



The foraging ecology of invasive black rats (*Rattus rattus*) differs in two nearby islands in a dry tropical archipelago in Brazil

Bruno de Andrade Linhares · Lucas Cabral Lage Ferreira ·
Leandro Bugoni

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Abstract Invasive predators on islands impact organisms they consume and lead to cascading effects that disrupt ecosystem functioning. Black rats (*Rattus rattus*) are a prevalent threat on tropical islands. Here, we used stable isotopes to reveal patterns in the foraging ecology of black rats ($n=43$) on two tropical islands in the Abrolhos archipelago, southwestern Atlantic Ocean. Contrary to our predictions, rats from the smaller island (3 ha), with greater seabird density, relied more on terrestrial resources than rats from the larger (31 ha) island, which were highly dependent (~50% of diet) on seabird resources. We attribute this finding to varying levels of spatial segregation among

habitats between the islands. On the smaller island, only rats sampled inside the colony had a high contribution from seabirds, while those sampled outside the colony had their foraging apparently constrained within the small patch of grassland habitat. On the larger island, however, individuals consumed seabird resources regardless of the sampling area, although the sampling locations were farer apart, suggesting lower spatial segregation. A greater foraging segregation in the smaller island could be related to a higher population density of rats, increasing competition and territoriality. Rats inside seabird colonies were larger and heavier than in grassland areas, likely by having access to marine-derived resources, suggesting these individuals could defend their prime foraging territory against others. Our results highlight the capacity of black rats to rely either on marine or terrestrial resources on tropical islands, providing population resilience for this island invader.

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B. A. Linhares (✉)
Programa de Pós-Graduação em Oceanografia Biológica,
Universidade Federal do Rio Grande - FURG, Rio Grande,
Rio Grande do Sul, Brazil
e-mail: brunolinhares.bio@gmail.com

B. A. Linhares · L. Bugoni
Laboratório de Aves Aquáticas e Tartarugas Marinhas
(LAATM), Instituto de Ciências Biológicas, Universidade
Federal do Rio Grande - FURG, Rio Grande,
Rio Grande do Sul, Brazil

L. C. L. Ferreira
Parque Nacional Marinho dos Abrolhos, Instituto Chico
Mendes de Conservação da Biodiversidade (ICMBio),
Praia do Kitongo, S/N, Caravelas, Bahia, Brazil

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Introduction

Invasive predators on islands may lead to several impacts on insular and adjacent aquatic ecosystems, as they consume native organisms and alter trophic interactions (Fukami et al. 2006; Jones et al. 2016). Animal and plant communities on islands are

susceptible to biological invasions once they are spatially isolated and, in some cases, have evolved without the presence of conspicuous terrestrial predators (Banks and Dickman 2007). Although island ecosystems are valuable for wildlife conservation due to high levels of endemism, most of the world's extinct or critically threatened species inhabit islands (Meyers et al. 2000; Ricketts et al. 2005; Tershy et al. 2015; Doherty et al. 2016). One of the most prevalent threats to these environments worldwide has been the introduction of invasive mammals (Townsend et al. 2006; Whittaker et al. 2007; Jones et al. 2008), especially commensal rats (*Rattus* sp.). The need for understanding the ecology of invasive rats on islands and implementation of effective conservation actions is thus evident.

Rats are estimated to occur in more than 90% of island archipelagos worldwide (Townsend et al. 2006). They thrive in tropical, temperate or even subpolar islands due to their generalist feeding habits, tolerance to diverse environmental settings and lack of predators or ecological competitors (Atkinson 1985; Pisanu et al. 2011; Rodríguez and Herrera 2013). Rats are omnivorous and feed opportunistically on almost any feeding resource available, thus implicating population-level dietary flexibility and adaptation to temporal or spatial fluctuations in resources (Caut et al. 2008a). On islands, rats are known to rely mainly on terrestrial organisms such as plants (roots, leaves, seeds and fruits), insects, reptiles and land birds (Stapp 2002; Cassaing et al. 2007; Clapperton et al. 2019; Gaiotto et al. 2020). Nonetheless, they are also able to supply their populations with allochthonous resources from marine origins, such as breeding seabirds, sea turtles or intertidal invertebrates (Hobson et al. 1999; Harper 2006; Caut et al. 2008a; Rodríguez and Herrera 2013). Indeed, marine resources are suspected to alleviate rats from environmental stress during, for example, seasonal drought periods experienced on some tropical or temperate islands (Caut et al. 2008a; Ruffino et al. 2013).

Conservation concerns refer primarily to the detrimental effects caused by rats on plants and animals they consume but also to the cascading top-down indirect effects over the entire insular ecosystem, e.g., through interruption of pollination, nutrient pathways, or seed predation (Townsend et al. 2006; Townsend 2009; Auld et al. 2010; Grant-Hoffmann and Barboza 2010; Graham et al. 2018). The negative effects on

seabird populations, for instance, which are mediated by predation on eggs, chicks or adults of several species globally (Jones et al. 2008), reduce the marine-terrestrial subsidy brought by seabirds to islands (Benkwitt et al. 2021). As these subsidies are known to support primary and secondary productivity on islands, even on nearshore coral reefs, rat invasion may disrupt some ecosystem functions (Jones 2010a; Graham et al. 2018). The single most effective measure to begin the restoration of invaded islands is to completely eradicate or control rat populations (Jones 2010a, b; Jones et al. 2016; Benkwitt et al. 2021), which requires some prior ecological information for adequate planning, such as on rat population dynamics, seasonality, movements and diet on different islands and habitats (Caut et al. 2009a; Harper et al. 2015).

However, both research on insular rat populations and eradication efforts concentrate on high-latitude temperate environments, even though tropical islands are biodiversity hotspots that host proportionally more threatened species and where rat invasion is one of the major threats (Ricketts et al. 2005; Varnham 2010; Harper and Bunbury 2015). Furthermore, the success of eradication attempts on islands is approximately 2–2.5 times lower in tropical areas, causing the focus of invasive rat research and management to progressively shift to these regions (Harper and Bunbury 2015; Russel and Holmes 2015). The most successful invasive rat species in the tropics is the black rat (*Rattus rattus*), reaching higher densities on tropical islands than those recorded for rats elsewhere (Shiels et al. 2013; Harper and Bunbury 2015). Black rats colonize a wide range of island habitats, from evergreen forests to arid sites with minimal vegetation cover (Rodríguez and Herrera 2013; Harper et al. 2015). The high population densities and lower eradication success may be due to one or several causes, such as year-round food availability, higher primary productivity, lack of seasonal cessation in breeding or more diverse food sources (Harper and Bunbury 2015; Russel and Holmes 2015). This broad range of potential causes suggests that rat ecology, management and even their impacts on tropical islands are poorly understood and thus evokes thorough studies on rat populations to advance planning on urgent management actions.

One way to characterize invasive rat ecological requirements and their intraspecific variations in

relation to intrinsic (sex, ontogeny, and individual preferences) or extrinsic (habitat and seasonal variation in rainfall) parameters is through dietary studies (Hobson et al. 1999; Stapp 2002; Caut et al. 2008a; Ruffino et al. 2011; Shiels et al. 2013). However, rat foraging activity is cryptic and mostly nocturnal, which makes diet determination difficult and feasible only through the analysis of gut or faecal contents or by using intrinsic markers such as stable isotopes. While analysis of gastrointestinal contents may allow the correct taxonomic identification of food items, it is impaired by unequal digestibility of different foods, rodent intensive maceration during ingestion, and by representing only the last ingested meal (Stapp 2002; Caut et al. 2008a). On the other hand, stable isotope analysis (SIA) provides information on food sources effectively assimilated to synthesize protein in tissues rather than ingested and informs diet over longer periods (e.g., the last week or month) depending on the tissue analysed, despite not providing accurate taxonomic resolution on food items (Hobson et al. 1999; Quillfeldt et al. 2008; Bodey et al. 2011). The most commonly used analysis, stable carbon isotope $^{13}\text{C}:^{12}\text{C}$ ratio (expressed as $\delta^{13}\text{C}$) analysis, reflects values of the food-web primary consumers closely, while nitrogen isotope $^{15}\text{N}:^{14}\text{N}$ ratios ($\delta^{15}\text{N}$) increase values in consumer tissues in relation to their food sources in a somewhat systematic manner, generally by 2–5‰, thus reflecting trophic level (DeNiro and Epstein 1981). Combining carbon and nitrogen SIAs of consumer tissues and their potential food sources thereby allows researchers to estimate the relative dietary proportions using sophisticated statistical methods such as isotopic mixing models implemented through a Bayesian approach (Parnell et al. 2013; Phillips et al. 2014). Moreover, cryptic patterns of niche partitioning and resource use among consumer groups are often assessed by quantifying the isotopic niche, a proxy for the trophic niche reflecting habitat and/or resource use (Newsome et al. 2007; Jackson et al. 2011; Rodríguez and Herrera 2013), which was recently improved by applying kernel densities to isotopic data (Eckrich et al. 2020). Indeed, historically, several studies have taken advantage of stable isotopes to study the feeding ecology of invasive rats on islands, revealing spatial variations (Stapp 2002), time-related shifts in diet (Caut et al. 2008a), dependency on allochthonous versus autochthonous resources and individual preferences (Quillfeldt et al. 2008; Ruffino et al. 2011; Rodríguez and Herrera 2013). Recent and on-going analytical

developments and improvements make this technique promising for revealing the feeding ecology, and thus the impact, of cryptic invasive animals such as rats on tropical islands.

