

First evidence of recruitment in critically endangered Galápagos pink land iguanas (*Conolophus marthae*)

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Abstract

We present the first estimate of population dynamics parameters for critically endangered Galápagos pink land iguanas, *Conolophus marthae*, leveraging mark-recapture data collected between 2006 and 2021. Demographic parameters were estimated using the POPAN formulation of the Jolly–Seber model. This approach provided a solid and robust estimate, consolidating the results obtained from previous estimates based on the Lincoln–Petersen method evaluating only two sampling occasions. Our results suggest that the abundance of males was higher than that of females at each sampling occasion, probably due to differences in sex-specific behavior during the reproductive season. Our analyses also provide no evidence of a change in population size during the sampling period, estimated at 150–270 adult individuals, while suggesting positive entry rates. Finally, by comparing the biometric features of first-captured versus recaptured iguanas, we found that the former have more juvenile-like characteristics (i.e., they are, on average, smaller) than the latter. Although juvenile pink iguanas have rarely been recorded (only four sampled juvenile-like individuals in over 16 years of field work), our combined results provide the first clear indication that the only known *C. marthae* population actively recruits new members from younger age classes. Such recruitment may have prevented any measurable population decline in the last 16 years, but it was also not sufficient to clearly increase the population size. These results are of the utmost importance for the conservation of this species. They will guide future high-

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priority actions: (i) aiming at increasing population size by removing or mitigating threats and (ii) increasing the number of individuals by implementing a headstart program and/or founding a second viable population, as identified in the recently published IUCN Conservation and Management Plan.

KEYWORDS

census population size, endangered species, Jolly–Seber, LMM, mark-recapture, population demography

1 | INTRODUCTION

Fundamental to any successful conservation strategy is knowledge of population parameters such as population size, recruitment, and growth rate, to be monitored and compared over time (Roman et al., 2015; Sim et al., 2011; Warret-Rodrigues et al., 2021). However, accurate estimation of these critical parameters often requires long-term, intensive research efforts, especially for populations inhabiting remote locations and for long-lived species with low fecundity. Despite recent methodological advancements allowing the estimation of some demographic parameters bypassing individual identification (Hostetler & Chandler, 2015; Royle, 2004), these approaches rely on crucial assumptions of an individual's detectability. Direct capture-mark-recapture (CMR), notwithstanding its costs, is still the most reliable approach for the estimation of demographic parameters (Link et al., 2018).

Galápagos pink land iguanas, *Conolophus marthae*, is one of the largest and most recently described reptile species from the Galápagos Islands (Gentile et al., 2009; Gentile & Snell, 2009). Shortly after their description, the species was listed as critically endangered (CR) by The IUCN Red List of Threatened Species™ (Gentile, 2012). The primary justifications for this assessment include an extremely limited distribution (ca. 25 km²), small population size, and the presence of introduced feral mammals (Gentile, 2012; Gentile et al., 2016). Currently, the only available estimate of population size is based on the application of the Lincoln–Petersen methodology to CMR data from only two visits in consecutive years (2009 and 2010; Gentile, 2012) and a general consensus on *C. marthae*'s abundance is still lacking. Even more critically, no information concerning recruitment for the *C. marthae* population is available. In fact, in almost 20 years of work on this species, only 4 juvenile individuals have ever been recorded. Very recently, and with the use of miniaturized tracking devices (Colosimo et al., 2022; Loreti et al., 2020), a nesting area has been identified and a few nests have been located. However, no evidence of population recruitment has been observed or documented.

Among the most serious threats potentially hampering juvenile recruitment of Galápagos pink land iguanas is the reported presence of feral cats (Gentile et al., 2016). Feral cats are known to prey on hatchlings and juvenile iguanas and have caused the extirpation or near extirpation of many island populations of *Cyclura carinata* rock iguanas in the Turks and Caicos Islands (Gerber & Iverson, 1999; Iverson, 1978). Unfortunately, we cannot ascertain when cats arrived on Wolf Volcano, but based on the documented introduction of other feral mammals, like dogs, on Isabela in 1868 (Barnett & Rudd, 1983), and the presence of a US military base on the northern end of Isabela throughout the Second World War (Astudillo & Jamieson, 2023; Woram, 1991), it is conceivable that cats have been on Wolf Volcano for a long time. By the beginning of our study in 2006, the presence of feral cats was already ascertained on Wolf Volcano (Gentile et al., 2016).

