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Endemic Top Predator Response to Goat Eradication on Santiago Island: the Galapagos Hawk and its Diet.

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A Thesis Submitted to the Graduate School at the University of Missouri – St. Louis in
partial fulfillment of the requirements for the degree
Master of Science in Biology with an emphasis in Ecology, Evolution and Systematics

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Abstract

The eradication of invasive species is becoming a common approach for the conservation of native communities around the world. However, few of the programs complete exhaustive studies and monitoring of the impact of these eradications. The current study is one component of a long-term monitoring of the Galapagos Hawk (*Buteo galapagoensis*) before, during and after the eradication of goats (*Capra hircus*) on Santiago Island in 2006. As the herbivory pressure was released, we foresaw that the rapid vegetation recovery would affect the hunting success of the Galapagos Hawk on its preferred terrestrial prey. We performed a comparative study on the feeding ecology of the hawk by direct observation of prey delivered to nests pre- (1999-2000) and post-goat eradication (2010-2011). We predicted that the Galapagos Hawk would adapt to its new environment by shifting its diet composition, from predominantly terrestrial prey before goat removal to a more arboreal prey base after goat removal, and that the effect would differ across habitat types. Additionally, we were interested in assessing the response of introduced rats (*Rattus rattus*) to the removal of goats. Contrary to our primary hypothesis, we were unable to find overall changes diet composition of terrestrial and arboreal prey. Nonetheless, the consumption of terrestrial prey did vary between vegetation types, confirming the influence of vegetation on the amount of prey consumed. Even though terrestrial prey consumption did not change much, it consisted of a much higher proportion of introduced rats. However, rat-trapping indicated no increases in abundance of rat populations, which coupled with the increased consumption of rats by hawks, suggests top predator control on the rodent invader. Moreover, it appears that the hawk's ability to hunt arboreal prey is hampered in areas with high vegetation, as consumption of arboreal prey in the higher transition zone habitat after eradication is significantly lower than before. Consequently, hawks in densely vegetated territories now depend largely on introduced rodents as a food source. Overall, we observed how the territorial population of the top predator in this community has, so far, been able to withstand these changes by adjusting to a new diet and possibly exert top down control on other potentially threatening invaders. Thus, we have learned that special consideration should be given to natural trophic interactions to understand the potential effects of invasive species eradication.

Introduction

Isolated island communities often develop in the absence of large herbivores (Bowen and Van Vuren 1997) and/or predators, and their lack of defenses against introduced species makes them especially vulnerable. The threat introduced species pose on the endemic fauna and flora has made such island communities a target of conservation efforts. Eradication is often the preferred method of invasive species management and has been very effective in preserving local habitats and their biodiversity (Donlan and Wilcox 2008). But when introduced species have been in a system long enough that they have displaced native species and replaced their function in the community, their removal could have unforeseen negative effects on native populations that have already adapted to their presence (Zavaleta et al. 2001). It is then of great importance for future management actions to identify the effects of such eradications on native communities and the mechanisms through which these effects appear.

Not exempt from the anthropogenic pressures exerted on them, the Galapagos Islands have been subjected to many biological invasions. During 200 years of human presence many species of domestic animals were intentionally brought to the islands, as a means of subsistence, and others inadvertently. Goats, *Capra hircus*, are thought to have been introduced first on Santiago Island in 1813 (as stated in Schofield 1989) and reached an approximate of 100,000 individuals by the 1970's (Calvopiña and De Vries 1975). For over a century, goats have grazed and damaged these ecosystems; it is possible then that some native organisms have ecologically adapted to their presence. Despite the threat they pose to many of the endemic species, goats may have benefited at least one, the Galapagos Hawk (*Buteo galapagoensis)*. During large periods of the eradication campaigns hunted goat carcasses were left on site, constituting a food item in the diet of juvenile hawks particularly (Levenstein 2008). Furthermore, by clearing large areas of vegetation cover (Calvopiña and de Vries 1975), goats likely enhanced the hawks' hunting success and eliminated refuges for ground prey. How, then, does the extirpation of this invasive grazer affect the ecology of the only diurnal raptor on the archipelago?

In 2006, Santiago Island (585 km^2) became the world's largest island on which eradication of goats was successfully completed (Cruz et al. 2009), resulting in a remarkable recovery of vegetation. This vegetation recovery is providing us with the unique opportunity to study its impact on the Galapagos Hawk population. Like on other islands from which goats were previously eradicated, Santa Fe and Pinta (De Vries 1977, Hamann 1979, Hamann 1993), recovery of vegetation on Santiago has been very rapid. Species-level studies have found that the populations of three highly threatened species, *Galvezia leucantha* subsp. *Porphyrantha*, *Scalesia atractyloides* and *Scalesia stewartii* are re-establishing (as reviewed in Atkinson et al. 2007). Currently on our James Bay study area, species of *Bursera*, *Cordia* and *Opuntia* already dominate arid and transitional landscapes, other shrubs (*Waltheria, Cryptocarpus, Scutia* spp.) have regenerated, and grasses and herbs such as *Mentzelia aspera* and even introduced species have spread swiftly, hindering our access to several areas (especially in the more humid transition zone) (Pers. obs.). At Sullivan Bay *Scalesia stewartii* now covers large areas that were nearly barren lava before goat eradication. This notable recovery of vegetation on Santiago Island could have a great impact on the hawks' hunting success.

The uncontrolled spread of dominant introduced plant species might exacerbate the impact of vegetation recovery; in fact, it is a rising concern in light of introduced species eradication worldwide (Kessler 2002, Bullock et al. 2002, Scowcroft and Conrad 1992). On James Bay the recovery of introduced plants is imminent; the spread of the introduced *Senna obtusifolia* is extremely apparent and covers large areas that were previously unvegetated (Pers. obs.). Outside our study area, in the highlands of Santiago, other introduced species of plants include *Citrus* spp., *Persea americana* (Avocado), *Rubus niveus* (Blackberry), and *Psidium guajava* (Guava). Perhaps the most important will be the spread of the introduced blackberry that has become even more evident on Santiago after the removal of introduced herbivores (Rentería et al. 2009). In spite of the rising efforts of scientists to control the blackberry population, no management approach has been found effective. The feared spread of blackberry could change the composition and abundance of Galapagos Hawk prey and even inhibit their success in hunting.

In addition to habitat degradation due to overgrazing on native vegetation, goats exert other pressures. The population of Galapagos Giant Tortoises, *Geochelone elephantopus*, has been largely decimated by hunting, damage and predation of eggs and hatchlings by feral pigs (*Sus scrofa*), eradicated on Santiago in 2000 (Cruz et al. 2005), and rats (*Rattus rattus*), among others. Goats have competed with and nearly displaced *G. elephantopus* (Trillmich 1992) on all invaded islands and surely replaced its role of herbivory on Santiago. The small population of tortoises remaining on Santiago is unable to regain its grazing role quickly enough to control the growth and dispersal of primary producers. In addition, another native herbivore, the land iguana (*Conolophus subcristatus*), is extinct on Santiago. High vegetation recovery rates in the absence of herbivorous vertebrates may pose a threat to the Galapagos Hawk and the other two birds of prey on the island, the Barn Owl (*Tyto alba*) and the Short-eared Owl (*Asio flammeus*).

Ongoing scientific investigations since the 1970's have made the Galapagos Hawk one of the most studied *Buteo* species in the world (Parker 2009). It has been studied extensively on Santiago Island, starting with Tjitte de Vries's eco-geographical (1973) and breeding biology (1975) studies. Several other scientists have studied its particular cooperative polyandry (Faaborg et al. 1980, Faaborg et al. 1995, DeLay et al. 1998); its morphological and genetic differences between sexes and among islands

(Bollmer et al. 2003, 2005); its inferred history of colonization (Bollmer et al. 2006; Hull et al. 2008); and its ecological and phylogeographic relationships with its ectoparasites (Whiteman and Parker 2004*a,b,* Whiteman et al. 2006, 2007, 2009), among others (Donaghy Cannon 2001, Levenstein 2008).

