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How removal of cats and rats from an island allowed a native predator to threaten a native bird

Santiago Ortega · **Cristina Rodríguez** · **Bryan Mendoza-Hernández** · **Hugh Drummond**

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Abstract The question of how to program the removal of two invasive mammals, typically cats and rats, from a marine island without increasing risk to native prey species has received two general answers based on ecological theory: removal of cats must be accompanied by control of their mesopredator prey, and risk is minimized by removing both invaders simultaneously. Nonetheless, a 31-year study showed that in a 82-ha tropical marine bird sanctuary, predation on a native prey, the blue-footed booby, by a native predator, the Atlantic Central American milk snake, apparently diminished after removal of cats then increased 11-fold after the additional removal of black rats. These novel effects are explained in terms of a hypothetical three-link trophic web in which cat removal released rats to increasingly compete with or prey on the snakes that feed on hatchling boobies, and subsequent rat removal released snakes from all remaining predation. The upshot is a disturbing scenario in which approximately 200 milk snakes currently aggregate annually in roughly 1 hectare of booby colony and predate roughly forty percent of the hatchlings. Where the lowest link of an insular trophic web is a native mesopredator that feeds on native prey, the predictions of the classic mesopredator release scenario can be inverted, and removal of invasive mammals may endanger native prey species.

Keywords Island · Mesopredator release · Invasive mammals · Marine bird · Snake predation

Introduction

Invasions of ecosystems by alien predators, particularly mammals, are an outstanding threat to biodiversity conservation because these animals have often depleted populations of native species or driven them to extinction. Invasive predators have contributed to the extinction of 142 species of birds, mammals and reptiles, and invasive mammals currently put close to 600 species at risk of extinction (Doherty et al. 2016). Islands are where species invasions have had the most devastating impacts on native species, including many endemics, and feral cats and rats, in particular, have depleted or driven extinct numerous populations of insular birds, mammals and reptiles (Bonnaud et al. 2011; Medina et al. 2011). Consequently, removal of invasive mammals is a conservation priority that has

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S. Ortega (✉) · C. Rodríguez · B. Mendoza-Hernández · H. Drummond
Instituto de Ecología, Universidad Nacional Autónoma de México, 04510 Ciudad de México, Mexico
e-mail: santiago.ortega@ecologia.unam.mx

S. Ortega
Posgrado en Ciencias Biológicas, Universidad Nacional Autónoma de México, 04510 Ciudad de México, Mexico

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been pursued on 181 islands worldwide (Jones et al. 2016), and followed by positive growth rates in 83% of local marine bird populations (Brooke et al. 2018).

However, because of trophic web complexity, removal of invasive mammals can also have unexpected and even counterproductive consequences (Zavaleta et al. 2001), and these must be explored and understood (Jones et al. 2016). For example, removal from islands of introduced apex predators such as feral cats can be followed by recovery of introduced rats which then prey increasingly on native prey species and may even extirpate them (Courchamp et al. 1999, 2003; Rayner et al. 2007). Increasing our ability to predict the ecosystem consequences of removals and control programs is thus an urgent priority for conservation biology, and in recent years has driven the development of experimental studies (Beggs et al. 2019; Bridgman et al. 2018) and theoretical models (Bode et al. 2015; Garcia-Diaz et al. 2019).

Here we report how removal of two invasive mammals from a tropical Pacific island inhabited by nine reproductive colonies of marine birds and seven reptiles was followed by increased predation by the Atlantic Central American milk snake (*Lampropeltis polyzona*) on a population of blue-footed boobies (*Sula nebouxii*). Snake predation on eggs is the leading cause of nest failure for most bird species in terrestrial ecosystems, and in North America accounts for nearly one third of nest predation events (Degregorio et al. 2014). Even so, the biologists and national park authorities who planned the removal of feral cats (*Felis catus*) and black rats (*Rattus rattus*) from the study island felt confident this would put an end to surplus killing of gull chicks by cats and probably benefit the marine bird colonies in general. They did not suspect that a two-step sequence of mesopredator release effects could threaten the survival of a colony of boobies and possibly other native vertebrates.

Initially, after removal of the cats, low-level predation of the milk snakes on hatchling boobies declined and stayed low, then 14 years later when the rats were removed, snake predation on hatchling boobies increased to unprecedented levels. We inferred that removal of cats released rats to increase their predation on snakes, and that subsequent removal of rats released snakes to increase their predation on boobies. We document this narrative by reporting from a single season (2018) on the snakes' extraordinary ability to aggregate in the booby colony and zero in on newly hatched chicks; and by estimating proportional consumption of hatchling boobies over a 31-year period, as the composition of the island's invasive mammal population passed through three phases. We finish by drawing attention to the vulnerability of marine birds to native snake mesopredators, which can be either suppressed or released by removal of invasive mammals.

