Rhesus macaque eradication to restore the ecological integrity of Desecheo National Wildlife Refuge, Puerto Rico

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Abstract A non-native introduced population of rhesus macaques (*Macaca mulatta*) was targeted for removal from Desecheo Island (117 ha), Puerto Rico. Macaques were introduced in 1966 and contributed to several plant and animal extirpations. Since their release, three eradication campaigns were unsuccessful at removing the population; a fourth campaign that addressed potential causes for previous failures was declared successful in 2017. Key attributes that led to the success of this campaign included a robust partnership, adequate funding, and skilled field staff with a strong eradication ethic that followed a plan based on eradication theory. Furthermore, the incorporation of modern technology including strategic use of remote camera traps, monitoring of radio-collared Judas animals, night hunting with night vision and thermal rifle scopes, and the use of high-power semi-automatic firearms made eradication feasible due to an increase in the probability of detection and likelihood of removal. Precision shooting and trapping were the primary methods used throughout the campaign. Long-term monitoring using camera traps and observed sign guided a management strategy that adapted over time in response to population density and structure. Lessons learnt include, 1) macaques quickly adjusted their behaviour in response to human presence and removal methods, 2) camera traps and thermal scopes provided high detection likelihood compared to other methods, and 3) the use of Judas animals and night hunting with thermal and night vision rifle-scopes facilitated removals. The removal of macaques from Desecheo Island appears to be the first introduced non-hominid primate eradication from an island.

Keywords: conservation, invasive species, island restoration, Judas, *Macaca mulatta,* primate

INTRODUCTION

Islands occupy ~5.5% of Earth's terrestrial surface area but contain more than 15% of terrestrial species (Kier, et al., 2009), 61% of all recently extinct species, and 37% of all critically endangered species on the International Union for Conservation of Nature (IUCN) Red List (Tershy, et al., 2015). Non-hominid primates (NHPs) are intelligent and adaptable animals (Fooden, 2000). World-wide, 78 introduced insular populations are known on 63 islands (Jones, et al., 2018). Despite their potential for ecological impacts, including being implicated in 69 insular species extinctions and extirpations globally (Jones, et al., 2018), management is problematic as NHP's demonstrate behavioural traits making them challenging to remove and few practitioners are experienced in their control or eradication (Evans, 1989; Feild, et al., 1997; Breckon, 2000; Kemp & Burnett, 2003; Strier, 2016; Jones, et al., 2018). Six eradication attempts have been documented globally and all were unsuccessful (Jones, et al., 2018). Desecheo Island (Desecheo), has been the site of half of these attempts targeting a population of invasive rhesus macaques (*Macaca mulatta*).

Historically, Desecheo was a major seabird rookery. In the early 1900s tens of thousands of seabirds representing seven species were nesting on the island (Bowdish, 1900; Wetmore, 1918; Struthers, 1927; Meier, et al., 1989; Noble & Meier, 1989). The most numerous species, brown boobies (*Sula leucogaster*), numbered 8,000 - 15,000 individuals (Danforth, 1931 cited by Noble & Meier, 1989; Wetmore, 1918) with red-footed boobies (*S. sula*), brown noddies (*Anous stolidus*), and bridled terns (*Sterna anaethetus*) accounting for another 12–14,000 birds. Humans shooting birds and harvesting eggs, habitat destruction through farming, ranching and military munitions training, and introduced feral goats (*Capra hircus*) and black rats (*Rattus rattus*) reduced populations of most seabird species and restricted many species to less accessible areas of the island (Wetmore, 1918; Struthers, 1927; Evans, 1989; Meier, et al., 1989). Feral goats were recently eradicated (2009; Hanson, unpublished data) while black rats were eradicated in 2016 after an initial attempt failed in 2012 (Will, et al., 2019). However, predation by rhesus macaques (macaques), introduced in 1966 for research purposes, resulted in the complete loss of seabird breeding on the island and was considered the most significant threat to wildlife on Desecheo (Evans, 1989; Meier, et al., 1989; Noble & Meier, 1989). In 1969, massive raids by macaques on booby nests were reported, with macaques pushing boobies off their nests and consuming an estimated 200–300 eggs per week (Noble & Meier, 1989). In 1987, although nests were built and eggs laid, brown and red-footed booby nesting success was zero (Noble & Meier, 1989). Macaques contributed to the extirpation of at least five seabird species, one land bird species, and led to the depauperate state of resident land birds on Desecheo (Noble & Meier, 1989; Island Conservation, 2007). Macaques on Desecheo have also been implicated in modifying vegetation structure, contributing to the extirpation of several plant species, and preying on native reptiles including three island-endemic lizards (Evans, 1989; Breckon, 2000; Island Conservation, 2007).