The Galapagos Hawk population is divided into territorial and non-territorial birds (De Vries 1975); juveniles attain sexual maturity around their third or fourth year when they join an already established breeding group (Faaborg et al. 1980). Territorial groups consist of one female that mates with up to eight unrelated males (Faaborg et al. 1995). Group members are highly territorial, defending against potential invaders all year round, and all males in a group copulate with the female and care equally for the offspring (DeLay et al. 1998 citing Faaborg and Patterson 1982). Hawks nest all throughout the year with a peak in reproductive activity in June-July and another slight peak in November-December. Overall, the hawk has been previously described as a successful predator on Santiago with a well established population of territorial birds and large numbers of juveniles waiting to attain breeding group membership.

The hawk's diet consists of a wide variety of animals including endemic snakes (*Alsophis* spp.), lava lizards (*Microlophus albemarlensis*), centipedes (*Scolopendra galapagoensis*), doves (*Zenaida galapagoensis*), mockingbirds (*Mimus parvulus*), finches (*Geospiza* spp.,*Camarhynchus* spp.), marine iguanas (*Amblyrhynchus cristatus*) and sea lion (*Zalophus californianus*) placenta (De Vries 1973); they prey as well on introduced rats and mice (*Mus musculus*) (Donaghy Canon 2001); and even on Pacific Green Turtle neonates (*Chelonia mydas*) (Pers. obs.), grasshoppers (*Schistocerca melanocera*) (Donaghy Canon 2001, Levenstein 2008, Pers. obs.), and goats (De Vries 1973, Donaghy Canon 2001, Levenstein 2008). In previous years hawks also preyed on young tortoises and land iguanas (De Vries 1973); thus, feral pig and introduced black rat predation on eggs of iguanas and tortoises possibly reduced young prey for Galapagos Hawks and influenced the predator negatively by resource competition.

The most recent study of hawks on Santiago Island showed that the goat eradication had a significant negative effect on the survivorship of adult hawks (Rivera et al. submitted). A severe decline of juvenile floaters that started in 2006 and continued in 2007, 2008 and 2010 was also attributed, by Rivera et al (submitted), to the end of the eradication campaign in 2006. The sudden decline in the population of hawks could be credited to the great impact of vegetation recovery on the hawk's hunting success. In order for the hawk to withstand its new environment, it could have undergone a shift in diet composition resulting from a change in availability or accessibility of certain prey items.

Shifts in diet composition after the removal of a species from an ecosystem are not uncommon. Prey switching by predators towards native or endemic prey has been seen when trying to eradicate other introduced species (e.g. Copson and Whinam 2001). On the California Channel Islands the eradication of pigs (*Sus scrofa*) caused the precipitous decline of island foxes (*Urocyon littoralis*) through increased predation by Golden Eagles (*Aquila chrysaetos*) (Coonan et al. 2005). Simultaneously, the insular skunk (*Spilogale gracilis amphiala*) has increased dramatically due to both its release from interference and resource competition with the island foxes and vegetation recovery (due to feral livestock removal) (Jones et al. 2007, Roemer et al. 2002). Although captive breeding programs of island foxes are intended to reestablish their population and stabilize the community, the result is still unknown given that the competitive forces have been completely unbalanced.

Eradication of goats on Santiago Island may have similarly tipped the balance of predator-prey interactions in the ecosystem; therefore, we will examine the subsequent impact of vegetation recovery by observing differences in the hawk's feeding ecology, pre- and post-goat removal. The prediction is that perhaps it shifted from a ground prey-based diet to a more arboreal one. Earlier diet observations, 1998-1999 (Donaghy Cannon, unpublished data) have shown that the diet of the Galapagos hawk consisted mostly of ground prey. At that time, 55.3% of the total prey biomass delivered to nests consisted of centipedes, lava lizards, rats, and others, whereas 32.3% of total prey biomass delivered at nests consisted of passerine birds. The distinction between arboreal and terrestrial prey is based in the prey's ability to fly or perch on trees, placing birds in the first category and other non-flying prey such as rats, centipedes, lizards, etc., in the second. Although, many of the birds found on Santiago spend a bulk of their time on the ground the particular dense ground cover could limit the hawk's hunting of these arboreal prey to aerial situations.

We are interested as well in determining the effect of goat eradication on the introduced rat, *Rattus rattus*, on Santiago. Introduced species eradications have caused the increase of other invaders in numerous instances (Towns 2002, Merton et al. 2002, Kessler 2002); thus vegetation recovery on Santiago could cause an increase in certain prey populations. *R. rattus* are food limited and their density and biomass correlate with vegetation biomass (Clark 1980). The outstanding recovery of the vegetation could provide more food resources and perhaps also enhanced cover from aerial predators. The period of instability of the hawk population can be expected to also have had a positive effect on the population density of this invader. Although important in the sense that they constitute a good portion of the hawk's diet, *R. rattus* represent imminent danger to the endemic rat of Santiago (*Nesoryzomys swarthi*) (Harris and Macdonald 2007) as well as other birds and reptiles, and they are consequently both competitors and prey for the Galapagos Hawk.

In summary, we are largely interested in determining if the Galapagos Hawk is able to adapt ecologically to its new environment by shifting its diet composition, from a terrestrial prey based diet to a more arboreal one. Hunting success of the Galapagos Hawk and prey composition in their diet would possibly differ between territories that include areas of lava with scarce vegetation and those located in the arid and transition zones, where vegetation is denser and recovers at a faster rate. Thus, we predict as well that ground prey will be least accessible in the transition zone as arboreal prey become more important in the hawk's diet. The main purpose is to determine how much of the variation in the diet is explained by periods pre- and post-goat eradication and how much by nest location (habitat type). At the same time, determining the response of major prey populations (emphasizing introduced rats) to the removal of goats could be useful to understand any changes that may present in the diet of this top predator. Therefore, we will assess introduced rat abundance during this study to couple with diet observations and also as a manner of monitoring the population of the introduced rodent.

Methods

Study area

We conducted this study at the two study sites established on Santiago during past years; James Bay with 23-25 territories at the western side of Santiago, and Sullivan Bay with 7-8 territories, at the eastern end of the island (Fig. 2).

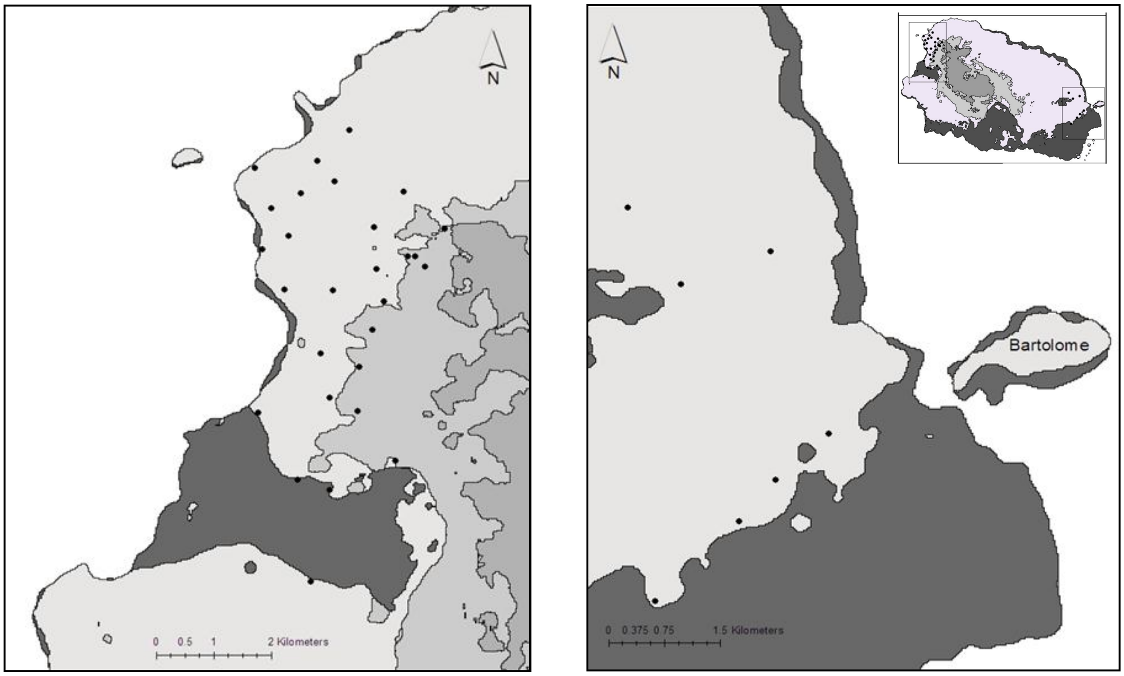

Figure 2. Major habitat types of Santiago Island and location of nests (black dots) on James Bay (left) and Sullivan Bay (right) study sites.

