

DEMOGRAPHIC ASSESSMENT AND MEDIUM-TERM
SUCCESS OF A REINTRODUCED POPULATION OF
Dasypsecta leporina

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Dedicado a
Alex Schomaker Bastos
uma estrela breve

*“Oh! Nem o tempo, amigo
Nem a força bruta
Pode um sonho apagar”*
Beto Guedes

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Like winds and sunsets, wild things
were taken for granted until progress
began to do away with them.
Now we face the question whether a
still higher 'standard of living' is
worth its cost in things natural, wild
and free.

Aldo Leopold

Elas foram outrora,
essas lindas colinas,
a verde coroa da jovem Guanabara,
hoje velha regateira,
calva de suas matas,
nua de seus prados.

José de Alencar,
sobre o Maciço da Tijuca

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A dois singulares indivíduos de *Macromys adorabilis* MONJEAU: Fernando Fernandez

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RESUMO

A reintrodução de populações extirpadas é uma ferramenta de conservação em crescente popularidade. No entanto, a taxa de sucesso de tais esforços é baixa, e o seu monitoramento cuidadoso só se tornou comum recentemente. Reintroduções possuem dois objetivos primários: aumentar a área de distribuição de espécies ameaçadas, e desse modo também aumentar sua persistência em escala global; e restaurar interações e processos ecológicos ao modo que eram antes da extinção da espécie em questão. A cutia-vermelha (*Dasyprocta leporina*) é um roedor *scatterhoarder*, conhecido por ser um bom dispersor de sementes de grande porte. Um projeto de reintrodução foi iniciado em 2009 para reestabelecer a população dessa espécie no Parque Nacional da Tijuca (RJ), com o objetivo de restaurar interações ecológicas como dispersão de sementes, desse modo aumentando o recrutamento de árvores. Trinta e dois indivíduos provenientes de populações de semi-cativeiro no Rio de Janeiro foram soltos entre 2009 e 2014. Destes, 20 sobreviveram às primeiras 12 semanas após a soltura, contribuindo para o crescimento populacional. Para avaliar o estabelecimento bem-sucedido dessa população reintroduzida, nós a monitoramos através de marcação-reavistamento de Novembro 2013 a Novembro 2015. Animais foram capturados usando armadilhas Tomahawk, e marcados individualmente através de descolorimento do pêlo e marcação a frio. O reavistamento foi realizado através de 30 dias de armadilhagem fotográfica após cada sessão de captura viva. Tamanho populacional e sobrevivência aparente foram estimados usando um modelo misto de design robusto marcação-reavistamento Poisson-log-normal. O recrutamento e crescimento populacional foram derivados a partir das estimativas anteriores através de *bootstrapping* paramétrico. Foram capturados 17 indivíduos, incluindo 13 animais nascidos na natureza. A sobrevivência estimada foi menor para indivíduos jovens do que para adultos. Os valores estimados também foram menores do que a sobrevivência pós-soltura reportado anteriormente para os animais reintroduzidos. O recrutamento foi baixo durante o período do estudo, com um pico pronunciado em Agosto 2014. No entanto, houve o crescimento da população nascida na natureza, com tamanhos populacionais estimados

indo de 10.63 a 29.31, com um pico de 82.66 em Agosto 2014. O aumento de densidade apresentado pode ter aumentando a mortalidade de indivíduos através de competição por recursos, agressão intra-específica ou predação por cães domésticos (*Canis lupus familiaris*), especialmente após a formação de uma imagem de busca por estes predadores. Durante o período do nosso estudo, poucos indivíduos reintroduzidos anteriormente foram registrados com vida. Desse modo, a maior parte do crescimento aqui reportado deve ter se dado devido ao sucesso reprodutivo da população nascida na natureza. Por que a população reintroduzida é capaz de crescimento não-assistido, nós concluímos que a reintrodução foi bem sucedida no médio-prazo. Logo, solturas devem ser interrompidas e esforços direcionados para o monitoramento continuado e investigação de possíveis ameaças a persistência da população, como predação por cães domésticos (foi observada durante o estudo para 12.5% dos animais reintroduzidos). Também deve se direcionar o monitoramento à quantificação do reestabelecimento de processos ecológicos, como a dispersão de sementes. Critérios de sucesso no nível ecossistêmico pode ser derivado de tal monitoramento. Como reintroduções de *D. leporina* podem ser bem sucedidas com baixos números de animais soltos, o manejo dessa espécie provê uma oportunidade para a compreensão de dinâmicas populacionais e os seus efeitos para a restauração ecossistêmica.

Palavras-chave: conservação, roedores, reintrodução, demografia, Mata Atlântica

ABSTRACT

Reintroduction of extirpated populations is an increasingly popular conservation tool. However, success rate of reintroduction efforts is low, and only recently careful monitoring of outcomes has become common. Reintroduction efforts have two main goals: first, to increase ranges of threatened species, and improve their long-term viability on the global scale; second, to restore lost interactions and ecosystem process to how they were before the species' extirpation. The red-humped agouti (*Dasyprocta leporina*) is a scatterhoarding rodent, known to be a good large-sized seed disperser. A reintroduction effort to reestablish a population of this species to Tijuca National Park (RJ) started in 2009 with the aim of restoring ecological interactions such as seed dispersal and thus improving tree recruitment. Thirty one individuals were released from semi-captive stocks in Rio de Janeiro from 2009 to 2014. Twenty of these survived the first 12 weeks after release, contributing to population growth. To assess the successful establishment of this reintroduced population, we monitored it through mark-resighting from November 2013 to November 2015. Individuals were captured using Tomahawk traps, and marked individually with fur bleaching and freeze-branding. Resighting was carried out through 30 days of camera trapping after each capture session. Population size and survival were estimated using a robust design Poisson-log-normal mixed-effects mark-resight model. Population recruitment and growth were derived from those estimates through parametric bootstrapping. We caught a total of 17 individuals, including 13 wild-born ones. Survival was lower for young individuals than for adults. Estimated survival was also lower than previously reported post-release survival of reintroduced animals. Recruitment was low throughout the study, with a peak on August 2014. However, overall growth of the wild-born population was positive, with estimated population size going from 10.63 to 29.31, with a peak of 82.66 on August 2014. The density increase may have increased mortality through competition for resources, higher intraspecific aggression or predation by domestic dogs (*Canis lupus familiaris*), especially after the latter developed a search image for agoutis. During our study, few released individuals were recorded

alive. Therefore, most of the growth observed is due to the reproductive success of the wild population. Because the reintroduced population is capable of unassisted growth, we conclude that the reintroduction has been successful on the medium-term. Thus, releases should be ceased and efforts redirected to continued monitoring and investigation of possible threats to persistence, such as predation from domestic dogs as was observed during the study for 12.5% of released animals. Monitoring should also be directed to quantifying the reestablishment of ecological processes such as seed dispersal by *D. leporina*. Success criteria at the ecosystem level can be derived from such monitoring. Because agouti reintroductions are able to succeed with low release numbers, management of this species provides a useful laboratory for understanding the dynamics of reintroductions and their effects on ecosystem restoration.

Keywords: conservation, rodents, reintroduction, demography, Atlantic Forest

CONTENTS

Agradecimientos	iv
Resumo	vi
Abstract	viii
Table of Contents	x
List of Figures	xi
List of Tables	xi
Introduction	1
Material and Methods	4
Study Site and Species	4
Capture and Marking	5
Resighting Surveys	7
Data Analysis	8
Results	12
Live Captures	12
Resighting Surveys	13
Demographic Estimates	13
Discussion	16
References	23
Appendix 1: Supplementary Tables	a.1
Appendix 2: R Code for Analysis	a.7
R Packages Used	a.7
Stepwise RDPNE Model Selection	a.8
Parametric Bootstrapping	a.21

LIST OF FIGURES

1	Study area and trapping grid.	4
2	Comparison of fur bleaching and freeze-branding techniques.	6
3	Number of individuals captured at each trapping session	12
4	Demographic estimates (and 95% confidence intervals) of agoutis in TNP	15

LIST OF TABLES

1	Individuals captured throughout the study	13
2	Comparison of open vs. closed model structures.	14
3	Best supported RDPNE models.	14
A.1	Summary table of resighting surveys' primary intervals	a.1
A.2	Encounter histories used as input for RDPNE analysis	a.2
A.3	Modeling of α in RDPNE models.	a.3
A.4	Modeling of σ in RDPNE models.	a.4
A.5	Modeling of ϕ in RDPNE models.	a.5
A.6	Final step of modeling (γ) in RDPNE models.	a.6

INTRODUCTION

One of the major consequences of the biodiversity crisis faced by conservation biology is defaunation, the local loss or decline of medium and large-sized vertebrates (Dirzo et al. 2014). Habitat loss, fragmentation and poaching are drivers of such local extinctions (Gilpin and Soulé 1986; Redford 1992). Ecosystems devoid of their large fauna suffer a plethora of consequences, such as meso-predator release (Crooks and Soulé 1999), reduced seed dispersal and lowered seedling survival (Dirzo and Miranda 1990; Terborgh et al. 2001). Local extinction of large frugivores is common (Ceballos and Ehrlich 2002; Canale et al. 2012), leading to changes in seed dispersal and predation (Asquith et al. 1999; Galetti et al. 2015), compromising community structure and diversity in tropical forests (Janzen 1970; Connell 1971). Defaunation can even have consequences over the evolutionary time scale, as it changes the selective pressures acting on species which had once interacted with those extirpated (Galetti et al. 2013).

Reintroduction is an increasingly common management measure (Seddon et al. 2007), undertaken to restore populations to where they were historically extirpated (IUCN/SSC 2013). By restoring populations of large sized vertebrates through such management actions, the process of defaunation can be effectively reversed (Oliveira-Santos and Fernandez 2010; Seddon et al. 2014). However, the success rate of reintroduction efforts is low, and unplanned, unmonitored releases do little to shed light on the causes of either failure or success (Fischer and Lindenmayer 2000). Without that kind of information, managers cannot know which actions should be taken to improve the probability of success of a given reintroduction (Nichols and Armstrong 2012). Nevertheless, because knowledge on reintroduced species and systems is imperfect, management decisions must be made in the face of uncertainty (Armstrong and Seddon 2008). Therefore, monitoring should be designed to fill gaps of ecological knowledge in order to help assessing the value of each possible management option (Nichols and Armstrong 2012; Runge 2013). A more experimental approach to reintroductions has been suggested as a means of resolving such uncertainties (Sarrazin and Barbault 1996; Seddon et al. 2007). This leads to a trade-off

between managing for conservation and managing for information, since the actions that would provide the most information about a system are not always the best alternatives to conserve it (McCarthy et al. 2012). By explicitly incorporating of the value of learning, active adaptive management is a useful decision framework for reintroduced populations (Armstrong et al. 2007). Moreover, there has been an urge for objective and quantitative criteria for reintroduction success, both on the short and long-term (Seddon 1999; Fischer and Lindenmayer 2000). The goal of most reintroductions is the achievement of a self-sustaining population, able to grow without the aid of further releases (Armstrong and Seddon 2008). Therefore, a well-established success criterion is positive, unassisted population growth (Armstrong and Seddon 2008; Schaub et al. 2009). Population monitoring and the estimation of parameters such as abundance, survival and fecundity are paramount to ascertain the fulfillment of this criterion (Sarrazin 2007; Converse et al. 2013).

The main focus of reintroductions has historically been on the recovery of threatened species, while efforts directed at restoring ecological processes have still been uncommon in the last decades, despite a growing trend of reintroduction initiatives and associated research (Polak and Saltz 2011). Nevertheless, it has already been argued that the scope of reintroduction biology as a science should be broadened to encompass questions about effects on ecosystem processes (Lipsey and Child 2007; Armstrong and Seddon 2008). Defaunated areas benefit from initiatives aiming not only to recover locally extirpated populations, but also to bring back interactions and processes that were lost following species' extinctions (Oliveira-Santos and Fernandez 2010). The agouti (*Dasyprocta* spp.) is an important species for restoration reintroductions, as its scatterhoarding behavior enhance seed dispersal and recruitment of large-seeded plants (Asquith et al. 1999). Reported seed dispersal distances for *Dasyprocta punctata* exceeds 100 meters (Jansen et al. 2012) and dispersal is directed towards areas with low conspecific plant density (Hirsch et al. 2012), thus actively increasing the probability of seed survival (Carson et al. 2008).

A reintroduction effort began in 2009 to reestablish *D. leporina* in Tijuca National Park, an Atlantic Forest reserve in Rio de Janeiro, Brazil. This effort has been under-

taken with the goals of (a) reestablishing a self-sustaining population of *D. leporina* and (b) restoring the recruitment of large-seeded plants, by bringing back this effective seed disperser (Cid et al. 2014). Releases of 31 individuals happened from 2010 to 2014. Released animals were captured in forested urban areas, where they had lived in semi-captivity. Most of the animals (93.55%) came from the same source population, a urban park named Campo de Santana. Cid et al. (2014) observed independence from food supplementation, establishment of home ranges, high post-release survival and reproductive events of released animals, concluding that the reintroduction effort was successful over the short-term (Griffith et al. 1989). Zucaratto (2013) found that in TNP seeds of *Astrocaryum aculeatissimum* (a large-seeded palm) were only buried in areas already occupied by *D. leporina*. As buried seeds are at lower predation risk than exposed ones (Jansen and Forget 2001), the agouti reintroduction has reestablished, to some extent, lost ecological interactions through dispersal and caching of large seeds.