In this study, we aimed to quantify intraspecific patterns in the diet of black rats on two tropical islands with varying sizes and settings, as well as rat and seabird densities in the Abrolhos archipelago, southeastern Brazil. In this dry tropical archipelago, black rats were recorded in high numbers by Darwin during the expedition aboard the *Beagle* in 1832 (Keynes 2003) and are thought to have caused reductions in seabird numbers since then, threatening with extinction the nationally “endangered” red billed tropicbird *Phaethon aethereus* (Sarmiento et al. 2014) but also masked (*Sula dactylatra*) and brown (*S. leucogaster*) boobies and magnificent frigatebirds (*Fregata magnificens*). Currently, actions to eradicate rats in Abrolhos are in progress and, if successful, will represent one of the few cases of rat eradication in a Brazilian archipelago, thus highlighting novel research on this site where rat ecology was never assessed. We expected that during the dry season, when terrestrial resources are depleted, the contribution of seabirds to the diet of black rats would be higher than autochthonous resources on both islands. However, we expected a larger dependency on seabirds in the smaller island due to larger seabird density and habitat constraints, while rats on the larger island would rely more on terrestrial resources due to the lower seabird density and more complex terrestrial habitats. Furthermore, we expected that rats sampled inside seabird colonies would be larger and heavier than those sampled in non-bird habitats due to better quality resources. Finally, based on previous studies on invasive rats elsewhere (Hobson et al. 1999; Quillfeldt et al. 2008; Ruffino et al. 2011), we expected limited dietary variation in response to sex, sampling year and tissue and a large variation in diet resulting from individual preferences in different areas.

Materials and methods

Study area and sampling

This study was carried out in the Abrolhos archipelago, ~70 km off the northeastern Brazilian coast,

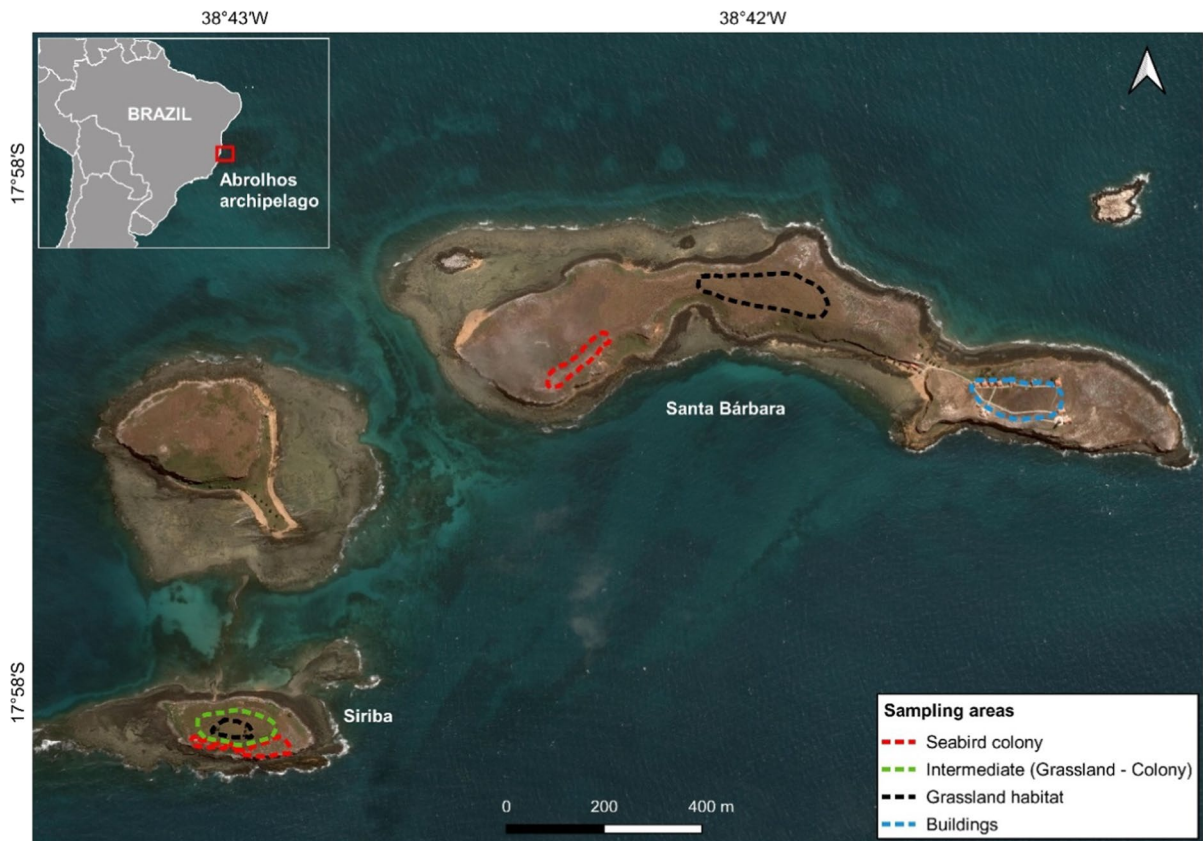


Fig. 1 Satellite image of the Abrolhos archipelago, southwestern Atlantic Ocean, highlighting the areas where black rats (*Rattus rattus*) were sampled on Santa Bárbara and Siriba islands between 2019 and 2021

Bahia state (Fig. 1). The climate is tropically warm and semiarid, with approximately 700 mm of annual rainfall mainly distributed in the colder winter months (May–August; Kemenes 2003). Vegetation is composed mainly of grasses, succulents and small shrubs (Kemenes 2003), with some bare ground rocky areas mainly inside colonies of the masked booby, the most widespread breeding seabird.

Sampling was conducted on two of the five islands of the archipelago, Santa Bárbara and Siriba. Santa Bárbara is the largest, with ~1.5 km in length and ~31 ha in area, and contains the greater number of seabird breeding pairs (~960). Siriba is 300 m in length, ~3 ha in area, holds ~410 seabird pairs, but has an approximately 4.5 times greater seabird biomass per hectare than Santa Bárbara (see Linhares and Bugoni 2023). The main breeding seabird on both islands is the masked booby, but red-billed tropicbirds and brown boobies also nest in lower numbers

(ICMBio 2020; Linhares and Bugoni 2023). Santa Bárbara has a small built-up area with a lighthouse and seven houses permanently inhabited by the Brazilian Navy and by the staff of the Abrolhos Marine National Park, which has jurisdictions on the other islands. In addition to black rats, Santa Bárbara has a population of 50–80 free-roaming, non-native goats.

Rats were trapped in Tomahawk traps at two distinct times: in September–October 2019 and in February 2021. Rats from 2019 were found dead and collected during a mark-recapture study conducted by the Abrolhos Marine National Park to estimate rat density and home range in support of rat eradication. In 2021, 10 Tomahawk traps baited with pineapple chunks were installed on four consecutive days either inside or outside masked booby colonies on Santa Bárbara and Siriba (Fig. 1) and checked every morning. The areas outside the seabird colonies on both islands were dominated by dense grassy

vegetation mainly composed of *Cyperus* sp. (hereafter “grassland” habitat), while the seabird colonies were scarcely vegetated with herbs, where bare soil and stones predominated. The distance between the sampled seabird colony and the grassland ranged from 25 to 50 m on Siriba and 250–350 m on Santa Bárbara. Rats from 2019 were only obtained in the grassland and near the houses on Santa Bárbara, and on Siriba, they were collected in an intermediate zone between the grassland and seabird colony (Fig. 1). Rats in 2021 were immediately euthanized under permits and following Brazilian guidelines for animal care. All rats were stored frozen until necropsy in the laboratory. Furthermore, in February 2020 and 2021, samples of potential food items used by rats were also collected for SIA as part of another ecological study (C3 and C4 plants, insects, arachnids and lizards; Linhares and Bugoni 2023), in accordance with food availability in Abrolhos and rat omnivorous feeding habits, following the same sampling areas of rats in 2021. Leaves of C3 (*Sida cordifolia* for Santa Bárbara and *Ipomea pes-caprae* for Siriba) and C4 (*Cyperus* sp.) plants were collected manually and stored frozen. One leg sample of spiders (family Theraphosidae) was removed nonlethally, and insects (order Orthoptera) were collected manually and stored in ethanol 70%. Lizards (*Tropidurus torquatus*) were captured with a noose and tail-tip samples (~ 10 mm) were collected with sterile scissors and stored in ethanol 70% before releasing the individual. Samples were stored from 3 to 7 months prior to laboratory analysis, and we assume that differences in storage protocol had a negligible effect on isotopic ratios (Hobson et al. 1997).