The study area includes littoral, arid and transition vegetation zones. The littoral zone is composed by sandy beaches and lava rocks; the main vegetation includes the button mangrove (*Conocarpus erectus*), white mangrove (*Laguncularia racemosa*), poison apple (*Hippomane mancinella*) and thorn shrub (*Scutia spicata)*. The arid zone is dry during most of the year and is dominated by prickly pear cactus (*Opuntia echios*) and other deciduous plants such as incense tree (*Bursera graveolens*), *Vallesia glabra, Castela galapageia* and *Cordia lutea. B. graveolens, C. lutea* and *Psidium galapageium* are common trees in the transition zone, as well as other shrubs and herbs like *Clerodendrum molle, Tournefortia* sp. and *Commicarpus tuberosus*. Additionally, large areas of our study sites include basaltic lava fields with scarce vegetation consisting mainly of lava cactus (*Brachycereus nesioticus*), thorn shrub, and *Scalesia stewartii.* As hawks mainly forage and nest in the transition, arid and lava fields these were considered the main habitat types. The narrow coastal strip of the littoral zone, below 10 masl, was excluded from the analysis because no nests were found there.

Focal observations of prey deliveries

A previous study of the feeding ecology of the hawk is available for pre-goat eradication (Donaghy Cannon, unpublished 1999-2000 data) with a data set that includes an average of 60 hour observations at each of 19 nesting attempts, for a total of 947 identified prey items, during June through August of 1999 and 2000. This data set was compared to diet observations post-goat eradication in 2010-2011: we monitored 18 hawk nests and recorded 481 prey items in the same study area with nearly similar sampling effort. We conducted these observations in June through December 2010 and June through August 2011. (Location and dates of territories observed are included in Appendix 1.)

When nestlings were found we conducted observations of prey deliveries at the nest. We set up an observation post, and constructed a blind using plastic/tarp, at a distance (20-80m) that allowed us to see the chicks without disturbing them but still identify prey with accuracy. We recorded the identity of the adult and prey item for each food delivery. One or two persons recorded prey deliveries using telescopes 10-60X, and binoculars 10X and 12X. Nests were watched approximately 9 hours per day (~7:30 through ~4:30). Prey deliveries at each nest were observed for 60 hours and each prey item was identified to species. Other data such as band number of the individual delivering prey, time, and general weather conditions and siblicide events were recorded.

Banding and re-banding

In order to identify individual hawks during diet observations it is necessary to band all individuals in each territory. Birds are attracted with the use of meat and captured with a long pole and rope, or with Bal-Chatri traps using introduced rats as bait. Morphological measures are taken from all birds captured and they receive a color-coded band bearing a unique alphanumeric code, identifiable from a distance, and a metallic band with a unique number. Birds that have already been banded are not disturbed unless bands are worn and unidentifiable from a distance; in this case, they would be recaptured and re-banded with a new color-coded band, and they retain the same metallic band (unique number).

Measures of rat abundance

To detect any changes in introduced rat (*Rattus rattus*) numbers we compared rat capture data from 2010-2011 to that obtained by Levenstein (2008). Rat captures were done using the same methodology as Levenstein (2008), to enable comparisons: 2002-2004 vs. 2010-2011. We set up 4 × 5 grids of Tomahawk live traps to sample for rat abundance. Two traps were placed at each of 20 stations, located 20 m apart. The traps were checked on three consecutive nights ($N = 120$ traps). A spot of dye was applied to rats to avoid double-counting individuals. Captures per sampling session were used as a measure of rat abundance. We were able to sample 6 territories in June – December 2010, and 14 territories in June – August 2011. (Location and dates of territories sampled are included in Appendix 2.)

Landscape Attributes

We performed Geographic Information Systems (GIS) spatial analyses in ArcMap 10 (Environmental Systems Research Institute Inc.). Territory boundaries were estimated by georeferencing detailed maps from a previous study (Donaghy Cannon 2001, unpublished). Donaghy Cannon delineated territory boundaries by assessing territorial bird’s behavior towards an intruding Osprey kite. Ospreys are occasional visitors of the archipelago and elicit a territorial response from Galapagos Hawks. These maps were created with the aid of GPS points taken at those places where individuals showed no more interest or aggression towards the kite and/or where other territories collided (assessing reaction of neighboring birds). Territory size and boundaries were useful in determining vegetation cover for each territory and in assigning territories to different habitat types. Territories that included large areas of lava were classified to the lava habitat type, other territories were assigned to arid and transition habitat types based on what vegetation zone constituted a greater portion of that territory.

We used an IKONOS image acquired on July 27 2011 to calculate NDVIs (Normalized Difference Vegetation Index) for each territory in our James Bay study area. A Digital Elevation Model (DEM), obtained from the Charles Darwin Foundation (Giermakowski and Snell 2004), was used to orthorectify the image. NDVI values were calculated in ArcMap 10. A proxy for vegetation cover in each territory was developed by dividing the number of pixels of NDVI value of 0.2 or above to the total number of pixels in a territory: values of 0.2 or above represent vegetation; values lower than 0.2 will correspond to sand, rocks, or other non-vegetated terrain, we used these values as percentages.

Statistical Analysis

Our primary prediction was that the hawk's diet would have a higher frequency of arboreal prey and a lower frequency of terrestrial prey in years post-eradication. In agreement with Donaghy Cannon (2001), we considered that the frequency of prey contributions did not adequately represent the value of each prey type so we converted them into prey units based on the average fresh weight of each prey type (Table 1). To investigate differences in prey frequency between treatments before and after eradication we constructed Generalized Linear Mixed Models (GLMMs), using the glmmADMB package (Skaug et al. 2011) in R (R Development Core Team 2011). The response variables used were prey frequency, in units, in each territory for both terrestrial and arboreal prey (assuming a negative binomial distribution and using a log link function). We used year as a random nested variable to account for variation within treatments (pre- and post-eradication). Treatment and habitat type (lava, arid and transition) were treated as fixed categorical variables. To account for any correlation of re-sampled territories across years, we conducted Spearman's rank correlations of terrestrial and arboreal prey delivered on each year against all other years. Since none of the correlations were significant we proceeded to include all, except one, territories in the analyses (see Appendix 1.). Other parameters such as brood size, chick age and number of males in a territory were included in all diet models to determine whether they had any influence in the amount of prey consumed.

Final model selection was based on Akaike Information Criteria (AIC) (Akaike 1974), a measure that balances goodness of fit and parsimony of a statistical model. In instances where Akaike values were very similar, we considered as well the significance of the parameters for model selection. Individual territories were not included as a random effect in the final model because models that included territory as a random effect had higher AICs and no significant correlations between territories in different years were found. To determine the significance of differences between each vegetation zone category we performed different combinations of the optimal model. The same approach was used to construct a model to investigate changes in the frequency of rats delivered to nests, where rat frequency was used as a response variable.

To test whether differences in rat frequency in the hawk's diet are due to an increased abundance of rats in the island we modeled rat capture numbers for treatment before (years 2002, 2003 and 2004) and after (years 2010 and 2011) eradication. Again, we used GLMMs, with the glmmADMB package (Skaug et al. 2011) in R (R

Development Core Team 2011), and employed a negative binomial distribution with a log link function. Treatment and habitat type (lava, arid and transition) were used as fixed effects and year was set as a nested random variable. In this case we did use territory as a random variable in the final model, because the model had lower AICs when including the term. Final model selection was based on AICs. To determine the significance of differences between each habitat type we performed different combinations of the optimal model.

To support our prediction about increased rat abundance due to increased vegetation, we compared percent vegetation cover with rat capture numbers in all territories where we obtained rat capture data on 2011. We used a one tailed Spearman's correlation test to examine the relationship between percent vegetation cover and number of rat captures in each territory, as we expected number of rat captures to increase as percentage cover increased. Finally, we compared the total log transformed frequency and the biomass of prey delivered at nests before and after goat eradication with a t-test to investigate discrepancies in the number of prey items recorded before and after goat removal (947, 481 respectively) in spite the similar sampling effort.

Table 1. Average weights and conversion units, for prey items used in the analyses.