In this study, we leverage CMR data collected by our team during eight expeditions to Wolf Volcano (Isabela Island, Galápagos, Ecuador) across 16 years to produce the first estimate of demographic parameters for *C. marthae*. In particular, we fitted a Jolly–Seber (JS) model to estimate adult population size, and population entry and exit rates (recruitment and population turn-over) for both sexes. Estimation of these demographic parameters is critical from a conservation perspective. We then compared biometric features of newly captured and recaptured iguanas using linear mixed-effect models (LMMs) to test the hypothesis that the observed population entry rate is at least partly attributable to recruitment rather than immigration of individuals from another (unknown) subpopulation of pink iguanas on Isabela Island.

2 | MATERIALS AND METHODS

2.1 | Target species and sampling strategies

Conolophus marthae are only found on the northwestern slopes of Wolf Volcano, Isabela Island (Gentile, 2012). Despite extended sampling efforts to identify additional

areas where these iguanas could occur, the most recent analyses indicate that *C. marthae* are restricted to an area of <math> < 25 \text{ km}^2 </math> (Figure 1; Gentile, 2012; Gentile et al., 2016; see also Marquez et al., 2010).

Between 2006 and 2021, we conducted eight CMR sampling expeditions within the known geographic distribution of the species. Our sampling efforts were concentrated in an area of approximately 2 km^2 near the northwest rim of the Wolf Volcano caldera, with altitude ranging from 1380 to 1660 m above sea level (a.s.l.; Figure 1, inset). In this area, adult iguanas congregate for 6–9 months every year (from January/February to August/September; Gentile et al., 2016), which roughly corresponds to the wet season and encompasses the reproductive season (Gentile et al., 2016; Onorati et al., 2016; Trueman & D'Ozouville, 2010). Pink iguanas appear to disperse to lower altitudes for the rest of the year (see Colosimo et al., 2022). Sampling only a portion of the overall distribution range may introduce a bias when extrapolating estimates of the total population. Nevertheless, as previous work indicates the congregation of *C. marthae* in the

sampled area during the time of the year when our captures were carried out, we expect our demographic parameter estimates to represent the total adult population.

Each sampling expedition involved between 5 and 10 scientists and park rangers. The shortest sampling period lasted 4 consecutive days, while the longest lasted 12 days. Iguanas were captured by hand or using a noose pole. Animal capture and handling were performed according to a protocol that minimizes stress and is approved by the Galápagos National Park Directorate (GNPD), the governmental authority that administers biodiversity in the Province of Galápagos. Newly captured individuals were branded with a unique progressive numerical code. They were also marked using Passive Integrated Transponder (PIT) tags. All iguanas were photographed from different angles. From the second sampling period on, all captured individuals were scanned for a PIT tag, and the brand was read. In a few instances, when the brand was visible but not readable and the PIT tag's code could not be read, photographs of the color pattern were compared, allowing individual