Materials and methods

Study site and species

Twenty-eight kilometres off the Pacific coast of Mexico (21° 50′ 57″ N, 105° 52′ 53″ W), Isla Isabel is an 82-ha volcanic island, mostly covered with a forest of garlic pear (*Crataeva tapia*) and papelillo trees (*Euphorbia schlechtendalii*), swathes of grass and sedge (*Cyperus ligularis, Jouvea pilosa* and *Cenchrus viridis*) and grassy beaches, and used for reproduction by many thousands of ground-, cliff-, and tree-nesting marine birds. The nine species are magnificent frigatebirds (*Fregata magnificens*), sooty terns (*Onychoprion fuscatus*), blue-footed boobies, brown boobies (*S. leucogaster*), Heermann's gulls (*Larus heermanni*), brown noddies (*Anous stolidus*), brown pelicans (*Pelecanus occidentalis*), red-billed tropicbirds (*Phaethon aethereus*), and red-footed boobies (*S. sula*). There are no native mammals but seven species of reptiles: Mexican spinytail iguanas (*Ctenosaura pectinata*), green iguanas (*I. iguana*), Clark's spiny lizards (*Sceloporus clarkii*), whiptail lizards (*Aspidoscelis costatus*), yellowbelly geckos (*Phyllodactylus tuberculosus*), Atlantic Central American milk snakes, and brahminy blind snakes (*Ramphotyphlops braminus*). The island lacks natural sources of usable fresh water but houses a hypersaline lake in a volcanic crater. It may never have been permanently settled but fishermen, biologists and ecotourists camp there periodically. It was declared a national park in 1980 and a Ramsar site in 2003.

There is little information on the colonization of Isla Isabel by vertebrates. Captain Petit-Thouars stated in 1836 that the island was arid and sterile (Petit-Thouars 1841), and local fishermen claim cats and rats were already present when they began camping there in the 1930s. In April 2009, Grupo de Ecología y

Conservación de Islas, A.C (GECI) estimated the density of black rats in the island at 49/hectare and a total 3700 rats on the island (Samaniego Herrera et al. 2009). We have been unable to find historical records of the presence of marine birds on the island. Most of the cats were eradicated by ecologists of the UNAM (Universidad Nacional Autónoma de Mexico) in the spring and summer of 1996, and the remainder intermittently over the next three years (Rodríguez et al. 2006). Since then, no cat has been observed on the island. Following an unsuccessful attempt at rat eradication by the UNAM in the spring of 2006, success was achieved completely by *GECI*, on behalf of the *Consejo Nacional de Áreas Naturales Protegidas*, in the spring of 2009 (Samaniego Herrera et al. 2011).

Blue-footed boobies are long-lived socially monogamous marine birds that lay clutches of 1–3 eggs in shallow unlined pits and hatch them at 4-day intervals after an average 40 days of incubation per egg (Nelson 2005). Parents jointly care for both clutch and brood, rarely leaving them unattended, but hatching failure and siblicidal elimination of youngest brood members are common (Drummond et al. 1986). Adult boobies are formidable birds with long dagger-shaped beaks and, on Isla Isabel at least, they are exempt from predation. However, their eggs are sometimes taken by gulls, despite their defensive pecking, and their newly hatched chicks are sometimes ingested by snakes, inside or beside the nest. On these occasions the brooding parents often seem not to recognize milk snakes as predators. There are no corvids on the island; there is a colony of about ten pairs of black-crowned night herons (*N. nycticorax*), but these have never been seen in the blue-footed booby colony. In 40 years of study of the Isla Isabel boobies, the only other species observed predating a hatchling (just once) was a great blue heron (*Ardea herodias*) and no more than one individual of that species has ever been seen (Drummond et al. 1986, Drummond unpublished data).

The Atlantic Central American milk snake is a slow-moving, terrestrial species, native to Isla Isabel as far as we know (first collected there in 1938; specimens UMMZ 84,256 and LACM 2467). It forages mostly during darkness or twilight. A 16-week dietary study on Isla Isabel in 1992, embracing forest, grassland and disturbed habitats outside the booby colony in both dry and rainy seasons, found that 70% of snakes had eaten lizards (24 whiptail lizards, 2 juvenile spinytail iguanas), 24% avian nestlings (5 sooty terns, 3 blue-footed booby hatchlings, 1 brown booby hatchling) and 5% eggs of whiptail lizards or spinytail iguanas (Rodríguez and Drummond 2000). Nocturnal vigils beside brown booby nests containing hatchlings revealed snakes attempting to enter, sometimes managing to seize the hatchling, other times being pecked and repelled, or even tossed away by the brooding adult, and sometimes returning minutes later (Cohen 1988).