Prey Type	Finch[a]	Dove[a]	Mockingbird[b]	S. Bird[c]	Lizard[a]	Centipede[a]	Rat[d]	Mouse[e]	Snake[a]
Fresh Mass g)	20	100	53	20	20	10	179	13	100
Units	2	10	5	2	2	1	18	1	10

a. Armas and De Vries (1976)
b. Grant et al. 2000 (took avg. of both sexes for *M. parvulus* on Genovesa)
c. Small bird, assigned a mass of finch.
d. Average during this study: 178.5g ± 49.9 (N= 132)
e. Donaghy Cannon (2001) : 13.1 ± 0.9 (N= 7)

Results

The model with only habitat type as predictor variable was selected between the two models with the lowest AICs because the brood size variable was not significant. Thus, habitat type was selected as the best predictor variable for the abundance of terrestrial prey in the hawk's diet (Table 2). This model shows how the consumption of terrestrial prey varies across habitats (Figure 3). We find that the consumption of terrestrial prey in the lava habitat is significantly lower than in both arid and transition habitats (Pr>|z| = 0.00006, Pr>|z| = 0.00091, respectively). Yet, the consumption of terrestrial prey does not differ significantly between arid and transition habitats (Pr>|z| = 0.85).

Table 2. AIC values for the set GLMMs performed for explaining the abundance of terrestrial prey in the diet of the Galapagos Hawk. The included random effects are shown between parentheses and the selected model is bolded. (B.size = brood size)

Model	AIC
Habitat + Treatment + Habitat * Treatment + Chick Age + No.males + B.size (year | territory)	469.9
Habitat + Treatment + Habitat * Treatment + Chick Age + B.size (year | territory)	468.1
Habitat + Treatment + Habitat * Treatment + Chick Age + B.size (year)	466.1
Habitat + Treatment + Habitat * Treatment + B.size (year)	464.2
Habitat + Treatment + B.size (year)	461.9
Habitat + B.size (year)	461.4
Habitat (year)	**461.6**

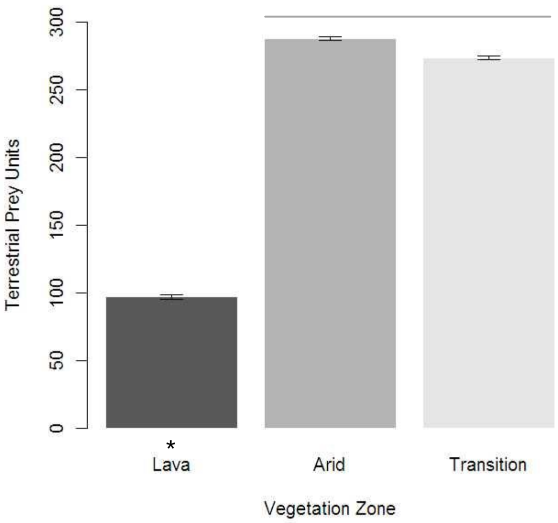

Figure 3. Terrestrial Prey Unit estimates for the optimal model, across habitat types. (Horizontal lines above the categories represent no significant differences. * Indicate significant differences.)

For arboreal prey, the optimal model included habitat type, treatment and the interaction between both (Table 3) (Figure 4). For the interaction between habitat type and eradication treatment, transition habitat in each treatment is different from both arid and lava habitats in the other treatment (Pr>|z| = 0.046, Pr>|z| = 0.0019, respectively). This model did not detect differences between pre-eradication and post-eradication for overall consumption of arboreal prey. However, with respect to the transition habitat there are significant differences between pre- and post-eradication treatments (Pr>|z| = 0.0094), with lower consumption of arboreal prey post-eradication. Differences between pre-eradication and post-eradication with respect to the other two habitats, arid and transition, are not significant and neither are differences between habitat types in treatment pre-eradication. On the other hand, habitat lava is significantly different from arid and transition habitats (Pr>|z| = 0.0025, Pr>|z| = 0.0001, respectively) in the post-eradication treatment, but habitat arid is not significantly different from transition habitat (Pr>|z| = 0.05969).

Table 3. AIC values for the set GLMMs performed for explaining the abundance of arboreal prey in the diet of the Galapagos Hawk. The included random effects are shown between parentheses and the selected model is bolded. (B.size = brood size)

Model	AIC
Habitat + Treatment + Habitat * Treatment + Chick Age + No.males + B.Size (year | territory)	362.7
Habitat + Treatment + Habitat * Treatment + Chick Age + B.Size (year | territory)	366.5
Habitat + Treatment + Habitat * Treatment + Chick Age + B.Size (year)	364.2
Habitat + Treatment + Habitat * Treatment + B.Size (year)	363.5
Habitat + Treatment + Habitat * Treatment (year)	**361.5**
Habitat + Treatment (year)	363.9
Treatment (year)	365.7
Habitat (year)	362.9

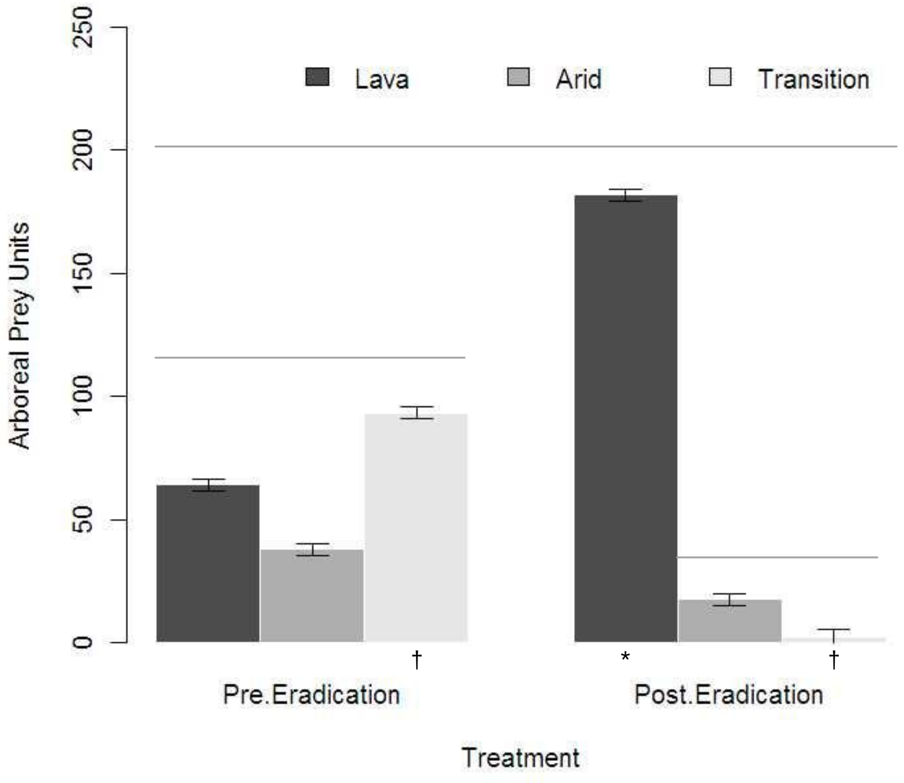

Figure 4. Arboreal Prey Unit estimates for the optimal model, across habitat types. (Horizontal lines above the categories represent no significant differences. * Indicate significant differences within treatments. Indicate significant differences between treatments.)

We found no significant differences between the total biomass of prey delivered before and after goat eradication (t= -1.3688, P = 0.1798) even though the frequency of prey delivered before eradication is significantly higher than after eradication (t = 3.567, P = 0.001082) (Figure 5.)