In 1976, Desecheo was designated a National Wildlife Refuge and the island was transferred from the Department of Health, Education, and Welfare to the U.S. Fish and Wildlife Service (USFWS). At this time the removal of macaques was identified as an objective to restore the island's ecological integrity (Island Conservation, 2007). Between 1976 and 1988, three eradication attempts took place with a total of 155 animals removed (Herbert, 1987; Evans, 1989; Breckon, 2000; USFWS, 2007). An initial attempt was reported to have insufficient funding to proceed (USFWS, 2007). The second eradication attempt required multiple removal methods to target wary individuals. After 246 days of effort it was assumed all individuals had been removed, but less than a year later 15 individuals were confirmed on the island (Evans, 1989). The third eradication attempt ended prematurely in 1988 due to a lack of resources; it was believed at that time that two

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. 249–255. Occasional Paper SSC no. 62. Gland, Switzerland: IUCN.

Fig. 1 Aerial images of Desecheo National Wildlife Refuge.

males and an unidentified juvenile were all that remained (USFWS, 2007). However, Breckon (2000) reported 11 animals in a single troop in 1996. Lack of funding, animals becoming educated to removal techniques, and unreliable detection methods contributed to the lack of eradication success. In April 2007, Island Conservation in partnership with USFWS developed a restoration plan (Island Conservation, 2007) that outlined a strategy and methods to eradicate macaques from the island. The planning effort coincided with the development of an environmental assessment covering the removal of non-hominid primates from the Commonwealth of Puerto Rico and its offshore islands (USDA, et al., 2008), including Desecheo. Here we report on the 2008–2017 eradication of macaques from Desecheo National Wildlife Refuge.

STUDY SITE

Desecheo is a small (117 ha) uninhabited hilly island (18° 23' N, 67° 29' W) situated roughly 21 km off the west coast of Puerto Rico. The vegetation is a mosaic of grassy patches, shrublands, woodlands, and semi-deciduous forest. The grassy patches and shrublands are on exposed ridges and screes, especially on the northern and north-eastern slopes, which face the prevailing winds. The woodlands are typically found covering coastal slopes, upper east- and south-facing slopes, along drainages, and within valley floors. The floral community of Desecheo is dry forest habitat. The island is composed primarily of Tertiary volcanic sandstones and rises to 218 m. Steep slopes fall away from five ridges interconnected by a perpendicular ridge which rises abruptly from the northeast coast (Fig. 1). There is no permanent surface water or spring on the island.

METHODS

Macaques carry B-virus (*Cercopithecine herpesvirus* 1), which can be lethal to humans (Huff & Barry, 2003), so animal handling was minimised where possible. The Desecheo macaque population originated from a population with a high occurrence of the disease (Shah & Morrison, 1969) and most likely had B-virus. When animals were handled, strict protocols were followed (Holmes, et al., 1995).

Several principles were employed to increase the likelihood of success: 1) target whole groups where possible, 2) limit opportunities to educate animals, 3) first utilise methods that would not impact the efficacy of other methods, 4) have sufficient methods to remove animals faster than the rate of reproduction, and 5) provide multiple detection methods that were independent of removal techniques, capable of detecting animals at very low densities. Variations of live-trapping and hunting were selected after a suite of possible techniques, including the use of toxicants, biological control, kill trapping, and immunocontraception, were evaluated for use on Desecheo (Island Conservation, 2007). The strategy to remove macaques was structured around three general phases and was adaptively managed from 2008 to 2017 (Fig. 2). The initial phase relied on live-trapping to provide a population reduction without educating animals to subsequent hunting methods. Select individuals captured were radio collared then released and tracked as sentinel (Judas) animals to facilitate hunting of a social species. The second phase aimed to remove remaining individuals through hunting and transitioned to a third phase where monitoring was anticipated to confirm eradication. A revised approach was required when macaques could only be detected by remote cameras. This involved specialised night hunting technology paired with the use of Judas animals and a distinct change in hunting strategy which primarily occurred outside of daylight hours.