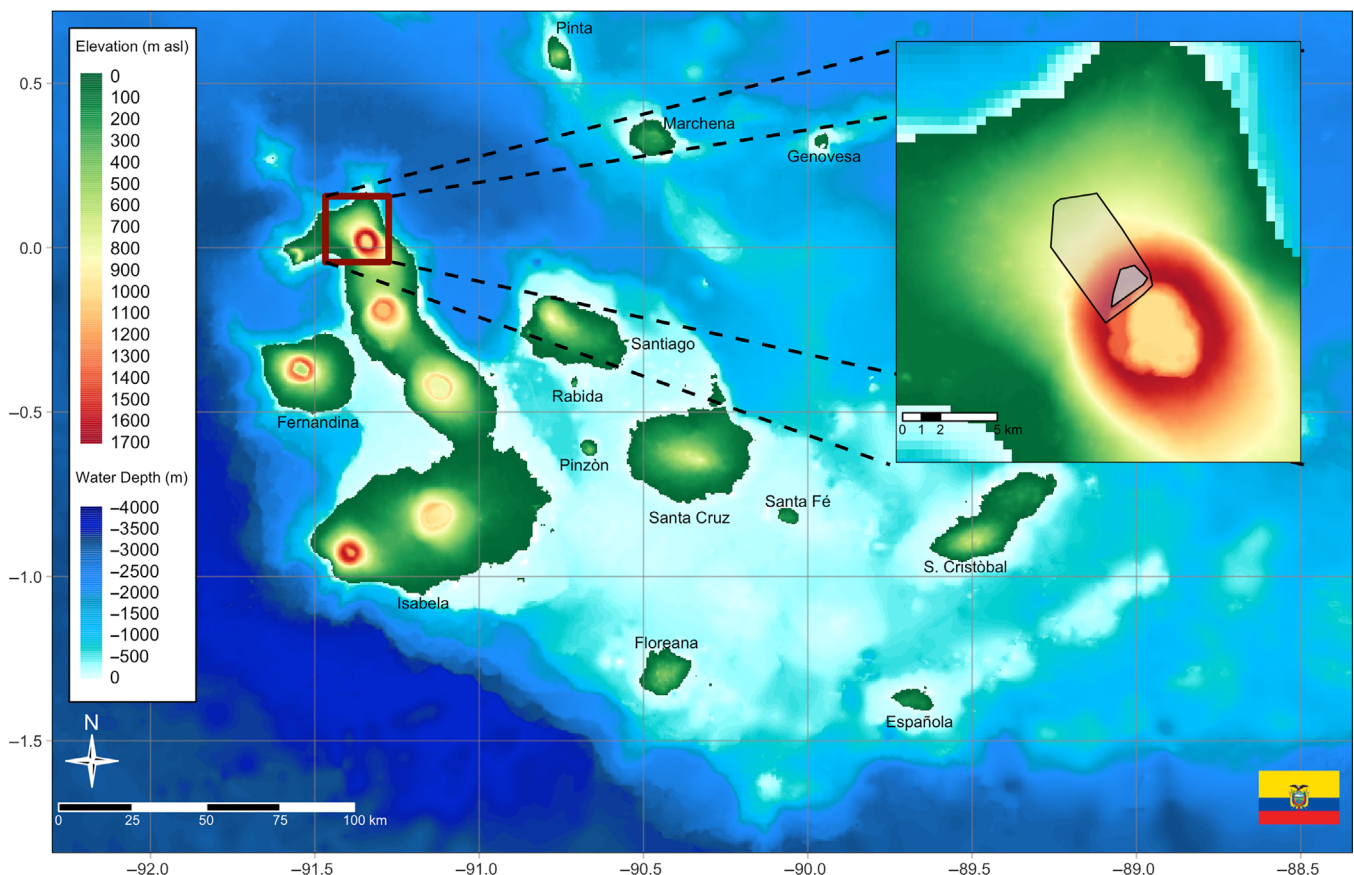


FIGURE 1 Map of the Galápagos Islands, an archipelago located approximately 900 km off the coasts of Ecuador. The inset shows a detail of Wolf Volcano, the tallest volcano (ca. 1700 m a.s.l.) in the Galápagos and the only location where pink iguanas persist in an area estimated at $< 25 \text{ km}^2$ (highlighted by the larger shaded minimum convex polygon). The smaller shaded minimum convex polygon represents the area where samples for this study were collected. See in text the explanation for further details.