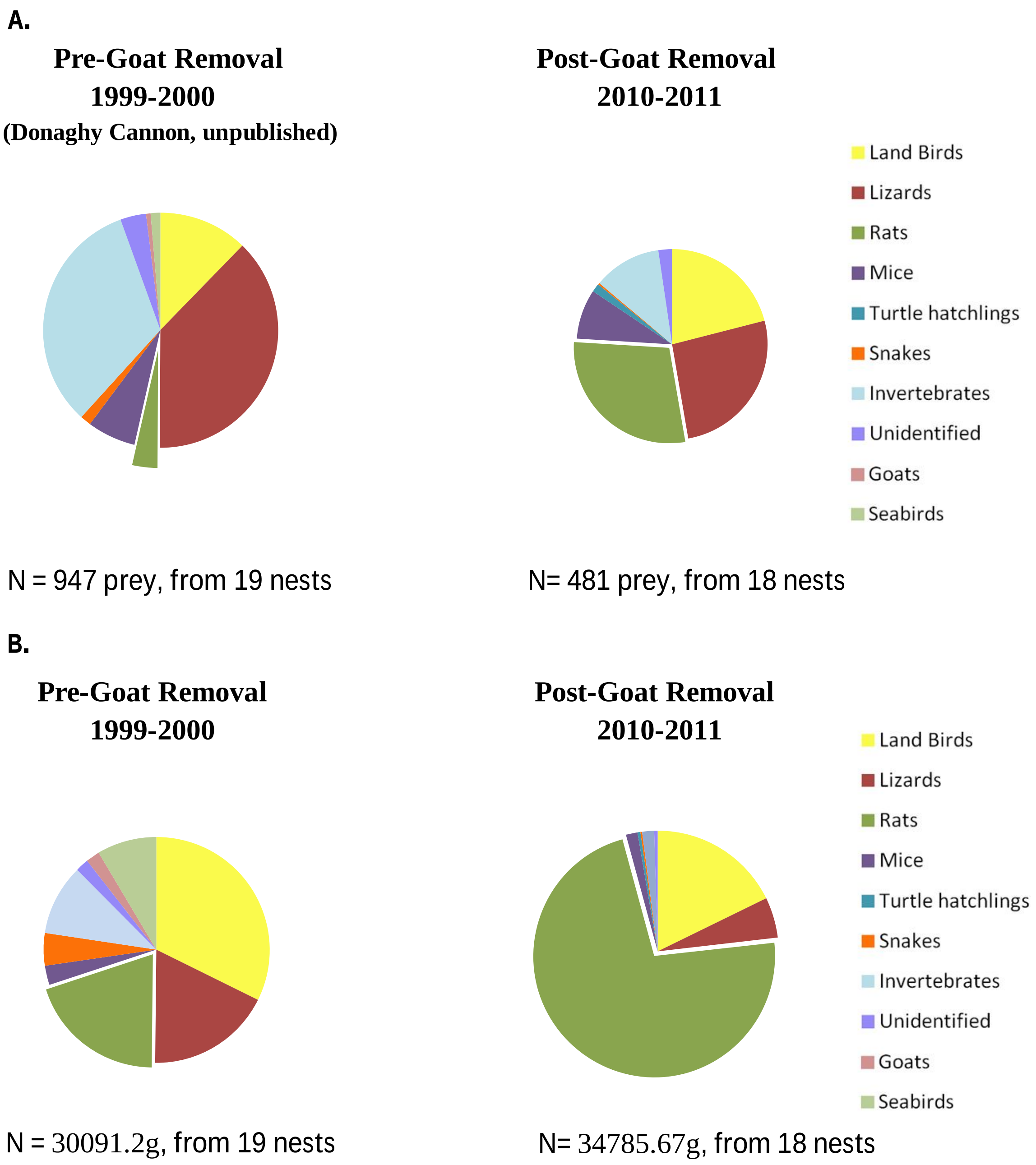

Figure 5. Prey frequency (A), biomass (B) and type of total prey items delivered at nests pre- and post- goat eradication. Pie chart size adjusted to show relative differences in number.

The best model for the frequency of rats in the hawk's diet includes habitat and eradication treatment but not the interaction between both (Table 4) (Figure 6). It includes as well the number of males in each territory, indicating an inverse relation between the number of males and the amount of arboreal prey delivered, but the term is not significant (Pr|>z|= 0.07245). The consumption of introduced rats has increased significantly in treatment post-eradication of goats (Pr|>z|= 0.00120). Overall, there is a significantly lower consumption of rats in the lava habitat compared to arid and transition habitats (Pr|>z|= 0.00057, Pr|>z|= 0.00686, respectively); but arid and transition habitats are not very different from each other (Pr|>z|= 0.7086).

Table 4. AIC values for the set GLMMs performed to explain differences in the frequency of rats in the diet of the Galapagos Hawk. The included random effects are shown between parentheses and the selected model is bolded. (B.size = brood size)

Model	AIC
Habitat + Treatment + Habitat * Treatment + Chick Age + B.size + No.males (year | territory)	178.5
Habitat + Treatment + Habitat * Treatment + Chick Age + B.size + No.males (year)	177.4
Habitat + Treatment + Habitat * Treatment + B.size + No.males (year)	176.6
Habitat + Treatment + Habitat * Treatment + No.males (year)	174.7
Habitat + Treatment + Habitat * Treatment (year)	175.8
Habitat + Treatment + No.males (year)	**173.8**
Treatment + No.males (year)	178.9
Habitat + No.males (year)	176.9

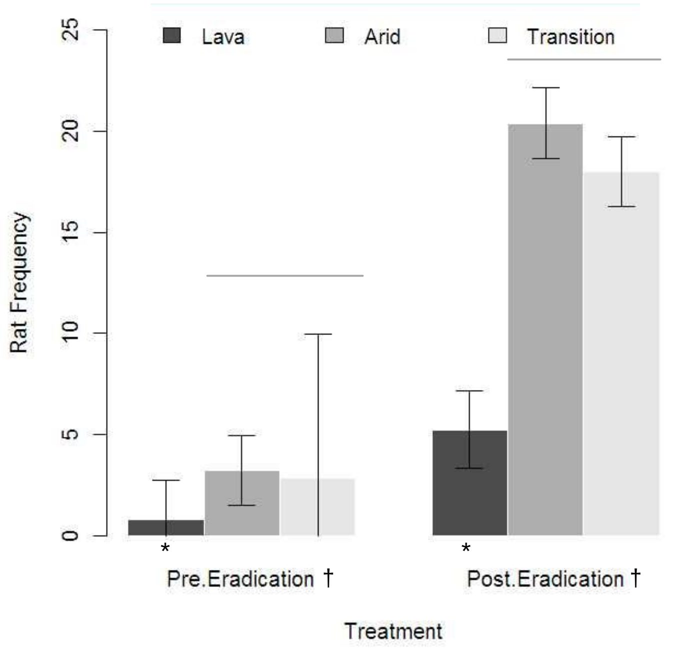

Figure 6. Rat Frequency estimates for the optimal model, across habitat types. (Horizontal lines above the categories represent no significant differences. * Indicate significant differences within treatments. † Indicate significant differences between treatments.)

Habitat type was the best predictor for the number of rat captures (Table 5) and it shows that there are significantly more rats captured in transition territories than in the arid territories (Pr|>z|= 0.017) (Figure 7). In addition, a weak positive relationship was found between the percent vegetation cover and the number of rat captures (Spearman's rho = 0.51, P = 0.03) (Figure 8).

Table 5. AIC values for the set GLMMs performed for rat captures. The included random effects are shown between parentheses and the selected model is bolded.

Model	AIC
Habitat + Treatment + Habitat * Treatment (year)	366.2
Habitat + Treatment + Habitat * Treatment (year | territory)	333.7
Habitat + Treatment (year | territory)	333.3
Habitat (year | territory)	**331.6**

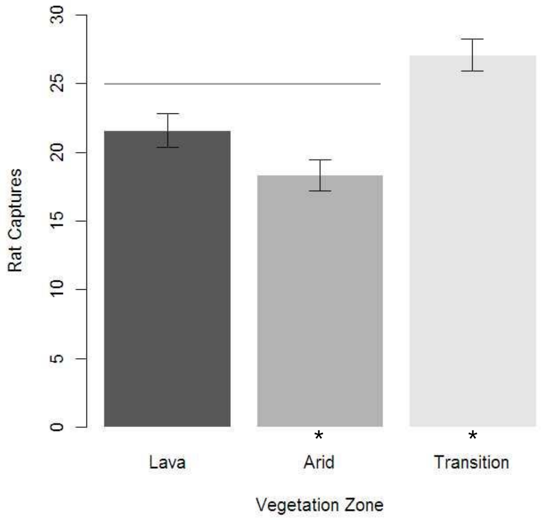

Figure 7. Rat capture estimates for the optimal model, across habitat types. (Horizontal lines above the categories represent no significant differences. * Indicate significant differences.)