Mammal presence and hatchling predation

To determine whether the probability of predation by a milk snake differed in the presence of both cats and rats (1989–1995), only rats (1996–2009), or no mammals (2010–2019), we analysed hatchling mortality in the reproduction database of our booby study area. This includes the main sub-colony, where snakes were sampled. The database includes contents of all nests every three days from shortly after the start of hatching until the end of fledging, during roughly 5 months of every year (Drummond et al. 2003), except 1992 and 2016 when the boobies largely abandoned reproduction during severe El Niño events. We attributed to snake predation all eggs that disappeared from the nest when they were 38–42 days old (expected hatching date). Although egg disappearance at other ages is likely due to predation by gulls, sudden disappearance at the age when hatching is expected implies hatching followed by prompt predation. We also attributed to snake predation disappearances from nests and their vicinity of hatchlings within an age range slightly larger than the observed age range of snake victims in 2018; that is, hatchlings observed on only 1 or 2 nest inspections (estimated age of death ≤ 6 days). Excluding hatchlings that disappeared after 2 observations would have meant excluding an unknown number of hatchlings that disappeared at age 4 days. Importantly, when chicks die of causes other than snake predation, rather than disappearing the cadaver is found trampled into the nest floor or within 2 m of it.

To analyse probability of predation of hatchlings over the 31-year period, we constructed a generalized linear mixed model with binomial distribution (predated or not) with a cloglog link function (appropriate for data with an excess of 0 s or 1 s; Zuur et al. 2009), in which nest identity and year were fitted as random effects. Nest was added because siblings from the same nest are not statistically independent, and year to account for unmeasured environmental conditions. All independent variables were standardized prior to model fitting to facilitate the interpretation of parameter estimates (Cade 2015; Grueber et al. 2011). The model tested for the separate effects of mammalian presence (3-levels: cats and rats, rats only or no mammals), hatch date (expressed as an annual proportion, values close to zero denoting early hatching), number of hatchlings aged $\leq$ 6 days present in the sub-colony when an egg hatched or when the hatchling was preyed upon, and environmental conditions (expressed as the average of the Multivariate El Niño/Southern Oscillation index, or MEI, values registered bi-monthly throughout each reproductive season from November to July). Hatch date tested whether early hatchers suffered less predation; number of hatchlings tested whether a higher number of currently available prey (due to synchronous laying) reduced the *per capita* risk of predation; and environmental conditions tested whether adverse weather conditions (positive MEI values) increased the probability of predation (due to the reduced number of birds reproducing during warm water years; Ancona et al. 2011). MEI data were obtained from the Physical Sciences Laboratory of the United States' National Oceanic and Atmospheric Administration (available at: https://psl.noaa.gov/enso/mei/). A two-way interaction between mammalian presence and number of hatchlings was included to determine whether the effect of number of hatchlings varied with mammalian presence. After finding that mammalian presence affected probability of predation, we tested whether effects of mammal removal were immediate or developed over time by re-running the model separately for each period of mammalian presence, including year and environmental conditions as fixed effects. All analyses were performed in R statistical environment (v3.6.3) (R Development Core Team 2020). Models were fitted with the *glmmTMB* package (Magnusson et al. 2020) and contrasts between categorical levels of interest, using Tukey's method, were calculated with the *emmeans* package (Lenth et al. 2021) Where appropriate, 95% confidence intervals (CI) are reported.

Snake-booby interactions

To quantify losses of hatchlings to snake predation, two monitors registered contents of all booby nests of the sub-colony every 3 days from January 22 through July 1, banded hatchlings according to hatch order, and searched for missing hatchlings in a 2-m radius of the nest (details in Drummond et al. 2003).

To quantify the presence and diet of snakes, and probe their ability to return to the subcolony after experimental translocation, every night from March 3 through July 5 in 2018 from 20:00 to 2300 h and 03:00 to 0600 h, two snake monitors slowly walked in single file along a fixed 972-m route meandering through two patches of nests in the main booby sub-colony along the island's eastern shore (Fig. 1). They scanned the forest floor and beach with red headlights, and bagged every snake detected within 5 m of the route. The snakes were measured (snout-vent length, cm) while stretched out on a table, obliged by ventral palpation (Carpenter 1952) to regurgitate stomach contents, given individual numbers by ventral scale clipping (Brown and Parker 1976) or identified from the number previously given, and retained in cloth collecting bags. Individuals $\geq$ 50 cm long were considered adults (Fitch and Fleet 1970) and their sex was determined from the length and width of the tail in relation to body size (Reed and Tucker 2012). Culmens of regurgitated booby hatchlings were measured to estimate age using growth curves of the local colony (all were $\leq$ 4 days old). Next night at 18:00 to 20:00 h snakes were liberated independently (one by one at separate spots and times) in one of two translocation zones, *Playa del Ocaso* and *Valle Central*, separated by 400–600 m from the sub-colony by watersheds and terrain of steep, forested slopes littered with boulders, brush and fallen trees (Fig. 1). On a few occasions when the number of captures exceeded our storage capacity, some snakes (total = 24) were liberated close to their capture locations. Data from the two patches were pooled in all analyses because patterns were similar, and the southern patch yielded too few data for comparing them. Permission for manipulation of milk snakes was granted by the *Secretaría de Medio Ambiente y Recursos Naturales* (SGPA/DGVS/012166/17), and the Animal Behavior Society's Guidelines For the Treatment of Animals in Behavioural Research and Teaching were followed.