Start	Stop	Tot.	Marked	Unmarked	Cumulative
2006-06-03	2006-06-09	32	0	32	32
2009-04-30	2009-05-13	85	15	70	102
2010-07-09	2010-07-16	59	33	26	128
2012-06-08	2012-06-19	82	54	28	156
2014-06-14	2014-06-23	56	43	13	169
2016-08-31	2016-09-03	15	9	6	175
2019-09-12	2019-09-26	15	5	10	185
2021-04-02	2021-04-05	23	10	13	198

Note: For each field expedition, we report the first and last dates of data collection (start and stop), total number of sampled individuals (Tot.), the number of recaptures (marked), and newly captured (unmarked) individuals. The last column (cumulative) lists the cumulative number of unique individuals sampled.

identification. The combined individual identification procedure minimized the risk of losing recapture information due to PIT tag malfunction or brand illegibility. Almost all sighted iguanas were captured and marked, which increases accuracy and reduces the effects of any differences in catchability. For each iguana capture, animal identification, GPS coordinates, sex, snout-vent-length (SVL, in cm), and head length (HL, in mm) were recorded. The final dataset consisted of 367 capture events. In total, 198 individuals (all adults) were captured and marked (85 females and 113 males; see Table 1 for details).

2.2 | Statistical analysis

All analyses were conducted in R v4.1.2 (R Core Team, 2021) running within R-Studio v2023.03.1+446 (R Studio Team, 2020). All graphics presented were generated within the same environment.

2.2.1 | Jolly–Seber model fitting

Demographic parameters were estimated by fitting a Jolly–Seber (JS) model to our CMR data (Jolly, 1965; Seber, 1965). JS models assume no difference in catchability (i) and survival (ii) between marked and unmarked animals within a constant area (iii), with no loss or misreading of tags (iv), and instantaneous sampling (v). Our sampling scheme was designed to ensure that (to the best of our knowledge) all the above-mentioned model assumptions were met. For instance, maximizing captures and the use of a combined approach to uniquely and permanently mark individuals helped us to meet assumptions (i), (ii), and (iv). The deliberate choice of always sampling within the same area is congruent with the assumption (iii). Finally, each year was considered as a separate sampling event so that the model

TABLE 1 Summary of the capture-mark-recapture (CMR) dataset.

would not violate assumption (v) since the duration of sampling periods was negligible compared to the lifespan of an iguana. To confirm that our sampling design would abide by the model assumptions, we performed goodness-of-fit (GOF) tests to our CMR data using the R package R2ucare version 1.0.2 (Gimenez et al., 2018). These tests were initially applied to our dataset as a whole without considering the sex of individuals. Most GOF results suggested that our dataset met the model assumptions, but we detected a violation of test 3.SR (p -val = .026, Table S1). Pradel et al. (1997) suggest that when all other GOF tests fail to reject the null hypothesis of equal capture probability among individuals between sampling occasions, a rejection of the null hypothesis by test 3.SR could indicate differences in apparent survival probability between individuals captured only once versus individuals captured more than once. Ultimately, without any information on the actual individual probability of survival, it is essentially impossible to ascertain if failure to capture an individual was because it had been permanently removed from a population (dead) or just temporarily removed from it (transient effect due to migration or other behavioral differences between individuals). In other species of iguanas (including *Conolophus*), females temporarily migrate from their home ranges at the end of the mating season to lay eggs (Christian & Tracy, 1982; Iverson et al., 2004; Krysko et al., 2007; Moss et al., 2020; Perez-Buitrago et al., 2016; Werner, 1983). We, therefore, deemed it possible that the elicited difference in survival probability could actually reflect a temporary displacement of females removing themselves from the sampling area to lay eggs. We thus performed a new set of GOF tests including the sex of individuals, and we did not detect violations in any test (Table S1).

We fitted the JS model to our CMR data using the R package RMark version 2.2.7 (Laake, 2014; White & Burnham, 1999). We used the POPAN formulation of the JS model, postulating the existence of a super-population

consisting of all animals that ever enter the real population during the study period (Schwarz & Arnason, 1996). This model allows us to directly estimate the size of the super-population (N_s), capture probability (p_c), annual apparent survival (φ), and probability of entry into the population between sampling events (β). The number of individuals entering in the population (B_i) and the abundance (N_i) during the i th sampling event can then be derived from these parameters (Table S2).