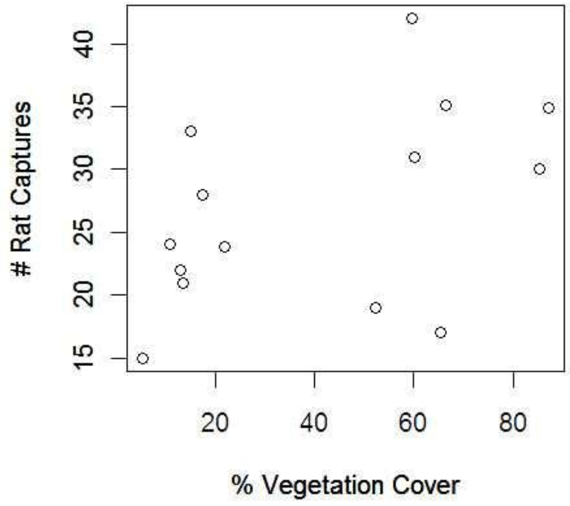

Figure 8. Scatter plot of the number of rat captures and the percent of vegetation cover in James Bay territories. (Spearman's rank correlation coefficient r_s= 0.51; P= 0.03).

Discussion

Contrary to our hypothesis of a lower consumption of terrestrial prey by Galapagos Hawks in the period after eradication, we found that the amount of terrestrial prey consumed did not change. The consumption of terrestrial prey does vary however between habitat types. We see that the lowest consumptions of terrestrial prey are found in territories close to the lava and that there is higher terrestrial prey consumption in both arid and transition habitats than in lava (Figure 3). This suggests that the amount of vegetation does influence the quantity of terrestrial prey consumed by hawks but perhaps it is due to a higher availability of prey. Our prediction of a lower amount of terrestrial prey in the period after eradication was based on the argument that the hawk's hunting ability would be jeopardized by the increasing ground cover. Given that consumption of terrestrial prey, besides introduced rats, is apparently much lower (See Figure 5.) it is possible that there is a negative effect on the hawk's hunting but is masked by a high consumption of rats.

The effect of the eradication of goats in the diet of the hawk with respect to arboreal prey is shown by a significant lower consumption of arboreal prey in the transition habitat post-eradication (Figure 4). On the other hand, arboreal prey consumption seems to have increased in lava territories, though not significantly. Thus, it appears that the hawk's ability to hunt arboreal prey is hampered in areas with denser vegetation; perhaps the increasing vegetation is an effective obstacle for arboreal prey hunting. Interestingly, arboreal prey consumption does not vary across habitat types pre-eradication; however, post eradication, the lava habitat is particularly different from both arid and transition habitats. This supports the inference that the amount of vegetation after eradication of this introduced herbivore influences how much arboreal prey we find in the hawk's diet.

In addition, we found a significantly higher frequency of rats in the diet after eradication (Figure 6). Therefore, even though the amount of terrestrial prey found in the hawk's diet has not changed significantly it consists of a much higher proportion of rats. This suggests that the number of other types of ground prey consumed has decreased, perhaps because of the difficulty of hunting smaller ground prey or because rats are a much more valuable prey item in terms of mass. In fact, in 1999-2000 (before goat eradication) Donaghy Cannon almost doubled the amount of prey items delivered in years in 2010-2011 (after goat eradication) with a comparable amount of effort. Nonetheless, no significant differences were found when comparing the total biomass delivered pre- and post goat eradication. This indicates that although the numbers of prey items delivered at nests are much lower these are constituted by larger prey, such as rats.

We found as well that the consumption of rats in the lava habitat is much lower than in the other two habitats and this relationship follows the same pattern in both periods before and after goat removal. This could be explained by the high amount of arboreal prey hunting in this area, since hawks are able to hunt numerous land birds in the lava they may not need to search for rats. It is puzzling however, how much the consumption of rats has increased in both arid and transition habitats (Figure 6) and how the hawks are able to capture as many rats in spite of ground cover being particularly dense, especially in the transition zone. We have been unable to detect whether this is due to a higher abundance of rats, as treatment before and after eradication did not explain differences in rat capture numbers. But we suggest that the reason why we have failed to detect any changes is because enhanced consumption of rats by hawks may be exerting top down control on rat populations.

The higher number of rat captures in the transition territories compared to the arid ones suggest that the amount of vegetation does have a direct influence in the abundance of rats. The lack of differences between lava and transition habitats could be explained by the lower consumption of rats in lava territories, hence more rats survive. It is also possible that there is capture bias in the lava territories, as bait could be more attractive to rats in a less productive environment. A slight positive correlation between percent vegetation cover and rat captures supports the hypothesis of the influence of recovery of vegetation on rat populations after the eradication of goats, even though significant differences have not been found. We conclude then that although we cannot be completely certain that an increase in abundance of rats has taken place, hawks are currently consuming them in much higher amounts. Thus, introduced rats have become an important part of the hawk’s diet and this is what could be allowing the territorial population of hawks to adapt to their new environment.

As much as a concern as it is that the main prey item in the diet of the only endemic raptor of the archipelago corresponds to an introduced rodent, constituting 73% of prey biomass consumed post-goat removal (Figure 5.B), it is possible as well that there is a positive top down effect that is controlling a rodent outburst. We have discussed previously how *R. rattus* represent high danger to the recently re-discovered endemic rat of Santiago (*N. swarthi*) (Harris and Macdonald 2007) as well as other birds and reptiles and that they are both competitors and prey for the Galapagos Hawk. However, hawk predation on the introduced rat populations may be controlling their impact on other flora and fauna on the island. It is likely as well that this sole prey item is what supports the remaining territorial hawk population in territories with dense vegetation.

Although, the number of territorial hawks during the past two years of this study (2010, 2011) has no longer declined (Parker, unpublished data), the severe drop in the juvenile population in 2006 that continued in 2007, 2008 and 2010 (Rivera et al. submitted), remains a concern. The large number of juveniles found before eradication was likely artificially inflated due to the abundance of goat carrion; however, it has given no indication of recovery. On the other hand, lava and arid territories produce a good number of fledglings even though reproduction has become highly asynchronous, but they are now rarely found again on Santiago after they have fledged. Furthermore, in the past few years we have been unable to locate many reproductively active nests in the transition zone, perhaps also as a consequence of the eradication of goats. Thus, further and innovative monitoring of juvenile hawks is necessary to determine whether they will be able to recover enough to succeed current territorial birds.

This is an example of a successful goat eradication in which the natural trophic interactions seem to be maintaining a temporary balance in the ecosystem. Care must be taken though in the planning of future eradications, as trophic cascades have been shown to take place in reality (Coonan et al. 2005, Roemer et al 2002, Jones et al. 2007) and in some cases cause drastic changes in ecosystems (Bergstrom et al. 2009). As suggested by Zavaleta et al. (2001), trophic interactions among and between exotics and natives and the functional roles of exotics should be cautiously evaluated before action is taken; and also post-eradication monitoring for both the target species and the ecosystem should be part of any eradication plan.

If eradication of introduced rodents is considered for Santiago in the future, we should pay close attention to availability of other prey items and also of the influence of vegetation in the hunting ability of the hawk, as it is certainly the case for arboreal prey hunting and perhaps also for smaller terrestrial prey. We recommend that a possible eradication of rats be coupled with, or posterior to eradication of invasive plants that may represent significant barriers for aerial predators. Invasive plants are still an alarming potential threat on Santiago's native plants and also on the endemic raptor of the island. *R. niveus* has been estimated to be able to invade the entire highlands of Santiago, a potential area of 4,000 ha (Atkinson et al. 2007). Therefore, we agree with Atkinson's et al. (2007) suggestions that the eradication of a single species for ecosystem restoration should be just the first step in a long-term project. The eradication of invasive species is not the only management strategy that should be employed. Santiago Island's ecosystem will also benefit from a re-established population of the remaining native herbivore, the Galapagos Tortoises. Although it should be expected that in the absence of competition they would be able to recover naturally, the process may take a long time and further monitoring of this species and its role in the community is highly recommended to assess its actual state.