Fig. 1 Isla Isabel (82 ha., 1.5 × 0.5 k) viewed from the southeast in April 2006. **a**, **b** two patches in the blue-footed booby colony where snakes were monitored. 1, 2: Playa del Ocaso and Valle Central, respectively, where translocated snakes were released. Photo by Daniel Anderson

Results

Mammal presence and hatchling predation

Across the 31-year period, 26,688 chicks of 16,062 nests hatched in the booby study area and, on average, 16% of them were predated by milk snakes during the first few days of life. Mammalian presence significantly affected this predation: when there were rats and cats the probability of a hatchling being predated was 5%, when there were only rats the probability appeared to drop by over half to 2% (although this difference was not supported; Table 1), and when there were no mammals at all it increased 11-fold to 22% (Fig. 2a). Importantly, the probability of hatchlings being predated was nearly four times as high in the absence as in the presence of both mammals (22% vs 5%; contrast: β = 1.572; 95% CI 0.701–2.440). In 2018, when milk snakes were studied, 41.1% of hatchlings were predated, and in several mammal-free years more than 50% were predated (Fig. 2b). The risk of predation was lower for boobies that hatched earlier in the season or when more hatchlings were simultaneously present, and this latter effect was greater when there were no mammals present than when there were only rats, but possibly absent when both rats and cats were present (Table 1). Furthermore, under adverse environmental conditions, associated with El Niño, the probability of being predated was higher (β = 1.129; 95% CI 0.644–1.614).

Within all three levels of mammalian presence, the probability of predation changed over time, increasing during the first seven years when cats and rats were present (β = 0.553; 95% CI 0.263–0.843), decreasing during the fourteen years after cat removal (β = − 1.070; 95% CI − 1.367 to − 0.772), and increasing during the ten years after rat removal (β = 1.032; 95% CI 0.781–1.074). Interestingly, while

Table 1 Effects of invasive mammalian presence, hatch date and presence of other hatchlings on probability of predation of 26,688 blue-footed booby hatchlings

Parameter	Estimate	CI 95%
Intercept	− 3.583	− 3.949, − 3.218
*Rats only**		
Rats and cats present	0.655	− 0.019, 1.33
No mammals	**2.227**	**1.669, 2.785**
Hatch date	**1.434**	**1.324, 1.543**
No. of hatchlings	**− 1.120**	**− 1.306, − 0.934**
*No. of hatchlings × Rats only**		
No. of hatchlings × Rats and cats present	− 0.320	− 0.927, 0.287
No. of hatchlings × No mammals	**− 0.720**	**− 1.030, − 0.409**

Terms whose regression coefficients were statistically different from zero are presented in boldface type. Asterisks (*) denote the reference level for the categorical parameters and interactions. Random effects: nest, $\sigma^2 = 1.43$; year, $\sigma^2 = 0.41$

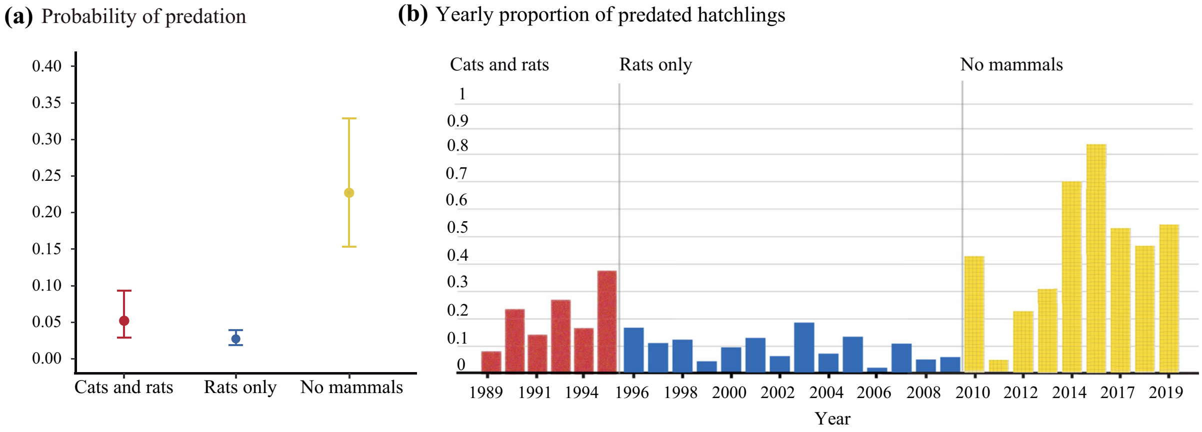

Fig. 2 **a** Mammalian presence influence on the hatchlings' probability of being predated and **b** annual observed proportion of hatchlings predated by milk snakes in the presence of cats and rats (Basal state), rats only (1st step) and no mammals (2nd step). In 1992 and 2016 monitoring was discontinued when the colony abandoned reproduction during severe El Niño events in the presence of cats and rats, rats only and no mammals. For **a**, mean values with their 95% confidence intervals are shown

adverse conditions increased the probability of being predated when both mammals were present ($\beta = 0.983$; 95% CI 0.665–1.302) and when both were absent ($\beta = 1.244$; 95% CI 1.032–1.456), they had no effect when only rats were present on the island ($\beta = 0.097$; 95% CI − 0.170 to 0.365) and predation on hatchling boobies was minimal.