We built a total of 24 models as a result of all plausible parameter combinations. In particular, we allowed the parameter φ to be either sex-dependent (\sim sex) or sex- and time-dependent (\sim t * sex), whereas constant (\sim) and time-varying (\sim t) scenarios were not considered due to the results of the test 3.SR. Since sampling effort varied among the sampling occasions, in terms of duration and number of observers, the parameter p_c was set to be either time- (\sim t), sex- (\sim s), or time- and sex- (\sim t * s) dependent. We allowed β to be time (\sim t) or sex and time (\sim t * s) varying to consider the time elapsed between sampling periods in our data. Indeed, the entry probability strongly depends on the length of the intervals between consecutive capture events. Finally, N_s could be constant (\sim) or sex dependent (\sim s) allowing to account for potential differences in total abundances between the sexes. The best model was selected using Akaike's information criterion (AIC), corrected for sample size (AICc; Akaike, 1998; Hurvich & Tsai, 1989), and its results were considered for making inference on *C. marthae* population dynamics.

2.2.2 | Linear mixed models

Models used to analyze CMR data are typically aimed at estimating population size and entrance/exit rates but cannot distinguish between permanent immigration into the population from an unsampled geographic area or from unsampled age cohorts. In our dataset, for example, very few obviously juvenile pink iguanas were captured. Recent data suggest that they may be, at least in part, spatially segregated from adults. Still, it is also reasonable that their size and behavior make them less detectable and thus less susceptible to capture. However, since iguanas grow indefinitely (Haines, 1969, but see Frydlova et al., 2019, 2020), if at least a significant fraction of the individuals entering the population consist of recruitment from younger age cohorts, we may predict that, on average, newly captured individuals will be smaller than recaptured individuals.

To preliminarily understand which biometric feature might be a more direct approximation of individual age, we fitted two LMMs with SVL and HL as response

variables. Both models included sex and the time elapsed between capture occasions (t) as fixed effects. Prior to the analysis, we scaled t to a mean of 0 and a standard deviation of 1. We set the sampling year as a random intercept to account for any possible systematic difference in morphological measurement between expeditions. Our models also included a random slope for the effect of t within individuals, to account for different growth rates among individuals. Growth patterns of large reptiles are generally described using von-Bertalanffy or logistic curves, with growth rates typically higher during earlier life stages and body size usually approaching an asymptote after reproduction begins (Avery, 1994; Rand & Bock, 1992; Shine & Charnov, 1992), and iguanas seem not to constitute an exception (Iverson, 2004). However, our data only comprise adult or nearly adult individuals and reasonably represent a very limited fraction of the species growth curve. We inspected the residuals of our LMMs to ensure that our data could be fit by a simple linear relation between t and the responses and found no sign of non-linearity.

The morphological feature best predicted by t was used as the response variable in another LMM, where the test predictor was whether the individual was captured for the first time or recaptured. Sex was included in this model as a control fixed effect (iguanas are sexually dimorphic), and the sampling year identity was included as a random intercept (see above). Data from the first capture event (2006) were not informative for this analysis and were excluded.

3 | RESULTS

3.1 | Jolly–Seber model

The model with time-varying catchability, sex-dependent survival, time-varying entry probability, and constant super population size [$p_{c(t)}\varphi_{(s)}\beta_{(t)}N_{s(c)}$] had the lowest AICc value (820.8409; see Table S3, reporting the 10 models with the lowest AICc values). Since capture and entry probabilities vary between sampling occasions, model parameters at the first and last capture events are confounded and non-identifiable (Schwarz et al., 1993; Schwarz & Arnason, 1996). The best model results do not show considerable differences in the total number of males and females occurring in the population over the study period, estimating an N_s of 189 iguanas (95% CI 145–264) for both sexes, whereas the apparent survival rate is \sim 0.962 (95% CI 0.887–0.988) for males and 0.899 (95% CI 0.831–0.941) for females. Catchability values strongly differ among capture events, reflecting differences in sampling effort, and ranging from 0.054 (95% CI