We monitored the reintroduced population (both the released and the wild-born individuals) through live capture and camera-trapping. A mark-resight approach was used to estimate population parameters such as abundance, survival rate, recruitment rate and sex ratio. Our main goal was to assess the medium-term success of the *D. leporina* reintroduction on TNP through monitoring of population growth, thereby evaluating the need for further releases or alternative management actions. We also aimed to identify threats to the long-term persistence of the population, as well as to direct future monitoring in order to provide useful information for the adaptive management of the reintroduced agoutis.

MATERIAL AND METHODS

STUDY SITE AND SPECIES

The study took place at Tijuca National Park (hereafter TNP), a 3.953-ha nature reserve located inside the city of Rio de Janeiro, Brazil (22°55'-23°00' S, 43°11'-43°19' W; Figure 1). Mean monthly temperatures vary between 18°C and 26°C, and annual rainfall exceeds 1200 mm, without marked seasons or water deficit (ICMBio 2008). The area that TNP now occupies was used for coffee farming up to the 19th century; it was then reforested with the intent of providing water to Rio de Janeiro (Pádua 2002). However, despite the reforestation many animal species and ecological process have not yet been restored, resulting in impoverished trophic webs (Oda 2000) and low recruitment of late-successional plants (Montezuma et al. 2005).

One of the species historically absent from TNP is the red-humped agouti (*D. lep-*



Figure 1: Study area and trapping grid. Filled dots represent stations deployed earlier in the study, while open dots represent stations deployed later (after the first two surveys). Inset shows Rio de Janeiro state and Tijuca National Park represented as a white star.

orina), a large-sized rodent, weighing from 3 to 6 kg (Reis et al. 2006). It is diurnal with primarily crepuscular activity. Its diet consists mainly of seeds, fruits and occasionally of leaves and insects. There are also anecdotal reports of opportunistic carnivory (Figueira et al. 2014). *Dasyprocta leporina* have not been recorded in TNP for nearly two decades, despite release efforts that took place in the 1970's (Coimbra-Filho et al. 1973). *Dasyprocta* is of great ecological importance due to its scatterhoarding behavior when food is abundant, it buries seeds in spaced caches for later consumption. Nonetheless, the animal may fail to retrieve them due to forgetfulness or mortality, and these buried seeds are then effectively (even if not willingly) dispersed (Jansen and Forget 2001; Pires and Galetti 2012). The disperser role *Dasyprocta* plays goes further than other scatterhoarders'. Recent studies show that *Dasyprocta punctata* is able to locate, steal and relocate seed caches from other individuals, increasing dispersal distance (Jansen et al. 2012). Furthermore, this competition drives *D. punctata* to use caches far from the seed's conspecific adults (Hirsch et al. 2012) which increases seed germination rate (Carson et al. 2008). Because of such traits, reintroductions of *D. leporina* are of great management interest for restoring animal-plant interactions.

CAPTURE AND MARKING

Six capture sessions were carried out every 3 months, from July 2013 to November 2014. Each session lasted 5 days until January 2014, when we increased our capture effort to 12 days. Individuals were captured using wire mesh traps (Tomahawk Live Trap Co., Hazelhurst - USA; Gabrisa Ltd., Cafelândia - Brazil), baited with sweet potato. Traps were checked after dusk, when all animals were supposed to have ceased foraging. All animals captured were sedated by veterinaries using a Ketamine-Midazolam solution. Adults were fitted with colored radio-collars, and when those were not available, simple plastic collars. We also marked the animal's fur with two different techniques: freeze-branding and fur bleaching. In both techniques we used individual codes of dots and bars. Freeze-branding consisted of shaving the of cooling an aluminum branding iron in dry-ice and 90% alcohol solution, and then applying it to the animal's skin for 70

seconds. This procedure kills the melanocytes on the epidermis, making the fur grow permanently white (Hadow 1972). This makes freeze-branding a most useful technique for long-term monitoring. However, the fur must be shaved before branding, making resighting only feasible a few months after marking, when it grows back. Marks achieved through fur bleaching are readily available for resighting, but they only last until the next molt. We believe these two techniques provide useful marks for camera trapping studies of mammals because (a) they are readable at a distance, (b) they do not rely on color identification, making them readable in black & white photographs (many camera-trap models use infrared light instead of flashes in low-light environments) and (c) they are complementary, with fur bleaching being temporary, but instantly available while freeze-branding is permanent, but requires months to reach readability (Figure 2).



Figure 2: Comparison of fur bleaching and freeze-branding techniques. (a) An adult female agouti 10 days after marking. Fur bleach is still clear, but freeze-branding is not visible. (b) The same animal, 404 days after marking. Despite bleached fur having already molted, the mark achieved through freeze-branding is visible.

RESIGHTING SURVEYS

Resighting surveys were carried out through camera trapping after each trapping session, from November 2013 to November 2014. We used a single camera trap per station to maximize number of stations and sampling area. Using one camera trap per station instead of two still allowed the use of both flanks for identification, because animals were marked on both sides. Traps were checked and baited with sweet potato every six days, for a total of 30 days in each survey. Lures may introduce individual heterogeneity in detection rate (Foster and Harmsen 2012), but we could explicitly model this effect, thus avoiding any biases (see Data Analysis). Cameras were set to take 3 pictures every 10 seconds, allowing a great number of photographic records of each individual resighted, especially when they stopped in front of the camera to feed on the bait. This allowed easier individual recognition through ear tags, collars and fur marks. Trap-failure events were recorded to track the variation in sampling effort (Foster and Harmsen 2012).

During the first two surveys, 21 stations were deployed in a grid covering a Minimum Convex Polygon (MCP) of 131.37 ha. Later in the study more cameras traps were available, so we increased our sampling effort to 33 stations. These new stations were deployed within the former grid, so that resighting effort increased while area sampled remained roughly similar (an 1.6% increase to 133.43 ha), allowing all surveys to be comparable (Figure 1). We accounted for the effort disparity between the first two surveys and subsequent ones by considering stations deployed later in the study as trap-failures before their deployment. Mean spacing between traps was originally $231 \pm 78\text{m}$ when using 21 stations, and decreased to $185 \pm 47\text{m}$ on subsequent surveys. The lower confidence limit of home range diameter of agoutis in the study area is 351 m (Cid et al. 2014). As trap spacing was always smaller than that, we could assure that all individuals in the sampling grid were subject to detection (Foster and Harmsen 2012). The MCP of the sampling grid was > 5 times greater than the average home range size estimated by Cid et al. (2014), therefore sampling area was sufficiently large according to Maffei and Noss (2008).

DATA ANALYSIS

Resightings from the same individual were considered independent when they were at least one hour apart or were made from different stations. We identified each photographic record using the following procedure: (a) Records with enough marks visible to allow the identification of a marked individual were assigned to that individual; (b) Records in which it was possible to determine that the individual is marked, but not its identity, were categorized as “Marked, But Unidentified”; (c) Records in which it was possible to assure that an individual did not have any marks (this is achievable with the clear identification of just one ear, since all marked individuals received ear-tags on both) were assigned as “Unmarked”; (d) When it was impossible to determine if an individual was marked or unmarked, the record was considered “Unidentifiable”. The latter were discarded from the analysis, providing information only on the rate of record loss (see later). Independent records were pooled for each six-day interval concomitant with rebaiting, so that an increase in trap visitation caused by the new bait would not cause resighting variation between periods. Thus, we could not assume that sampling in each interval was without replacement (i.e., each individual could be recorded more than once). We excluded records from the first 45 days after release of captive individuals to separate survival in the wild from post-release survival (following Armstrong and Reynolds (2012)).

We used McClintock and White 2009’s robust design Poisson-log-normal mixed-effects mark-resight model (RDPNE) to estimate population size N and apparent survival ϕ (The complement of both mortality and permanent emigration). Other parameters estimated are U (number of unmarked individuals), α (intercept for mean resighting rate, on the log scale), σ (individual heterogeneity in detection rate, on the log scale), γ (probability of temporary moving out of the study area) and γ' (probability of remaining outside of the study area). RDPNE’s assumptions are (a) population closure (spatial and demographic) within each primary sampling interval; (b) no loss of marks within each primary interval; (c) perfect distinction between marked and unmarked animals; (d) independently and identically distributed resighting probabilities for marked and unmarked animals.

We assumed closure within each primary interval, but we were also interested in assessing if each 30-day survey could be considered closed as well. To evaluate whether population was statistically closed within resighting surveys, we compared two RDPNE model structures, namely open and closed structures. Both structures modeled all parameters as constant except abundance of unmarked individuals (U). The open structure modeled U as a function of each primary interval, and estimated transition parameters (ϕ , γ'' , γ') for every interval. On the other hand, the closed structure modeled U as a function of each survey, and fixed transition parameters for all intervals except the ones between surveys (ϕ was fixed as 1, γ' and γ'' as 0). We assessed model fit to both structures, and used the best one for subsequent analysis.

We computed two different resighting rate covariates: “Sampling effort” (eff) was calculated as the sum of all trap-days from each resighting station (accounting for trap-failures); it is fairly clear that eff influences positively the number of independent records. “Record loss” ($rloss$) was calculated as the proportion of unidentifiable records (when an individual could not be identified as marked nor unmarked) over each interval. We included $rloss$ because there were occasions in which a camera trap station was fully operational and yet, due to various issues (e.g., bad angulation, dirty lenses, strong IR flashes), some records were unidentifiable. We also used the variance of eff and $rloss$ between resighting stations as measures of spatial heterogeneity of resighting rates. We assumed that spatial heterogeneity translates to individual heterogeneity because animals have relatively stable home ranges, not moving randomly through a given area (Spencer 2012).

Because RDPNE estimates six parameters simultaneously, the potential number of models can be large. Therefore we used a step-wise approach to model selection. We began modelling α while keeping the other parameters constant, and used only the best models (those with a ΔAIC_c smaller than 2) for estimation of a subsequent parameter, at which point we repeated the same process (for σ , ϕ , γ'' and γ' , in that order). The interval between six-day intervals within the same survey is instantaneous, therefore different values of ϕ for each one of them is illogical. Because of that we constrained values of ϕ to

be constant within each survey. Parameters were modelled as constant or as a function of either animal origin (*captv*), age (*age*), sex (*sex*), resighting occasion (*time*), resighting survey (*survey*), sampling effort (*eff*), effort spatial variance (*eff var*), record loss (*rloss*) and record loss spatial variance (*rloss var*). σ only was a function of *eff var* or *rloss var* in models that had an effect of *eff* or *rloss* on α . We always modelled γ'' and γ' together (i.e., as a function of the same covariates). Geographic closure and individual heterogeneity were assessed by incorporating models with γ' and γ'' , as well as σ , fixed as 0. U was modelled simply as time-dependent in all cases.

We used parameters estimates from RDPNE to derive parameters of interest for population management. Population recruitment was calculated as

$$\hat{B}_t = \hat{N}_t - (\hat{N}_{t-1} \times \hat{\phi}_t^*) \quad (1)$$

where $\hat{\phi}_t^*$ is uncorrected, or realized, survival (this distinction is important because most estimation softwares correct transition parameters for a constant period of time).

A straight-forward measure of reintroduction success is the assessment of population growth, or finite rate of increase λ . Positive growth ($\lambda > 1$) without the aid of additional releases is an indicator of population persistence (Ostermann et al. 2001; albeit being deterministic and not quite robust). The finite rate of increase over a period $t - 1$ to t is calculated as

$$\hat{\lambda}_t = \frac{\hat{N}_t}{\hat{N}_{t-1}} \quad (2)$$

We were also interested on the average change the population underwent during the duration of our study (“trend”, or T), which is simply the geometric mean of all $\hat{\lambda}_t$:

$$\hat{T} = \left(\prod_{t=1}^t \hat{\lambda}_t \right)^{1/y} \quad (3)$$

where y is the overall study length, in years. Since \hat{N}_t and $\hat{\phi}_t^*$ are both estimated parameters with associated standard errors, we were able to derive standard errors for \hat{B}_t , $\hat{\lambda}_t$ and \hat{T} through parametric bootstrapping, assuming a log-normal distribution for \hat{N}

and a normal distribution for $\hat{\phi}^*$ on the logit scale (Williams et al. 2002). All analyses were conducted in the R v.3.2.0 environment (Statistical Package 2009), using the package ‘RMark’ for interface with the software MARK (White and Burnham 1999). See Appendix 2 for other packages used.

RESULTS

LIVE CAPTURES

After a total of 51 live-trapping nights, we obtained 37 captures from 17 different individuals. Capturability was highest in August 2014 and lowest in November 2014 (See Figure 3). Many of the animals captured were young (47.1%), specially during August 2014 (57.1%). The sex-ratio of individuals caught was extremeley biased, with 70.6% of captured animals being females ($\chi^2_{\text{Yates}}=2.88$; $p = 0.09$). Taking into account only wild-born animals, this number rises to 76.9% ($\chi^2_{\text{Yates}}=5.4$; $p = 0.02$; see Table 1 for a summary of captures).