Laboratory procedures

In the laboratory, rats were sexed by examination of external genitalia, measured in body length (nose tip to the base of the tail), weighed and then necropsied to obtain liver and muscle samples for SIA. The liver has a high turnover rate and represents the diet integrated over the previous week, while muscle has a slower turnover of approximately one month (Kurle 2009). Stomachs were also collected, but preliminary laboratory work showed that the pineapple bait was intensively consumed by rats; thus, a visual analysis of stomach contents was not possible. Liver and muscle samples from rats as well as insects, spiders and

lizard samples were washed in a Soxhlet apparatus with a 2:1 chloroform:methanol solution as solvent in three 6 h cycles to remove lipids that could alter results targeting the protein fraction of tissues. Rat and animal food source samples were freeze-dried, and C3 and C4 plants were oven-dried. Then, all samples were ground, homogenized, weighed in tin capsules and sent for analysis in an isotope ratio mass spectrometer at the *Centro Integrado de Análises* (CIA-FURG, Brazil). Differences between ratios of sample values and the international reference standards (Vienna Pee Dee Belemnite limestone for carbon and atmospheric air for nitrogen) were expressed in δ notation as parts per thousand (‰; Bond and Hobson 2012), where $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ (‰) = $(R_{\text{sample}}/R_{\text{standard}}) - 1$, where R is $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. Based on repeated measurements of laboratory standards (glutamic acid, caffeine and acetazolamide), the measurement precision was 0.07‰ for $\delta^{13}\text{C}$ and 0.8‰ for $\delta^{15}\text{N}$.

Body size and mass

Independent Kruskal–Wallis tests were used to test for differences in body mass (g) and length (cm) of rats between islands (Santa Bárbara and Siriba) and the sampling area (colony vs. grassland). Rats sampled in other habitats (i.e., the built-up area on Santa Bárbara and the intermediate zone on Siriba) were excluded from this analysis due to low sample sizes. Only sexually mature individuals were used for analysis to avoid ontogenetic bias, using the body mass threshold of 120 g to assign and exclude immature individuals (see Ruffino et al. 2013). A nonparametric test was used for both the body length and mass since body lengths did not show a Gaussian distribution.

Univariate differences in stable isotope values

Generalized linear models (GLMs) were constructed to examine the effect of sex (male and female), sampling year (2019 and 2021), island (Santa Bárbara and Siriba), sampling habitat (colony and grassland), the interaction of island and habitat, and body length and mass (continuous variables) on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in the liver and muscle samples of black rats. For this analysis, the few samples collected around the houses in Santa Bárbara ($n=3$) and in the intermediate area in Siriba ($n=5$) were assigned to the ‘grassland’

habitat due to low sample sizes from only 2019 and to the scant seabird nests in these areas. Models for each stable isotope were built separately for muscle and liver given that the metabolic routes of tissue synthesis vary between tissues (Hobson et al. 1999; Caut et al. 2008b, 2009b; Phillips et al. 2014); thus, their stable isotope ratios are not directly comparable.

Full model assumptions for a Gaussian distribution were validated in diagnostic plots. Then, model selection was performed by ranking potential models based on their second-order Akaike's information criterion corrected for small sample size (AICc) (Hurvich and Tsai 1989) using the dredge function in the MuMIn R package (Barton 2017; R Core Team 2021). Models with lowest AICc were used for analysis and variable performances were accessed through the deviance percentage explained, obtained with ANOVA tables.

Stable isotope mixing models

The relative contribution of different food items to the diet of black rats of Santa Bárbara and Siriba islands was estimated for each island with Bayesian mixing models implemented in the 'simmr' R package (Parnell 2021), also separately for muscle and liver. Potential dietary sources were selected based on previous studies on rat diet and sample availability from Abrolhos. Thus, we used island-specific data of C3 and C4 plant leaves, insects and lizards collected concomitantly with rat sampling in February 2021; spiders collected in February 2020 on Santa Bárbara; and data on the blood of seabirds (masked and brown boobies and red-billed tropicbirds), collected in Santa Bárbara during fieldwork in February–March 2019–2022, obtained from the database of the Waterbirds and Sea Turtles Laboratory (FURG, Brazil) (see Table S1 for sample sizes and source values used). We assume that these seabird data represent seabird-derived sources broadly, although we lack values from eggs or chicks which may be more susceptible to predation by rats. These sources were set to represent isotopic ratios of plants, terrestrial animals and marine-derived sources (seabirds) that may be consumed by rats in Abrolhos. In addition to island population models, given the large variation in stable isotope ratios of individual rats (see Results), individual-level mixing models were built for both liver and muscle.

Three sets of trophic discrimination factors (TDFs) for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, specific for liver or muscle, were selected and tested with the dietary data (see Table S2 for TDF values tested). Before running mixing models, the adequacy of sources and candidate TDFs was verified using simulated mixing polygons (see Smith et al. 2013), using the 'sp' and 'splancs' R packages, with 1500 iterations. First, we tested the regression approach for TDF estimation based on the diet isotopic ratio provided by Caut et al. (2008b) in an experimental study with black rats; however, once this approach was further criticized due to a lack of a functional explanation on derived TDFs and from potential experimental and statistical biases (see Auerwald et al. 2010 and Perga and Grey 2010), we also tested the TDFs directly measured in rat tissues for the diet Types A (fish meal) and C (alfalfa meal; see Caut et al. 2008b) in our animal and vegetal sources, respectively. In addition, we tested TDFs measured experimentally for house mice (*Mus musculus*) fed cane sucrose, fish meal, and soybean oil (Arneson and MacAvoy 2005). Whenever TDF standard deviations were not provided by references, we arbitrarily set them to 1‰.

Isotopic niche size and overlap

We used the 'rKIN' package (Eckrich et al. 2020) to estimate the kernel utilization density (hereafter KUD) isotopic niches for each sex (male and female), year (2019 and 2021) and island (Santa Bárbara and Siriba), separately for tissues. The KUD approach aims are similar to those of traditionally used Bayesian standard ellipses (Jackson et al. 2011), but KUDs were found to better represent multimodal data non-normally distributed in the bivariate space, such as when cryptic trophic preferences occur within the population (related to social behavior, ontogeny; see Eckrich et al. 2020). Niche size and overlap are reported for 50% and 75% KUD contours.

Results

A total of 43 rats were analyzed for stable isotopes. Among the samples from 2019, nine rats were obtained on Santa Bárbara, of which six were from the grassland and three from the area around Navy buildings, while five rats were collected on Siriba in

the intermediate zone between the colony and grassland. In 2021, seven samples were obtained inside the seabird colony on Santa Bárbara, and eight were obtained in the grassland area; for Siriba, six individuals were obtained from the grassland, and eight were obtained from the seabird colony (Table S3).

Body size and mass

Statistical differences ($p < 0.05$) were found in the body mass and length of black rats between areas but not between islands (Table S4). Rats ($n = 32$) sampled inside the seabird colonies were larger (18.04 ± 0.97 cm) and heavier (171.43 ± 25.90 g) than those sampled in the grassland habitat (length = 16.84 ± 1.16 cm; mass = 161.22 ± 26.17 g).

Univariate differences in stable isotope values

For the $\delta^{15}\text{N}$ in both liver and muscle of black rats, selected GLM models only included island, habitat, the interaction (island:habitat) and body mass as explanatory variables (Table 1). These models explained more than 50% of deviance in data, with habitat and island explaining the largest proportion and body mass the lowest (Table S5). The only significant effect ($p < 0.05$) observed in these models was

from the interaction (Table 1), indicating that the differences between colony and grassland habitats varied between the islands. There seem to be a greater variation in $\delta^{15}\text{N}$ among habitats in Siriba (Table 1), with rats presenting much higher values in the grassland and intermediate sites than in the seabird colony (Fig. S1). In Santa Bárbara, $\delta^{15}\text{N}$ values were generally lower than Siriba, with the difference between habitats also occurring but with a greater overlap (Fig. S1). Island-specific patterns were highlighted by the GLM summaries despite the assignment of rats from the intermediate and building areas to grassland habitats, which may have added noise to the models (Table 1, Fig. S1).

For $\delta^{13}\text{C}$, selected models included only the island and habitat variables, with both showing significant effects (Table 1, Table S5). It seems that Siriba presented overall higher $\delta^{13}\text{C}$ values than Santa Bárbara, while lower values occurred in the grassland than in the seabird colony habitats (Table 1).