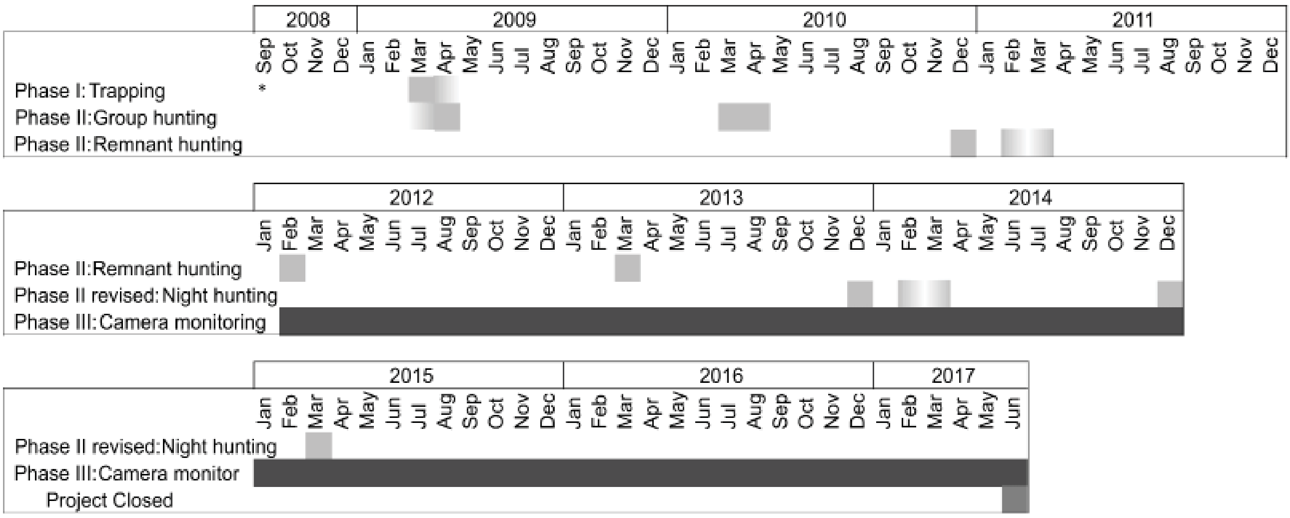

Fig. 2 Project timeline of events. (*) field work initiated by seasoning traps on site.

Phases relied on a team temporarily camped at one of two sites on the island with all equipment and supplies being delivered then removed each trip. The first campsite, serviced by helicopter, was located near the peak of the island. This site supported up to nine staff, was utilised from project initiation through the duration of group hunting (see Fig. 3) and allowed centralised access to the entire island. A second site was later established along the coastline to allow boat access and minimise logistic expenses for a reduced field team to complete the eradication.

Phase I. Trapping and Judas animal release (2008–2009)

Eighteen *#208 dual-door cage traps* (Tomahawk Live Trap, Hazelhurst, WI) were placed in groups of three across the island at sites of known macaque activity. Trap dimensions of 107 × 38 × 38 cm were considered large enough to capture multiple animals, based on mainland Puerto Rico trapping efforts (López Ortiz, 2015). Concurrently, a single, large 5 m wide group-style trap (Day, 2004) was built upon a flat, ridgetop location. This trap was constructed in an octagon shape with a wood frame, cyclone fence sides and skirt. A 60 cm overhanging eave and 60 cm vertical wall made from sheet metal faced internally to prevent animals from exiting. A remote-controlled drop-net was used in another site, comprising an 11 × 11 m reinforced net elevated above the ground by roughly 2 m around the edge with a tented peak of 5 m. Pre-baiting took place across all trap sites for two weeks with whole and sliced oranges. Oranges were chosen based on successful results experienced during previous eradication campaigns (Evans, 1989). Prior to departing the island, all cage traps and a single side of the octagon trap were wired open for animals to become familiar with their presence.