Snake-booby interactions

Over 18 weeks of nightly monitoring of the 9718-m^2 sampling area in the booby sub-colony in 2018, 211 individual snakes were captured, including 77 females measuring 56–111 cm (88.38 ± 11.37 cm; $\overline{X}$± standard deviation), 96 males measuring 56–112 cm (92.97 ± 11.01 cm; snout-vent), 32 adults of undetermined sex, and 6 juveniles. Including recaptures of snakes translocated to release sites, there were a total 911 captures, 7.29 ± 6.45 snakes per night ($\overline{X}$± standard error, range = 0–29). For the 205 individuals that were recaptured at least once, the minimum period they apparently remained in the sampled area (except during translocations) was 40.02 ± 34.14 days, an underestimate of their persistence in the booby sub-colony because they could have spent time there outside our snake sampling period or area, and because snakes can spend much time concealed in fissures, particularly after eating or during ecdysis. The most persistent female and male were captured repeatedly over a total 114 days and 113 days, respectively.

The distribution of booby hatching dates was bimodal, as commonly observed in this colony, whereas snake abundance was approximately unimodal, not peaking until just after the second hatching mode (Fig. 3). Few new individuals were captured after May 17, indicating that after that date, arrival/emergence of snakes in the sub-colony was minimal or absent (whether the snakes hibernate is not known). Between May 5 and June 15, when snake abundance was declining, 15 females oviposited in the collection bag, and none of these regurgitated prey.

In the 66 adults that were recaptured at least four times, interval to recapture in the sampling area was 15.24 ± 14.30 days ($\overline{X}\pm$ s.d.) after the first translocation, and 8.91 ± 8.88 days, 7.88 ± 7.71 days and 8.42 ± 9.54 days after the next three, indicating that learning during the first translocation enabled subsequent returns in a little more than half the original time. The snakes probably arrived back in the sampling area well before being recaptured, so these values overestimate the time taken to return after a 400–600 m translocation. The shortest latencies to recapture were 3 h 20 min, 9 h, 24 h, and 24 h (3 instances) for females, and 4.5–5.0 h (4 instances), 9 h, and 24 h for males.

All 28 snakes with stomach contents regurgitated blue-footed booby hatchlings, including four individuals that did so twice and one that did so three times, and one that simultaneously regurgitated two hatchlings. Thirty-four of 911 captures (3.7%) resulted in regurgitation. No snake shorter than 80 cm regurgitated a hatchling, indicating that smaller snakes are unable to gape widely enough to swallow booby hatchlings. Culmen lengths and estimated ages of regurgitated hatchlings were 17.66 ± 1.54 mm ($\overline{X}\pm$ s.d; range 12–21 mm) and 1.28 ± 0.73 d (range 1–4 days), with similar values for female and male snakes, consistent with hatchlings ≥ 4 days old being too large for milk snakes to swallow.

Discussion

Initial removal of feral cats from the island was a conservation success, followed during 14 years by an apparent reduction in the probability of predation on booby chicks. Subsequent removal of black rats was a conservation disaster, followed by an 11-fold increase in the probability of predation. Thus, successive removal of the two invasive mammalian species that