Isotope mixing models

The highest number of individuals inside the 95% probability contours of mixing polygons of muscle and liver of rats from Santa Bárbara and Siriba islands was obtained with a TDF reported in Caut

Table 1 Parameter estimates for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in the liver and muscle of black rats (*Rattus rattus*) collected in the Abrolhos archipelago, Brazil, obtained from selected Generalized Linear Models

	Parameter	Estimate	Std. error	<i>t</i> -value	<i>p</i> -value
<i>Liver</i>					
$\delta^{15}\text{N}$	Intercept	19.68	2.28	8.65	<0.0001
	Island (Siriba)	1.05	1.38	0.76	0.4511
	Habitat (Grassland)	2.02	1.20	1.68	0.1014
	Mass	−0.02	0.01	−1.93	0.0605
	Island (Siriba):Habitat (Grassland)	3.53	1.72	2.05	0.0476
$\delta^{13}\text{C}$	Intercept	−16.67	0.62	−26.93	<0.0001
	Island (Siriba)	1.81	0.63	2.90	0.0061
	Habitat (Grassland)	−2.18	0.65	−3.35	0.0018
<i>Muscle</i>					
$\delta^{15}\text{N}$	Intercept	19.63	2.00	9.83	<0.0001
	Island (Siriba)	0.41	1.21	0.34	0.7368
	Habitat (Grassland)	0.84	1.06	0.80	0.4292
	Mass	−0.02	0.01	−1.74	0.0901
	Island (Siriba):Habitat (Grassland)	3.99	1.51	2.64	0.0119
$\delta^{13}\text{C}$	Intercept	−17.40	0.63	−27.69	<0.0001
	Island (Siriba)	2.72	0.63	4.28	0.0001
	Habitat (Grassland)	−1.92	0.66	−2.91	0.0059

Variables with *p*-value less than 0.05 are presented in bold

et al. (2008b) for rats fed with fish and alfalfa meals (Fig. S2), which was therefore used in the mixing models. The most marked difference between islands detected by mixing models was that seabirds constituted a much higher proportion in the diet of rats on Santa Bárbara (0.47 ± 0.7 , mean \pm SD in liver) than on Siriba (0.15 ± 0.1) (Fig. 2; Fig. S3). On Santa Bárbara, dietary contributions among tissues were maintained, with seabirds contributing the most (47–51%) and other sources held between 6 and 15% each. On Siriba, results were similar between tissues, but slight differences occurred, with lizards contributing the most (24%) in liver, followed by C4 plants (22%) and C4 plants in muscle (30%).

Mixing models ran separately for each rat demonstrated a large variation in consumption of food sources between individuals within Santa Bárbara and Siriba islands (Fig. 3). Despite whole-population patterns, for instance, some individuals from Santa Bárbara showed a reduced (< 20%) contribution from seabirds, and a few individuals (five or six depending on tissue) from Siriba exhibited a high dietary contribution from seabirds (> 25%). Interestingly, on Siriba, only some individuals from the seabird colony and intermediate zone showed a higher contribution

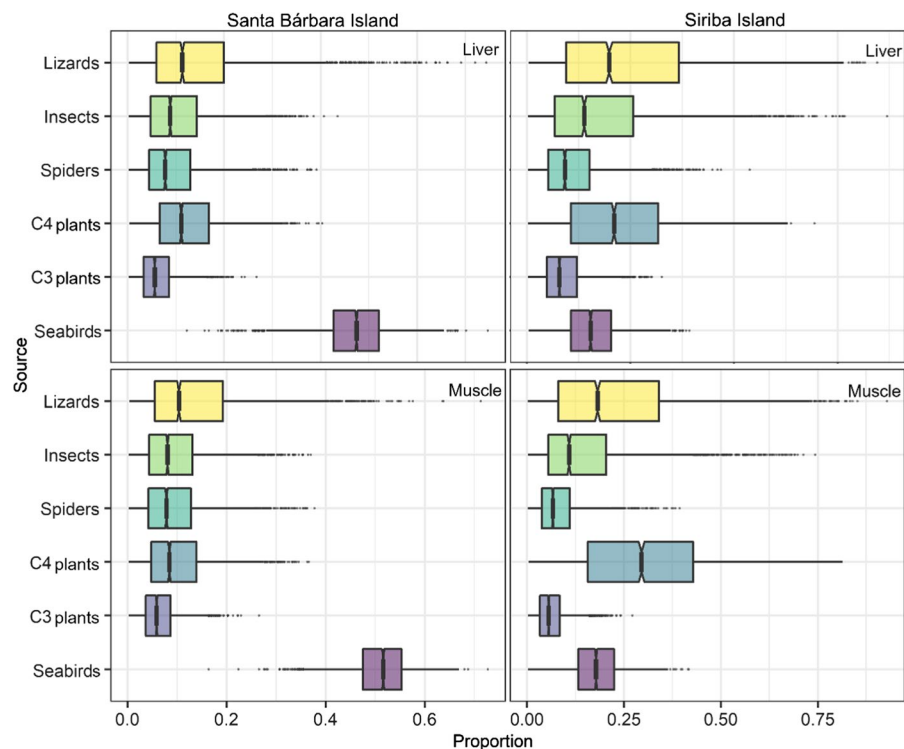
from seabirds, while the majority of individuals from Santa Bárbara showed a high seabird contribution regardless of the sampling location (Fig. 3, Table S3). Nonetheless, limited within-individual temporal variation in diet was detected based on results from liver and muscle (Fig. 3).

Isotopic niche width and overlap

Isotopic niche widths were larger in females than males and in 2021 larger than in 2020 in both liver and muscle samples, while they were variable for islands, with Santa Bárbara having a wider niche in liver and Siriba in muscle (Table 2). The niche of female rats was higher among all, followed by that of rats captured in 2021.

Isotopic niche overlap was the highest between sexes in both liver and muscle, spanning from ~54.7 to 76.2% depending on the KUD of inference, but some females showed higher $\delta^{15}\text{N}$ than males (Fig. 4a, Table 2). The overlap between sampling years was from ~22 to 67% and was especially low considering the 50% contour in the liver (22.3–24.6%). The KUD delineated a multimodal distribution of core areas (50% contour) of rats from

Fig. 2 Output of Bayesian stable isotope mixing models representing the estimated contributions (mean, 25% and 75% percentiles) of different food sources for the carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopic values in the liver and muscle of invasive black rats (*Rattus rattus*) collected on Santa Bárbara and Siriba islands in the Abrolhos archipelago, Brazil



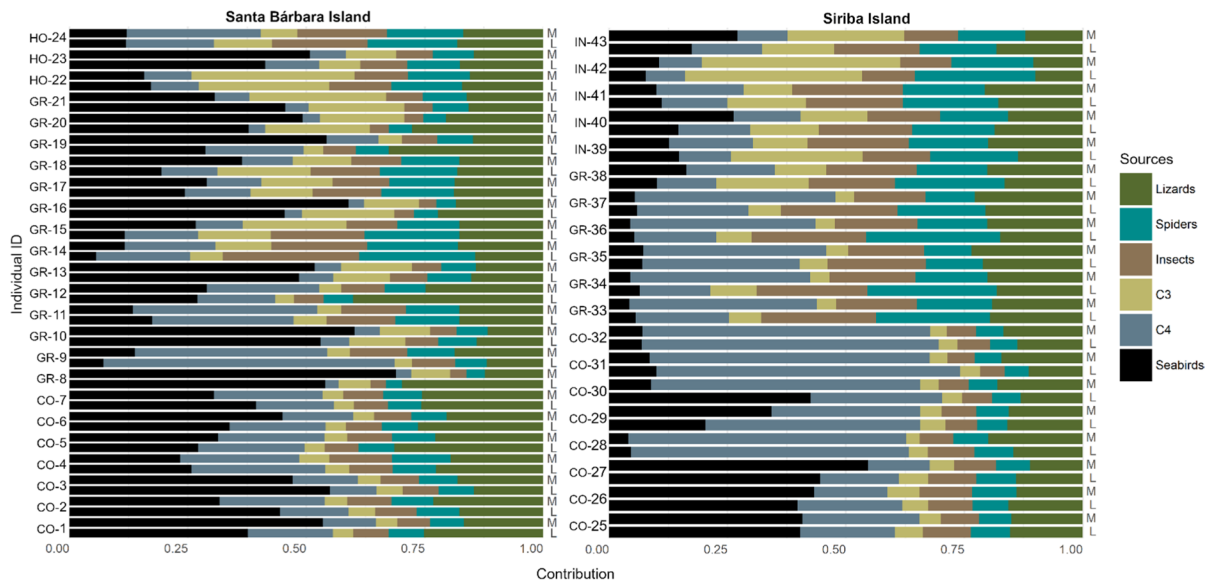


Fig. 3 Bayesian mixing model estimated mean contributions of food sources to the carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopic values of each individual black rat (*Rattus rattus*) collected in the Abrolhos archipelago, Brazil. Contributions are shown in paired sets for each individual, indicating results from liver (L) and muscle (M) samples (tissue highlighted in

the right side of each panel). Letters in individual ID refer to the area where each rat was captured: CO Seabird colony; GR Grassland; HO Houses (Santa Bárbara only); IN Intermediate habitat (Siriba only). For further details on sampling year, or sex, see Table S3 in the supplementary material

Table 2 Estimates of isotopic niche size ($\%c^2$) and overlap between black rats (*Rattus rattus*) from different islands, sexes and years in the Abrolhos archipelago, Brazil, based on kernel utilization densities at 50 and 75% contour

