Survival analysis of two endemic lizard species before, during and after a rat eradication attempt on Desecheo Island, Puerto Rico

J.L. Herrera-Giraldo[1], C.E. Figuerola-Hernández[1], N.D. Holmes[1], K. Swinnerton[1,2], E.N. Bermúdez-Carambot[3], J.F. González-Maya[4] and D.A. Gómez-Hoyos[4]

[1]Island Conservation, 2100 Delaware Avenue, Suite 1, Santa Cruz, CA 95060, USA. <jose.herrera@islandconservation.org>. [2]Current affiliation: The Island Endemics Foundation, P.O. Box 1908, Boquerón, Puerto Rico 00622. [3]US Fish and Wildlife Service -Vieques National Wildlife Refuge, Vieques, Puerto Rico. [4]ProCAT International/The Sierra to Sea Institute, Las Alturas, Puntarenas, Costa Rica.

Abstract Rodent eradications are a key island restoration activity to counteract extinction and endangerment to native species. Despite the widespread use of brodifacoum as a rodenticide for island restoration, there has been little examination of its potential negative effects on native reptiles. Here we examined the survival of two endemic insular lizard populations before, during and after a brodifacoum-based rodent eradication using a mark-recapture study. We found no evidence of an effect from baiting in *Anolis desechensis* and evidence of a change in recapture rates after baiting for *Ameiva desechensis*. Effects of baiting on survival rates were not measurable due to a small sample size. Results suggest that brodifacoum did not result in population-level impacts during the three-week study period after brodifacoum exposure. For invasive species eradications using toxicants, potential risks to non-target species should be assessed against the expected benefits to native biota from the removal of threats posed by invasive mammals. We recommend continued studies that directly examine non-target risk to native reptile populations derived from toxicant baiting programs, particularly on tropical islands that are home for high numbers of endemic reptiles.

Keywords: brodifacoum, mark-recapture, non-target species, reptiles, rodent eradication

INTRODUCTION

Islands represent approximately 5% of the land area of the Earth, yet 61% of extinctions have been insular species, and 37% of species listed by the IUCN as critically endangered are confined to islands (Tershy, et al., 2015). Invasive species are a major driver of species extinctions on islands and remain a significant risk to threatened species (Bellard, et al., 2016; Doherty, et al., 2016). Invasive rats have been introduced to approximately 80% of the archipelagos of the world, and have wide-ranging negative impacts on native flora and fauna (Towns, et al., 2006). Techniques to eradicate invasive rodents from islands are available and the practice is increasing in scope, scale, and application (Howald, et al., 2007; Keitt, et al., 2011), with restoration benefits being accrued when eradication is achieved (Jones, et al., 2016). To date there have been over 650 eradication attempts of rats (*Rattus* spp.) on more than 500 islands worldwide (Russell & Holmes, 2015).

Successful rodent eradication from islands larger than 5 ha primarily relies on the use of anticoagulant rodenticide (Howald, et al., 2007). Second generation anticoagulants are the most commonly used toxicant in invasive rodent eradication programmes (Holmes, et al., 2015). When using toxicants for rodent eradication on islands, the risk to non-target native species is typically assessed. Efforts to reduce this risk during eradication operations commonly include application of bait when susceptible species are absent, temporary captive-holding of species during potential periods of exposure, and alternative delivery methods to reduce bait access (Howald, et al., 2007). While reptiles have been known to consume cereal-based rodent baits (Merton, 1987; Marshall & Jewell, 2007), they have typically been considered at lower risk (Hoare & Hare, 2006), in part because of decreased susceptibility due to differences in blood chemistry and physiology compared to mammals and birds (Merton, 1987; Hoare & Hare, 2006). Although evidence of population level impact to reptiles is sparse, observations from an increasing number of rodenticide-based eradications, plus targeted studies, have suggested the risk is low (Harper, et al., 2011). Nevertheless, additional studies are required to improve general knowledge of the risk of rodenticides to reptiles during rodent eradication operations.