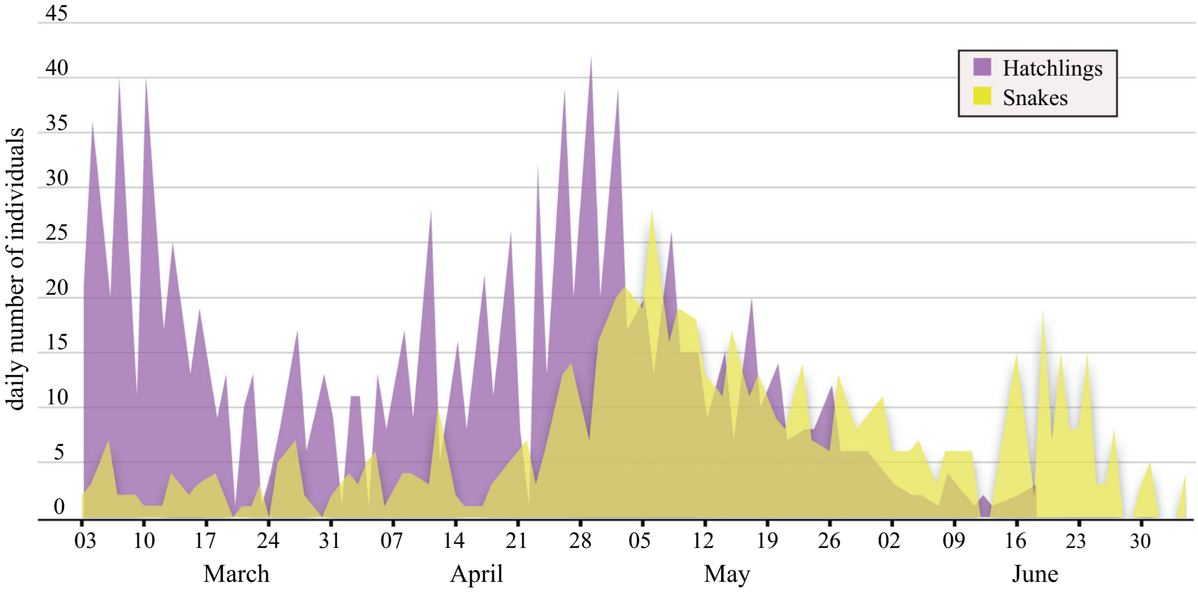

Fig. 3 Daily counts of newly hatched boobies and captured snakes in the booby colony across the 2018 nesting season

have most commonly reduced biodiversity in the world's insular ecosystems, and which tend to extirpate native species synergistically (McCreless et al. 2016), resulted in one native species intensifying its predatory exploitation of another, nearly quadrupling the probability of blue-footed booby hatchlings being predated every season.

The feeding ecology of the two invasive predators was not studied on Isla Isabel, and for the milk snakes we have dietary information only for 4 months of one year before removal of the cats and rats, no information on their predators and no information on their abundance during the 30 years of the study. However, studies of cats, rats and snakes elsewhere allow us to make tentative inferences about the trophic interactions responsible for the observed impacts on boobies. It is likely that removal of cats released rats, the mesopredator that was probably controlling milk snake abundance, resulting in a decline in the snake population and an apparent reduction in the probability of hatchlings being predated, from 5 to 2%. Subsequently, removal of rats probably released the milk snakes, enabling them to progressively increase their predation on hatchlings from 2 to 22%.

Plausibility of the above interpretation is buttressed by observations in other insular ecosystems. Feral cats on Pacific islands prey principally on mammals (Duffy et al. 2012), and a review of 72 studies of 40 islands worldwide found that, although cats on islands take a wide variety of vertebrates and invertebrates, they mainly consume rats (Bonnaud et al. 2011). Black rats on Pacific islands mostly eat fruits and seeds, along with diverse vertebrates and invertebrates, but they can drive reptile populations to the edge of extinction, including a population of Atlantic Central American milk snakes. Caribbean islands populated by black rats support substantially fewer Antiguan racers (*Alsophis antiguae*), another ground-dwelling, slow-moving, lizard-eating snake, than those without. Moreover, removal of rats from a Caribbean island was followed by improvement in the snakes' body condition (including reduction in rodent bite marks), body lengths (a proxy for longevity) and abundance (Daltry et al. 2013). Further, a supposedly extinct population of Atlantic Central American milk snakes on Isla San Pedro Martir, 972 km northwest of Isla Isabel in the Gulf of California, "reappeared" 2 years after black rats were removed (Shiels et al. 2014).

We cannot rule out the alternative hypothesis that snakes increased their predation on booby hatchlings after 2009 because one or more of their other prey, such as whiptail lizards, or hatchlings of sooty terns or brown boobies, declined in abundance. Although changes in species abundance on the island occur in relation to the fluctuations of El Niño Southern Oscillation, these are on the scale of just a few years rather than spans of 9 or 14 years, and they have not been systematically monitored. We are not aware of any change in abundance of alternative prey that appears to correlate with intensity of snake predation on blue-footed booby hatchlings. Certainly, our ability to make inferences about factors affecting snake predation on booby hatchlings would have benefitted from long-term or before-and-after monitoring of the abundance and diets of all the likely players in the island ecosystem, including milk snakes, blue-footed and brown boobies, sooty terns, rats, cats, spinytail iguanas and whiptail lizards.

On Isla Isabel, the cats could have suppressed the black rats by preying on them or competing with them for prey; and the rats could have suppressed the milk snakes by preying on their eggs or the snakes themselves, or by competing with them for eggs or adults of the island's other birds and reptiles, or for space. It is unlikely that removal of cats from Isla Isabel released the milk snakes directly because the snakes delayed 10 years in increasing their predation on boobies and, anyway, cats on islands rarely prey on snakes (Table 7 in Bonnaud et al. 2011).

In years with adverse environmental conditions, hatchlings had a higher probability of being predated, possibly because in adverse conditions fewer boobies reproduce and they do so later in the season (in early March; Ancona et al. 2011), when snake abundance is greater (Fig. 3). Across the 14-year period when rats were the only mammals on the island, the probability of predation was unaffected by environmental conditions. This lack of effect may be due to all El Niño events in the period being weak ones (Hu and Fedorov 2019), and being accompanied by four rapid shifts between the cold, neutral, and warm phases of the Pacific Decadal Oscillation (PDO; Jet Propulsion Laboratory 2021) –a phenomena often described as the leading mode of sea surface temperature anomalies in the North Pacific (Mantua and Hare 2002)–. When ENSO and PDO are out of phase (e.g. El Niño event occurring during a cold PDO phase), the weather anomalies of ENSO are weakened and tend to be neutral (e.g. Hu and Huang 2009). Consequently, Isla Isabel's biota did not experience adverse environmental conditions during this period. In contrast, El Niño events during both the period with cats and rats and the period without mammals occurred during the warm phase of the Pacific decadal oscillation, which exacerbates the temperature and precipitation anomalies in Mexico associated with El Niño (Llanes-Cárdenas et al. 2020; Pavia 2009).