Seven months later all traps were activated and a network of 48 padded leg-hold traps was installed along areas suspected to have macaque activity. Traps were typically set in groups of two or more and each were accompanied by a magnetically triggered trap-monitor. Monitors were in place to support near-real-time monitoring of each trap's status which was communicated by radio-transmitter to a R-1000 telemetry receiver (Communications Specialist, Orange, CA); traps were monitored several times daily. A second pre-baiting effort took place during this time. To supplement oranges and provide greater variety, additional bait types including mangos, chicken eggs, and a water drip pan were utilised and replaced regularly. A remote-controlled audio lure (FoxPro Crossfire, Lewistown, PA) programmed with macaque calls also was deployed in association with baits at the drop-net location. Various leg-hold traps were set with lures including mirrors, wind chimes, streamers, feathers, or brightly coloured objects suspended above the trap site. Traps that did not receive a lure were set as a blind set with no distinguishing features separating it from the original site.

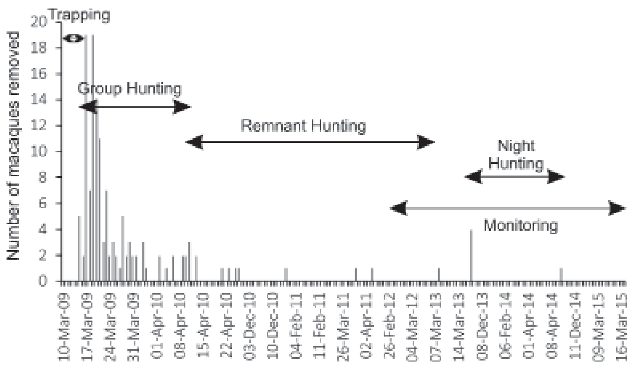

Fig. 3 Number of macaques removed over time in relation to project phase.

During this timeframe, a wild-caught adult male macaque from mainland Puerto Rico was quarantined, sterilised by vasectomy, radio-collared (Telenax, TXE-311C, Playa del Carmen, Mexico), and transported to Desecheo. This individual was released upon arrival and monitored daily as a Judas animal.

Phase II. Hunting (2009–2013)

Trapping activities from Phase I overlapped with this phase for one field trip. Hunting was intended to remove remnant individuals that were avoiding trap sets. Timing of this phase was based on the seasonally deciduous dominant tree species (*Bursera simaruba*) which leafed-out in response to rainfall. Field staff were selected from within Island Conservation and from White Buffalo Inc. (Connecticut, USA) based on their experience in precision shooting and demonstration of eradication ethic. In preparation, key vantage points were identified while conducting a census of the population before any removals took place. This assessment effort also was used to identify concealed shooting hides that offered a wide field of view for observation and clear shooting lanes. Hunting was considered capable of placing all individuals at risk of removal, particularly once population numbers were reduced with a successful trapping phase.

Troop removal (2009–2010)

Hunting predominately relied on an ambush-then-stalk strategy that collected troop characteristics (number of individuals, body size of individuals) and movements at dusk while macaques located a location to roost. In certain circumstances, where specific trees were identified as a roost site, field staff would proceed with hunting in the middle of the night while utilising spotlights and close-range shooting. In most circumstances, staff would wait until nightfall before returning to camp to develop a strategy of engagement for the following day. Before first light, field staff would be dispatched to pre-established hides or to new locations thought to offer a better vantage point of a troop's roost location. Field staff were equipped with high-capacity centrefire semi-automatic .223 Remington or 6.5 Grendel rifles with telescopic sights ranging from 4.5× to 20× magnification and reticles matched to each firearm's ballistics. Other field staff were stationed along known escape routes with high capacity 12-gauge semi-automatic shotguns.