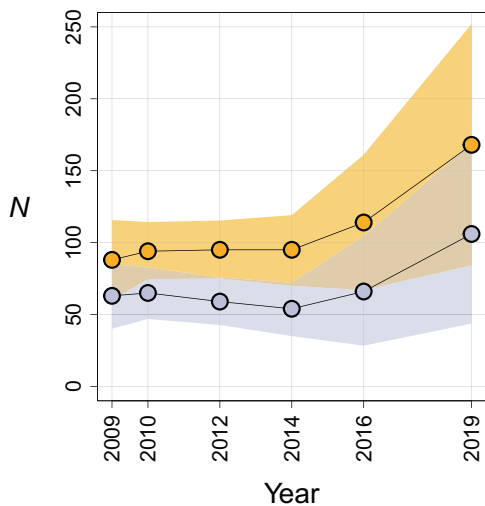


FIGURE 2 Population size of pink land iguana males (orange) and females (light blue) during the sampling period applying the Jolly–Seber (JS) POPAN formulation model. Dots represent abundance values (N) at capture events; shaded areas show the 95% confidence intervals (CI). Abundance estimates at the first and at the last sampling events are not reliably calculated by our Jolly–Seber model, and therefore these estimates are not reported in the chart.

0.026–0.109) in 2019 to 0.559 (95% CI 0.374–0.728) in 2009 (Table S4).

Deriving abundances for each study year, we found that, while point estimates vary from 88 to 168 males and from 54 to 106 females, all confidence intervals were largely overlapping (e.g., 2009 95% CI 60–116 males, 2019 95% CI 84–252 males; 2009 95% CI 40–85 females, 2021 95% CI 44–169 females; see Figure 2; Table S5). The total population size resulting from the sum of male and female abundances ranged from 150 to 274 individuals. Model results also suggest that the number of individuals of both sexes entering the population (B_i) was ≥ 1 between each sampling occasion, varying from ~ 6 (95% CI 1–32) to 66 (95% CI 27–167) males and from ~ 6 (95% CI 1–28) to 58 (95% CI 22–150) females.

3.2 | Linear mixed model results

LMM results revealed that HL significantly increased over time, whereas SVL did not show any significant correlation with t (Table S6), suggesting that HL may be used as a proxy for age in our data. Hence, we selected HL as the response variable in the LMM aimed to detect age differences between recaptured individuals and individuals captured for the first time within each sampling period. As expected, males had significantly longer heads than females. Most importantly, however, for each

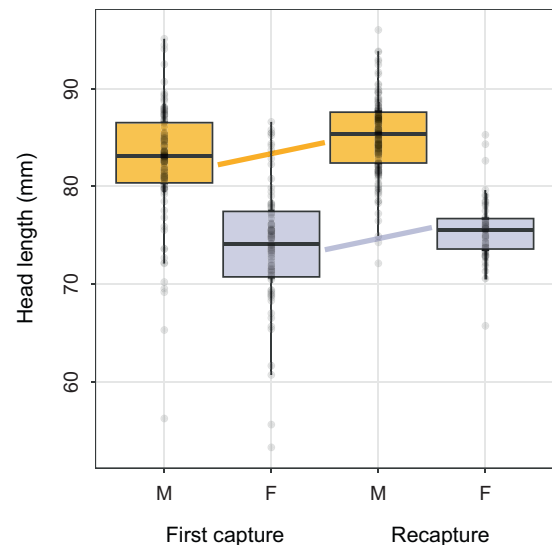


FIGURE 3 Results of the linear mixed model fitted to investigate differences in head length (HL, in mm) between individuals captured for the first time and recaptured, divided in males (M; in orange) and females (F; in light blue). Dots and box plots report the real data of HL. Lines connect the mean HL estimates of first captures and recaptures for both sexes. Horizontal black lines correspond to median HL values. Lower and upper edges of boxes correspond to first and third data quartile. Whiskers extending from the boxes describe the variability outside the lower and upper quartiles.

sampling year, we found that individuals that were captured for the first time had significantly shorter heads (smaller HL) than recaptured individuals (Figure 3 and Table 2).