During 2012, an eradication of *Rattus rattus* using rodenticide bait was attempted on Desecheo Island located approximately 21 km off the north-west coast of Puerto Rico. Black rats were introduced in the early 1900s and are considered an important threat on Desecheo, including impacts on native reptiles from direct predation and habitat modification via seed and seedling predation and soil nutrient changes (U.S. Fish and Wildlife Service, 2016). An additional potential threat from rats to native reptiles could include competition for space and food resources, consistent with rat impacts on reptiles elsewhere (Shiels, et al., 2014; Harper & Bunbury, 2015). Two years prior to the eradication operation, exposure of bait to the endemic Desecheo ameiva (*Ameiva desechensis*) and Desecheo anole (*Anolis desechensis*) was assessed through a placebo non-toxic bait biomarker study. The study found no evidence of ameivas (n=18 marked, n=5 recaptured) interacting with bait, but 21% of anoles recaptured were exposed (n=97 marked, n=20 recaptured) (Herrera & Bermúdez-Carambot, 2010). However, because these species occur only on Desecheo, and thus had high conservation value, the fate of both lizard species was followed during the application of toxic bait during the eradication operation. Here we report the results of a mark-recapture study to monitor the short-term survival of the ameivas and the anoles before, during and after the 2012 rodent eradication operation on Desecheo Island.

MATERIALS AND METHODS

Study area

Desecheo Island is a 117 ha hilly island located approximately 21 km off the north-west coast of the Commonwealth of Puerto Rico (18^{o} 23’ N, 67^{o} 29’ W; Fig. 1). It was declared a U.S. National Wildlife Refuge (NWR) in 1976 and is currently administered and managed by the U.S. Fish and Wildlife Service. Sub-tropical dry forest (i.e. woodland) is present primarily on the leeward slopes and valleys, and is dominated by the semi-deciduous almácigo tree (*Bursera simaruba*). The windward slopes and ridges also harbour cacti, shrubs and open grasslands. The annual

In: C.R. Veitch, M.N. Clout, A.R. Martin, J.C. Russell and C.J. West (eds.) (2019). Island invasives: scaling up to meet the challenge, pp. 191–195. Occasional Paper SSC no. 62. Gland, Switzerland: IUCN.

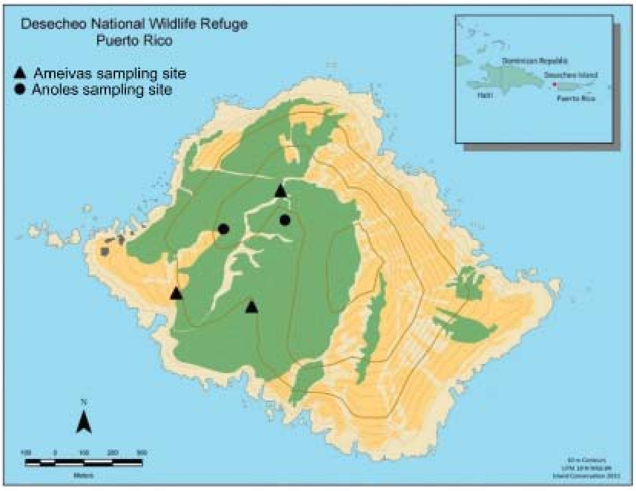

Fig. 1 Location of Desecheo Island and sampling sites for *Anolis desechensis* and *Ameiva desechensis* impact assessment during black rat eradication operations.

rainfall average is 828 mm (range 750–1039 mm; Morrison & Menzel, 1972) with a seasonal dry period between January and March, followed by a rainy season between July and November. The island supports five single-island endemic species (three lizards and two arachnids) as well as one of the three remaining populations of the threatened higo chumbo cactus (*Harrisia portoricensis*). Previous anthropogenic activities on the island included livestock grazing, military operations (e.g. bombing and gunnery range) and the introduction of invasive mammals: black rats (*Rattus rattus*), goats (*Capra hircus*), feral cats (*Felis catus)*, and rhesus macaques (*Macaca mulatta)*. The extirpation of nesting seabirds from Desecheo Island has been linked to the presence of these invasive mammals (U.S. Fish and Wildlife Service, 2016). The island is currently closed to the public due to the existence of unexploded ordnance.