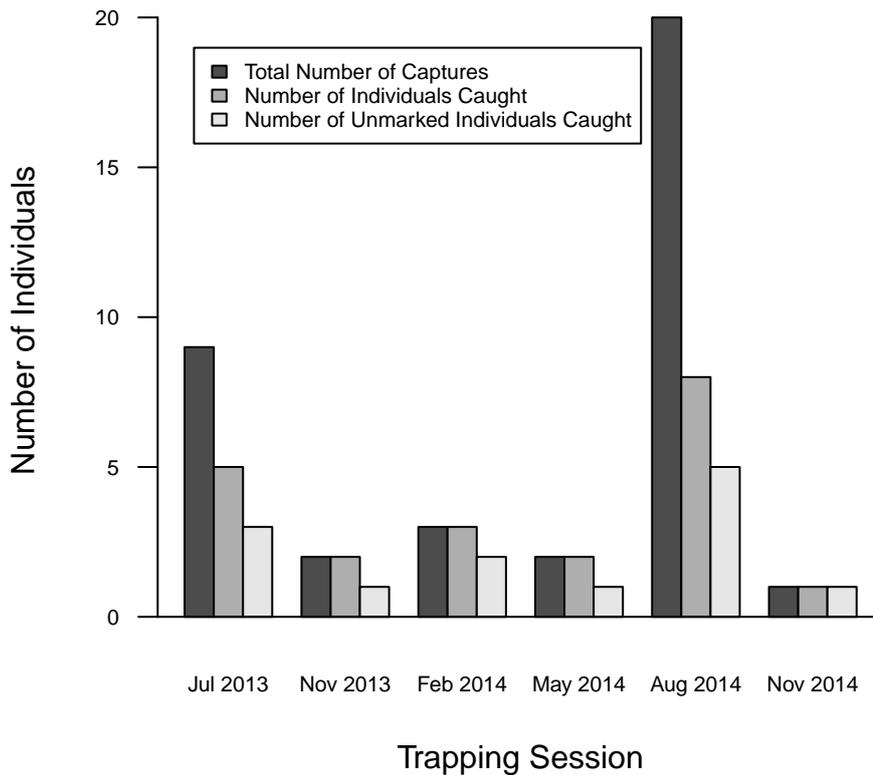


Figure 3: Number of individuals captured at each trapping session. It should be noted that the first three sessions (from Jul 2013 to Feb 2014) lasted five days, while subsequent ones lasted 12 days.

Table 1: Individuals captured throughout the study

Individual	Origin	Sex	Age at Marking	Date of Marking	Trapping Month
Bella	Captivity	Female	Adult	2013-07-22	Jul 2013
Negra	Captivity	Female	Adult	2013-11-08	Nov 2013
Roland	Captivity	Male	Adult	2014-08-20	Aug 2014
Wallace	Captivity	Male	Adult	2014-08-25	Aug 2014
Primo	Wild-born	Male	Young	2013-07-23	Jul 2013
Chico	Wild-born	Male	Young	2013-07-24	Jul 2013
Anathema	Wild-born	Female	Adult	2013-07-25	Jul 2013
Neguinha	Wild-born	Female	Young	2013-11-06	Nov 2013
Lili	Wild-born	Female	Adult	2014-02-04	Feb 2014
Luna	Wild-born	Female	Adult	2014-02-05	Feb 2014
Malu	Wild-born	Female	Young	2014-05-12	May 2014
Bjork	Wild-born	Female	Young	2014-08-20	Aug 2014
Grey	Wild-born	Female	Young	2014-08-20	Aug 2014
Luke	Wild-born	Male	Adult	2014-08-20	Aug 2014
Maia	Wild-born	Female	Young	2014-08-20	Aug 2014
Lolita	Wild-born	Female	Young	2014-08-25	Aug 2014
Sol	Wild-born	Female	Adult	2014-11-10	Nov 2014

RESIGHTING SURVEYS

Total sampling effort from resighting surveys was 3787 trap-days, with a mean of 151 ± 33 per 6-day period. Trap-failure rate was high (23.49%). It should be noted that this number is inflated since we considered traps not yet deployed as failures. True failure rate was 10.47%. Moreover, we explicitly incorporated variation in sampling effort when estimating resighting rates, therefore we believe such variation did not bias our estimates. We obtained a total of 2989 independent records of agoutis, from which 16.46% were discarded because they were considered “Unidentifiable”. This was due mainly to poor image quality or the animal being partially seen.

DEMOGRAPHIC ESTIMATES

The open-survey model structure achieved greater fit than closed-survey’s (ΔAIC_c of 68.4, see Table 2), so we kept the former structure for subsequent analysis. After running the step-wise model selection for all parameters, two models had an ΔAIC_c smaller than 2. However, model-averaged estimates did not differ relevantly from the best model. We thus report here the best-fitting model estimates instead of model-averaged ones. None

of the final models incorporated individual heterogeneity (i.e., variation of resighting rate α was sufficiently explained). Age had a consistent positive effect on apparent survival ($\hat{\beta}_{age}$: 2.25, 95% CI: 0.37 – 4.13). Captivity did not influence apparent survival (none of the final models included it); it did however have a positive effect on resighting rates ($\hat{\beta}_{captv}$: 0.41, 95% CI: 0.21 – 0.62).

Table 2: Comparison of open vs. closed model structures (in relation to a 30-day survey period). Closed structure assumed constant population size and absence of mortality or emmigration within each survey, while open structure makes the same assumptions for each six-day sampling interval only. AIC_c of the open model structure is much greater than the closed model's, despite the latter having fewer estimable parameters.

Model Structure	k	AIC_c	ΔAIC_c	w_i	Deviance
Open	30	876.80	0.00	1.00	799.74
Closed	10	945.21	68.41	0.00	923.51

Table 3: Best supported robust design Poisson-log-normal mixed-effects mark-resight (RDPNE) models. Estimated parameters from this model are α (intercept on the log scale of the resighting rate), σ (variation on resighting rate due to individual heterogeneity), U (number of unmarked individuals in the population), ϕ (apparent survival), γ'' (probability of temporarily emmigrating out of the study area) and, γ' (probability of remaining outside of the study area). *eff* denotes effort in trap-days, *rloss* denotes the rate of record loss, *captv* denotes origin (wild-born or captive), *age* denotes individual's age (pup or adult), *rain* denotes precipitation over six days, *sex* denotes gender and '.' denotes a constant parameter. $\gamma_{(0)}$ models indicate geographic closure and $\sigma_{(0)}$ models indicate lack of unexplained individual heterogeneity. Parameter U is omitted because it was always modeled as time-dependent. Only models with w_i greater than 0.01 are shown; consult Appendix for a full list of models run.

Model	k	AIC_c	ΔAIC_c	w_i	Deviance
$\alpha_{(eff+rloss+captv+sex)}\sigma_{(0)}\phi_{(age)}\gamma_{(.)}$	34	861.68	0.00	0.61	771.02
$\alpha_{(eff+rloss+captv+sex)}\sigma_{(0)}\phi_{(.)}\gamma_{(.)}$	33	863.39	1.71	0.26	776.22
$\alpha_{(eff+rloss+captv+sex)}\sigma_{(0)}\phi_{(age)}\gamma_{(sex)}$	36	867.59	5.91	0.03	769.73
$\alpha_{(eff+rloss+captv+sex)}\sigma_{(0)}\phi_{(age)}\gamma_{(age)}$	36	867.80	6.12	0.03	769.94
$\alpha_{(eff+rloss+captv+sex)}\sigma_{(0)}\phi_{(age)}\gamma_{(captv)}$	36	868.33	6.65	0.02	770.46
$\alpha_{(eff+rloss+captv+sex)}\sigma_{(0)}\phi_{(.)}\gamma_{(age)}$	35	868.74	7.06	0.02	774.51
$\alpha_{(eff+rloss+captv+sex)}\sigma_{(0)}\phi_{(.)}\gamma_{(sex)}$	35	869.17	7.48	0.01	774.93
$\alpha_{(eff+rloss+captv+sex)}\sigma_{(0)}\phi_{(.)}\gamma_{(captv)}$	35	869.89	8.20	0.01	775.66

Estimated population sizes of wild individuals were lowest on November 2013 (10.00; 95% CI: 7.36 – 13.58) and highest on August 2014 (82.66; 95% CI: 76.18 – 89.69), declining to as low as 24.75 (95% CI: 20.03 – 30.59) on the last survey, on November 2014 (see Figure 4a). Mean apparent survival $\hat{\phi}$ was estimated as 0.94 ± 0.03 for adults and 0.61 ± 0.18 for young animals. Estimated recruitment between surveys was low throughout the study, with a peak of 55.93 (95% CI: 46.68 – 66.66) individuals from May 2014 to August 2014.

Overall finite rate of increase $\hat{\lambda}_{1,t}$ throughout the study was 2.81 (95% CI: 1.91 – 4.02). Yearly trend \hat{T} was estimated as 4.11 (95% CI: 2.41 – 6.66).

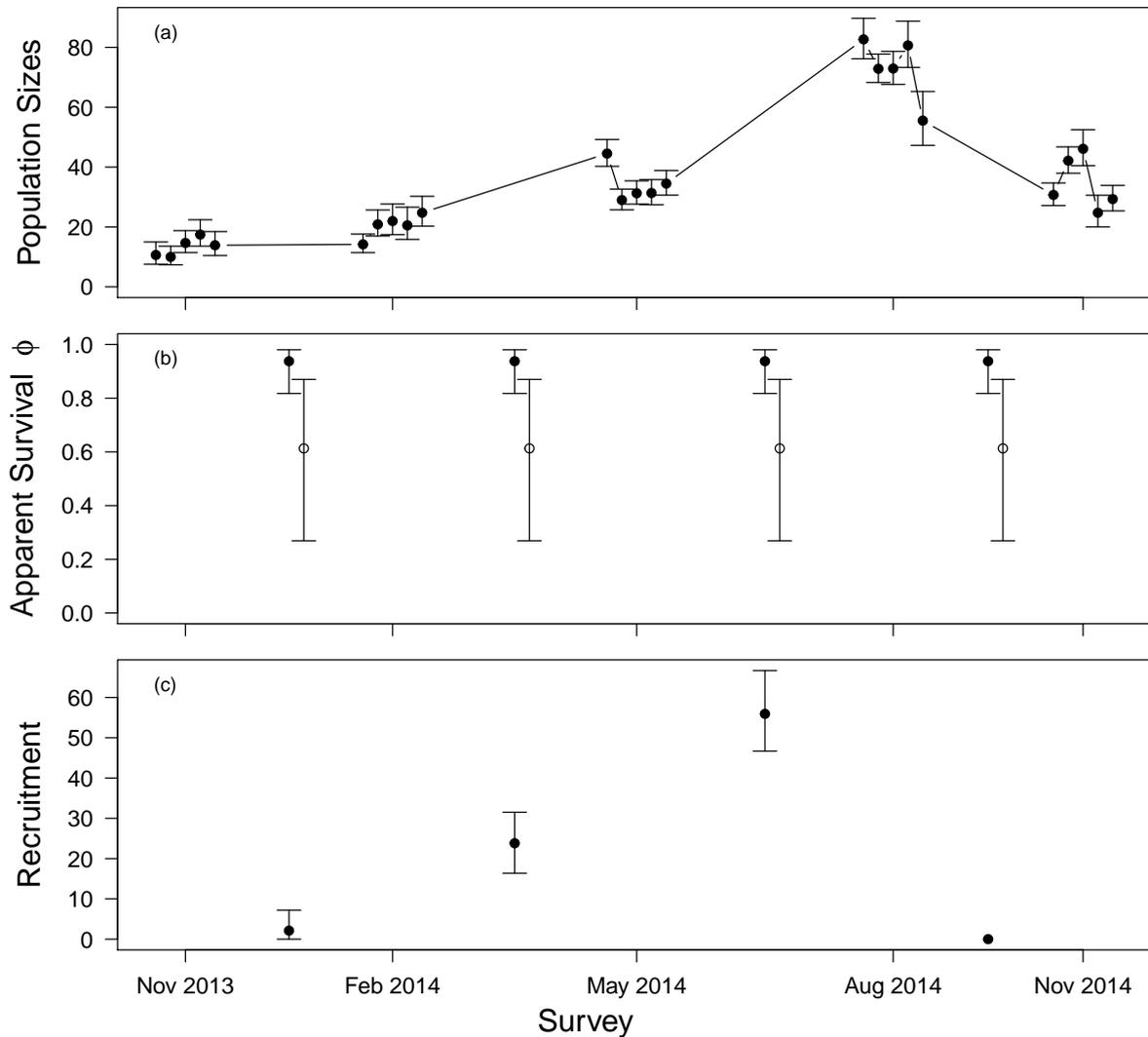


Figure 4: Demographic estimates (and 95% confidence intervals) of agoutis in TNP. (a) Abundance estimates of wild animals for each sampling occasion. There's a regular increase in population size until August 2014, followed by a small decline in November 2014. (b) Survival estimates for adult (filled circles) and young (open circles) animals. (c) Derived recruitment estimates between surveys (because recruitment is zero-truncated, we report the median).

DISCUSSION

A crucial assumption for estimating population parameters is that all animals inside a given sampled area are subject to detection (Williams et al. 2002). We used the home range size distribution of agoutis released in 2010-2011 reported by Cid et al. (2014) to define the minimum trap spacing needed to assure that all individuals could be recorded in our surveys. However, such home ranges are larger than those estimated for *D. leporina* in other studies (Silvius and Fragoso 2003; Jorge and Peres 2005). Cid et al. (2014) argued that this difference might be due to a difference in resource availability in each study area, with agoutis from TNP having larger home ranges to obtain a similar amount of resources than individuals from Silvius and Fragoso (2003) and Jorge and Peres (2005). An alternative hypothesis is that the first animals released established large home ranges due to lack of intra-specific competition. If this is true, and home ranges individuals established after the founders' are smaller than previously reported, trap spacing may be insufficient to assure that all individuals have a chance to be recorded. Such violation would cause a negative bias in abundance estimates and consequently conservative results. This was probably not the case, since most marked adults were recorded in more than one trapping station. In addition, estimated home range size for one adult wild-born female fell within the range of estimates from Cid et al. (2014) (26.98 ha, kernel 95% h_{ref}).