Groups		Niche size ($\%c^2$)		Niche overlap	
		50%	75%	50%	75%
<i>Liver</i>					
Islands	Santa Bárbara	41.2	79.6	44.5	57.7
	Siriba	37.3	69.2	40.3	50.1
Sex	Male	42.8	80.2	67.7	68.6
	Female	48.2	89.2	76.2	76.2
Years	2019	35.9	75.2	22.3	56.6
	2021	39.6	81.4	24.6	61.3
<i>Muscle</i>					
Islands	Santa Bárbara	32.8	61.2	32.0	44.5
	Siriba	40.9	71.0	39.9	51.7
Sex	Male	37.1	67.8	54.7	59.3
	Female	44.4	84.2	65.5	73.6
Years	2019	37.8	68.6	40.1	55.3
	2021	41.8	83.3	44.4	67.2

Levels the niche overlap provided in each line is the percentage of each group area over the other group in comparison

2021 in the isospace for both liver and muscle, with a distinct smaller group with high $\delta^{15}\text{N}$ and a larger group with lower $\delta^{15}\text{N}$ (Fig. 4b). The multimodal pattern from 2021 did not occur in samples from 2019. Furthermore, niche overlap between rats from Santa Bárbara and Siriba spanned from 32.0 to 57.7%, generally lower than detected in all other comparisons for the 75% contour. The core area for rats from Santa Bárbara had lower $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, while rats from Siriba had more variable $\delta^{15}\text{N}$ values, with some individuals having low and intermediate $\delta^{15}\text{N}$ values overlapping with those of Santa Bárbara and others having substantially higher $\delta^{15}\text{N}$ (Fig. 4c). The group in 2021 and the females with distinguished high $\delta^{15}\text{N}$ were individuals from Siriba, with the exception of one outlier from Santa Bárbara (Fig. 4). Overall, the patterns of KUD niche width, overlap, and geometry were similar between tissue types.

Discussion

Overall, our results revealed that the diet of black rats in the Abrolhos archipelago is composed of a

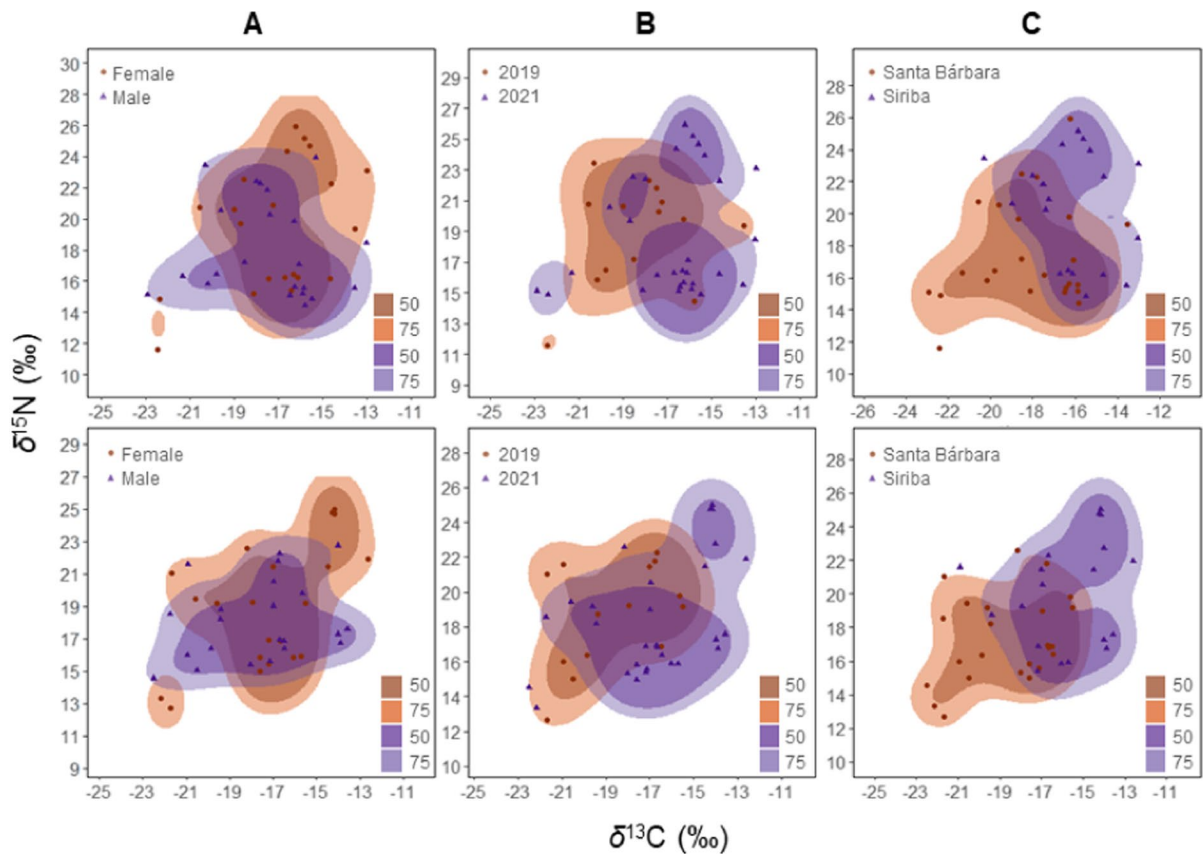


Fig. 4 Stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopic niches based on the liver (above) and muscle (below) of invasive black rats (*Rattus rattus*) collected in the Abrolhos archipelago, Brazil. Comparisons are shown between sex (A), sam-

pling year (B) and island (C). Kernel utilization density was generated for the 50% (darker colors) and 75% (lighter colors) contour levels

mixture of terrestrial resources and marine-derived foods from seabird colonies. Strikingly, seabirds seem to contribute up to ~50% to the protein in tissues of black rats, a pattern that was maintained in the short term of a week (liver samples) to approximately a month during the dry season (muscle samples); the annual period when terrestrial resources are assumed to be depleted in a tropical-arid archipelago (Harper and Bunbury 2015). This is comparable with previous studies that demonstrated that during food shortages on islands, rats may heavily depend on marine resources such as seabird colonies or intertidal invertebrates (Stapp 2002; Ruffino et al. 2011, 2013). This may partly be evidence of rat predation or scavenging on seabirds, their eggs and chicks, but also of the consumption of other seabird-derived resources, such as fish remains, ectoparasites or scavenging arthropods

relying on seabird carrion. Nevertheless, stable isotope ratios and diet varied substantially between Santa Bárbara and Siriba islands, suggesting island-specific foraging strategies.

Generalized linear models highlighted spatial variables (island and habitat) as the most important in explaining the variation in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of black rats. Moreover, Bayesian mixing models indicated different diet of rats between the islands, where seabirds contribute to approximately 50% of protein in rat tissues on Santa Bárbara, while in Siriba, the contribution of seabirds was less than 20% and terrestrial resources were more important. This finding contradicted our predictions, given that Siriba is a much smaller island with an almost 5 times greater biomass concentration of seabirds than Santa Bárbara (Linhares and Bugoni 2023); thus,

we expected a much larger importance of seabirds for rats there. Nonetheless, we propose some potential explanations for this finding. First, the grassland on Siriba is in the center of the island and is almost immediately surrounded by breeding seabirds. Given that seabirds enhance the nutritional content in plants and provide several resources (e.g., fish remains and carcasses) that may result in boosted primary and secondary productivity on islands (Polis and Hurd 1996; Barret et al. 2005; Young et al. 2010; Hentati-Sundberg et al. 2020), it is possible that rats encounter higher food availability of plants and arthropods in grassland habitats on Siriba, allowing individuals to rely more on terrestrial resources even during the dry season (e.g., Major et al. 2006; Quillfeldt et al. 2008). On Santa Bárbara, however, the main colony and grassland habitats are separated by 200–300 m, and grasses may be impacted by herbivory and trampling by a herd of introduced goats (Campbell and Donlan 2005; Gangoso et al. 2006), potentially leading to a lower quality foraging habitat for rats. Notwithstanding, grassland areas on both islands may be important habitats not only for foraging but also for providing shelter during daytime and likely supporting an adequate environment for breeding (authors' pers. obs.; Quillfeldt et al. 2008).

Second, the dietary difference between the islands also appears to be a result of different levels of spatial segregation in foraging territories within the islands, among different habitats. Rats from Siriba showed clear intra-island differences in $\delta^{15}\text{N}$, with much higher $\delta^{15}\text{N}$ in the grassland habitat, which was attributed to a high consumption of ^{15}N -enriched terrestrial resources from the grassland (Linhares and Bugoni 2023), while most individuals in the colony rely heavily on seabirds (Fig. 3). Furthermore, on Santa Bárbara, despite the larger distance between habitats, values of nitrogen isotope ratios in rat tissues was lower and less variable between habitats, and we found that the use of seabirds was substantial (> 25%) even for some individuals from the grassland (Fig. 3). Thus, although distances between habitats are minimal, it seems that the spatial differences in the diet of rats are much greater in Siriba. This pattern was apparently maintained in the short and long terms, as demonstrated by similar results obtained from liver and muscle samples, respectively.