Understanding not only the natural processes of communities but also their response to manipulation and management is a key to the conservation of species. By focusing on the top predator of this community we were able to get an overview of the predator-prey interactions and the whole community impact resulting from the introduction and subsequent removal of a dominant herbivore. We have seen that vegetation has recovered swiftly, that immediate and long term monitoring of the ecosystems can detect other potential threats hidden below the surface that in the case of introduced herbivore eradications applies particularly to invasive plants. We have observed how the territorial population of the top predator in this community has, so far, been able to withstand these changes by adjusting to a new diet and is possibly exerting top down control on other potentially threatening invaders. Thus, we have learned that trophic cascades are important when looking at the whole community impact and that a thorough analysis of these could help predict and plan possible interventions for some of the undesired events after eradication of invasive species.

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APPENDIX 1.a.

Location and dates of territories observed by Donaghy Cannon (2001) in 1999 and 2000.

Territory	Year	Habitat	Hours Observed
Cave	1999	Transition	60.33
Coast	1999	Arid	60.33
Cowan 2	1999	Arid	60.50
Guayabillo	1999	Transition	60.75
Malgenio	1999	Lava	61.67
Peak	1999	Transition	63.48
Peregrino	1999	Arid	61.75
Valley	1999	Arid	60.58
Cave	2000	Transition	52.08
Cowan 2	2000	Arid	50.23
Espino	2000	Lava	50.50
Gully	2000	Arid	54.35
Lagoon	2000	Arid	64.18
Lava	2000	Lava	51.50
Mordor	2000	Lava	56.67
Peregrino	2000	Arid	50.42
Red Mtn	2000	Transition	36.03
Shangri La	2000	Transition	52.58
Valley	2000	Arid	51.18

APPENDIX 1.b.

Location and dates of territories observed in 2010 and 2011.

Territory	Year	Habitat	Date	Hours Observed
Bingo Bongo	2010	Lava	16 - 23 Jun	60.18
1st Caldera	2010	Lava	18 - 23 Jun	60.00
Gully	2010	Arid	27 Jun - 3 Jul	60.93
Gaona	2010	Lava	3 - 11 Jul	60.00
Buena Suerte	2010	Transition	12 - 19 Jul	60.00
Eureka	2010	Arid	4 - 10 Sep	60.00
Young Guns	2010	Arid	6 - 12 Sep	60.00
Lagoon	2010	Arid	9 - 14 Sep	60.00
Landslide	2010	Arid	13 -15 Sep	30.00
Gully *	2010	Arid	9 - 15 Dec	60.00
Manzano	2010	Transition	3 - 9 Dec	60.00
Lejos	2011	Lava	14 - 20 Jun	60.00
Lagoon	2011	Arid	22 - 27 Jun	60.00
Valley	2011	Arid	28 Jul - 3 Aug	60.00
Middleton	2011	Transition	23 - 29 July	60.00
Gaona	2011	Lava	18 - 25 Jun	60.00
Chachay	2011	Lava	18 - 24 July	60.00
Young Guns	2011	Arid	27 Jul - 3 Aug	60.00

*Not included in Prey Consumption Models.

APPENDIX 2.a.

Location and dates of territories where rat captures where performed by Levenstein (2008) in 2002, 2003 and 2004.

Year	Territory	Habitat	Captures
2002	Valley	Arid	51
2002	Guayabillo	Transition	27
2002	Young Guns	Arid	25
2002	Cowan1	Arid	27
2002	Cowan2	Arid	16
2002	Peak	Transition	35
2002	Espumilla	Transition	38
2003	Middleton	Transition	17
2003	Landslide	Arid	8
2003	Valley	Arid	15
2003	Young Guns	Arid	18
2003	Cowan1	Arid	13
2003	Espumilla	Transition	28
2003	1stcaldera	Lava	14
2003	Cave	Transition	30
2004	Landslide	Arid	5
2004	Lagoon	Arid	17
2004	Lava	Lava	29
2004	Espino	Lava	22
2004	Gully	Arid	14
2004	Malgenio	Lava	17
2004	Bucanero	Arid	22
2004	Coast	Arid	4
2004	Rocky	Lava	14

APPENDIX 2.b.

Location and dates of territories where rat captures where performed in 2010 and 2011.

Year	Territory	Habitat	Start Date	End Date	Captures
2010	Middleton	Transition	23-Apr	25-Apr	23
2010	Landslide	Arid	27-Apr	29-Apr	5
2010	Valley	Arid	7-Jun	9-Jun	17
2010	Guayabillo	Transition	30-Jun	2-Jul	28
2010	Buena Suerte	Transition	4-Sep	6-Sep	25
2010	Lagoon	Arid	7-Sep	9-Sep	34
2011	Middleton	Transition	15-Jun	17-Jun	35
2011	Guayabillo	Transition	19-Jun	21-Jun	17
2011	Red Mtn.	Transition	22-Jun	24-Jun	35
2011	Espumilla	Transition	25-Jun	27-Jun	31
2011	Valley	Arid	28-Jun	30-Jun	24
2011	Landslide	Arid	1-Jul	3-Jul	19
2011	Buena Suerte	Transition	9-Jul	11-Jul	30
2011	Lagoon	Arid	14-Jul	16-Jul	42
2011	Lava	Lava	17-Jul	20-Jul	28
2011	Espino	Lava	20-Jul	22-Jul	21
2011	Young Guns	Arid	24-Jul	26-Jul	24
2011	Cowan 1	Arid	27-Jul	29-Jul	33
2011	Gully	Arid	30-Jul	1-Aug	15
2011	Eureka	Arid	2-Aug	4-Aug	22

APPENDIX 3. Model Results (obtained in R with the glmmadmb package)

Terrestrial Prey Model

Habitat (year)	**AIC : 461.6**

Model 1 Terrestrial

```
Coefficients:
                 Estimate    Std. Error    z value    Pr(>|z|)
(Intercept)       5.663        0.309        18.31     < 2e-16 ***
Lava             -1.089        0.271        -4.02       5.8e-05 ***
Transition       -0.052        0.277        -0.19       0.85
---
Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Number of observations: total=36, =4
Random effect (year) variance: (intercept) 0.27526

Negative binomial dispersion parameter: 2.2547 (std. err.: 0.57447)
Log-likelihood: -225.797
```

Model 2 Terrestrial

```
Coefficients:
                 Estimate    Std. Error    z value    Pr(>|z|)
(Intercept)       4.575        0.341       13.41     < 2e-16 ***
Arid              1.089        0.271        4.02        5.8e-05 ***
Transition        1.037        0.313        3.32        0.00091 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Number of observations: total=36, =4
Random effect (year) variance:  (intercept) 0.27526

Negative binomial dispersion parameter: 2.2547 (std. err.: 0.57447)
Log-likelihood: -225.797
```

Model 3 Terrestrial

```
Coefficients:
                  Estimate    Std. Error    z value    Pr(>|z|)
(Intercept)        5.611       0.345        16.26      < 2e-16 ***
Arid               0.052       0.277         0.19       0.85138
Lava              -1.037       0.312        -3.32       0.00091 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Number of observations: total=36, =4
Random effect (year) variance:  (intercept) 0.27526

Negative binomial dispersion parameter: 2.2547 (std. err.: 0.57447)
Log-likelihood: -225.797
```

Arboreal Prey Model

Habitat + Treatment + Habitat * Treatment (year) **AIC: 361.5**

Model 1 Arboreal

```
Coefficients:
                              Estimate    Std. Error    z value    Pr(>|z|)
(Intercept)                    3.637        0.906        4.01      6e-05 ***
Lava                           0.522        0.873        0.60      0.550
Transition                     0.899        0.972        0.93      0.355
Treat After                   -0.775        1.205       -0.64      0.520
Lava: Treat After              1.819        1.164        1.56      0.118
Transition : Treat After      -2.871        1.441       -1.99      0.046 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Number of observations: total=36, =4
Random effect (year) variance:  (intercept) 0.7168

Negative binomial dispersion parameter: 0.508 (std. err.: 0.1418)
Log-likelihood: -172.755
```

Model 2 Arboreal

```
Coefficients:
                         Estimate   Std. Error   z value    Pr(>|z|)
(Intercept)                2.862      0.793       3.61      0.00031 ***
Lava                       2.341      0.775       3.02      0.00253 **
Transition                -1.972      1.047      -1.88      0.05969 .
Treat Before               0.775      1.205       0.64      0.52007
Lava : Treat Before       -1.819      1.164      -1.56      0.11812
Tran : Treat Before        2.871      1.441       1.99      0.04635 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Number of observations: total=36, =4
Random effect (year) variance:  (Intercept)     0.7168

Negative binomial dispersion parameter: 0.508 (std. err.: 0.1418)
Log-likelihood: -172.755
```