Age was the main driver of variation on $\hat{\phi}$; adults had higher probabilities of surviving than young. High mortality of young animals has also been reported for *Dasyprocta punctata* on Barro Colorado Island, Panama (Smythe 1978). Most of mortality reported for *Dasyprocta* has been attributed from mammalian predators (e.g., white-nosed coatis (*Nasua narica*), ocelots (*Leopardus pardalis*); (Smythe 1978; Silvius and Fragoso 2003; Suselbeek et al. 2014). There are no large-sized native mammals in TNP that could prey upon adult agoutis (ICMBio 2008). The South American coati (*Nasua nasua*) is abundant, nevertheless, and is a potential predator of young agoutis. However, since the beginning of the reintroduction we did not observe *N. nasua* chasing nor preying upon *D. leporina*; in fact, we observed a released animal foraging alongside a group of *N. nasua*.

Despite the absence of native, large-sized predators in TNP, we believe a major driver of agouti mortality is predation by domestic dogs (*Canis lupus familiaris*). We repeatedly observed *C. lupus familiaris* chasing agoutis (both released and wild-born). In addition, one animal was killed by two dogs that entered the acclimatization pen before release (Cid et al. 2014) and four released animals that were found dead in the wild had distinctive signs of predation by dogs (personal observation).

Release into the wild is frequently associated with reduced survival, specially when released animals are of captive origin (Jule et al. 2008; Tavecchia et al. 2009; Aaltonen et al. 2009). We found the opposite situation in our study; Cid et al. 2014 reported higher post-release survival (monthly $\hat{\phi}$: 0.98) in 2010-2011 than the survival we estimated for adult animals, regardless of their origin, in 2013-2014. Such differences in survival may be explained by two non-exclusive hypotheses. First, as population size and density increased since the time of release, an increase in competition for food would reduce mean individual body condition and increase intra-specific aggression. Second, predation by *C. lupus familiaris* may have increased since the 2010 releases due to individuals residing in TNP forming a search image as encounters with *D. leporina* became more frequent (Ishii and Shimada 2010). Because we could only estimate apparent survival ϕ and not true survival S , we cannot distinguish mortality from permanent emigration (Williams et al. 2002). Our sampled area is not geographically closed (as demonstrated by the high AIC_c of $\gamma_{(0)}$ models), thus it is plausible that low survival is partially explained by individuals dispersing away from the area sampled, especially juveniles (Greenwood 1980).

Young animals were recorded on all surveys. Their high capturability in the middle of the year and high recruitment in the same period suggests a period when reproduction is more intense, as already described for *Dasyprocta* (Dubost et al. 2005; Smythe 1978). The only recorded decrease in abundance occurred after this peak in recruitment; at this time population returned to roughly the same size of the survey prior to the recruitment event. While such decrease was certainly due to young individuals' higher mortality, losses must also have been caused partially by dispersal of young individuals away from the sampling area (Greenwood 1980). Besides an increase in population size, spatial expansion is also

expected in thriving reintroduced populations (Bar-David et al. 2005; Molinari-Jobin et al. 2010). Population sampling outside the immediate release area is needed to assess expansion over TNP and to distinguish mortality from dispersal. Our sampling lasted just about one year, hence it was not suitable to evaluate seasonality. However, if natality is indeed higher during June-August, future releases should take place a few months before that period, so that more released females are already established and possible negative post-release effects on fecundity are no longer present (Dickens et al. 2010).

Most of the wild animals captured were females. This bias is either an artifact of the capture process (males would be more wary of traps and thus less catchable) or a result of a biased sex ratio in the population. If the latter is the case, it could be caused by differential mortality or dispersal of males due to intra-specific aggression (Smythe 1978). We did not detect a significant effect of sex on ϕ that would have confirmed such differences. Nevertheless, because the number of males captured was remarkably low we probably did not achieve enough sample sizes to detect such an effect, have it existed.

A study of hunted *D. leporina* on the Amazon forest also wielded a significantly female biased sex-ratio (0.42, $\chi^2_{Yates}=4.22$, $p = 0.04$; Dubost et al. 2005). However, it is not clear in that study if this pattern resulted from a true population bias or from an artifact from differential vulnerability to hunting. Smythe (1978), on the other hand, reports higher mortality in males of *Dasyprocta punctata*, and hypothesized it was caused by aggression from adults. Both studies support the notion that agouti populations are female biased to some extent. Sex ratio deviations can amplify Allee effects (Deredec and Courchamp 2007), namely low mate-encounter rates and thus negatively affect growth in small populations (Courchamp et al. 1999). Such deviations may happen in the first years after reintroduction (Larkin et al. 2002).

Even if agouti sex ratio is in fact biased in TNP, it does not seem to prevent production of offspring and population growth. At the same time, if there are in fact demographic Allee effects taking place in virtue of biased sex-ratios, releases of more males might improve further population growth in TNP. Releases of a preferred sex is an obvious management measure to alleviate sex-ratio deviations (Ferrer et al. 2009). Still, if male

mortality is indeed higher in *D. leporina*, subsequent releases of this sex may be vain as individuals would perish before being able to reproduce. Therefore, such a practice would not be recommended, as it would be a waste of financial resources and captive stock, raising serious animal welfare issues. Therefore, one must be sure that such sex-ratio deviations are random, or at least driven by male dispersal as opposed to male mortality.

In total, 31 individuals were released throughout the project. From this founder pool, 11 animals died shortly after release (less than 12 weeks) or were removed, hence the number of individuals which were successfully established (hereafter referred to as “effective release group”) was 20. By November 2014, numbers of wild-born individuals fluctuated around 35 individuals. The number of wild-born individuals thus has surpassed the effective release group size. Furthermore, the number of individuals reported in this study is a conservative estimate, because our sampling grid was not geographically closed and the population most likely had already expanded beyond it. Even so, since we do not know the spatial extension of the population nor whether habitat suitability for *D. leporina* is comparable in and outside the sampling grid, we cannot estimate a population density for the whole area through extrapolation (Foster and Harmsen 2012).

Moreover, when monitoring of the wild population began, only two released individuals were still to be found on the study area. We released twelve individuals from captivity on June 2014; however, seven of these animals were dead 12 weeks after release and only one of them was recorded in the study area in our surveys. Therefore, most of the growth herein reported is due to the reproductive success of the wild population. Unassisted population increase is a basic criteria for success of reintroduced populations (Armstrong and Seddon 2008) and represents a critical demographic landmark that many reintroduction efforts do not achieve (Fischer and Lindenmayer 2000). We therefore conclude that the reintroduction effort of *D. leporina* on TNP has been successful on the medium-term, and the population has entered the growth phase proposed by Sarrazin (2007).

IUCN/SSC (2013) lists elimination of the local cause of extinction as a major requirement of reintroduction projects. Given the history of TNP, the local cause of extinction

of *D. leporina* before the 19th century was most likely habitat loss and hunting. Such habitat has been restored since, and there are no records of significant hunter activity on TNP. However, we are not aware of what caused Coimbra-Filho et al. (1973)'s effort to fail to establish a population. The number of animals released was low (25 individuals), thus release group was vulnerable to demographic stochasticity. Besides that, releases were sparse both in space and time; individuals were released at an average rate of 1.5 animals per month, on the location with most releases. Domestic dogs are known to hunt terrestrial vertebrates (Galetti and Sazima 2006; Campos et al. 2007). Moreover, Galetti and Sazima (2006) suggest that dogs may be in fact the reason behind the absence of *D. leporina* on their study site. We recorded *C. lupus familiaris* on TNP both visually and through camera-traps, and at least four released agoutis were killed by this invasive species. Individuals from Coimbra-Filho et al. (1973)'s release could also have been killed by domestic dogs from neighboring sites roaming the park or even illegal hunters. However, lack of subsequent monitoring prevents us to precise the cause of extinction and thus assure that it is not present in TNP today. Despite a positive trend in growth, the same threats may still be present in TNP and render the agouti population vulnerable to extirpation. Continuous monitoring of the population and further investigations on the drivers of high mortality on all age classes are needed to assess the viability of the population on the long-term and to consider different management strategies.

Despite overall positive growth, population size is still small in absolute numbers, and thus is vulnerable to demographic stochasticity (Caughley 1994). Additional releases may increase persistence probability and population growth. On the other hand, population grew during the last two years with practically no effective release group. Financial resources for reintroduction projects are limited, and should be allocated in management strategies that will contribute the most to reintroduction success or provide the most useful information for future decisions (Canessa et al. 2014). Therefore, it is important to assess when such reinforcements may cease to be cost-effective, i.e., when releases no longer significantly increase viability (Schaub et al. 2009; Martínez-Abraín et al. 2011; Armstrong and Ewen 2001) and financial and logistical resources should be directed to

other management actions (such as predator control) or monitoring programs.

For example, one of the main goals of the *D. leporina* reintroduction in TNP is to restore the recruitment of large-seeded plants (Cid et al. 2014). Evidence of the ecological role of *D. leporina* as a seed disperser in TNP is still scarce; Zucaratto (2013) found seed burial of *Astrocaryum aculeatissimum* is conditional on the local presence of *D. leporina*. Moreover, there is no quantitative information on the influence of local abundance on the rate of seed burial and dispersal distance. In Barro Colorado Island, intraspecific competition in *Dasyprocta punctata* drives increased dispersal distances through cache theft (Jansen et al. 2012), and scatterhoarding is directed to areas with low conspecific tree densities so as to avoid such thefts (Hirsch et al. 2012). Because these behaviors contribute positively to seed dispersal and their frequency should increase with increased density, monitoring of *D. leporina* density and its effect on large-seeded plant demography is needed to establish a minimum density threshold as a success criteria for the goal of restoring ecological interactions (Polak and Saltz 2011).

Despite medium-term success of the reintroduction, one must bear in mind that TNP lacks native agouti predators, and reintroductions in areas subject to mesopredator release may face more adverse conditions than reported here, since predation is a major driver of reintroduction failures (Short et al. 1992; Armstrong et al. 2006). Monitoring of *C. lupus familiaris* impact on *D. leporina* survival may provide insights on the feasibility of reintroductions in areas where natural predators such as *L. pardalis* are still present.

We were able to catch and mark few individuals, which was detrimental to the precision of survival ($\hat{\phi}$) and recruitment (\hat{B}) estimates. Short time-span, low number of marked individuals and consequently low precision of demographic estimates prevents us to make more inferences on the processes ultimately leading to variation on vital rates and population size. Even in the absence of management actions, an adaptive management approach to reintroduction implicates a need for continued monitoring of both released and wild-born individuals (Nichols and Armstrong 2012). Information on vital rates derived from monitoring is essential for understanding population processes in reintroductions (Sarrazin 2007), and reliable knowledge derived from such efforts is needed

to push forward the field of reintroduction biology (Sarrazin and Barbault 1996; Seddon et al. 2007).

Efforts to reintroduce *D. leporina* to defaunated areas in an attempt to restore lost ecological interactions are only the first step towards “refaunation”, the restauration of whole faunas so as to reestablish ecological processes lost in historical times (Oliveira-Santos and Fernandez 2010). *Dasyprocta leporina* is a promising candidate for reintroduction as a part of such projects due to its scatterhoarding behavior, which enhances large-seeded plant recruitment (Asquith et al. 1999; Hirsch et al. 2012; Jansen et al. 2012). Despite the high failure rate of reintroduction attempts (Fischer and Lindenmayer 2000), some projects may succeed even with a small number of founders (Taylor et al. 2005; Reynolds et al. 2012). This was the case of this study, which achieved success on the medium-term after the release of less than 40 animals. Thus, *D. leporina* has a potential for achieving high numbers with small release groups. As a result, reintroducing this species is cost-effective in terms of total population size per dollar invested. This makes management of *D. leporina* an useful tool to understand the dynamics of reintroduced medium-large mammals populations in defaunated areas, and also their effect at the ecosystem level.

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APPENDIX 1: SUPPLEMENTARY TABLES

Table A.1: Summary table of resighting surveys' primary intervals. # of Records refers to independent records (one-hour apart) only, but includes "Unidentifiable" records.

Interval Start	Interval End	Survey Month	# of Records	<i>eff</i>	<i>eff var</i>	<i>rloss</i>	<i>rloss var</i>
2013-11-15	2013-11-20	Nov 2013	43	96	8.96	0.19	0.04
2013-11-21	2013-11-26	Nov 2013	47	96	8.71	0.13	0.01
2013-11-27	2013-12-02	Nov 2013	75	114	7.94	0.08	0.02
2013-12-03	2013-12-08	Nov 2013	84	120	8.36	0.17	0.04
2013-12-09	2013-12-14	Nov 2013	65	115	8.38	0.17	0.04
2014-02-07	2014-02-12	Feb 2014	65	126	8.59	0.06	0.03
2014-02-13	2014-02-18	Feb 2014	103	126	8.59	0.08	0.01
2014-02-19	2014-02-24	Feb 2014	94	126	8.59	0.17	0.02
2014-02-25	2014-03-02	Feb 2014	75	114	9.07	0.07	0.00
2014-03-03	2014-03-08	Feb 2014	123	126	8.59	0.10	0.04
2014-05-17	2014-05-22	May 2014	145	139	7.05	0.08	0.01
2014-05-23	2014-05-28	May 2014	111	168	4.77	0.14	0.01
2014-05-29	2014-06-03	May 2014	130	180	3.07	0.22	0.03
2014-06-04	2014-06-09	May 2014	133	174	3.95	0.08	0.01
2014-06-10	2014-06-15	May 2014	173	173	3.63	0.13	0.03
2014-08-29	2014-09-03	Aug 2014	213	166	4.78	0.16	0.05
2014-09-04	2014-09-09	Aug 2014	196	172	3.61	0.16	0.05
2014-09-10	2014-09-15	Aug 2014	151	166	4.09	0.17	0.02
2014-09-16	2014-09-21	Aug 2014	187	171	3.34	0.24	0.07
2014-09-22	2014-09-27	Aug 2014	144	151	5.63	0.23	0.04
2014-11-14	2014-11-19	Nov 2014	149	192	1.09	0.13	0.02
2014-11-20	2014-11-25	Nov 2014	125	185	1.62	0.20	0.05
2014-11-26	2014-12-01	Nov 2014	136	198	0.00	0.25	0.09
2014-12-02	2014-12-07	Nov 2014	98	198	0.00	0.29	0.09
2014-12-08	2014-12-13	Nov 2014	124	195	0.27	0.31	0.08

Table A.2: Encounter histories used as input for RDPNE analysis. Each cell represents number of independent photographic records over a 6-day period. “.” denotes not yet marked individuals, or in which it was known have been absent from the population (due to removal, mortality or emmigration). “+0” denotes absence of records from an individual, yet it was known to be available for resighting. An encounter was only assigned as “+0” when its primary interval was immediately after the capture of the animal. “-0” denotes absence of records from an individual and uncertainty around its fate.