We suggest that the higher spatial segregation in the diet of black rats from Siriba could be a result of

more intense population processes, such as competition and territoriality, derived from differing rat population densities between islands (e.g., Ruffino et al. 2011). A mark-recapture study conducted during five days by the Abrolhos Marine National Park team estimated a density of 69 (CI 95%: 52–93) rats/ha on Siriba, with a home range of 7.76 m² (6.64–9.07), in contrast to 14 (10–23) rats/ha and 19 m² (16–24) home range in the Santa Bárbara grassland (L.C.L. Ferreira, unpublished results), although home ranges in grassland areas could be higher than detected (e.g. Ringler et al. 2014). A much higher rat density in Siriba could induce an increase in behavior interactions, such as territoriality and social dominance of rats holding prime territories towards subordinate individuals in lower quality habitats (e.g. Spencer and Cameron 1983; Jensen et al. 2005). We showed that rats found in colonies were larger and heavier than in grassland areas, likely from having access to energy-rich marine resources associated with seabird colonies (Ruffino et al. 2011; Caut et al. 2012; Linhares and Bugoni 2023). Thus, one possible explanation is that, in Siriba, larger individuals dominate the seabird colony, while smaller individuals are constrained within the patch of grassland habitat, which is a similar spatial segregation found elsewhere (e.g., Hobson et al. 1999; Major et al. 2006; Ruffino et al. 2011; Russel and Ruffino 2012). In contrast, the fairly low density of rats on Santa Bárbara appears to allow individuals to roam more among island habitats in search of more profitable resources, such as those occurring within seabird colonies, suggesting that the social pressure is less important on this larger island (Quillfeldt et al. 2008). To our knowledge, this is the first study using stable isotopes to reveal such contrasting resource use of invasive rats on islands with differing rat and seabird densities. However, our sampling based on only two islands in two years prevents the extrapolation of our results to other contexts, and additional information is needed to better understand the effect of population density and social relationships in driving differences in foraging segregation between islands.

Despite the difference between islands and habitats, there was limited variation in isotope ratios in relation to 'sex', 'sampling year', 'body mass' and 'length', evidenced both by GLMs and isotopic niches using KUDs. This finding highlights the importance of the spatial context in explaining

isotopic variation for rats rather than other intrinsic factors. Indeed, at KUDs, the few distinct individuals with high $\delta^{15}\text{N}$ among females and rats from 2021 were those few rats collected in the grassland of Siriba Island. Nonetheless, the performance of KUDs in delineating the irregular geometry of isotopic niches of rats highlighted advantages over the widely used standard ellipses of the Bayesian approach (see Jackson et al. 2011; Eckrich et al. 2020), allowing the identification of cryptic intra-group foraging strategies, such as the multimodal pattern in rats collected in 2021 and intra-island variations from Siriba habitats. Interestingly, some patterns in niche geometry were maintained over the timelines represented by the two different tissues analysed. Nonetheless, the resolution in the niche analysis would likely benefit from a larger sample size and if sampling habitats were maintained between sampling years. The inherent characteristics of the KUD approach may be useful to access the resource use of other generalist consumers with high inter-individual foraging variation, such as the invasive rats in Abrolhos.

Indeed, individual mixing models showed that the relative use of resources varied widely between individual rats, even among those from the same island and habitat (Fig. 3), but with limited within-individual temporal variation. This is similar to previous studies that evidenced individual consistency in the food habits of individual rats by analyzing the stable isotopes of tissues with different turnover rates (Hobson et al. 1999; Quillfeldt et al. 2008). Similarity in results obtained from the liver and muscle of most rats highlights a stable diet over a period of a week to over a month (Kurle 2009). A consistent individual's diet but with high inter individual variation may minimize intraspecific competition by reducing overlap in resource use for a generalist invader during the dry season (Bolnick et al. 2007), thereby potentially enhancing the colonization capacity of black rats in different island habitats worldwide, allowing the high densities often observed. A nondestructive sampling of the same individuals year-round, such as using rat hair instead of liver or muscle (Caut et al. 2008b), could help us to understand dietary variation within and between individuals over different and greater periods (e.g., dry vs. wet) and their role in the population-level resilience of rats on islands.

Conservation implications

Overall, our results showed that rats in Abrolhos rely heavily on seabird-derived nutrients, although there were high inter-individual differences. Under high rat population densities in Siriba, resource use was apparently spatially constrained, with only the few individuals captured within seabird colonies accessing seabird-derived resources. In Santa Bárbara, under lower population density, spatial constraints were apparently lower, potentially due to reduced competition, and more individuals seem to have access to seabird resources (Quillfeldt et al. 2008). While the high estimated contribution from seabirds may also represent the consumption of other seabird-derived resources, a potentially high level of seabird predation by rats in Abrolhos is nonetheless alarming. Importantly, this finding was derived from some rats sampled in September–October, at the peak of the nesting season of the most widespread seabird in Abrolhos, the masked booby, but also in February, when there were only post-fledged boobies on the island (ICMBio 2020; Linhares and Bugoni 2023). In the absence of boobies, predation on seabirds may shift to the more vulnerable, burrow-nesting and nationally threatened red-billed tropicbird, which breeds year-round in Abrolhos (ICMBio 2020), and the scant nests of white-tailed tropicbirds (*P. leucurus*) (Mancini et al. 2016). Abrolhos is the only Brazilian archipelago where red-billed tropicbirds breed in substantial numbers, and it is one of the most southerly breeding sites and thus an important peripheral population (Eckert et al. 2008; Sarmiento et al. 2014; Mancini et al. 2016), with low genetic diversity and high vulnerability to extinction (Nunes et al. 2017). Furthermore, it was suggested that seabirds exposed to black rats, especially those who nest in burrows, are the most likely to suffer population declines (Jones et al. 2008). It has already been estimated that predation from invasive rats threatens the population viability of tropicbirds in Abrolhos, likely promoting population decline in the near future (Sarmiento et al. 2014).

Therefore, our results highlight the urgency of controlling or eradicating black rats in Abrolhos to protect the local breeding seabirds. Effective management would benefit the whole insular ecosystem, as it was recently demonstrated that seabirds provide nutrients that subsidize productivity in the terrestrial

environment but also in nearshore coral reefs in Abrolhos (Linhares and Bugoni 2023). Moreover, we demonstrated that rats also used plants, arthropods and even lizards as main food sources, especially on Siriba, thus evidencing the direct impact on the terrestrial native biota. Several studies have shown the highly detrimental effect that rats have on vegetation (Auld et al. 2010), lizards (Gollin et al. 2021) and invertebrates (Townsend et al. 2009), affecting pollination, plant growth (Auld et al. 2010), and seedbanks (Shiels 2011), potentially leading to ecosystem function breakdown. Rat management is, thus, a key action for ecosystem recovery in this tropical dry archipelago.

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Author contributions BAL and LB formulated the idea and developed the methodology. BAL performed sample preparation, data analysis and writing under the supervision of LB. LCLF carried out fieldwork for early rat samples and provided unpub. data on rat density and home range. All authors reviewed and provided contributions to the content and offered editorial advice.

Data availability Data analyzed during this study are available in IsoBank datasource under number 482, with the exception of data on seabirds, which was updated during review after the inclusion in the repository. <https://isobank.tacc.utexas.edu/>

Declarations

Conflict of interest The authors declare that they have no conflicts of interest.

Ethical approval This study was carried out in accordance with Brazilian law and ethical standards on animal care. The Brazilian Federal Environmental Agency (*Instituto Chico Mendes de Conservação da Biodiversidade*—ICMBio) approved the study through license No. SISBIO 73603. The Animal Ethics Committee (CEUA-FURG) issued Permit No. P007/2022.