Rat eradication

Aerial bait broadcast for rodent eradication was carried out on Desecheo between March 13 and 23, 2012. The bait used for the eradication was "Brodifacoum Conservation-25D" manufactured by Bell Laboratories in Madison, Wisconsin, USA. The bait was a 2 g extruded pellet, dyed green, and contained 25 ppm of the toxin brodifacoum. The bait broadcast was completed in two aerial applications separated by 10 days and with a ground application rate of 17 kg/ha for the first application and 9.1 kg/ha for the second application. There is no weather station on Desecheo Island and data were obtained from weather stations located in Rincon (13 miles from Desecheo) and Isabela (29 miles) and the Standard Precipitation Index (SPI) produced by Caribbean Regional Climate Center. January and March are usually a dry period but data from two weather stations and comparisons with 2008 and 2010 vegetation cover indicate that in 2012 Desecheo received greater than average rainfall.

Study species

The Desecheo ameiva (Fig. 2a) is a common lizard species found in coastal areas, including shoreline margins, in habitats of maximum solar exposure but frequently near some vegetation cover or shade (Evans, et al., 1991). Adult females tend to be smaller (SVL <90 mm) than males (average SVL 97 mm). Field surveys conducted in 2009 and 2010 estimated the island population at 7,469 individuals (95% CI 1,800–13,137) (McKown, et al., 2010). The Desecheo anole (Fig. 2b) is present throughout the island, but is most common in forested areas (e.g. valleys) and their margins (Evans et al., 1991). Average size for adult males is 57 mm (SVL) and for females 45 mm (SVL). Field surveys in 2009 and 2010 estimated the island population at 52,111 individuals (95% CI 31,464–72,758) (McKown et al., 2010).

Reptile monitoring

During the eradication, we implemented a reptile monitoring program between February and April 2012. We used a standard mark-recapture methodology (Jolly, 1965; Seber, 1965) over three discrete sampling periods of six days each, which coincided with bait application stages during the eradication. The first period began 21 days prior to the first bait application, the second between the first and second bait application, and the third began three days after the second bait application. The sampling sites were randomly located in five different locations within the woodland habitats in the Long and West Valleys (Fig. 1). Ameivas were sampled within one 100 × 10 m plot and

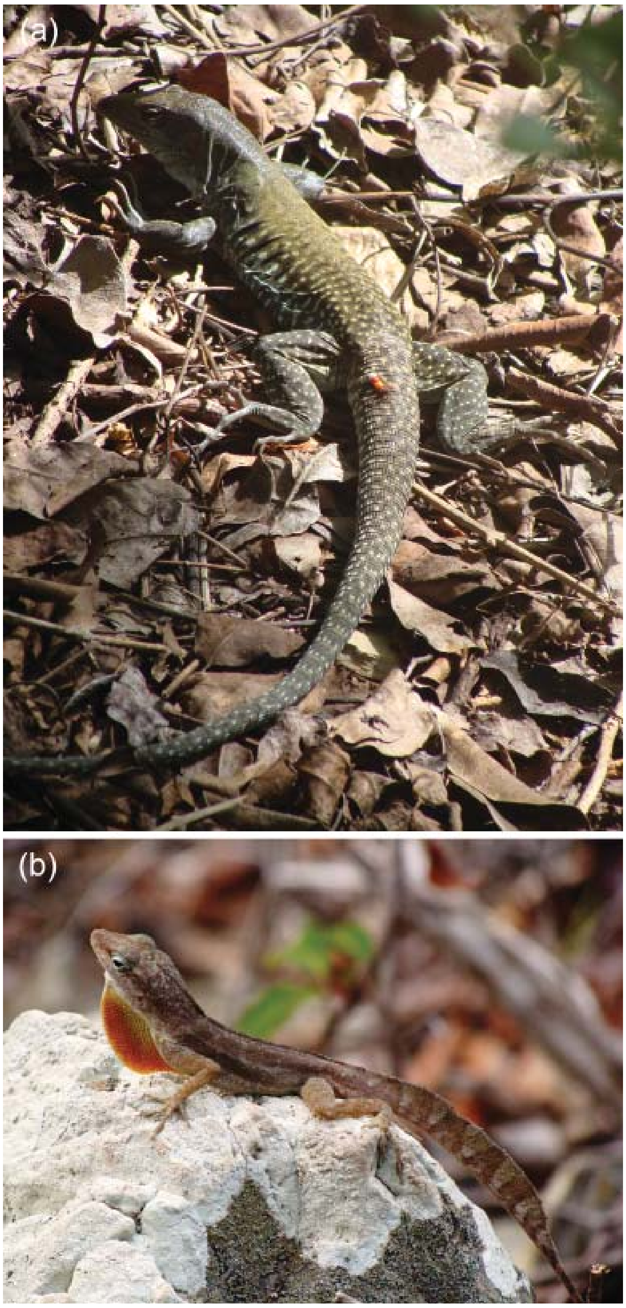

Fig. 2 *Ameiva desechensis* (a) and *Anolis desechensis* (b).