Shooters would communicate via 2-way radio to assess the troop and attempt to identify the number of individuals, their hierarchy, and body size. Body size class was estimated based on body mass and ranked as one through five. Groups would only be engaged if it was considered a high likelihood that all individuals could be removed. Field staff that had a visual on the dominant individual would engage with the first shot, with other staff following by removing individuals that presented a lethal shot opportunity. Adult females (often dominant) were removed first, followed by adult males and juveniles. Field staff would continue to monitor the site while supporting shooters would be redistributed to areas where escapes were thought to have possibly occurred. Once macaque activity ceased in the canopy, field staff equipped with close-range firearms would enter the site to remove any remnant individuals. Removals were tallied and the animals' body size classes would be recorded. Follow-up visual confirmation of carcasses occurred whenever possible. Any known escapes were recorded, along with their size class. Confirmed removals and escapes would be cross-referenced with the troop size estimate. To improve the detection of roosting troops during this phase a commercial-grade handheld thermal camera (FLIR, P620, Wilsonville, Oregon, USA) was trialled.

Remnant removal (2011–2013)

After the initial knock-down of the macaque population, the project shifted focus to the detection and removal of lone individuals and reconstituted groups created after troops were fractured. Before dawn, field staff were stationed across the island to conduct focused observations over as much landscape as possible. Visual observation of canopy movement and audible cracks of tree limbs and masticated seeds were the primary cues of macaque presence prior to direct observation. If a detection was made, the number of animals was estimated and, if confidence existed that the group or individual could be removed, field staff would proceed by removing individuals through shooting. When assistance was required, additional field staff would be guided to the site offering the highest likelihood of removing the entire group. If escapes were thought to be probable, the team would reassess the opportunity and hold off until another situation presented greater confidence in removal.

Phase II revision. Night hunting (2013–2015)

Remote cameras (see monitoring) continued to detect macaques that were undetectable to field staff. Methods employed were re-analysed, leading to detection dogs and night hunting technology being considered. Dogs that could effectively track animals traveling on the ground and through forest canopy were considered necessary and a breed of mountain cur that is used to pursue squirrels was identified. Additionally, managers of NHPs on mainland Puerto Rico had sourced effective thermal hunting optics and began demonstrating success with night hunting.

In 2013, three macaques were selected from mainland Puerto Rico to be used as Judas animals to support night hunting. Young female macaques were chosen as they were considered more likely to readily associate with remnant animals on Desecheo. Replicating methods developed for Judas goats, each macaque was sterilised via tubal ligation, fitted with a radio-telemetry collar (ATS, M2950B, Isanti, Minnesota, USA), and received a Compudose® 200 (25.7 mg estradiol; Elanco, Indianapolis, USA) implant to induce prolonged oestrus (Zehr, et al., 1998; Campbell, et al., 2005; Campbell, et al., 2007). Radio telemetry collars had infrared (IR) reflective patches sewn in and a solar powered light-emitting diode (LED) epoxied to them to facilitate detection at night. Judas macaques were transported to Desecheo via boat and released.

Hunting methodology changed to working strictly at night, initially incorporating mainland Puerto Rico staff and their equipment to train the project team. Based on the success of these methods, thermal weapons scopes with a built in adjustable reticle (BAE Systems, Inc. ATS-6000M, Arlington, Virginia, USA), a 3rd generation night vision clip-on unit (Knight Optics Ltd., Krystal 950, Harrietsham, Kent, UK) used in combination with pre-existing telescopic firearms optics, and an IR laser illuminator (Jager-Pro LLC., JP-IR Laser, Fortson, Georgia, USA) were procured to improve detection and facilitate removals. Night operations continued with 2–3 field staff using the thermal scope to detect heat signatures of macaques in conjunction with telemetry scans for Judas animals (described in Phase III). When no Judas animals were present in a group all were targeted. When Judas animals were present night vision in conjunction with infrared illuminators were used to detect IR reflective patches sewn into collars to determine which macaque in the group was the Judas, facilitating removal of only uncollared macaques.

Phase III. Monitoring (2012–2017)

Monitoring occurred simultaneously with the removal of remnants and night hunting in Phase II. The presence of macaques was assessed through active and passive monitoring techniques; each independent of removal methods. Active monitoring occurred through visual observation of animals and the detection of fresh sign. Passive monitoring trialled acoustic recording units (Wildlife Acoustics, Maynard, MA), but relied primarily on a network of 16–26 Hyperfire PC900 no-glow cameras (Reconyx, Holmen WI). Cameras were placed in locations known to have had previous macaque activity or at sites which offered a clear field of view across a travel route. Specific attention was given to rocky bluffs, exposed patches of slope, or within tree canopies that were dominated by horizontal tree branches. Tuning the camera field-of-view used an integrated "walk-test" function which indicated where the camera would be triggered by movement. Lures made from cord passed through brightly coloured balls were installed at sites which could accommodate a swinging item without triggering the camera's motion sensor. Cameras were serviced every 3–9 months, where memory cards (32GB, 95mb/s write speed) were switched for empty ones and batteries were replaced if below 60% charge. Camera operational settings were programmed to operate from one hour prior to dawn to one hour after dusk, provide the highest sensor sensitivity, take five photos in succession, and reset immediately after a trigger event.