Anathema	03	01	02	-0	01	03	05	05	04	07	04	02	08	01	04	03	06	02	06	04	11	07	04	02	04
Bjork	+0	05	-0	-0	-0	-0	-0	-0	-0	-0
Grey	05	03	01	01	-0	-0	-0	-0	-0	-0
Lili	+0	02	01	-0	01	-0	-0	-0	-0	-0	-0	-0	-0	-0	-0	-0	-0	-0	-0	-0
Luke	04	-0	06	06	05	-0	-0	-0	-0	-0
Luna	02	02	03	03	04	02	-0	-0	07	07	02	03	01	01	02	02	02	05	03	04
Maia	+0	-0	-0	02	-0	-0	-0	-0	-0	-0
Malu	07	11	04	07	06	02	07	02	05	04	-0	-0	01	01	-0	-0
Negra	05	10	06	04	07	05	08	05	-0	06	05	09	01	-0	-0	-0	-0	-0	-0	-0	-0	-0	-0	-0	-0
Sol	+0	-0	-0	-0	-0
Wallace	01	03	02	-0	02	04	01	-0	-0	01
X	02	03	05	08	05	06	04	03	-0	06	06	04	05	08	08	08	04	05	05	-0	09	06	03	05	05
Lolita	+0	-0	-0	-0	-0	-0	-0	-0	-0	-0
Unmarked	25	27	56	58	41	45	74	61	63	87	106	69	80	97	105	147	125	100	112	91	98	77	86	61	63
Marked Unid.	0	0	0	0	0	0	0	0	0	0	3	1	4	3	4	6	9	6	5	3	6	3	2	1	8
Unidentif.	8	6	6	14	11	4	8	16	5	12	12	15	28	10	23	35	31	26	44	33	19	25	34	28	39

Table A.3: Robust design Poisson-log-normal mixed-effects mark-resight (RDPNE) modeling of α . Estimated parameters from these models are α (intercept on the log scale of the resighting rate), σ (variation on resighting rate due to individual heterogeneity), U (number of unmarked individuals in the population), ϕ (apparent survival), γ (probability of temporarily emigrating out of the study area) and, γ' (probability of remaining outside of the study area). *eff* denotes effort in trap-days, *rloss* denotes the rate of record loss, *captv* denotes origin (wild-born or captive), *age* denotes individual's age (pup or adult), *sex* denotes gender and “.” denotes a constant parameter. Parameter U is omitted because it was always modeled as time-dependent. Models with an ΔAIC_c smaller than 2 were kept for the subsequent step, modelling of σ (See Table A.4)

Model	k	AIC_c	ΔAIC_c	w_i	Deviance	Included
$\alpha(\text{eff}+\text{rloss}+\text{captv}+\text{sex})\sigma(\cdot)\phi(\cdot)\gamma(\cdot)$	34	866.89	0.00	0.50	776.22	Yes
$\alpha(\text{eff}+\text{rloss}+\text{captv}+\text{age}+\text{sex})\sigma(\cdot)\phi(\cdot)\gamma(\cdot)$	35	868.90	2.01	0.18	774.67	No
$\alpha(\text{eff}+\text{rloss}+\text{captv})\sigma(\cdot)\phi(\cdot)\gamma(\cdot)$	33	868.96	2.07	0.18	781.79	No
$\alpha(\text{eff}+\text{rloss}+\text{captv}+\text{age})\sigma(\cdot)\phi(\cdot)\gamma(\cdot)$	34	870.57	3.68	0.08	779.90	No
$\alpha(\text{eff}+\text{captv}+\text{sex})\sigma(\cdot)\phi(\cdot)\gamma(\cdot)$	33	873.01	6.12	0.02	785.84	No
$\alpha(\text{eff}+\text{captv}+\text{age}+\text{sex})\sigma(\cdot)\phi(\cdot)\gamma(\cdot)$	34	874.30	7.41	0.01	783.63	No
$\alpha(\text{eff}+\text{rloss})\sigma(\cdot)\phi(\cdot)\gamma(\cdot)$	32	874.69	7.80	0.01	790.95	No
$\alpha(\text{eff}+\text{captv})\sigma(\cdot)\phi(\cdot)\gamma(\cdot)$	32	875.65	8.76	0.01	791.91	No
$\alpha(\text{eff}+\text{captv}+\text{age})\sigma(\cdot)\phi(\cdot)\gamma(\cdot)$	33	876.38	9.49	0.00	789.21	No
$\alpha(\cdot)\sigma(\cdot)\phi(\cdot)\gamma(\cdot)$	30	876.80	9.91	0.00	799.74	No
$\alpha(\text{eff}+\text{rloss}+\text{sex})\sigma(\cdot)\phi(\cdot)\gamma(\cdot)$	33	877.17	10.28	0.00	790.00	No
$\alpha(\text{eff}+\text{rloss}+\text{age})\sigma(\cdot)\phi(\cdot)\gamma(\cdot)$	33	877.90	11.01	0.00	790.73	No
$\alpha(\text{eff})\sigma(\cdot)\phi(\cdot)\gamma(\cdot)$	31	880.11	13.22	0.00	799.74	No
$\alpha(\text{eff}+\text{rloss}+\text{age}+\text{sex})\sigma(\cdot)\phi(\cdot)\gamma(\cdot)$	34	880.57	13.68	0.00	789.91	No
$\alpha(\text{eff}+\text{sex})\sigma(\cdot)\phi(\cdot)\gamma(\cdot)$	32	881.94	15.05	0.00	798.20	No
$\alpha(\text{eff}+\text{age})\sigma(\cdot)\phi(\cdot)\gamma(\cdot)$	32	882.81	15.92	0.00	799.07	No
$\alpha(\text{eff}+\text{age}+\text{sex})\sigma(\cdot)\phi(\cdot)\gamma(\cdot)$	33	885.00	18.11	0.00	797.83	No

Table A.4: Robust design Poisson-log-normal mixed-effects mark-resight (RDPNE) modeling of σ . Estimated parameters from these models are α (intercept on the log scale of the resighting rate), σ (variation on resighting rate due to individual heterogeneity), U (number of unmarked individuals in the population), ϕ (apparent survival), γ (probability of temporarily emigrating out of the study area) and, γ' (probability of remaining outside of the study area). *surv* denotes an effect of the resighting survey, *time* denotes a 6-day sampling interval, *eff* denotes effort in trap-days, *eff var* denotes spatial variance of effort, *rloss* denotes the rate of record loss, *rloss var* denotes spatial variance of record loss, *captv* denotes origin (wild-born or captive), *age* denotes individual's age (pup or adult), *sex* denotes gender and "." denotes a constant parameter. $\sigma_{(0)}$ models indicate lack of unexplained individual heterogeneity. Parameter U is omitted because it was always modeled as time-dependent. Models with an ΔAIC_c smaller than 2 were kept for the subsequent step, modelling of ϕ (See Table A.5).

Model	k	AIC_c	ΔAIC_c	w_i	Deviance	Included
$\alpha(\text{eff+rloss+captv+sex})\sigma_{(0)}\phi(\cdot)\gamma(\cdot)$	33	863.39	0.00	0.80	776.22	Yes
$\alpha(\text{eff+rloss+captv+sex})\sigma(\cdot)\phi(\cdot)\gamma(\cdot)$	34	866.89	3.50	0.14	776.22	No
$\alpha(\text{eff+rloss+captv+sex})\sigma(\text{eff var})\phi(\cdot)\gamma(\cdot)$	35	870.18	6.79	0.03	775.95	No
$\alpha(\text{eff+rloss+captv+sex})\sigma(\text{rloss var})\phi(\cdot)\gamma(\cdot)$	35	870.45	7.06	0.02	776.22	No
$\alpha(\text{eff+rloss+captv+sex})\sigma(\text{eff var+rloss var})\phi(\cdot)\gamma(\cdot)$	36	871.46	8.07	0.01	773.60	No
$\alpha(\text{eff+rloss+captv+sex})\sigma(\text{surv})\phi(\cdot)\gamma(\cdot)$	38	880.51	17.11	0.00	775.16	No
$\alpha(\text{eff+rloss+captv+sex})\sigma(\text{time})\phi(\cdot)\gamma(\cdot)$	58	968.15	104.76	0.00	767.65	No

Table A.5: Robust design Poisson-log-normal mixed-effects mark-resight (RDPNE) modeling of ϕ . Estimated parameters from these models are α (intercept on the log scale of the resighting rate), σ (variation on resighting rate due to individual heterogeneity), U (number of unmarked individuals in the population), ϕ (apparent survival), γ (probability of temporarily emigrating out of the study area) and, γ' (probability of remaining outside of the study area). *surv* denotes an effect of the resighting survey, *eff* denotes effort in trap-days, *rloss* denotes the rate of record loss, *captv* denotes origin (wild-born or captive), *age* denotes individual's age (pup or adult), *sex* denotes gender and “.” denotes a constant parameter. $\sigma_{(0)}$ models indicate lack of unexplained individual heterogeneity. Parameter U is omitted because it was always modeled as time-dependent. Models with an ΔAIC_c smaller than 2 were kept for the subsequent step, modelling of ϕ (See Table A.6).

Model	k	AIC_c	ΔAIC_c	w_i	Deviance	Included
$\alpha_{(eff+rloss+captv+sex)}\sigma_{(0)}\phi_{(age)}\gamma_{(.)}$	34	861.68	0.00	0.45	771.02	Yes
$\alpha_{(eff+rloss+captv+sex)}\sigma_{(0)}\phi_{(.)}\gamma_{(.)}$	33	863.39	1.71	0.19	776.22	Yes
$\alpha_{(eff+rloss+captv+sex)}\sigma_{(0)}\phi_{(age+sex)}\gamma_{(.)}$	35	864.52	2.83	0.11	770.28	No
$\alpha_{(eff+rloss+captv+sex)}\sigma_{(0)}\phi_{(captv+age)}\gamma_{(.)}$	35	864.91	3.22	0.09	770.67	No
$\alpha_{(eff+rloss+captv+sex)}\sigma_{(0)}\phi_{(captv)}\gamma_{(.)}$	34	864.98	3.29	0.09	774.31	No
$\alpha_{(eff+rloss+captv+sex)}\sigma_{(0)}\phi_{(sex)}\gamma_{(.)}$	34	866.82	5.14	0.03	776.16	No
$\alpha_{(eff+rloss+captv+sex)}\sigma_{(0)}\phi_{(captv+age+sex)}\gamma_{(.)}$	36	867.52	5.84	0.02	769.66	No
$\alpha_{(eff+rloss+captv+sex)}\sigma_{(0)}\phi_{(captv+sex)}\gamma_{(.)}$	35	868.08	6.39	0.02	773.85	No
$\alpha_{(eff+rloss+captv+sex)}\sigma_{(0)}\phi_{(surv)}\gamma_{(.)}$	37	873.23	11.54	0.00	771.66	No
$\alpha_{(eff+rloss+captv+sex)}\sigma_{(0)}\phi_{(surv+captv)}\gamma_{(.)}$	38	875.63	13.95	0.00	770.28	No
$\alpha_{(eff+rloss+captv+sex)}\sigma_{(0)}\phi_{(surv+sex)}\gamma_{(.)}$	38	876.77	15.09	0.00	771.43	No
$\alpha_{(eff+rloss+captv+sex)}\sigma_{(0)}\phi_{(surv+captv+sex)}\gamma_{(.)}$	39	879.48	17.80	0.00	770.28	No

Table A.6: Robust design Poisson-log-normal mixed-effects mark-resight (RDPNE) modeling of γ . Estimated parameters from these models are α (intercept on the log scale of the resighting rate), σ (variation on resighting rate due to individual heterogeneity), U (number of unmarked individuals in the population), ϕ (apparent survival), γ (probability of temporarily emigrating out of the study area) and, γ' (probability of remaining outside of the study area). *surv* denotes an effect of the resighting survey, *eff* denotes effort in trap-days, *rloss* denotes the rate of record loss, *captv* denotes origin (wild-born or captive), *age* denotes individual's age (pup or adult), *sex* denotes gender and "." denotes a constant parameter. $\gamma_{(0)}$ models indicate geographic closure and $\sigma_{(0)}$ models indicate lack of unexplained individual heterogeneity. Parameter U is omitted because it was always modeled as time-dependent.

