	time	oil (1)	effort	23	-1253.47	0.03	-1251.75	0
sex	time	1	effort	22	-1252.40	1.10	-1250.82	0.928
sex	time	1	time	41	-1251.79	1.71	-1246.27	5.482
sex	time	oil (1)	effort + temperature + moon	25	-1251.51	1.99	-1249.48	2.271
sex	time	oil (1)	effort + temperature	24	-1251.46	2.04	-1249.59	2.163
sex	time	oil (2)	effort	23	-1251.25	2.24	-1249.54	2.214
sex	time	1	effort + moon	23	-1250.87	2.63	-1249.15	2.604
sex	time	sex	effort	23	-1250.54	2.95	-1248.83	2.924
sex	time	oil (1)	time	42	-1250.48	3.02	-1244.68	7.068

Table S3.5: Model selection for the Ilot Vacoas Lesser Night Gecko CMR, 10 models with lowest AIC shown. Oil (1) denotes where the oil spill covariate was split into one value for surveys before and one value for all surveys after the oil spill, for oil (2) the covariate was one values for all surveys apart from the one directly following the oil spill.

N	*β*	*ϕ*	*P*	*k*	*AIC*	*ΔAIC*	AICc	*ΔAICc*
sex	time	1	1	10	-509.90	0	-508.69	0
sex	time	1	effort	11	-508.41	1.491	-506.95	1.739
sex	time	1	temperature	11	-508.00	1.916	-506.53	2.164
sex	time	1	sex	11	-507.93	1.970	-506.48	2.219
sex	time	oil (2)	1	11	-507.93	1.971	-506.47	2.219
sex	time	1	moon	11	-507.92	1.978	-506.47	2.226
sex	time	oil (1)	1	11	-507.90	2.001	-506.44	2.249
sex	time	sex	1	11	-507.89	2.001	-506.44	2.250
sex	time	oil (1)	effort	12	-507.18	2.716	-505.46	3.237
sex	time	1	sex + temperature	13	-506.85	3.043	-504.83	3.863

Table S3.6: Model selection for the Ile aux Fouquets Bojer's skink CMR, 10 models with lowest AIC shown. Oil (1) denotes where the oil spill covariate was split into one value for surveys before and one value for all surveys after the oil spill.

N	*β*	*ϕ*	*P*	*k*	*AIC*	*ΔAIC*	AICc	*ΔAICc*
sex	time	sex	sex + effort + temperature	17	-2955.25	0	-2954.24	0
sex	time	sex	sex	13	-2953.23	2.027	-2952.63	1.612
sex	time	sex	sex + effort	15	-2952.68	2.578	-2951.88	2.357
sex	time	1	sex + effort + temperature	16	-2952.37	2.887	-2951.47	2.773
sex	time	sex + oil (1)	sex + effort + temperature	19	-2951.97	3.288	-2950.7	3.538
sex	time	1	sex	12	-2951.95	3.302	-2951.44	2.802
sex	time	oil	sex	13	-2951.76	3.490	-2951.17	3.075
sex	time	sex + oil (1)	sex	15	-2951.46	3.789	-2950.67	3.568
sex	time	oil (1)	sex + effort + temperature	17	-2951.36	3.893	-2950.35	3.893
sex	time	sex	sex + temperature	15	-2951.30	3.958	-2950.50	3.736

Table S3.7: Model selection for the Ile de la Passe Bojer's skink CMR, 10 models with lowest AIC shown. Oil (1) denotes where the oil spill covariate was split into one value for surveys before and one value for all surveys after the oil spill, for oil (2) the covariate was one values for all surveys apart from the one directly following the oil spill.

N	*β*	*ϕ*	*P*	*k*	*AIC*	*ΔAIC*	AICc	*ΔAICc*
sex	time	time	sex + temperature	18	-2139.48	0	-2137.99	0
sex	time	time	1	15	-2138.56	0.923	-2137.52	0.473
sex	time	oil (2)	sex + temperature	14	-2138.45	1.031	-2137.54	0.451
sex	time	sex	sex + temperature	14	-2138.40	1.075	-2137.50	0.495
sex	time	1	sex + temperature	13	-2137.76	1.713	-2136.98	1.011
sex	time	time	sex + effort + temperature	20	-2137.53	1.946	-2135.70	2.292
sex	time	sex + oil (2)	sex + temperature	16	-2137.38	2.096	-2136.21	1.787
sex	time	oil (2)	1	11	-2137.37	2.110	-2136.80	1.190
sex	time	time	effort + temperature	17	-2137.16	2.320	-2135.83	2.161
sex	time	time	effort	16	-2137.16	2.321	-2135.98	2.012

Table S3.8: Model selection for the Ilot Vacoas Bojer's skink CMR, 10 models with lowest AIC shown. Oil (1) denotes where the oil spill covariate was split into one value for surveys before and one value for all surveys after the oil spill, for oil (2) the covariate was one values for all surveys apart from the one directly following the oil spill.