References

- Arneson LS, MacAvoy SE (2005) Carbon, nitrogen, and sulfur diet–tissue discrimination in mouse tissues. *Can J Zool* 83:989–995. <https://doi.org/10.1139/z05-083>
- Atkinson IAE (1985) The spread of commensal species of *Rattus* to oceanic islands and their effects on island avifaunas. In: Moors PJ (ed) *Conservation of island birds*. ICBP Tech, Cambridge, pp 35–81
- Auerswald K, Wittmer MH, Zazzo A, Schäufler R, Schnyder H (2010) Biases in the analysis of stable isotope discrimination in food webs. *J Appl Ecol* 47:936–941. <https://doi.org/10.1111/j.1365-2664.2009.01764.x>
- Auld TD, Hutton I, Ooi MK, Denham AJ (2010) Disruption of recruitment in two endemic palms on Lord Howe Island by invasive rats. *Biol Invasions* 12:3351–3361. <https://doi.org/10.1007/s10530-010-9728-5>
- Banks P, Dickman C (2007) Alien predation and the effects of multiple levels of prey naiveté. *Trends Ecol Evol* 22:229–230. <https://doi.org/10.1016/j.tree.2007.02.006>
- Barrett K, Anderson W, Wait A, Grismer L, Polis G, Rose M (2005) Marine subsidies alter the diet and abundance of insular and coastal lizard populations. *Oikos* 109:145–153. <https://doi.org/10.1111/j.0030-1299.2005.13728.x>
- Barton K (2017) MuMIn: multi-model inference. R package version 1.9.18. <https://CRAN.R-project.org/package=MuMIn>
- Benkwitt C, Gunn R, Le Corre M, Carr P, Graham N (2021) Rat eradication restores nutrient subsidies from seabirds across terrestrial and marine ecosystems. *Curr Biol* 31:2704–2711.e4. <https://doi.org/10.1016/j.cub.2021.03.104>
- Bodey TW, Bearhop S, McDonald RA (2011) Invasions and stable isotope analysis—informing ecology and management. In: Veitch C, Clout M, Townsend D (eds) *Island invasions: eradication and management*. International Union for Conservation of Nature, Gland, pp 148–151
- Bolnick DI, Svanbäck R, Araújo MS, Persson L (2007) Comparative support for the niche variation hypothesis that more generalized populations also are more heterogeneous. *Proc Natl Acad Sci USA* 104:10075–10079. <https://doi.org/10.1073/pnas.0703743104>
- Bond AL, Hobson KA (2012) Reporting stable-isotope ratios in ecology: recommended terminology, guidelines and best practices. *Waterbirds* 35:324–331. <https://doi.org/10.1675/063.035.0213>
- Campbell K, Donlan CJ (2005) Feral goat eradications on islands. *Conserv Biol* 19:1362–1374. <https://doi.org/10.1111/j.1523-1739.2005.00228.x>
- Cassaing J, Derré C, Moussa I, Cheylan G (2007) Diet variability of Mediterranean insular populations of *Rattus rattus* studied by stable isotope analysis. *Isotopes Environ Health Stud* 43:197–213. <https://doi.org/10.1080/10256010701562919>
- Caut S, Angulo E, Courchamp F (2008a) Discrimination factors ($\Delta^{15}\text{N}$ and $\Delta^{13}\text{C}$) in an omnivorous consumer: effect of diet isotopic ratio. *Funct Ecol* 22:255–263. <https://doi.org/10.1111/j.1365-2435.2007.01360.x>
- Caut S, Angulo E, Courchamp F (2008b) Dietary shift of an invasive predator: rats, seabirds and sea turtles. *J Appl*

- Ecol 45:428–437. <https://doi.org/10.1111/j.1365-2664.2007.01438.x>
- Caut S, Angulo E, Courchamp F (2009a) Avoiding surprise effects on Surprise Island: alien species control in a multitrophic level perspective. *Biol Invasions* 11:1689–1703. <https://doi.org/10.1007/s10530-008-9397-9>
- Caut S, Angulo E, Courchamp F (2009b) Variation in discrimination factors ($\Delta^{15}\text{N}$ and $\Delta^{13}\text{C}$): the effect of diet isotopic values and applications for diet reconstruction. *J Appl Ecol* 46:443–453. <https://doi.org/10.1111/j.1365-2664.2009.01620.x>
- Caut S, Angulo E, Pisanu B, Ruffino L, Faulquier L, Lorvelec O, Chapuis J, Pascal M, Vidal E, Courchamp F (2012) Seabird modulations of isotopic nitrogen on islands. *PLoS ONE* 7:e39125. <https://doi.org/10.1371/journal.pone.0039125>
- Clapperton BK, Maddigan F, Chinn W, Murphy EC (2019) Diet, population structure and breeding of *Rattus rattus* L. in South Island beech forest. *NZ J Ecol* 43:1–8. <https://doi.org/10.20417/nzj ecol.43.22>
- DeNiro M, Epstein S (1981) Influence of diet on the distribution of nitrogen isotopes in animals. *Geochim Cosmochim Acta* 45:341–351. [https://doi.org/10.1016/0016-7037\(81\)90244-1](https://doi.org/10.1016/0016-7037(81)90244-1)
- Doherty TS, Glen AS, Nimmo DG, Ritchie EG, Dickman CR (2016) Invasive predators and global biodiversity loss. *Proc Natl Acad Sci USA* 113:11261–11265. <https://doi.org/10.1073/pnas.1602480113>
- Eckert CG, Samis KE, Loughheed SC (2008) Genetic variation across species' geographical ranges: the central–marginal hypothesis and beyond. *Mol Ecol* 17:1170–1188. <https://doi.org/10.1111/j.1365-294X.2007.03659.x>
- Eckrich CA, Albeke SE, Flaherty EA, Bowyer RT, Ben-David M (2020) rKIN: kernel-based method for estimating isotopic niche size and overlap. *J Anim Ecol* 89:757–771. <https://doi.org/10.1111/1365-2656.13159>
- Fukami T, Wardle D, Bellingham P, Mulder C, Towns D, Yeates G, Bonner K, Durrett M, Grant-Hoffman M, Williamson W (2006) Above- and below-ground impacts of introduced predators in seabird-dominated island ecosystems. *Ecol Lett* 9:1299–1307. <https://doi.org/10.1111/j.1461-0248.2006.00983.x>
- Gaiotto J, Abrahão C, Dias R, Bugoni L (2020) Diet of invasive cats, rats and tegu lizards reveals impact over threatened species in a tropical island. *Persp Ecol Conserv* 18:294–303. <https://doi.org/10.1016/j.pecon.2020.09.005>
- Gangoso L, Donázar JA, Scholz S, Palacios CJ, Hiraldo F (2006) Contradiction in conservation of island ecosystems: plants, introduced herbivores and avian scavengers in the Canary Islands. *Biodivers Conserv* 15:2231–2248. <https://doi.org/10.1007/s10531-004-7181-4>
- Gollin JF, Gorman N, Armstrong DP (2021) Twenty years on: changes in lizard encounter rates following eradication of rats from Kāpiti Island. *NZ J Ecol* 45:3423. <https://doi.org/10.20417/nzj ecol.45.13>
- Graham N, Wilson S, Carr P, Hoey A, Jennings S, MacNeil M (2018) Seabirds enhance coral reef productivity and functioning in the absence of invasive rats. *Nature* 559:250–253. <https://doi.org/10.1038/s41586-018-0202-3>
- Grant-Hoffman MN, Barboza PS (2010) Herbivory in invasive rats: criteria for food selection. *Biol Invasions* 12:805–825. <https://doi.org/10.1007/s10530-009-9503-7>
- Harper GA (2006) Habitat use by three rat species (*Rattus* spp.) on an island without other mammalian predators. *NZ J Ecol* 30:321–333
- Harper GA, Bunbury N (2015) Invasive rats on tropical islands: their population biology and impacts on native species. *Glob Ecol Conserv* 3:607–627. <https://doi.org/10.1016/j.gecco.2015.02.010>
- Harper GA, van Dinther M, Russell JC, Bunbury N (2015) The response of black rats (*Rattus rattus*) to evergreen and seasonally arid habitats: informing eradication planning on a tropical island. *Biol Conserv* 185:66–74. <https://doi.org/10.1016/j.biocon.2014.11.044>
- Hentati-Sundberg J, Raymond C, Sköld M, Svensson O, Gustafsson B, Bonaglia S (2020) Fueling of a marine-terrestrial ecosystem by a major seabird colony. *Sci Rep* 10:15455. <https://doi.org/10.1038/s41598-020-72238-6>
- Hobson KA, Gloutney ML, Gibbs HL (1997) Preservation of blood and tissue samples for stable-carbon and stable-nitrogen isotope analysis. *Can J Zool* 10:1720–1723. <https://doi.org/10.1139/z97-799>
- Hobson KA, Drever MC, Kaiser GW (1999) Norway rats as predators of burrow-nesting seabirds: insights from stable isotope analyses. *J Wildl Manag* 63:14–25. <https://doi.org/10.2307/3802483>
- Hurvich CM, Tsai CL (1989) Regression and time series model selection in small samples. *Biometrika* 76:297–307. <https://doi.org/10.1093/biomet/76.2.297>
- ICMBio (2020) Relatório anual do Programa de Monitoramento das Aves Marinhas do Parque Nacional Marinho dos Abrolhos. ICMBio, Caravelas
- Jackson AL, Inger R, Parnell AC, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER—stable isotope Bayesian ellipses in R. *J Anim Ecol* 80:595–602. <https://doi.org/10.1111/j.1365-2656.2011.01806.x>
- Jensen SP, Gray SJ, Hurst JL (2005) Excluding neighbours from territories: effects of habitat structure and resource distribution. *Anim Behav* 69:785–795. <https://doi.org/10.1016/j.anbehav.2004.07.008>
- Jones HP (2010a) Prognosis for ecosystem recovery following rodent eradication and seabird restoration in an island archipelago. *Ecol Appl* 20:1204–1216. <https://doi.org/10.1890/09-1172.1>
- Jones HP (2010b) Seabird islands take mere decades to recover following rat eradication. *Ecol Appl* 20:2075–2080. <https://doi.org/10.1890/10-0118.1>
- Jones H, Tershy B, Zavaleta E, Croll D, Keitt B, Finkelstein M, Howald G (2008) Severity of the effects of invasive rats on seabirds: a global review. *Conserv Biol* 22:16–26. <https://doi.org/10.1111/j.1523-1739.2007.00859.x>
- Jones H, Holmes N, Butchart S et al (2016) Invasive mammal eradication on islands results in substantial conservation gains. *Proc Natl Acad Sci USA* 113:4033–4038. <https://doi.org/10.1073/pnas.1521179113>
- Kemenes A (2003) Distribuição espacial da flora terrestre fanerogâmica do Parque Nacional Marinho de Abrolhos, BA. *Rev Bras Bot* 26:141–150. <https://doi.org/10.1590/S0100-84042003000200001>