4 | DISCUSSION

Our study reports the first estimates of population size dynamics and the first evidence of recruitment in critically endangered *C. marthae* iguanas, leveraging on CMR data collected over 16 years of fieldwork. We estimated abundance for both sexes for each sampling year, with results ranging from 88 to 168 for males and from 54 to 106 for females, and suggesting a total population size of *ca.* 150–270 individuals between 2009 and 2019 (Figure 2). Our measures are comparable with the first abundance estimate reported in the IUCN Red List of Threatened Species, computed applying the Lincoln–Petersen approach on 2009–2010 CMR data (Gentile, 2012), and confirm the classification of *C. marthae* as “critically endangered” following criterion C of IUCN guidelines (IUCN, 2022).

Confidence intervals of male and female estimates are narrower in the early-middle portion of the study period,

TABLE 2 Estimated coefficients for the linear mixed model fitted to investigate morphological differences between captured individuals.

Term	Estimate	SE	<i>t</i>	df	χ^2	<i>p</i> -val
Intercept	75.756	0.846	-	-	-	-
Cap:fc	-2.269	0.641	-3.538	1	12.471	<.001
Sex:M	8.659	0.618	14.009	1	154.796	<.001

Note: The table shows the output of the model fitted to investigate head length (HL) differences between individuals captured for the first time or recaptured (cap). The table reports the estimated model value (estimate), standard error (SE), *t*-score (*t*), degrees of freedom (df), and the χ^2 statistic for likelihood ratio test with the corresponding *p*-values (*p*-val). The estimate of cap is expressed for first captured individuals (fc) while sex for males (M).

whereas CIs are considerably wider in the last years (Figure 2), reflecting sampling effort, as the number of captured animals was highest between 2009 and 2014 (Table 1). Confidence intervals for the estimated abundances broadly overlap throughout the whole study period, so that our results do not provide evidence of any change in population size. Most importantly, however, a dramatic decrease in abundance over the study period is not compatible with our estimates.

Annual survival probability of *C. marthae* individuals is high: 0.962 (95% CI 0.887–0.988) for males and 0.899 (95% CI 0.831–0.941) for females. These estimates are similar to survival rates reported in other studies regarding long-lived iguanas. For instance, the Galápagos marine iguana (*Amblyrhynchus cristatus*) survival rate was estimated to be ~0.910 for females and 0.880 for males in years not affected by El Niño (Laurie & Brown, 1990). The survival rate of *Cyclura carinata* in the Turks and Caicos Islands was reported to be ~0.900 for females and 0.950 for males (Iverson, 1979) and, in *Cyclura cychlura*, this parameter was estimated at 0.870–0.930 (Iverson et al., 2006).

The best JS model suggests no considerable differences in the total number of males and females in the sampled population over the study period, even though abundance estimates at capture events are always lower for females than males. Since the sampling location corresponds to the reproductive area of *C. marthae*, the dissimilarities in point abundances between sexes may reflect a difference in their reproductive behavior. Indeed, females of other Galápagos iguana species usually leave male territories after mating to reach nesting grounds (Trillmich, 1983; Werner, 1983; Wikelski et al., 1996), and this behavior was also observed for *C. marthae* through the application of miniaturized tracking devices. Based on this evidence, the lower number of females at each sampling occasion can be explained by their different patterns of movement. In other words, if females remain within the mating area for shorter periods than males, the stock of catchable females during sampling activities is probably smaller than males.

Since no hatchlings and only a few juveniles were observed until recently during field activities, it was

hypothesized that recent recruitment rates for this species could be negligible and non-effective, possibly due to the presence of introduced predators (feral cats) in the area (Gentile, 2012). Challenging this hypothesis, our analyses estimated positive entry rates.