Model	k	AIC _c	Δ AIC _c	w_i	Deviance
$\alpha(\text{eff+rloss+captv+sex})\sigma_{(0)}\phi(\text{age})\gamma(\cdot)$	34	861.68	0.00	0.61	771.02
$\alpha(\text{eff+rloss+captv+sex})\sigma_{(0)}\phi(\cdot)\gamma(\cdot)$	33	863.39	1.71	0.26	776.22
$\alpha(\text{eff+rloss+captv+sex})\sigma_{(0)}\phi(\text{age})\gamma(\text{sex})$	36	867.59	5.91	0.03	769.73
$\alpha(\text{eff+rloss+captv+sex})\sigma_{(0)}\phi(\text{age})\gamma(\text{age})$	36	867.80	6.12	0.03	769.94
$\alpha(\text{eff+rloss+captv+sex})\sigma_{(0)}\phi(\text{age})\gamma(\text{captv})$	36	868.33	6.65	0.02	770.46
$\alpha(\text{eff+rloss+captv+sex})\sigma_{(0)}\phi(\cdot)\gamma(\text{age})$	35	868.74	7.06	0.02	774.51
$\alpha(\text{eff+rloss+captv+sex})\sigma_{(0)}\phi(\cdot)\gamma(\text{sex})$	35	869.17	7.48	0.01	774.93
$\alpha(\text{eff+rloss+captv+sex})\sigma_{(0)}\phi(\cdot)\gamma(\text{captv})$	35	869.89	8.20	0.01	775.66
$\alpha(\text{eff+rloss+captv+sex})\sigma_{(0)}\phi(\text{age})\gamma(\text{age+sex})$	38	873.82	12.14	0.00	768.48
$\alpha(\text{eff+rloss+captv+sex})\sigma_{(0)}\phi(\text{age})\gamma(\text{captv+sex})$	38	873.90	12.22	0.00	768.55
$\alpha(\text{eff+rloss+captv+sex})\sigma_{(0)}\phi(\cdot)\gamma(\text{age+sex})$	37	874.55	12.86	0.00	772.98
$\alpha(\text{eff+rloss+captv+sex})\sigma_{(0)}\phi(\text{age})\gamma(\text{captv+age})$	38	875.03	13.34	0.00	769.68
$\alpha(\text{eff+rloss+captv+sex})\sigma_{(0)}\phi(\cdot)\gamma(\text{captv+sex})$	37	875.77	14.09	0.00	774.20
$\alpha(\text{eff+rloss+captv+sex})\sigma_{(0)}\phi(\cdot)\gamma(\text{captv+age})$	37	875.84	14.16	0.00	774.27
$\alpha(\text{eff+rloss+captv+sex})\sigma_{(0)}\phi(\text{age})\gamma(\text{captv+age+sex})$	40	880.90	19.21	0.00	767.76
$\alpha(\text{eff+rloss+captv+sex})\sigma_{(0)}\phi(\cdot)\gamma(\text{captv+age+sex})$	39	881.87	20.18	0.00	772.67
$\alpha(\text{eff+rloss+captv+sex})\sigma_{(0)}\phi(\text{age})\gamma(\text{surv})$	42	885.55	23.87	0.00	764.31
$\alpha(\text{eff+rloss+captv+sex})\sigma_{(0)}\phi(\cdot)\gamma(\text{surv})$	41	886.84	25.15	0.00	769.69
$\alpha(\text{eff+rloss+captv+sex})\sigma_{(0)}\phi(\cdot)\gamma(\text{surv+captv})$	43	892.80	31.12	0.00	767.39
$\alpha(\text{eff+rloss+captv+sex})\sigma_{(0)}\phi(\text{age})\gamma(\text{surv+sex})$	44	893.07	31.39	0.00	763.39
$\alpha(\text{eff+rloss+captv+sex})\sigma_{(0)}\phi(\cdot)\gamma(\text{surv+sex})$	43	893.07	31.39	0.00	767.66
$\alpha(\text{eff+rloss+captv+sex})\sigma_{(0)}\phi(\text{age})\gamma(\text{surv+captv})$	44	893.56	31.88	0.00	763.88
$\alpha(\text{eff+rloss+captv+sex})\sigma_{(0)}\phi(\cdot)\gamma(\text{surv+captv+sex})$	45	900.65	38.97	0.00	766.61
$\alpha(\text{eff+rloss+captv+sex})\sigma_{(0)}\phi(\text{age})\gamma(\text{surv+captv+sex})$	46	901.33	39.64	0.00	762.83
$\alpha(\text{eff+rloss+captv+sex})\sigma_{(0)}\phi(\text{age})\gamma_{(0)}$	32	2217.53	1355.85	0.00	2133.80
$\alpha(\text{eff+rloss+captv+sex})\sigma_{(0)}\phi(\cdot)\gamma_{(0)}$	31	2224.35	1362.67	0.00	2143.98

APPENDIX 2: R CODE FOR ANALYSIS

R PACKAGES USED

```
##IMPORTING PACKAGES

##Statistical packages
require(RMark)
require(msm)
require(combinat)

##Data-management packages
require(lubridate)
require(gtools)
require(stringr)
require(zoo)

##Graphical packages
require(plotrix)
require(graphics)

##Spatial tools packages
require(maptools)
require(rgdal)
require(rgeos)
```

STEPWISE RDPNE MODEL SELECTION

```
#####  
###RMark PROCESSING DATA###  
#####  
agout.proc<-process.data( ##Processing encounter history data  
  data=eh.df, ##data.frame containing encounter histories and indiv. covariates  
  model="PoissonMR", #character object containing type of model ran  
  counts=list( #list of count vectors  
    "Unmarked Seen"=eh.unmark, #unmarked individuals  
    "Marked Unidentified"=eh.mark.n.id, #marked, but unidentified individuals  
    "Known Marks"=kmark), #known number of marks at each sampling occ. (0 means unknown)  
  begin.time=1, #arbitrary start time of analysis  
  time.intervals=(interval_cov$time.interval.months[-1]) #intervals between each samping occ.  
  )  
###Dummy object of processed data (using Minimum Number Kown Alive as the known number of marks)  
dummy.agout.proc<-process.data( ##Processing encounter history data  
  data=eh.df, ##data.frame containing encounter histories and indiv. covariates  
  model="PoissonMR",#character object containing type of model ran  
  counts=list( #list of count vectors  
    "Unmarked Seen"=eh.unmark, #unmarked individuals  
    "Marked Unidentified"=eh.mark.n.id, #marked, but unidentified individuals  
    "Known Marks"=dummy.kmark), #known number of marks at each sampling occ. (0 means unknown)  
  begin.time=1, #arbitrary start time of analysis  
  time.intervals=(interval_cov$time.interval.months[-1]) #intervals between each samping occ.  
  )  
#####  
###RMark DESIGN DATA###  
#####  
agout.ddl<-make.design.data(agout.proc)  
###Adding time indexes to design data  
interval_cov$time<-force.numeric(agout.ddl$alpha$time[1:no_int])  
interval_cov$survey.mean<-rep(  
  tapply(interval_cov$time,interval_cov$sample_month,mean),  
  each=5)  
#time vector of beginnings resighting surveys  
survey.beg<-tapply(interval_cov$time,interval_cov$sample_month,min)  
interval_cov$survey.beg<-rep(survey.beg,each=5)  
#time vector of ends of resighting surveys  
survey.end<-tapply(interval_cov$time,interval_cov$sample_month,max)  
interval_cov$survey.end<-rep(survey.end,each=5)  
#time vector transitions between resighting surveys  
survey.trans<-(survey.end[1:(length(survey.end)-1)] + survey.beg[2:length(survey.beg)]) / 2  
interval_cov$survey.trans<-interval_cov$survey.end
```

```

interval_cov$survey.trans[1:(length(survey.trans)*5)]<-rep(survey.trans,each=5)
##Formating individual covariates
agout.proc$data$captive<-as.numeric(agout.proc$data$captive)
agout.proc$data$sex<-agout.proc$data$sex.female*1
#replace missing values for mean values
agout.proc$data$sex[is.na(agout.proc$data$sex)]<-mean(agout.proc$data$sex,na.rm=TRUE)
agout.proc$data$young.mark<-agout.proc$data$marked.as.young*1
##Time-varying age
temp<-matrix(ncol=no_int,nrow=nrow(agout.proc$data),dimnames=list(
  rownames=rownames(agout.proc$data),colnames=paste("age.t",interval_cov$time,sep="")))
for (i in 1:nrow(agout.proc$data)){ #for each individual
  #time since release
  tsr<-difftime(interval_cov$start,agout.proc$data$date.mark.rel[i],units="days")
  tsr[tsr<0]<-NA
  #values before it's first capture (NA's)
  a<-rep(NA,length(which(interval_cov$start<agout.proc$data$resig.cohort[i])))
  #sampling occ. spent as young
  b<-rep((agout.proc$data$marked.as.young[i]==F)*1,length(which(tsr<=60)))
  #sampling occ. spent as adult
  c<-rep(1,no_int-length(c(a,b)))
  temp[i,]<-c(a,b,c) #full vector of ages for individual
  temp[i,which(interval_cov$start>=agout.proc$data$date.rm[i])<-NA} #missing values after removal
##Replace age missing values
age.means<-apply(temp,2,mean,na.rm=TRUE) #mean of binary ages at each sampling occ.
for(c in 1:ncol(temp)){temp[is.na(temp[,c]),c]<-age.means[c]} #replacing missing values for means
##Binding age data to processed data
agout.proc$data<-cbind(agout.proc$data,temp)
dummy.agout.proc$data<-agout.proc$data
##Adding interval covariates to design data
des.cov<-interval_cov #desired covariates to merge (all interval covariates)
###Merging covariates to all parameter classes
agout.ddl$Phi<-merge_design.covariates(
  ddl=agout.ddl$Phi, df=des.cov,bytime=T)
agout.ddl$alpha<-merge_design.covariates(
  ddl=agout.ddl$alpha, df=des.cov,bytime=T)
agout.ddl$sigma<-merge_design.covariates(
  ddl=agout.ddl$sigma, df=des.cov,bytime=T)
agout.ddl$U<-merge_design.covariates(
  ddl=agout.ddl$U, df=des.cov,bytime=T)
agout.ddl$GammaDoublePrime<-merge_design.covariates(
  ddl=agout.ddl$GammaDoublePrime, df=des.cov,bytime=T)
agout.ddl$GammaPrime<-merge_design.covariates(
  ddl=agout.ddl$GammaPrime, df=des.cov,bytime=T)
##Specifying fixed parameters

```

```

agout.ddl.full<-agout.ddl #object without any fixed parameter
##Creating 'fixed' column for parameters of interest
  agout.ddl$Phi$fix<-NA
  agout.ddl$GammaPrime$fix<-NA
  agout.ddl$GammaDoublePrime$fix<-NA
##Vector of times to fix parameters
  exist.cohort<-interval_cov$time[ #existing release cohorts
    as.character(interval_cov$start)
    %in%
    levels(as.factor(agout.proc$data$resig.cohort))]
  month.ends<-as.vector(          #ends of months (resig. surveys)
    tapply(
      force.numeric(interval_cov$time),interval_cov$sample_month,max))
##Fixing transition parameters for non-existent cohorts
  agout.ddl$Phi$fix[agout.ddl$Phi$cohort%in%exist.cohort==F]<-1
  agout.ddl$GammaPrime$fix[agout.ddl$GammaPrime$cohort%in%exist.cohort==F]<-0
  agout.ddl$GammaDoublePrime$fix[agout.ddl$GammaDoublePrime$cohort%in%exist.cohort==F]<-0
##Saving parameter structure for open populations (relative to resighting surveys)
  op.agout.ddl<-agout.ddl
##Fixing transition parameters for closed populations (relative to resighting surveys)
  #There only estimated parameters at the end of each survey
  agout.ddl$Phi$fix[agout.ddl$Phi$time%in%month.ends==F]<-1
  agout.ddl$GammaPrime$fix[agout.ddl$GammaPrime$time%in%month.ends==F]<-0
  agout.ddl$GammaDoublePrime$fix[agout.ddl$GammaDoublePrime$time%in%month.ends==F]<-0
##Saving parameter structure for open populations (relative to resighting surveys)
  cl.agout.ddl<-agout.ddl
#####
####RUNNING RMark MODELS####
#####
###Running a dummy model (of easy convergence) without unknown number of marks
  dummy.dot.fix.siman<-mark(
    dummy.agout.proc, #Dummy input data
    op.agout.ddl,     #Open model structure (more parameters)
    options="SIMANNEAL",#'Simulated' annealing method of convergence
    threads=-1)      #Using full CPU capacity
###Running a simple model, with unknown number of marks, from previous model
  dot.fix.init.siman<-mark(
    agout.proc,      #Actual input data
    op.agout.ddl,    #Open model structure (more parameters)
    initial=dummy.dot.fix.siman, #'Borrowing' initial beta values from previous model
    options="SIMANNEAL", #'Simulated' annealing method of convergence
    threads=-1)     #Using full CPU capacity
#####
###EVALUATING POPULATION CLOSURE###