two 50 × 10 m plots. Anoles were sampled within two 100 × 10 m plots. Each plot was surveyed by two observers, each responsible for sampling one side (5 m) of a central transect through the plot. Each sampling day accounted for 8 hours of intensive searches for both species, and included the detection and capture of each observed individual. Individuals were captured using a pole and noose and by hand capture. Each anole was marked on the hind limb with a unique visible alphanumeric implant tag and each ameiva was marked with a unique combination of coloured glass beads sewed to the base of the tail (Fig 2a), and a unique combination of clipped toes (Censky, pers. comm. and modified from Fisher & Muth, 1989). Each individual was released at their capture location.

Statistical analyses

Survival of individuals was estimated using a mark-recapture model based on multiple capture histories within each sampling period (Cooch & White, 2015). We estimated the probability of recapture based on time and apparent survival to assess any potential impacts on either species as a result of the rodent bait application. We used MARK 5.0 (White & Burnham, 1999) to model factors influencing variation in survival. The Cormack-Jolly-Seber (CJS) model based on live animal recaptures in an open population (Lebreton, et al., 1992) was used to estimate the apparent survival (phi or ø). Models were constructed based on the recapture rates (*p*) and apparent survival (ø) remaining constant (.) or changing in time (*t*), and according to the bait dispersal events – before, during, and after (*asp*). The best performing model was selected using the Akaike Information Criteria (AIC) through the proportion test with Akaike weights (AICw; Burnham & Anderson, 2002). The assumptions of the CJS model were tested using TEST 2 and TEST 3 in the U-CARE program version 2.3 M 7.5 (Choquet, et al., 2005). To evaluate the fit of the set of models to the data, a Global TEST was conducted to calculate the variance inflation factor (ĉ).

RESULTS

A total of 452 anoles and 57 ameivas were captured and marked across 18 days of field sampling and 144 person-hours of sampling effort in the five study sites (Table 1). Although ameivas were detected less frequently across the study sites, they had a higher rate of recapture (35 recaptures, 61.4%) than anoles (92 recaptures, 20.4%; Table 1).

The best supported model for anoles explained the probability of recapture according to time and with apparent survival remaining constant (Table 2). For ameivas, the best supported model was the one in which the recapture probability varied across the sampling periods (i.e. bait application) and when apparent survival remained constant (Table 2). Both models indicated no changes in apparent survival along the three periods (asp) of bait applications. TEST 2 and TEST 3 showed no differences in the probability of recaptures and survival for the marked individuals (p>0.61). Global TEST indicated a sub-dispersion in the data (ĉ<1), thus no effect on the variance, therefore this parameter was not modified in the models (Cooch & White, 2015).

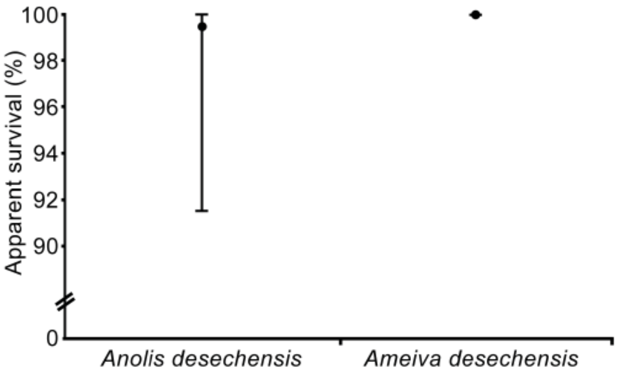

Fig. 3 Apparent survival percentage of *Anolis desechensis* and *Ameiva desechensis* during a black rat eradication on Desecheo Island (Error bars: 95% confidence intervals).