In our JS model, the lower 95% CI limit for estimates of the number of individuals of both sexes entering the population between sampling events (B_i) was ≥ 1 during the entire sampling period (Table S4). The observation of positive entry rates in the CMR dataset per se simply indicates that iguanas enter the capturable stock from a reservoir of non-capturable individuals. However, our LMMs provide a very strong indication that, at least in part, entries in the capturable stock do represent recruitment from juvenile age classes. We first showed that the HL significantly and positively correlates with the time elapsed since the first capture of an individual, and then found that, controlling for sex and within each sampling occasion, iguanas captured for the first time had significantly shorter heads than recaptured animals (Figure 3 and Table 2). In summary, our data (i) demonstrate turnover and recruitment in the reproductive (capturable) population of *C. marthae* and (ii) do not support a significant decline in the species abundance.

Compiled together, these results indicate that, among other threats, the impact of predation on hatchlings by feral cats on population turnover was not significant enough to cause a discernible negative demographic decline. However, it must be remarked that the width of confidence intervals in our estimates of demographic dynamics (Figure 2) still allows for a less pronounced decline, and the life cycle of *C. marthae* remains poorly known, and it is therefore possible that the time required for hatchlings to enter the reproductive population is long enough that the effects of predation by cats are yet to become apparent. Continuous population size monitoring and feral mammal control are among the high-priority actions indicated by the IUCN Conservation and Management Plan 2022–2027 for the species (Rueda et al., 2023), and both are fundamental conservation actions for Galápagos pink land iguanas. We also want to emphasize that our finding of recruitment and lack of evidence of significant population decline are

insufficient elements to justify downlisting of the IUCN risk status for *C. marthae* from critically endangered to endangered. Our estimates of population abundance are, in fact, lower than the threshold for CR under criterion C, and we add no new information concerning the species' extent of occurrence or number of distinct populations (criterion B). For long-lived reptiles with high and constant survival rates, reproduction and survival of hatchlings and juveniles were reported to markedly influence population dynamics (Briggs-Gonzalez et al., 2017; Warret-Rodrigues et al., 2021). Conservation actions aimed at enhancing reproductive success and juvenile survival can, thus, constitute a fundamental practice for the preservation of Galápagos pink land iguanas. Following the CAMP, the Galápagos National Park Directorate is considering a headstart or captive breeding program. Indeed, although the study of reproductive biology is listed as a priority action in the IUCN risk assessment (Gentile, 2012), our current knowledge of *C. marthae* still suffers from a serious lack of information on ecological aspects of reproduction and early life stages. For these reasons, in addition to pursuing an effective conservation strategy aimed at lowering the risk status of the species, future research should also investigate ecological aspects of pink iguana reproduction and pre-breeding life stages, such as nesting behavior, reproductive success, hatchlings dispersion, juvenile growth and survival rates, and age at sexual maturity. By providing the first estimates of demographic dynamics and recruitment for critically endangered *C. marthae*, our study represents a crucial starting point for planning future efficient management practices.

POSITION STATEMENT

Our study reports the first estimates of population size dynamics and the first evidence of recruitment in critically endangered *Conolophus marthae* iguanas. These results are of the utmost importance for the conservation of this species. They will guide future high-priority actions (i) aiming at increasing population size by removing or mitigating threats and (ii) increasing the number of individuals by implementing a headstart program and/or founding a second viable population, as identified in the recently published IUCN Conservation and Management Plan.

AUTHOR CONTRIBUTIONS

Study conception and design: Lorenzo Garizio, Marco Gargano, Giuliano Colosimo, Paolo Gratton, and Gabriele Gentile. *Data acquisition:* Giuliano Colosimo, Gregory Lewbart, Christian Sevilla, and Gabriele Gentile. *Data analysis:* Lorenzo Garizio, Marco Gargano, and Paolo Gratton. *Data interpretation:* Lorenzo Garizio, Marco Gargano, Giuliano Colosimo, Paolo Gratton, and

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data analyzed in this article is the raw count of captured and marked individuals over a 16-year period. Raw counts are presented as is in the article. We have also deposited the raw capture history matrix used in the Jolly-Saber model in datadryad.org repository. The link to access such count is forthcoming.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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