RESULTS

A total of 140 macaques were removed from Desecheo Island between 2009 and 2015, excluding Judas animals translocated from mainland Puerto Rico (Fig. 3). The cost of the 2007–2017 campaign was US$ 1.229m. The majority of costs (73%) were associated with implementation and monitoring from 2009 to 2015 at US$ 893k. Planning and preparation in 2007/8 utilised US$ 214k and US$ 121k was spent on confirmation over 2015–2017.

Phase I. Trapping

Baiting to encourage macaques into traps was ineffective. Additional lures such as a water drip and audio lures also proved unsuccessful as evidenced by camera traps. Non-target species, primarily black rats and hermit crabs, would consume any bait not suspended from the ground. Bait that did persist required regular replacement due to the arid climate on the island; fruits quickly desiccated and non-boiled eggs rapidly spoiled. After 26 days, unsuccessful traps that were located in remote sites and not easily accessible by field staff were closed to ration bait and improve the efficiency of trap monitoring. Traps left open were outfitted with florescent flagging as a visual lure and left open. A total of 546 trap nights accrued between cage traps, the group-style octagon trap, and the drop net with zero trap success.

Padded leg-hold traps were in place for 1,344 trap nights and resulted in the capture of 13 macaques; 10.7% of the population. Three received radio collars and were released as Judas animals; all but one was sterilised. Traps equipped with novel visual lures, particularly reflective materials, demonstrated a higher catch rate than non-reflective items. Two blind sets established as a part of a three-trap grouping, demonstrated success simultaneously. Traps placed at the base of trees where macaques would leap into the tree were particularly successful.

The adult male Judas animal transported to Desecheo from mainland Puerto Rico was found dead 16 days after its release for unknown reasons.

Phase II. Hunting

Hunting reduced the population of macaques to near undetectable levels by removing 118 individuals (84% of 140 macaques removed) over the span of two trips (46 days where hunting took place) across two years. Estimates of animals remaining at the end of each trip significantly underestimated the population. Three animals were known to be present at the end of the second trip, one of which was a sterilised Judas macaque. Follow-up hunting focused on the detection and removal of remnant macaques, which removed four individuals in five field trips (66 days where hunting took place) over three years. At this time, camera monitoring indicated six individuals remained and evidence of population recruitment, shown by one newborn juvenile.

Phase II. Revision

The introduction of night hunting strategies supported by thermal and night vision technology, field staff's intimate knowledge of the island's terrain, and leveraging Judas animal behaviour resulted in five macaque removals over five trips (50 days where hunting took place) over 2.5 years.

Phase III. Monitoring

The single most effective monitoring tool proved to be the remote camera network. Camera density ranged from one camera per 4.5–7.25 ha. Roughly 450,000 images were collected throughout the entire campaign. The volume of images varied greatly depending on the length of a monitoring period (2–9 months) with a mean of ~50K images. More than 2K macaque detections were compiled. Camera placement was impacted by vegetation growth over time leading to the majority of images being false captures. Once population numbers were reduced to five individuals the entire group could be tracked with at least one detection of each individual occurring per monitoring period. Judas animals, with unique physical and collar characteristics, could be identified within camera images and were used to indicate camera network efficacy; all Judas animals were detected per monitoring session and were easily distinguishable from wild individuals due to the presence of the collar.

Acoustic recording units were trialled but did not result in confident detections by monitoring macaque vocalisation. This tool was quickly discounted as an effective option to monitor animals at low density. The lack of vocalisation was corroborated by field staff who indicated macaques no longer vocalised with the same frequency once the population was reduced to less than ten individuals.