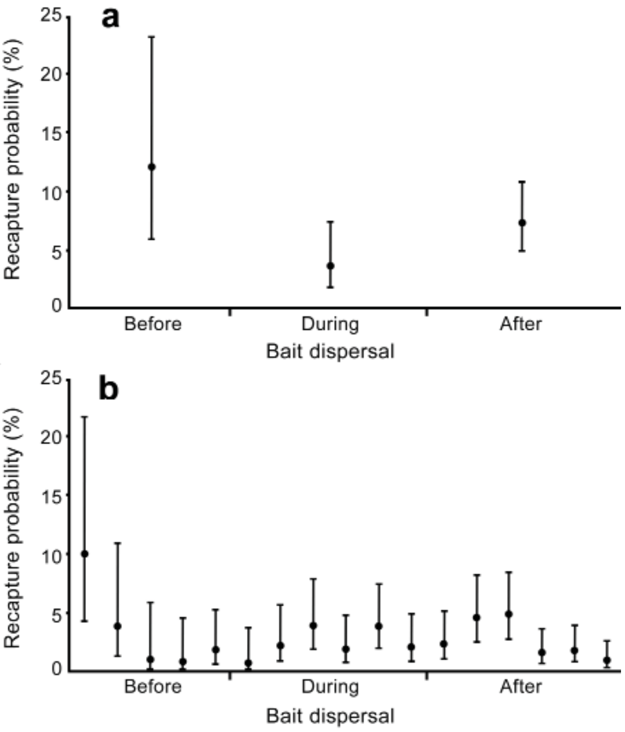

Fig. 4 Recapture probability for (a) *Anolis desechensis* and (b) *Ameiva desechensis* before, during and after bait dispersal for a black rat eradication on Desecheo Island (Error bars: 95% confidence intervals). We retain individual survey events in Figure 3b as these were found to be associated with recapture probability.

Apparent survival for both lizard species during the study period was estimated to be time-invariant and close to 100% (anoles: ø = 0.99, 95% CI = 0.91–0.99; ameivas: ø = 1, 95% CI = 1–1; Fig. 3). However, the precise apparent

Table 1 *Anolis desechensis* and *Ameiva desechensis* previously unmarked and accumulated recaptures (in parenthesis) according to sampling site and bait application stage during the black rat eradication on Desecheo Island.

Bait application stage	*Anolis desechensis*			*Ameiva desechensis*			
	Site1	Site 2	Total	Site1	Site2	Site3	Total
Before	89(2)	126(11)	215(13)	7(0)	12(3)	8(4)	27(7)
During	49(6)	46(37)	95(43)	8(3)	5(7)	3(4)	16(14)
After	75(24)	67(68)	142(92)	7(13)	3(13)	4(9)	14(35)

Table 2 Comparison of models to estimate the apparent survival (ø) and probability of recapture (*p*), according to the bait application stage (asp: before, during and after) and time (t) for *Anolis desechensis and Ameiva desechensis* during black rat eradication operations at Desecheo Island.

Model	AICc	ΔAICc	AICc weights	k	Deviance
Anolis desechensis					
ø(.) p(t)	888.04	0	0.788	18	249.89
ø(asp) p(t)	891.79	3.76	0.120	20	249.33
ø(.) p(.)	893.33	5.29	0.059	2	288.51
ø(asp) p(.)	895.79	7.76	0.016	4	286.92
ø(asp) p(asp)	896.42	8.39	0.012	6	283.46
ø(.) p(asp)	897.23	9.19	0.008	4	288.36
ø(t) p(.)	915.12	27.09	0	18	276.98
ø(t) p(asp)	915.68	27.64	0	20	273.22
ø(t) p(t)	918.92	30.89	0	33	247.56
***Ameiva desechensi*s**					
ø(.) p(asp)	268.91	0	0.615	1	163.39
ø(.) p(.)	270.44	1.52	0.287	0	169.26
ø(asp)p(asp	273.47	4.55	0.063	0	163.39
ø(asp) p(.)	274.67	5.76	0.034	0	169.15
ø(.) p(t)	287.42	18.51	<0.001	0	144.47
ø(asp) p(t)	294.05	25.13	0	0	144.47
ø(t) p(.)	311.42	42.50	0	0	168.46
ø(t) p(asp)	312.15	43.23	0	0	162.57
ø (t) p(t)	348.35	79.44	0	0	143.76

survival estimate for ameivas was not realistic due to the small sample size (Fig. 3). An effect of time across bait dispersal over the recapture probability was found in the ameiva, with a tendency to decrease during and after bait dispersal (Fig. 4a). In contrast, for the recapture probability of the anoles there was no pattern associated with bait dispersal, but this variation was related to survey events (Fig. 4b). No mortality was observed for either species.