```

```

#####

open.model<-mark(          #Running model with an 'open' parameter structure
  agout.proc,              #input data
  op.agout.ddl,            #open parameter structure
  initial=dot.fix.init.siman, #initial beta values
  threads=-1,              #Using full CPU capacity
  model.parameters=list(    #Modeling U as a function of sampling occ.
    U=list(formula=~1+time)))

clos.model<-mark(          #Running model with a 'closed' parameter structure
  agout.proc,              #input data
  cl.agout.ddl,            #closed parameter structure
  initial=dot.fix.init.siman, #initial beta values
  threads=-1,              #Using full CPU capacity
  model.parameters=list(    #Modeling U as a function of resighting survey
    U=list(formula=~1+sample_month)))

#Collecting both models for comparison
open.close.models<-collect.models(
  lx=c("clos.model","open.model"),type="PoissonMR")

##Evaluating closure
#If closed (simpler) model DeltaAIC is > 2
if(clos.model$results$AICc - open.model$results$AICc > 2){
  true.agout.ddl<-op.agout.ddl #discard it, keeping open structure
  closed.months<-FALSE} else{
#else, keep close structure
  closed.months<-TRUE
  true.agout.ddl<-cl.agout.ddl}

#####
###STEPWISE MODELING###
#####

###Defining covariate classes
time.cont.cov<-c( #Temporal, continous covariates
  "effort.trapdays","recordloss.agout.total","effort.var","recordloss.agout.var","age.t")
time.catg.cov<-c( #Temporal, categorical covariates (effect of occasion or survey)
  "time","sample_month")
indiv.cov<-c( #Individual covariates
  "captive","age.t","sex","group")

###Function to be applied to an covariate combinations object, removing impossible combinations
imposib.mod<-function(x){ #x is a vector of covariate names,
  any(c(
#models with a categorical and continuous temporal effect
  (any(x%in%time.catg.cov) & any(x%in%time.cont.cov)),
#models with an effect of both surveys and sampling occasions
  (any(x=="sample_month") & any(x=="time"))))==FALSE}

#####

```

```

###ALPHA MODEL SELECTION (STEP 1)##
#####

##Creating enviroment for alpha model selection
agout.models.alpha<-function(threads,run,initial,data,options,ddl){
##Modeling U as a function of time
  if(closed.months==TRUE){U.time<-list(formula=~1+sample_month)} else{
    U.time<-list(formula=~1+time)}
###alpha possible models###
  alpha.dot<-list(formula=~1) #constant model
  alpha.covariates<-c(      #definig covariates used
    "captive","age.t","sex","effort.trapdays","recordloss.agout.total","time")
#Empty objects to be filled in 'for loop'
  mod.list<-list()
  formulas<-character()
  f<-1 #index addressing the number of formulas generated
#Loop generating possible combinations of covariates
  for(m in 2:length(alpha.covariates)){ #
    temp<-as.matrix(combn(alpha.covariates,m))
    temp<-temp[,apply(temp,2,imposib.mod)]
    mod.list[[m]]<-as.matrix(temp)
    if(any(dim(mod.list[[m]])==0)){
      mod.list[[m]]<-NULL
      break} else {
      formulas[f:(f-1+ncol(mod.list[[m]]))<-paste("~1 +",apply(
        mod.list[[m]],2,paste0,collapse="",sep="+"))
      f<-length(formulas)+1}
    }
#Formatting formulas
  formulas<-gsub('.{1}$', '', formulas)
#Creating univariate formulas
  formulas[f:(f-1+length(alpha.covariates))<-paste("~1",alpha.covariates,sep="+")
#Leaving only formulas with 'effort' as a covariate
  formulas<-formulas[str_detect(formulas,"effort")]
#Assigning formulas to models to be run
  alpha<-list() #empty object
  for (f in 1:length(formulas)){ #for each formula, assignit to enviroment
    alpha[[f]]<-list(formula=as.formula(formulas[f]))
    names(alpha)[f]<-paste("alpha",f,sep=".")
    environment(alpha[[f]]$formula)<-environment(alpha.dot$formula)
    assign(names(alpha)[f], alpha[[f]])}
##Other parameters are kept constant
  sigma.dot<-list(formula=~1)
  Phi.dot=list(formula=~1)
  GammaPrime.dot<-list(formula=~1)

```

```

GammaDoublePrime.dot<-list(formula=~1)

##Finishing function
  cml<-create.model.list("PoissonMR")
  results=mark.wrapper(cml,data=data,
  adjust=TRUE,
  initial=initial,
  threads=threads, realvcv=TRUE,
  ddl=ddl,run=run)
  return(results)
}

##Running models for alpha
start.computing<-now()
agout.results.alpha<-agout.models.alpha(
  run=TRUE,
  data=agout.proc,
  ddl=true.agout.ddl,
  initial=dot.fix.init.siman,
  threads=-1)
run.time.alpha<-difftime(now(),start.computing,units="hours") #time run for all alpha models

##Step 1 of model selection
agout.results.alpha.bkp<-agout.results.alpha #Creating backup object of all models run
temp<-agout.results.alpha$model.table[ #Temporary object of model selection table
  order(agout.results.alpha$model.table$weight,decreasing=T),]

##Removing models that didn't converge (Negative infinite AICc)
if(any(temp$AICc==Inf)){
  agout.results.alpha<-remove.mark(
    agout.results.alpha,as.numeric(rownames(agout.results.alpha$model.table[
      agout.results.alpha$model.table$AICc==Inf,])))}

##Defining criteria for keeping models for next step
cut<-as.numeric(rownames(temp[temp$DeltaAICc > 2,])) #DeltaAICc smaller than 2
#Keeping dropped models in a separate object, removing from main object
drop.agout.results.alpha<-remove.mark(agout.results.alpha,as.numeric(setdiff(rownames(temp),cut)))
agout.results.alpha<-remove.mark(agout.results.alpha,cut)

#####
###SIGMA MODEL SELECTION (STEP 2)###
#####

##Creating enviroment for sigma model selection
agout.models.sigma<-function(threads,run,initial,data,options,ddl){
  ##Modeling U as a function of time
  if(closed.months==TRUE){U.time<-list(formula=~1+sample_month)} else{
    U.time<-list(formula=~1+time)}
  ###sigma possible models###
  sigma.dot<-list(formula=~1) #constant model
  sigma.zero<-list(formula=~1,fixed=0)#sigma as zero (without indiv. heterogeneity)

```

```

sigma.covariates<-c(          #definig covariates used
      "time","sample_month","effort.var","recordloss.agout.var")
#Empty objects to be filled in 'for loop'
mod.list<-list()
formulas<-character()

f<-1 #index addressing the number of formulas generated
for(m in 2:length(sigma.covariates)){
  temp<-as.matrix(combn(sigma.covariates,m))
  temp<-temp[,apply(temp,2,imposib.mod)]
  mod.list[[m]]<-as.matrix(temp)
  if(any(dim(mod.list[[m]])==0)){
    mod.list[[m]]<-NULL
    break} else {
  formulas[f:(f-1+ncol(mod.list[[m]]))<-paste("~1 +",apply(
    mod.list[[m]],2,paste0,collapse="",sep="+"))
  f<-length(formulas)+1
  }
}

#Formatting formulas
formulas<-gsub('.{1}$', '', formulas)

#Creating univariate formulas
formulas[f:(f-1+length(sigma.covariates))<-paste("~1",sigma.covariates,sep="+")

#Character vector of sigma models containing variance in effort or record loss
effort.sigma.models<-paste("sigma",which(str_detect(formulas,"effort")),sep=".")
recloss.sigma.models<-paste("sigma",which(str_detect(formulas,"recordloss")),sep=".")

#Assigning formulas to models to be run
sigma<-list()
for (f in 1:length(formulas)){
  sigma[[f]]<-list(formula=as.formula(formulas[f]))
  names(sigma)[f]<-paste("sigma",f,sep=".")
  environment(sigma[[f]]$formula)<-environment(sigma.dot$formula)
  assign(names(sigma)[f], sigma[[f]])}

##Recovering selected models for 'alpha'
alpha<-list()
for (m in 1:nrow(agout.results.alpha$model.table)){
  alpha[[m]]<-agout.results.alpha[[m]]$model.parameters$alpha}
names(alpha)<-paste("alpha",1:length(alpha),sep=".")
for (l in 1:length(alpha)){
  environment(alpha[[l]]$formula)<-environment(sigma.dot$formula)}
for (l in 1:length(alpha)){
  assign(names(alpha)[l], alpha[[l]])}

#Character vector of alpha models containing effort or record loss
effort.alpha.models<-paste("alpha",as.character(which(sapply(alpha,function(x){
  any(str_detect(as.character(x$formula),"effort"))}))),sep=".")

```

```

        recloss.alpha.models<-paste("alpha",as.character(which(sapply(alpha,function(x){
            any(str_detect(as.character(x$formula),"recordloss"))}))),sep=".")
##Other parameters are kept constant
    Phi.dot=list(formula=~1)
    GammaPrime.dot<-list(formula=~1)
    GammaDoublePrime.dot<-list(formula=~1)
##Finishing function
    cml<-create.model.list("PoissonMR")
    #Removing sigma models in which a variance used as a covariate
    ###does not have respective covariate in alpha formula
        cml<-cml[(
            ( cml$sigma%in%effort.sigma.models & (cml$alpha%in%effort.alpha.models==FALSE) ) |
            ( cml$sigma%in%recloss.sigma.models & (cml$alpha%in%recloss.alpha.models==FALSE) ) )
            ==FALSE,]
    results=mark.wrapper(cml,data=data,
        adjust=TRUE,
        initial=initial,
        threads=threads, realvcv=TRUE,
        ddl=ddl,run=run)
    return(results)
}
##Running models for sigma
start.computing<-now()
agout.results.sigma<-agout.models.sigma(
    data=agout.proc,
    ddl=true.agout.ddl,
    run=TRUE,
    initial=dot.fix.init.siman,
    threads=-1)
run.time.sigma<-difftime(now(),start.computing,units="hours") #time run for all sigma models
##Step 2 of model selection
agout.results.sigma.bkp<-agout.results.sigma#Creating backup object of all models run
temp<-agout.results.sigma$model.table[      #Temporary object of model selection table
    order(agout.results.sigma$model.table$weight,decreasing=T),] #temp com tabela dos modelos
#Removing models that didn't converge (Negative infinite AICc)
if(any(temp$AICc==-Inf)){
    agout.results.sigma<-remove.mark(
        agout.results.sigma,as.numeric(rownames(agout.results.sigma$model.table[
            agout.results.sigma$model.table$AICc==-Inf,])))}
#Defining criteria for keeping models for next step
cut<-as.numeric(rownames(temp[temp$DeltaAICc > 2,])) #DeltaAICc smaller than 2
#Keeping dropped models in a separate object, removing from main object
drop.agout.results.sigma<-remove.mark(agout.results.sigma,as.numeric(setdiff(rownames(temp),cut)))
agout.results.sigma<-remove.mark(agout.results.sigma,cut)

```

```

#####
###PHI MODEL SELECTION (STEP 3)###
#####

##Creating enviroment for Phi model selection

agout.models.Phi<-function(threads,run,initial,data,options,ddl){

  ##Modeling U as a function of time

  if(closed.months==TRUE){U.time<-list(formula=~1+sample_month)} else{
    U.time<-list(formula=~1+time)}

  ###Phi possible models###

  Phi.dot<-list(formula=~1) #constant model

  Phi.covariates<-c( #definig covariates used
    "captive","sample_month","age.t","sex")

  #Empty objects to be filled in 'for loop'

  mod.list<-list()

  formulas<-character()

  f<-1 #index addressing the number of formulas generated

  #Loop generating possible combinations of covariates
  for(m in 2:length(Phi.covariates)){

    temp<-as.matrix(combn(Phi.covariates,m))

    temp<-temp[,apply(temp,2,imposib.mod)]

    mod.list[[m]]<-as.matrix(temp)

    if(any(dim(mod.list[[m]])==0)){

      mod.list[[m]]<-NULL

      break} else {

      formulas[f:(f-1+ncol(mod.list[[m]]))<-paste("~1 +",apply(
        mod.list[[m]],2,paste0,collapse="",sep="+"))

      f<-length(formulas)+1

    }

  }

  #Formatting formulas

  formulas<-gsub('.{1}$', '', formulas)

  #Creating univariate formulas

  formulas[f:(f-1+length(Phi.covariates))<-paste("~1",Phi.covariates,sep="+")

  #Assigning formulas to models to be run

  Phi<-list() #empty object

  for (f in 1:length(formulas)){ #for each formula, assign to enviroment

    Phi[[f]]<-list(formula=as.formula(formulas[f]))

    names(Phi)[f]<-paste("Phi",f,sep=".")

    environment(Phi[[f]]$formula)<-environment(Phi.dot$formula)

    assign(names(Phi)[f], Phi[[f]])}

  ##Recovering selected models for 'alpha' and 'sigma'

  alpha<-list()

  for (m in 1:nrow(agout.results.sigma$model.table)){

    alpha[[m]]<-agout.results.sigma[[m]]$model.parameters$alpha}