N	***β***	***ϕ***	***P***	***k***	***AIC***	***ΔAIC***	**AICc**	***ΔAICc***
sex	time	1	sex + time	23	-2449.29	0	-2447.30	0
sex	time	oil (2)	sex + time	24	-2447.54	1.756	-2445.37	1.933
sex	time	oil (1)	sex + time	24	-2447.46	1.830	-2445.29	2.007
sex	time	sex	sex + time	24	-2447.34	1.952	-2445.17	2.129
sex	time	sex + oil (2)	sex + time	26	-2443.64	5.650	-2441.09	6.205
sex	time	sex + oil (1)	sex + time	26	-2443.61	5.682	-2441.06	6.238
sex	time	time	sex + time	28	-2440.90	8.392	-2437.94	9.358
sex	sex + time	1	sex + time	29	-2440.64	8.649	-2437.47	9.831
sex	sex + time	1	sex + time	29	-2440.64	8.649	-2437.47	9.831
sex	sex + time	oil (2)	sex + time	30	-2438.93	10.363	-2435.53	11.770

Table S3.9: Model selection table for lesser night gecko populations on the southeast islets, Mauritius. Left column shows results for Generalised linear mixed models (including individual as a random effect) and right for linear models (no random effects).

Fixed Effects	GLMM with ID as random effect			Linear model with extended dataset		
	df	AIC	ΔAIC	df	AIC	ΔAIC
Time	10	-728.966	0	12	-1000.06	0
Time + Sex	11	-728.826	0.139706	13	-998.233	1.828674
Time + Island	11	-727.567	1.399022	14	-996.865	3.196639
Time + Island + Sex	12	-727.442	1.523618	15	-995.062	4.999906
Oil (1)	4	-665.565	63.40112	3	-910.743	89.31844
Sex + Oil (1)	5	-665.237	63.72916	5	-906.808	93.2543
Island + Oil (1)	5	-663.785	65.18074	4	-910.279	89.78323
Sex + Island + Oil (1)	6	-663.471	65.49515	6	-906.36	93.70193
Oil (2)	4	-574.608	154.3582	3	-811.827	188.2353
Island + Oil (2)	5	-574.433	154.5324	4	-814.582	185.4799
Sex + Oil (2)	5	-574.411	154.5547	5	-808.162	191.8995
Sex + Island + Oil (2)	6	-574.211	154.7551	6	-810.913	189.1484
Season + Island	6	-547.126	181.84	5	-774.012	226.0502
Island + Sex + Season	7	-546.61	182.3553	7	-770.318	229.7439
Season	5	-545.364	183.6014	4	-766.083	233.979
Season + Sex	6	-544.864	184.1015	6	-762.491	237.5709
Island	4	-530.289	198.677	3	-764.165	235.8968
1 (Null)	3	-529.762	199.2039	2	-760.52	239.5415
Island + Sex	5	-529.262	199.7032	5	-760.319	239.7425
Sex	4	-528.754	200.2122	4	-756.771	243.2912

Table S3.10: Model selection table for Bojer’s skink populations on the southeast islets, Mauritius. Left column shows results for Generalised linear mixed models (including individual as a random effect) and right for linear models (no random effects).