DISCUSSION

We estimated the survival and recapture rates of two native reptile species during a black rat eradication on Desecheo Island, Puerto Rico. During our study, we found no significant change in apparent survival rates across the sampling periods in anoles or ameivas, indicating that the application of rodenticide bait did not result in any detectable mortality or negative effect on both populations. Furthermore, the recapture probabilities for anoles varied through time (between survey events), but were not dependent on bait application, suggesting that while anoles were exposed to rodent bait (23% of individuals), exposure did not impact survivorship within the sampling period. For ameivas, the placebo-bait biomarker study found no direct or indirect exposure of ameivas to rodent bait. For the current study, the precise apparent survival estimate for ameivas was influenced by the small sample size and was not considered statistically valid. The recapture probability estimate for the species decreased during bait application and then increased following the bait application, which may have been an artefact of increased human activity during the operation affecting movement of these animals.

Behavioural ecology, diet, and foraging habitat of lizards are important considerations in understanding potential pathways of exposure to rodenticides. Although we did not observe anoles or ameivas feeding directly on the placebo biomarker or toxic bait, other studies have shown direct consumption of bait by different reptile species (Merton, 1987; Merton, et al., 2002). Bait availability monitoring showed bait disappeared three days after the second bait application, thus removing a pathway of direct exposure (consumption) for ameivas and anoles. However, we anticipate that anoles were exposed to bait via indirect pathways through consumption of invertebrates feeding on bait. Few anole species are dietary specialists and most species, including the Desecheo anole, consume a wide variety of insects and fruit (Meier & Noble, 1991). The ameiva, a larger species than the anole, primarily forages on the ground where it could be easily exposed to bait through secondary pathways (e.g. ground-foraging beetles and ants that feed on bait).

Delayed response to toxicant impacts on reptiles has been previously reported. Telfair’s skinks (*Leiolopisma telfairii*) on Round Island, Mauritius, showed an apparent increased mortality three to six weeks after a brodifacoum bait application (Merton, 1987) and Harper et al. (2011) estimated 4.5% mortality of the Galápagos marine iguana up to two months following rat eradication using brodifacoum. While toxicant as the cause of death was not confirmed during these events, a cautious approach suggests it be considered a risk. While our study was undertaken for approximately three weeks (22 days) after bait was dispersed, the impacts of the rodenticide could not be assessed beyond this timeframe.

This study focused on the survivorship of two reptile species because of the high conservation value of these single-island endemics. Rodenticide application risk assessments should also consider the role of lizards as prey items, and thus as potential toxin pathways to other native species. Food web models that include rodenticide introduction can inform risk assessments, including potential pathways and levels of exposure. Residue analyses can help confirm these assessments. Ultimately, risk assessments for rodent eradication operations using toxicants must evaluate the cost and benefit impacts of these efforts (i.e. negative impacts from using toxicants versus positive impacts from removing rats). Whereas reports of individual reptile mortality during rodenticide-based eradications are evident (Merton, 1987; Harper, et al., 2011) a greater body of evidence suggests that reptile populations benefit following rodent eradication (Jones, et al., 2016). Studies such as ours provide another case study to evaluate the value of island restoration efforts on reptiles. The combination of studies such as these can help managers make informed decisions about the potential negative impacts of rodenticides used during eradication operations versus the expected positive impact to native biota from the permanent removal of threats posed by invasive species.