Additional monitoring took place though the tracking and assessment of Judas animals. Of the three animals captured on-island, one unsterilised male was found dead due to unknown causes, a second sterilised male was inadvertently shot during the hunting phase of the project, and a third sterilised female experienced a collar failure and integrated back into the population. This individual was one of the last macaques removed. Of the three additional Judas animals later captured on mainland Puerto Rico and released in Phase III, none experienced collar failure although the installed LED lights did not function in the field. After release, one was indistinguishable amongst a group of wild macaques and shot while night hunting with thermal optics. The remaining two Judas macaques formed an independent pair. One Judas animal was later removed to disrupt the social balance which resulted in a more consistent interaction between the remaining Judas animal and the two known remnant animals. Field staff removed one remnant animal before the final Judas animal was found dead in 2016. This Judas animal was associating with the last wild macaque known to remain on island.

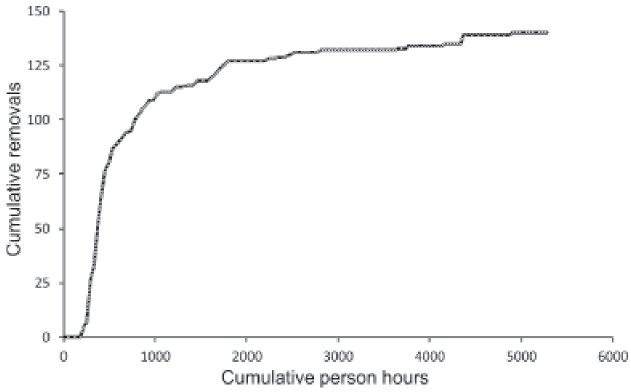

Fig. 4 Number of removals in relation to effort expended over time.

Twelve hunting trips were conducted totalling 5,280 detection hours (Fig. 4). A single wild adult matching the description of the last known wild macaque was detected on 15 occasions by the camera trap network over approximately 41 months indicating that this was the only wild individual that remained. Over the same timeframe, no juveniles were shot or detected, reflecting no reproduction. As a result, the project was closed in June 2017 with the understanding that the population was functionally extinct.

DISCUSSION AND LESSONS LEARNT

The campaign to remove macaques from Desecheo took 10 years, 17 field trips, variations of two primary methods – trapping and hunting – and a network of remote monitoring cameras to complete.

Pre-baiting attempts were unsuccessful, resulting in the ineffectiveness of baited traps. Trapping efforts may have benefited from trials and a longer pre-baiting period which also would take into account timing to allow learnt behaviours to transfer through the population. Locally available food items including nuts and berries were considered but discounted as they were found in abundance across Desecheo. Having a diet with limited exposure to novel food items on Desecheo is thought to have contributed to their disinterest in baits provided. Once baited trapping ceased, hunting and leg-hold trapping were then relied upon as the sole methods. Trapping efforts on mainland Puerto Rico that utilise a variety of fruits have resulted in up to 50% of project removals (López Ortiz, 2015) suggesting that trap success is variable across sites and should remain a management consideration.

When hunting was initiated, only troops where all individuals were thought to be at risk of removal were targeted. Although this method proved to be effective and efficient, it became apparent that escapes likely occurred unbeknownst to field staff as macaques quickly adjusted their behaviour in response to human presence and removal methods. Macaques increasingly avoided detection during the day, and if field staff were detected, would regularly select a route of escape that placed an object between them and the observer, limiting shot opportunities, as they fled to an adjacent watershed. This behaviour eventually nullified daylight hunting and required revised methods and tactics to improve the probability that an individual would be detected.

Advanced night hunting equipment facilitated both detections and removals. In many instances macaques were detectable only with a thermal scope, even when field staff knew the location of the animal. As a result, an integrated shooting reticle with the ability to remove and return the scope to the firearm without having any shift in the scope's point of aim was considered critical. Furthermore, having the ability to de-couple the night vision from traditional hunting scopes proved valuable as the firearm's point of aim did not need to be recalibrated for daylight hunting; only the thermal scope could be used in daylight without damaging the equipment or losing the capability to continue hunting into dawn with the firearm paired with night vision. A less sophisticated general-use FLIR thermal camera was trialled early in the project although low image resolution limited the unit's detection range. At ranges beyond ~150 m, individual pixels were estimated to be larger than a macaque's heat signature. The camera's limited range resulted in zero detections and thus general-use thermal tools were abandoned.