- Keynes RD (2003) Fossils, finches, and Fuegians: Darwin's adventures and discoveries on the Beagle. Oxford University Press, New York
- Kurle CM (2009) Interpreting temporal variation in omnivore foraging ecology via stable isotope modelling. *Funct Ecol* 23:733–744. <https://doi.org/10.1111/j.1365-2435.2009.01553.x>
- Linhares BA, Bugoni L (2023) Seabirds subsidize terrestrial food webs and coral reefs in a tropical rat-invaded archipelago. *Ecol Appl* 33:e2733. <https://doi.org/10.1002/eap.2733>
- Major HL, Jones IL, Charette MR, Diamond AW (2006) Variations in the diet of introduced Norway rats (*Rattus norvegicus*) inferred using stable isotope analysis. *J Zool, Lond* 271:463–468. <https://doi.org/10.1111/j.1469-7998.2006.00230.x>
- Mancini P, Serafini P, Bugoni L (2016) Breeding seabird populations in Brazilian oceanic islands: historical review, update and a call for census standardization. *Rev Bras Ornitol* 24:94–115. <https://doi.org/10.1007/BF03544338>
- Myers N, Mittermeier R, Mittermeier C, Da Fonseca G, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* 403:853–858. <https://doi.org/10.1038/35002501>
- Newsome SD, Martinez del Rio C, Bearhop S, Phillips DL (2007) A niche for isotopic ecology. *Front Ecol Environ* 5:429–436. <https://doi.org/10.1890/060150.1>
- Nunes GT, Efe MA, Freitas TR, Bugoni L (2017) Conservation genetics of threatened red-billed tropicbirds and white-tailed tropicbirds in the southwestern Atlantic Ocean. *Condor* 119:251–260. <https://doi.org/10.1650/CONDOR-16-141.1>
- Parnell A, Phillips D, Bearhop S, Semmens B, Ward E, Moore J, Jackson A, Grey J, Kelly D, Inger R (2013) Bayesian stable isotope mixing models. *Environmetrics* 24:387–399. <https://doi.org/10.1002/env.2221>
- Parnell A (2021) *simmr*: a stable isotope mixing model. R package version 0.4.5. <https://CRAN.R-project.org/package=simmr> Accessed 26 Jan 2022
- Perga ME, Grey J (2010) Laboratory measures of isotope discrimination factors: comments on Caut, Angulo & Courchamp (2008, 2009). *J Appl Ecol* 47:942–947. <https://doi.org/10.1111/j.1365-2664.2009.01730.x>
- Phillips DL, Inger R, Bearhop S, Jackson AL, Moore JW, Parnell AC, Semmens BX, Ward EJ (2014) Best practices for use of stable isotope mixing models in food web studies. *Can J Zool* 92:823–835. <https://doi.org/10.1139/cjz-2014-0127>
- Pisanu B, Caut S, Gutjahr S, Vernon P, Chapuis JL (2011) Introduced black rats *Rattus rattus* on Ile de la Possession (Iles Crozet, Subantarctic): diet and trophic position in food webs. *Polar Biol* 34:169–180. <https://doi.org/10.1007/s00300-010-0867-z>
- Polis G, Hurd S (1996) Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. *Am Nat* 147:396–423. <https://doi.org/10.1086/285858>
- Quillfeldt P, Schenk I, McGill RA, Strange IJ, Masello JF, Gladbach A, Roesch V, Furness RW (2008) Introduced mammals coexist with seabirds at New Island, Falkland Islands: abundance, habitat preferences, and stable isotope analysis of diet. *Polar Biol* 31:333–349. <https://doi.org/10.1007/s00300-007-0363-2>
- R Core Team (2021) R: a language and environment for statistical computing. Vienna
- Ricketts TH, Dinerstein E, Boucher T et al (2005) Pinpointing and preventing imminent extinctions. *Proc Natl Acad Sci USA* 102:18497–18501. <https://doi.org/10.1073/pnas.0509060102>
- Ringler D, Russell J, Jaeger A, Pinet P, Bastien M, Le Corre M (2014) Invasive rat space use on tropical islands: implications for bait broadcast. *Basic Appl Ecol* 15:179–186. <https://doi.org/10.1016/j.baae.2014.01.005>
- Rodriguez MAM, Herrera LGM (2013) Isotopic niche mirrors trophic niche in a vertebrate island invader. *Oecologia* 171:537–544. <https://doi.org/10.1007/s00442-012-2423-8>
- Ruffino L, Russell J, Pisanu B, Caut S, Vidal E (2011) Low individual-level dietary plasticity in an island-invasive generalist forager. *Popul Ecol* 53:535–548. <https://doi.org/10.1007/s10144-011-0265-6>
- Ruffino L, Russell J, Vidal E (2013) Anthropogenic subsidies mitigate environmental variability for insular rodents. *Oecologia* 172:737–749. <https://doi.org/10.1007/s00442-012-2545-z>
- Russell JC, Holmes ND (2015) Tropical island conservation: rat eradication for species recovery. *Biol Conserv* 185:1–7. <https://doi.org/10.1016/j.biocon.2015.01.009>
- Russell JC, Ruffino L (2012) The influence of spatio-temporal resource fluctuations on insular rat population dynamics. *Proc R Soc Lond B Biol Sci* 279:767–774. <https://doi.org/10.1098/rspb.2011.1121>
- Sarmiento R, Brito D, Ladle RJ, Leal GR, Efe MA (2014) Invasive house (*Rattus rattus*) and brown rats (*Rattus norvegicus*) threaten the viability of red-billed tropicbird (*Phaethon aethereus*) in Abrolhos National Park, Brazil. *Trop Conserv Sci* 7:614–627. <https://doi.org/10.1177/2F194008291400700403>
- Shiels AB (2011) Frugivory by introduced black rats (*Rattus rattus*) promotes dispersal of invasive plant seeds. *Biol Invasions* 13:781–792. <https://doi.org/10.1007/s10530-010-9868-7>
- Shiels AB, Flores CA, Khamsing A, Krushelnycky PD, Mosher SM, Drake DR (2013) Dietary niche differentiation among three species of invasive rodents (*Rattus rattus*, *R. exulans*, *Mus musculus*). *Biol Invasions* 15:1037–1048. <https://doi.org/10.1007/s10530-012-0348-0>
- Smith JA, Mazumder D, Suthers IM, Taylor MD (2013) To fit or not to fit: evaluating stable isotope mixing models using simulated mixing polygons. *Meth Ecol Evol* 4:612–618. <https://doi.org/10.1111/2041-210X.12048>
- Spencer SR, Cameron GN (1983) Behavioral dominance and its relationship to habitat patch utilization by the hispid cotton rat (*Sigmodon hispidus*). *Behav Ecol Sociobiol* 13:27–36. <https://doi.org/10.1007/BF00295073>
- Stapp P (2002) Stable isotopes reveal evidence of predation by ship rats on seabirds on the Shiant Islands, Scotland. *J Appl Ecol* 39:831–840. <https://doi.org/10.1046/j.1365-2664.2002.00754.x>
- Tershy BR, Shen KW, Newton KM, Holmes ND, Croll DA (2015) The importance of islands for the protection of

- biological and linguistic diversity. *Bioscience* 65:592–597. <https://doi.org/10.1093/biosci/biv031>
- Towns DR (2009) Eradications as reverse invasions: lessons from Pacific rat (*Rattus exulans*) removals on New Zealand islands. *Biol Invasions* 11:1719–1733. <https://doi.org/10.1007/s10530-008-9399-7>
- Towns DR, Atkinson IA, Daugherty CH (2006) Have the harmful effects of introduced rats on islands been exaggerated? *Biol Invasions* 8:863–891. <https://doi.org/10.1007/s10530-005-0421-z>
- Towns D, Wardle D, Mulder C, Yeates G, Fitzgerald B, Parrish G, Bellingham P, Bonner K (2009) Predation of seabirds by invasive rats: multiple indirect consequences for invertebrate communities. *Oikos* 118:420–430. <https://doi.org/10.1111/j.1600-0706.2008.17186.x>
- Varnham KJ (2010) Invasive rats on tropical islands: their history, ecology, impacts and eradication. RSPB Conservation Science Department, Research Report No. 41. Royal Society for the Protection of Birds, Sandy, Bedfordshire, UK
- Whittaker RJ, Fernández-Palacios JM (2007) Island biogeography: ecology, evolution, and conservation, 2nd edn. Oxford University Press, New York
- Young H, McCauley D, Dunbarb R, Dirzoa R (2010) Plants cause ecosystem nutrient depletion via the interruption of bird-derived spatial subsidies. *Proc Natl Acad Sci USA* 107:2072–2077. <https://doi.org/10.1073/pnas.0914169107>

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