ACKNOWLEDGEMENTS

This study was supported in part by the United States Fish and Wildlife Service (USFWS), the National Fish and Wildlife Foundation, the David and Lucile Packard Foundation, and private donors to Island Conservation. The views and conclusions contained in this document are those of the authors and should not be interpreted as representing the opinions or policies of the National Fish and Wildlife Foundation. Mention of trade names or commercial products does not constitute their endorsement by the National Fish and Wildlife Foundation. The USFWS Caribbean Islands National Wildlife Refuge Complex provided logistical support and technical assistance during the study period. Thanks to the editor and reviewers for providing insightful comments and suggestions that significantly improved this manuscript. We want to express our deepest gratitude to the field assistants from Island Conservation, USFWS and local biologists for their dedication and commitment that made these conservation efforts on Desecheo possible.

REFERENCES

Bellard, C., Cassey, P. and Blackburn, T.M. (2016). ‘Alien species as a driver of recent extinctions’. *Biology Letters* 12: 20150623.

Burnham, K.P. and Anderson, D.R. (2002). *Model Selection and Multi Model Inference: A Practical Information-theoretic Approach*. New York: Springer-Verlag.

Choquet, R, Reboulet, A.M., Lebreton, J.D., Gimenez, O. and Pradel, R. (2005). *U-care 2.2 User´s Manual. CEFE, Montpellier, France*. <https://ftp.cefe.cnrs.fr/biom/Soft-CR/>.

Cooch, E. and White, G. (2015). *Program MARK: A Gentle Introduction. Colorado State University, Fort Collins*. < http://www.fwspubs.org/doi/suppl/10.3996/122012-JFWM-110R1/suppl_file/10.3996_122012-jfwm-110r1.s8.pdf?code=ufws-site>.

Doherty, T.S., Glen, A.S., Nimmo, D.G., Ritchie, E.G and Dickman, C.R. (2016). ‘Invasive predators and global biodiversity loss’. *Proceedings of the National Academy of Sciences’* 113: 11261–11265.

Evans, M., Herbert, H.J. and Rohnke, K. (1991). ‘Observations on the Status of the Herpetofauna of Desecheo Island National Wildlife Refuge, Puerto Rico’. In: J.A. Moreno (ed.) *Estatus y Distribución de los Reptiles y Anfibios de la Región de Puerto Rico*, pp. 34–36. San Juan: Departamento de Recursos Naturales de Puerto Rico.

Fisher, M. and Muth, A. (1989). ‘A technique for permanently marking lizards’. *Herpetological Review* 20: 45–46.

Harper, G.A. and Bunbury, N. (2015). ‘Invasive rats on tropical islands: Their population biology and impacts on native species’. *Global Ecology and Conservation* 3: 607–627.

Harper, G.A., Zabala, J. and Carrion, V. (2011). ‘Monitoring of a population of Galapagos land iguanas (*Conolophus subcristatus*) during a rat eradication using brodifacoum’. In: C.R. Veitch, M.N. Clout and D.R. Towns (eds.) *Island invasives: eradication and management*, pp. 309–312. Occassional Paper SSC no. 42. Gland, Switzerland: IUCN and Auckland, New Zealand: CBB.

Herrera, J.L. and Bermúdez-Carambot, E.N. (2010). *Survey of the Desecheo Dwarf Sphaero,* Sphaerodactylus levinsi *(Squamata: Gekkonidae) and a Mark-recapture Study with* Anolis desechensis *and* Ameiva desechensis*, Desecheo Island, Puerto Rico*. Internal report to Island Conservation. Unpublished.

Hoare, J.M. and Hare, K.M. (2006). ‘The impact of brodifacoum on non-target wildlife: Gaps in knowledge’. *New Zealand Journal of Ecology* 30: 157–167.

Holmes, N.D., Griffiths, R., Pott, M., Alifano, A., Will, D., Wegmann, A.S. and Russell, J.C. (2015). ‘Factors associated with rodent eradication failure’. *Biological Conservation* 185: 8–16.

Howald, G., Donlan, C.J, Galvan, J.P., Russell, J.C., Parkes, J., Samaniego, A., Wang, Y., Veitch, D., Genovesi, P., Pascal, M., Saunders, A. and Tershy, B. (2007). ‘Invasive rodent eradication on islands’. *Conservation Biology* 21: 1258–1268.

Jolly, G.M. (1965). ‘Explicit estimates from capture-recapture data with both death and immigration-stochastic model’. *Biometrika* 52: 225–247.