If the project had been initiated with advanced night hunting thermal equipment and Judas animals it is estimated that its duration and cost would have been significantly reduced. Hunting activities could have taken place regardless of seasonal variation in vegetation, detections would have been more frequent, and entire groups could have been removed with greater confidence, precision, and frequency. Furthermore, the incorporation of suppressed firearms with subsonic ammunition would have offered additional advantages. Suppressed firearms would likely have reduced the flight response of any associated macaques due to abated firearm report, projectile "crack," and identification of shot origin.

Camera traps provided high detection likelihood as compared to other passive detection methods, particularly once the density of animals was reduced to near-zero. Camera placement, and the decision to increase the size of the network, was guided by weeks of observation before and after removals took place and is believed to have significantly improved detection probability. Staff were familiar with the use of the same cameras with feral cats (*Felis catus*), however, a greater awareness of the camera's field-of-view and trigger window was necessary when setting cameras to monitor a three-dimensional environment. The presence of an accurate walk-test function offered confidence that cameras were set to detect animals at varying elevations and distances. In addition, a robust camera design offered confidence that cameras would have a low failure rate regardless of adverse field conditions including hurricanes, intense heat, and sustained humidity. Failures generally included screen malfunctions, walk-test function ceasing to work, and component corrosion due to termites burrowing into the camera case.

Ongoing commitment from the partners throughout a dynamic project enabled the eradication to succeed. There was a significant investment up front to start the project and the initial projected methodologies and associated tools did not result in eradication. As a result, the project lasted longer than expected and overall costs were higher than anticipated. These costs may have been reduced if the funding was available in larger amounts rather than in annual allocations, allowing higher intensity effort over a shorter period of time. However, it is also believed that the long periods between hunting trips was beneficial because macaques became less agitated, resumed routine behaviours, and were more likely to be detected.

Macaques becoming educated to removal techniques, unreliable detection methods, and a lack of funding were linked to previous failures on Desecheo. To reduce the probability that similar issues would impact the success of this attempt, the partnership routinely and transparently reassessed all aspects of the project including the funding required to proceed, equipment and field trips considered necessary to achieve eradication, and how to interpret results. These factors guided an adaptive management strategy that supported principles outlined within original project planning. This shared effort resulted in a robust relationship that was capable of addressing a dynamic project and uncertainty in a solution-oriented, step-by-step manner. As a result, a project with no precedent of success – incentivised by a high conservation reward – was completed in a conscious and calculated fashion.

CONCLUSION

Desecheo Island is the location of the first successful removal of introduced non-hominid primates from an island that we are aware of. The project was contingent on the strength of the partnership, specialised equipment, and commitment of an experienced field team with a strong eradication ethic that followed a plan based on eradication theory. These factors were all critical to the project's success after a protracted time-period. The challenges of this eradication required several revisions to the original methodologies and strategies, as well as continued funding beyond the original budget projections.

Desecheo Island, and the unique species that are found there are now safe from invasive mammals after nearly a century. This restoration action should enable the island's return as the most important seabird colony within the region.

ACKNOWLEDGEMENTS

This work was made possible by the generous support of our philanthropic donors and funding from the United States Fish and Wildlife Service. We also would like to thank W. Wolfrom and B. Mancial, J. Padilla, F. Boyd, L. Figueroa, M. Evans, J. Herbert, J. Schwagerl, E. Melendez, A. Saunders, B. Tershy, J. Bonham, C. Bergman, L. Bennett, W. Jolley, D. Will, E. Oberg, J.L. Herrera-Giraldo, K. Swinnerton, C. Figuerola-Hernandez, R. Rodts, T. Robinson, W. Shockley, M. Garcia, O. Acevedo, and many other USFWS, DNER, Puerto Rico law enforcement, and IC staff for assisting with planning, field work or logistical support. Mayaguez Zoo and Puerto Rico DNER provided support with sourcing and preparing Judas macaques. USDA Wildlife Services and DNER staff assisted with two field trips and graciously shared their skills and knowledge acquired from their own night fieldwork.

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