Fixed Effects	GLMM with ID as random effect			Linear model with extended dataset		
	df	AIC	ΔAIC	df	AIC	ΔAIC
Island + Sex + Season	9	2645.039	0	9	4391.876	0
Season + Island	8	2653.008	7.96944	7	4418.971	27.09518
Time + Island + Sex	15	2703.513	58.47421	16	4463.502	71.62552
Time + Island	14	2710.248	65.20886	14	4491.051	99.17518
Season + Sex	7	2717.78	72.74141	7	4419.446	27.56949
Season	6	2729.387	84.34842	5	4451.771	59.89511
Sex + Island + Oil (2)	7	2735.35	90.31123	7	4505.062	113.1855
Island + Oil (2)	6	2742.781	97.74194	5	4525.51	133.6336
Sex + Island + Oil (1)	7	2795.584	150.5453	7	4566.527	174.6508
Time + Sex	13	2803.484	158.4452	14	4489.625	97.7489
Island + Oil (1)	6	2806.552	161.5134	5	4582.774	190.8983
Time	12	2817.813	172.7742	12	4530.742	138.866
Sex + Oil (2)	5	2827.29	182.2511	5	4528.804	136.928
Oil (2)	4	2838.249	193.2106	3	4560.399	168.5232
Island + Sex	6	2838.849	193.81	6	4594.581	202.7052
Island	5	2845.583	200.5444	4	4606.121	214.2452
Sex + Oil (1)	5	2878.276	233.2377	5	4589.531	197.6552
Oil	4	2892.706	247.667	3	4615.352	223.4761
Sex	4	2913.371	268.3325	4	4613.329	221.4526
1 (Null)	3	2923.34	278.3015	2	4633.227	241.3508

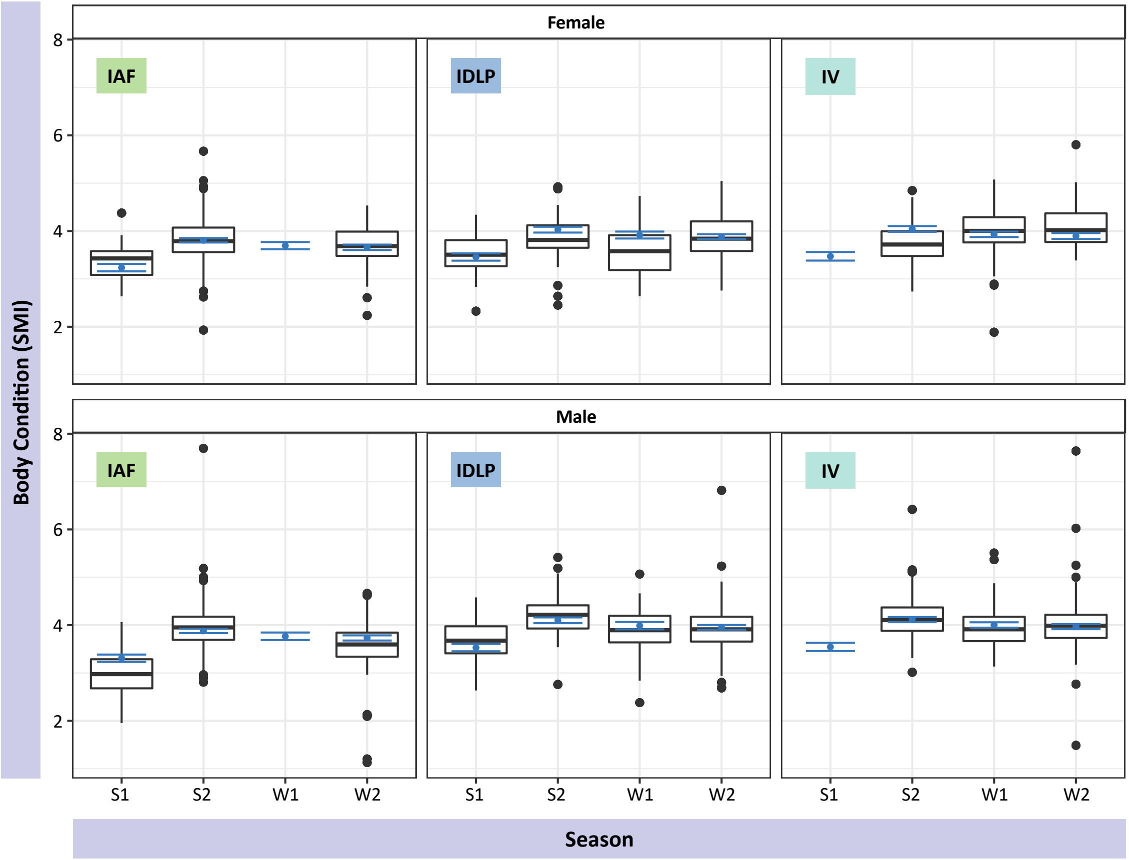

Figure S3.1: Variation in body condition of the Bojer's skink by season, sex and island (IAF: Ile aux Fouquets; IDLP: Ile de la Passe; IV: Ilot Vacoas). Red points indicate predictions from the highest ranked model for each (4.6 Supplementary Information: Table S3.10) and error bars show 95% confidence intervals.