Jones, H.P., Holmes, N.D., Butchart, S.H.M., Tershy, B.R., Kappes, P.J., Corkery, I., Aguirre-Muñoz, A., Armstrong, D.P., Bonnaud, E., Burbidge, A.A., Campbell, K., Courchamp, F., Cowan, P.E., Cuthbert, R.J., Ebbert, S., Genovesi, P., ‘Howald, G.R., Keitt, B.S., Kress, S.W., Miskelly, C.M., Oppel, S., Poncet, S., Rauzon, M.J., Rocamora, G., Russell, J.C., Samaniego-Herrera, A., Seddon, P. J., Spatz, D.R., Towns, D.R. and Croll, D.A. (2016). ‘Invasive mammal eradication on islands results in substantial conservation gains’. *Proceedings of the National Academy of Sciences* 113: 4033–4038.

Keitt, B., Campbell, K., Saunders, A., Clout, M., Wang, Y., Heinz, R., Newton, K and Tershy, B. (2011). ‘The Global Islands Invasive Wertebrate Eradication Database: A Tool to Improve and Facilitate Restoration of Island Ecosystems’. In: C.R. Veitch, M.N. Clout and D.R. Towns (eds.) *Island invasives: eradication and management*, pp. 74–77. Occassional Paper SSC no. 42. Gland, Switzerland: IUCN and Auckland, New Zealand: CBB.

Lebreton, J.D., Burnham, K.P., Clobert, J. and Anderson, D.R. (1992). ‘Modelling survival and testing biological hypotheses using marked animals: A unified approach with case studies’. *Ecological Monographs* 62: 67–118.

Marshall, J.E. and Jewell, T. (2007). ‘Consumption of non-toxic baits by grand (*Oligosoma grande*) and Otago (*O. otagense*) skinks’. *DOC Research and Development Series* 272: 5–11.

McKown, M., Swinnerton, K. and Herrera-Giraldo, J.L. (2010). *Desecheo Reptile Monitoring Data.* Internal report to Island Conservation. Unpublished.

Meier, A.J. and Noble, R.E. (1991). ‘Notes on the natural history of *Anolis desechensis’*. *Florida Field Naturalist* 19: 17–18.

Merton, D. (1987). ‘Eradication of rabbits from Round Island, Mauritius: A conservation success story’. *Dodo* 24: 19–43.

Merton, D., Climo, G., Laboudallon, V., Robert, S. and Mander, C. (2002). ‘Alien mammal eradication and quarantine on inhabited islands in the Seychelles’. In: C.R. Veitch and M.N. Clout (eds.) *Turning the tide: the eradication of invasive species*, pp. 182–198. Occasional Paper SSC no. 28. IUCN SSC Invasive Species Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.

Morrison, J.A and Menzel Jr, E.W. (1972). ‘Adaptation of a free-ranging rhesus monkey group to division and transplantation’. *Wildlife Monographs* 31: 1–79.

Russell, J.C. and Holmes, N.D. (2015). ‘Tropical island conservation: Rat eradication for species recovery’. *Biological Conservation* 185: 1–7.

Seber, G.A.F. (1965). ‘A note on the multiple recapture census’. *Biometrika* 52: 249–259.

Shiels, A.B., Pitt, W.C., Sugihara, R.T. and Witmer, G.W. (2014). ‘Biology and impacts of Pacific Island invasive species. 11. *Rattus rattus*, the black rat (Rodentia: Muridae)’. *Pacific Science* 68: 145–184.

Tershy, B.R., Shen, K.W., Newton, K.M., Holmes, N.D. and Croll, D.A. (2015). ‘The importance of islands for the protection of biological and linguistic diversity’. *BioScience*: 10.1093/biosci/biv031.

Towns, D.R., Atkinson, I.A.E. and Daugherty, C.H. (2006). ‘Have the harmful effects of introduced rats on islands been exaggerated?’ *Biological Invasions* 8: 863–891.

U.S. Fish and Wildlife Service (2016). *Final Environmental Assessment: Desecheo National Wildlife Refuge Rat Eradication Project*. U.S. Department of the Interior Fish and Wildlife Service, San Juan. <https://www.fws.gov/caribbean/refuges/desecheo/>.

White, G.C. and Burnham, K.P. (1999). ‘Program MARK: Survival estimation from populations of marked animals’. *Bird Study* 46: 120–138.