Considering the number of hunting snakes in 2018, the high proportions of booby hatchlings annually predated, and the increase in predatory risk as the number of available hatchlings falls, local extinction or abandonment of the booby colony now seem possible. More than two hundred individual snakes aggregated in roughly 1 hectare of the booby subcolony during 18 weeks. Many remained there for several weeks (despite occasional translocations), and some females oviposited there at the end of the hatching period. Snake abundance was relatively low during the first 9 weeks of 2018, and across 31 booby breeding seasons early nests suffered less hatchling predation, possibly because of an ecological constraint such as cool winter and spring air temperatures. Few snakes were captured with a hatchling in the stomach, probably because snakes tend to refuge in crevices after ingesting prey. However, while in the subcolony, snakes ate little or nothing but booby hatchlings, predating 41.1% of the total and doing so during the brief age span (0–4 days) permitted by the snakes' mandibular gape.

Snakes may be a greater threat to insular marine bird populations than has been realized. To our knowledge, snake predation on insular marine bird colonies is virtually unstudied, but anecdotal observations have revealed that diverse snake species, including venomous ones, prey on eggs and nestlings of cormorants, shearwaters, storm petrels, gulls, terns, ibises and penguins (Dyer 1996; Underhill et al. 2009). The prevalence and impact of this predation is unknown, but the extraordinary toll of the milk snakes of Isla Isabel on blue-footed boobies proves that it can be great. Those milk snakes showed us that native snake populations on islands are capable of rapidly converging on marine bird colonies and consuming a large proportion of the offspring, and that island-nesting birds can lack effective behavioral defenses against them. Furthermore, the snakes oviposited in or close to the booby colony, possibly positioning their offspring for eventual predation on its hatchlings. However, the snakes were constrained, possibly by an environmental variable such as air temperature, to postpone their most intense foraging until after most chicks hatched, and booby parents mitigated predatory risk by hatching their chicks earlier in the season and synchronously with other boobies.

Conservationists who would eliminate invasive species from islands to prevent their impacts on biodiversity are fully aware that removal of apex predators such as cats can be followed by release of their prey, and that those prey, whether carnivores or herbivores, may devastate populations of native animals (Rayner et al. 2007). Indeed, the risk of this is considered so high that managers are generally recommended to remove apex predators and mesopredators (e.g., cats and rats) simultaneously, to protect native species from the latter (Courchamp et al. 2003, Griffiths et al. 2011; but see Bode et al. 2015). However, faced with the complexity of trophic webs, progress will depend on systematically identifying additional webs ("ecosystem motifs") and designing adequate removal strategies for them using modeling approaches and empirical testing (Bode et al. 2015, Morrison et al. 2011). On Isla Isabel, the relevant food web for booby conservation has not the usual two but three trophic links, and the lowest link transforms the conservation dynamic (Fig. 4). Removal of cats (apex predator) released rats (1st mesopredator) to increasingly prey on or compete with the snakes (2nd mesopredator), which consequently reduced their predation on boobies. Subsequent removal of rats released the 2nd mesopredator, allowing it to prey on boobies with unprecedented intensity. Outcomes of changes in trophic webs due to invasive species removal are often non-intuitive (Courchamp et al. 2003), but it is likely that a similar outcome would have occurred if in 1996 cats and rats had been removed simultaneously. In the particular three-link motif of Isla Isabel, the survival of blue-footed boobies (and possibly other common prey of the island's milk snakes including brown boobies, sooty terns, whiptail lizards and spinytail iguanas, none of which were monitored) was maximized by removing only the apex predator. And the boobies' survival was severely prejudiced by removing both apex predator and 1st mesopredator, outcomes which