```

```

    names(alpha)<-paste("alpha",1:length(alpha),sep=".")
    for (l in 1:length(alpha)){environment(alpha[[l]]$formula)<-environment(Phi.dot$formula)}
    for (l in 1:length(alpha)){assign(names(alpha)[l], alpha[[l]])}
    sigma<-list()
    for (m in 1:nrow(agout.results.sigma$model.table)){
      sigma[[m]]<-agout.results.sigma[[m]]$model.parameters$sigma
      names(sigma)<-paste("sigma",1:length(sigma),sep=".")
      for (l in 1:length(sigma)){environment(sigma[[l]]$formula)<-environment(Phi.dot$formula)}
      for (l in 1:length(sigma)){assign(names(sigma)[l], sigma[[l]])}
##Other parameters are kept constant
      GammaPrime.dot<-list(formula=~1)
      GammaDoublePrime.dot<-list(formula=~1)
##Finishing function
      cml<-create.model.list("PoissonMR")
      ##Keeping previous combinations of models
      cml<-cml[substr(cml$alpha,6,nchar(cml$alpha))==substr(cml$sigma,6,nchar(cml$sigma)),]
      results=mark.wrapper(cml,data=data,
        adjust=TRUE,
        initial=initial,
        threads=threads, realvcv=TRUE,
        ddl=ddl,run=run)
}

##Running models for Phi
start.computing<-now()
agout.results.Phi<-agout.models.Phi(
  run=TRUE,
  data=agout.proc,
  ddl=true.agout.ddl,
  initial=dot.fix.init.siman,
  threads=-1)
run.time.Phi<-difftime(now(),start.computing,units="hours") #time run for all Phi models
##Step 3 of model selection
agout.results.Phi.bkp<-agout.results.Phi #Creating backup object of all models run
temp<-agout.results.Phi$model.table[ #Temporary object of model selection table
  order(agout.results.Phi$model.table$weight,decreasing=T),]
##Removing models that didn't converge (Negative infinite AICc)
if(any(temp$AICc==-Inf)){
  agout.results.Phi<-remove.mark(
    agout.results.Phi,as.numeric(rownames(agout.results.Phi$model.table[
      agout.results.Phi$model.table$AICc==-Inf,])))}
##Defining criteria for keeping models for next step
cut<-as.numeric(rownames(temp[temp$DeltaAICc > 2,])) #DeltaAICc smaller than 2
##Keeping dropped models in a separate object, removing from main object
drop.agout.results.Phi<-remove.mark(agout.results.Phi,as.numeric(setdiff(rownames(temp),cut)))

```

```

agout.results.Phi<-remove.mark(agout.results.Phi,cut)

#####

###GAMMA MODEL SELECTION (STEP 4)##

#####

##Creating enviroment for Gamma model selection

agout.models.Gamma<-function(threads,run,initial,data,options,ddl){
##Modeling U as a function of time
  if(closed.months==TRUE){U.time<-list(formula=~1+sample_month)} else{
    U.time<-list(formula=~1+time)}
###Gamma possible models###
##Constant models
  GammaPrime.dot<-list(formula=~1)
  GammaDoublePrime.dot<-list(formula=~1)
##Gamma as zero (geographic closure)
  GammaPrime.zero<-list(formula=~1,fixed=0)
  GammaDoublePrime.zero<-list(formula=~1,fixed=0)
GammaPrime.covariates<-c( #definig covariates used
  "captive","sample_month","age.t","sex")
#Empty objects to be filled in 'for loop'
  mod.list<-list()
  formulas<-character()
  f<-1 #index addressing the number of formulas generated
#Loop generating possible combinations of covariates
  for(m in 2:length(GammaPrime.covariates)){
    temp<-as.matrix(combn(GammaPrime.covariates,m))
    temp<-temp[,apply(temp,2,imposib.mod)]
    mod.list[[m]]<-as.matrix(temp)
    if(any(dim(mod.list[[m]])==0)){
      mod.list[[m]]<-NULL
      break} else {
      formulas[f:(f-1+ncol(mod.list[[m]]))<-paste("~1 +",apply(
        mod.list[[m]],2,paste0,collapse="",sep="+"))
      f<-length(formulas)+1
    }
  }
}
#Formatting formulas
  formulas<-gsub('.{1}$', '', formulas)
#Creating univariate formulas
  formulas[f:(f-1+length(GammaPrime.covariates))<-paste("~1",GammaPrime.covariates,sep="+")
#Assigning formulas to models to be run
  GammaPrime<-list() #empty object
  GammaDoublePrime<-list()#empty object
  for (f in 1:length(formulas)){
    GammaPrime[[f]]<-list(formula=as.formula(formulas[f]))

```

```

GammaDoublePrime[[f]]<-GammaPrime[[f]]
names(GammaPrime)[f]<-paste("GammaPrime",f,sep=".")
names(GammaDoublePrime)[f]<-paste("GammaDoublePrime",f,sep=".")
environment(GammaPrime[[f]]$formula)<-environment(GammaPrime.dot$formula)
environment(GammaDoublePrime[[f]]$formula)<-environment(GammaPrime.dot$formula)
assign(names(GammaPrime)[f], GammaPrime[[f]])
assign(names(GammaDoublePrime)[f], GammaDoublePrime[[f]])}
##Recovering selected models for 'alpha' and 'sigma' and 'Phi'
alpha<-list()
for (m in 1:nrow(agout.results.Phi$model.table)){
alpha[[m]]<-agout.results.Phi[[m]]$model.parameters$alpha}
names(alpha)<-paste("alpha",1:length(alpha),sep=".")
for (l in 1:length(alpha)){
environment(alpha[[l]]$formula)<-environment(GammaPrime.dot$formula)}
for (l in 1:length(alpha)){
assign(names(alpha)[l], alpha[[l]])}
sigma<-list()
for (m in 1:nrow(agout.results.Phi$model.table)){
sigma[[m]]<-agout.results.Phi[[m]]$model.parameters$sigma}
names(sigma)<-paste("sigma",1:length(sigma),sep=".")
for (l in 1:length(sigma)){
environment(sigma[[l]]$formula)<-environment(GammaPrime.dot$formula)}
for (l in 1:length(sigma)){
assign(names(sigma)[l], sigma[[l]])}
Phi<-list()
for (m in 1:nrow(agout.results.Phi$model.table)){
Phi[[m]]<-agout.results.Phi[[m]]$model.parameters$Phi}
names(Phi)<-paste("Phi",1:length(Phi),sep=".")
for (l in 1:length(Phi)){
environment(Phi[[l]]$formula)<-environment(GammaPrime.dot$formula)}
for (l in 1:length(Phi)){
assign(names(Phi)[l], Phi[[l]])}
##Finishing function
cml<-create.model.list("PoissonMR")
##Keeping previous combinations of models
cml<-cml[
(substr(cml$alpha,6,nchar(cml$alpha))==substr(cml$sigma,6,nchar(cml$sigma))) &
(substr(cml$sigma,6,nchar(cml$sigma))==substr(cml$Phi,4,nchar(cml$Phi))),]
##Removing models where GammaPrime and GammaDoublePrime are modelled with different covariates
cml<-cml[
substr(cml$GammaPrime,11,nchar(cml$GammaPrime))
==
substr(cml$GammaDoublePrime,17,nchar(cml$GammaDoublePrime)),]
results=mark.wrapper(cml,data=data,

```

```

    adjust=TRUE,
    initial=initial,
    threads=threads, realvcv=TRUE,
    ddl=ddl,run=run)
}
##Running models for Gamma
start.computing<-now()
agout.results.Gamma<-agout.models.Gamma(
run=TRUE,
data=agout.proc,
ddl=true.agout.ddl,
initial=dot.fix.init.siman,
threads=-1)
run.time.Gamma<-difftime(now(),start.computing,units="hours")           #run time for Gamma models
run.time.total<-sum(run.time.alpha+run.time.sigma+run.time.Phi+run.time.Gamma) #run time for all models
##Step 4 of model selection
agout.results.Gamma.bkp<-agout.results.Gamma #Creating backup object of all models run
temp<-agout.results.Gamma$model.table[      #Temporary object of model selection table
order(agout.results.Gamma$model.table$weight,decreasing=T),]
#Removing models that didn't converge (Negative infinite AICc)
if(any(temp$AICc==-Inf)){
agout.results.Gamma<-remove.mark(
agout.results.Gamma,as.numeric(rownames(agout.results.Gamma$model.table[
agout.results.Gamma$model.table$AICc==-Inf,])))}
agout.results<-agout.results.Gamma #full results of final step
#best supported models of final step
agout.results.subset<-remove.mark(
agout.results.Gamma,as.numeric(rownames(temp[temp$DeltaAICc > 2,])))

```

PARAMETRIC BOOTSTRAPING

```
#####  
###PARAMETRIC BOOTSTRAPING (DERIVED PARAMETERS)###  
#####  
  
###Empty lists for storing generated values from fitted distributions  
  N.mc<-list() #population sizes  
  Phi.mc<-list() #apparent survival values  
  Recrut.mc<-list() #Recruitment values  
  Fin.rate.inc.mc<-list() #Finite rate of increase values  
  Trend.mc<-list() #Yearly trends  
  
###Empty lists for storing generated values from fitted distributions  
  Trend.stats<-list()  
  Recrut.stats<-list()  
  Fin.rate.inc.stats<-list()  
  
###Simulation parameters  
  n.simu<-10000 #number of generated values for each demographic parameter  
  intervals<-na.omit(agout.proc$time.intervals[ #vector of monthly time distance between sampling occ.  
    cumsum(c(agout.proc$begin.time,agout.proc$time.intervals))  
    %in%  
    pop.sizes$estimates$time])  
  
###Formatting used survival values  
  Phi.temp<-survival$estimates[ #extracting survival values referent  
    survival$estimates$time #to estimable population sizes  
    %in%  
    pop.sizes$singular.estm$time==FALSE,]  
  Phi.temp<-Phi.temp[ #ordering survival by time  
    order(Phi.temp$interval,decreasing=FALSE),]  
  Phi.temp.vcv<-survival$vcv[ #extracting referent variance-covariance matrix  
    as.character(Phi.temp$par.index),  
    as.character(Phi.temp$par.index)]  
  
###Generating random values from already estimated parameters  
  for (n in 1:nrow(pop.sizes$estimates)){ #for each abundance estimate  
    N.mc[[n]]<-rlnorm( #generate from a log-Normal distribution  
      n.simu, #ten thousand values with  
      #mean equal estimated value (log-transformed)  
      meanlog = log(pop.sizes$estimates[n,"estimate"]),  
      #std. deviation equal std. error from estimate (log-transformed through delta method)  
      sdlog = deltamethod(g=~log(x1),  
        mean=pop.sizes$estimates[n,"estimate"],  
        cov=pop.sizes$vcv[n,n],ses=TRUE))  
  }  
  if(n!=nrow(pop.sizes$estimates)){ #for all but the last interval  
    Phi.mc[[n]]<-rnorm( #generate survivals from a Normal distribution  
      n.simu, #ten thousand values with
```

```

#mean equal the central estimate (logit transformed)
  mean = logit(Phi.temp[n,"estimate"]),
#std. dev. equal the std. error, logit transformed through delta method)
  sd = deltamethod(g=~log(x1/(1-x1)),
    mean=Phi.temp[n,"estimate"],
    cov=Phi.temp.vcv[
      as.character(Phi.temp[n,"par.index"]),as.character(Phi.temp[n,"par.index"])],
    ses=TRUE))
}
}
####Generating derived parametersf
for(n in 1:(nrow(pop.sizes$estimates)-1)){ #for all but the last sampling occasions
###Finite rate of increase (lambda)
  Fin.rate.inc.mc[[n]]<-N.mc[[n+1]]/N.mc[[n]] #10.000 generated values for each sampling occasions
  Fin.rate.inc.stats$time[n]<-force.numeric(pop.sizes$estimates$time[n])
###Summary of estimates
  Fin.rate.inc.stats$mean[n]<-mean(Fin.rate.inc.mc[[n]])
  Fin.rate.inc.stats$se[n]<-sd(Fin.rate.inc.mc[[n]])
###Confidence interval
  Fin.rate.inc.stats$lcl[n]<-quantile(Fin.rate.inc.mc[[n]],0.025)
  Fin.rate.inc.stats$ucl[n]<-quantile(Fin.rate.inc.mc[[n]],0.975)
###Recruitment
  Recrut.mc[[n]]<-N.mc[[n+1]]-((inv.logit(Phi.mc[[n]])^intervals[n]) * N.mc[[n]])
  Recrut.mc[[n]][Recrut.mc[[n]]<0]<-0 #Transform negative derived values to 0
###Summary of estimates
  Recrut.stats$mean[n]<-quantile(Recrut.mc[[n]],0.5) #median value
  Recrut.stats$se[n]<-sd(Recrut.mc[[n]])
###Confidence interval
  Recrut.stats$lcl[n]<-quantile(Recrut.mc[[n]],0.025)
  Recrut.stats$ucl[n]<-quantile(Recrut.mc[[n]],0.975)
  Recrut.stats$time[n]<-force.numeric(pop.sizes$estimates$time[n])
}
###Converting derived estimates to data.frame, with interval covariated appended
  Recrut.estm<-merge(as.data.frame(Recrut.stats),interval_cov,by="time")
  Fin.rate.inc.estm<-merge(as.data.frame(Fin.rate.inc.stats),interval_cov,by="time")
###Overall tendencies
###Finite rate of increase (from the first to last occasion)
  Fin.rate.overall<-N.mc[[nrow(pop.sizes$estimates)]]/N.mc[[1]]
  Fin.rate.ov.mean<-mean(Fin.rate.overall)
  Fin.rate.ov.se<-sd(Fin.rate.overall)
  Fin.rate.ov.lcl<-quantile(Fin.rate.overall,0.025)
  Fin.rate.ov.ucl<-quantile(Fin.rate.overall,0.975)
###Yearly trend (geometric mean of growth)
  study.length<-max(interval_cov$cum.time_elaps.days,na.rm=TRUE)/365 #study length, in years

```

```
Trend.mc<-apply(simplify2array(Fin.rate.inc.mc),1,prod)^(1/study.length)
Trend.stats$mean<-mean(Trend.mc)
Trend.stats$se<-sd(Trend.mc)
Trend.stats$lcl<-quantile(Trend.mc,c(0.025))
Trend.stats$ucl<-quantile(Trend.mc,c(0.975))
Trend.estm<-as.data.frame(Trend.stats)
```