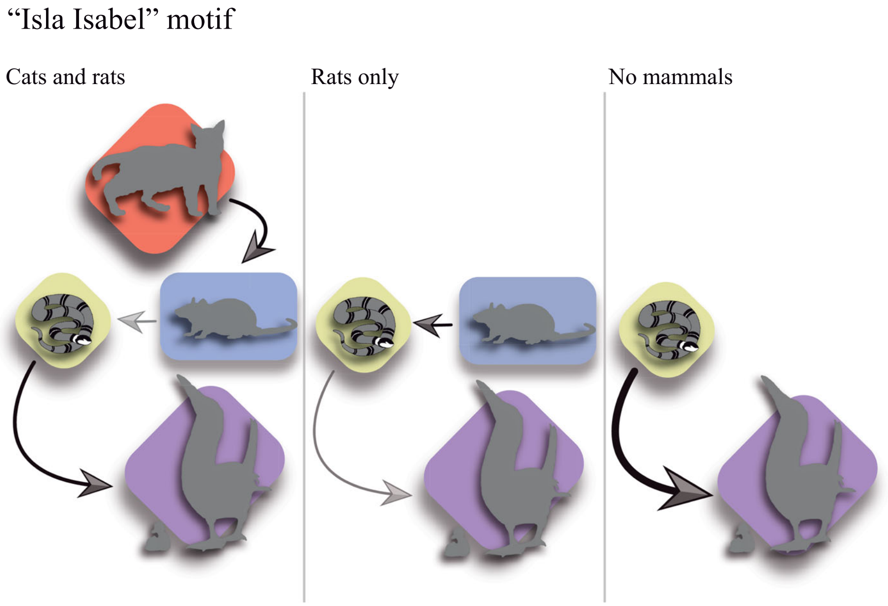

Fig. 4 Hypothetical Isla Isabel motif, showing the trophic links inferred to explain the changes (shown in Fig. 2) in probability of blue-footed booby hatchlings being predated after removal of cats and subsequently rats from the island

are the exact opposite of the pattern predicted in the classic scenario of mesopredator release theory.

Implications for conservation

We share the optimism of conservationists who have proposed that where removal of invasive mammals is contemplated in defence of seabird colonies, just a few common motifs may be sufficient to adequately describe the relevant trophic webs and guide removal objectives and strategies; for example, (1) two invasive predators plus a native prey or (2) invasive superpredator plus an invasive mesopredator and a native prey (Bode et al. 2015). To this nascent taxonomy we can add the hypothetical "Isla Isabel" motif that emerged from the present study: an invasive predator, plus an invasive mesopredator, plus a 2nd -level native mesopredator (possibly not preyed upon by the invasive predator), plus a native prey. It remains to be determined whether the Isla Isabel motif applies to the milk snakes' other prey on that island: brown boobies, sooty terns, whiptail lizards and spinytail iguanas. Ideally, this question should be answered before designing an invasive mammal removal strategy (Courchamp et al. 2003). A similar motif but without the invasive apex predator (see panel 2 of Fig. 4) could operate elsewhere, for example in the marine bird-dominated ecosystem of the desertic island of San Pedro Martir, where Atlantic Central American milk snakes "reappeared" 2 years after removal of black rats (Shiels et al. 2014). There too, invasive rats might have suppressed probable milk snake predation on chicks of blue-footed and brown boobies. Either or both of these motifs could be common on tropical islands where rich biodiversity underpins complex trophic webs, and could be the basis for deciding, controversially, not to remove or even to reintroduce, invasive mesopredators that control native predators of native species.

Conclusions

On an 82-ha. tropical marine island with no native mammals but invasive cats and black rats, removal of cats was followed by a 14-year period of apparently reduced predation by Atlantic Central American milk snakes on newly hatched boobies. Subsequent removal of rats was followed by a 9-year period of greater predation by milk snakes on booby hatchlings. We inferred a novel three-link trophic web in which removal of cats allowed rats to exert greater control of milk snakes, to the benefit of boobies, and removal of rats terminated that control of milk snakes, to the detriment of boobies. Both of these outcomes contradict the expectations of the mesopredator release theory that currently guides programs of invasive mammal removal from marine islands, and they do so because the lowest link of Isla Isabel's trophic web involves a native mesopredator preying on a native prey. A similar (but two-link) trophic web without the apex predator would generate similar outcomes.

Despite only being able to ingest hatchlings up to 4 days old, the milk snakes had a devastating impact on booby reproduction when uncontrolled by rats. More than 200 individuals foraged in roughly 1 ha. of the colony over a period of several months in 2018 and because booby parents, not always recognizing them as predators, frequently failed to repel them, the snakes managed to consume 41% of hatchlings that season. On islands where the lowest link of the trophic web is occupied by a native predator that feeds on native prey, removal of invasive mammals may be contraindicated when it could lead to extirpation of native species. Snakes may represent a special mesopredator threat to marine bird colonies because their stealth can enable them to bypass the defences of even formidable species like boobies and they can aggregate in large numbers to exploit seasonally available prey.

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Author contributions SO: Writing—review & editing, Methodology, Formal analysis, Software, Visualization, Supervision. CR: Conceptualization, Writing—review & editing, Investigation, Data curation, Supervision, Project administration. BM-H: Investigation – data collection, Writing—review & editing. HD: Conceptualization, Methodology, Writing – original draft, Investigation, Funding acquisition, Project administration.

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Availability of data and materials Dataset is available as supplementary material.

Code availability No custom code was used for analyses, all functions in statistical analyses were acknowledged and respective R packages were cited.

Declarations

Conflict of interest The authors have no competing interests to declare.

Consent to participate Not applicable.

Consent for publication Not applicable.

Ethics approval The study was conducted in Parque Nacional Isla Isabel under the permit SGPA/DGVS/012166/17.

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