Model 3 Arboreal

```
Coefficients:
                             Estimate   Std. Error   z value    Pr(>|z|)
(Intercept)                    4.159      0.971        4.28     1.8e-05 ***
Arid                          -0.522      0.873       -0.60     0.5500
Transition                     0.378      1.003        0.38     0.7064
Treat After                    1.044      1.285        0.81     0.4165
Arid : Treat After            -1.819      1.164       -1.56     0.1181
Transition : Treat After      -4.690      1.510       -3.11     0.0019 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Number of observations: total=36, =4
Random effect (year) variance: (Intercept)     0.7168

Negative binomial dispersion parameter: 0.508 (std. err.: 0.1418)
Log-likelihood: -172.755
```

Model 4 Arboreal

```
Coefficients:
                         Estimate    Std. Error    z value     Pr(>|z|)
(Intercept)               5.203        0.837        6.22       5e-10 ***
Arid                     -2.341        0.775       -3.02       0.0025 **
Transition               -4.312        1.111       -3.88       0.0001 ***
Treat Before             -1.044        1.285       -0.81       0.4165
Arid: Treat Before        1.819        1.164        1.56       0.1181
Transition: Treat Before  4.690        1.510        3.11       0.0019 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Number of observations: total=36, =4
Random effect (year) variance: (Intercept)     0.7168

Negative binomial dispersion parameter: 0.508 (std. err.: 0.1418)
Log-likelihood: -172.755
```

Model 5 Arboreal

```
Coefficients:
                    Estimate    Std. Error    z value     Pr(>|z|)
(Intercept)           4.536       0.850        5.34       9.3e-08 ***
Arid                 -0.899       0.972       -0.93       0.3546
Lava                 -0.378       1.003       -0.38       0.7064
Treat After          -3.646       1.404       -2.60       0.0094 **
Arid : Treat After    2.871       1.441        1.99       0.0463 *
Lava : Treat After    4.690       1.510        3.11       0.0019 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Number of observations: total=36, =4
Random effect (year) variance: (Intercept)     0.7168

Negative binomial dispersion parameter: 0.508 (std. err.: 0.1418)
Log-likelihood: -172.755
```

Model 6 Arboreal

```
Coefficients:
                       Estimate    Std. Error    z value    Pr(>|z|)
(Intercept)              0.89         1.11         0.80     0.4244
Arid                     1.97         1.05         1.88     0.0597 .
Lava                     4.31         1.11         3.88     0.0001 ***
Treat Before             3.65         1.40         2.60     0.0094 **
Arid : Treat Before     -2.87         1.44        -1.99     0.0463 *
Lava : Treat Before     -4.69         1.51        -3.11     0.0019 **
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Number of observations: total=36, =4
Random effect (year) variance: (Intercept)     0.7168

Negative binomial dispersion parameter: 0.508 (std. err.: 0.1418)
Log-likelihood: -172.755
```

Rat Frequency Model

Habitat + Treatment + No.males (year)	**173.8**

Model 1 Rat Frequency

```
Coefficients:
               Estimate    Std. Error    z value    Pr(>|z|)
(Intercept)      1.173        0.538        2.18     0.02924 *
Lava            -1.359        0.394       -3.45     0.00057 ***
Transition      -0.125        0.334       -0.37     0.70858
Treat After      1.843        0.569        3.24     0.00120 **
No.males        -0.271        0.151       -1.80     0.07245 .
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Number of observations: total=36, =4
Random effect (year) variance: (Intercept)     0.22134

Negative binomial dispersion parameter: 3.0553 (std. err.: 1.8317)
Log-likelihood: -79.9021
```

Model 2 Rat Frequency

```
Coefficients:
              Estimate    Std. Error    z value     Pr(>|z|)
(Intercept)     3.015        0.550        5.48      4.3e-08 ***
Lava           -1.359        0.394       -3.45       0.00057 ***
Transition     -0.125        0.334       -0.37       0.70858
Treat Before   -1.843        0.569       -3.24       0.00120 **
No.males       -0.271        0.151       -1.80       0.07245 .
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Number of observations: total=36, =4
Random effect (year) variance:  (Intercept)     0.22134

Negative binomial dispersion parameter: 3.0553 (std. err.: 1.8317)
Log-likelihood: -79.9021
```

Model 3 Rat Frequency

```
Coefficients:
              Estimate    Std. Error    z value     Pr(>|z|)
(Intercept)    -0.186        0.654       -0.28      0.77594
Arid            1.359        0.394        3.45      0.00057 ***
Transition      1.234        0.456        2.70      0.00686 **
Treat After     1.843        0.569        3.24      0.00120 **
No.males       -0.271        0.151       -1.80      0.07245 .
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Number of observations: total=36, =4
Random effect (year) variance: (Intercept)     0.22134

Negative binomial dispersion parameter: 3.0553 (std. err.: 1.8317)
Log-likelihood: -79.9021
```

Model 4 Rat Frequency

```
Coefficients:
               Estimate   Std. Error   z value    Pr(>|z|)
(Intercept)     1.657       0.650        2.55     0.01076 *
Arid            1.359       0.394        3.45     0.00057 ***
Transition      1.234       0.456        2.70     0.00686 **
Treat Before   -1.843       0.569       -3.24     0.00120 **
No.males       -0.271       0.151       -1.80     0.07245 .
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Number of observations: total=36, =4
Random effect (year) variance:  (Intercept)     0.22134

Negative binomial dispersion parameter: 3.0553 (std. err.: 1.8317)
Log-likelihood: -79.9021
```

Model 5 Rat Frequency

```
Coefficients:
               Estimate   Std. Error   z value   Pr(>|z|)
(Intercept)     1.048       0.535        1.96     0.0503 .
Arid            0.125       0.334        0.37     0.7086
Lava           -1.234       0.456       -2.70     0.0069 **
Treat After     1.843       0.569        3.24     0.0012 **
No.males       -0.271       0.151       -1.80     0.0724 .
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Number of observations: total=36, =4
Random effect (year) variance:  (Intercept)     0.22134

Negative binomial dispersion parameter: 3.0553 (std. err.: 1.8317)
Log-likelihood: -79.9021
```

Model 6 Rat Frequency

```
Coefficients:
              Estimate    Std. Error   z value    Pr(>|z|)
(Intercept)     2.890        0.555       5.21     1.9e-07 ***
Arid            0.125        0.334       0.37     0.7086
Lava           -1.234        0.456      -2.70     0.0069 **
Treat Before   -1.843        0.569      -3.24     0.0012 **
No.males       -0.271        0.151      -1.80     0.0724 .
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Number of observations: total=36, =4
Random effect (year) variance(s):  (Intercept)    0.22134

Negative binomial dispersion parameter: 3.0553 (std. err.: 1.8317)
Log-likelihood: -79.9021
```

Rat Captures Model

Habitat (year | territory)	331.6

Model 1 Rat Captures

```
Coefficients:
              Estimate    Std. Error   z value    Pr(>|z|)
(Intercept)    2.909        0.142       20.44     <2e-16 ***
Lava            0.163        0.199        0.82      0.413
Transition      0.389        0.163        2.39      0.017 *
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Number of observations: total=44, =5, =22
Random effect variance(s):
  year  (Intercept)    0.044121
  territory  (Intercept)    0.052431

Negative binomial dispersion parameter: 21.679 (std. err.: 13.024)
Log-likelihood: -157.159
```

Model 2 Rat Captures

```
Coefficients:
             Estimate  Std. Error   z value  Pr(>|z|)
(Intercept)    3.072      0.197      15.59   <2e-16 ***
Arid          -0.163      0.199      -0.82   0.41
Transition     0.226      0.220       1.03   0.30
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1


Number of observations: total=44, =5, =22
Random effect variance(s):
  year  (Intercept)    0.044121
  territory  (Intercept)    0.052431

Negative binomial dispersion parameter: 21.679 (std. err.: 13.024)
Log-likelihood: -157.159
```

Model 3 Rat Captures

```
Coefficients:
            Estimate   Std. Error   z value    Pr(>|z|)
(Intercept)   3.298       0.155      21.34     <2e-16 ***
Arid         -0.389       0.163      -2.39      0.017 *
Lava         -0.226       0.220      -1.03      0.304
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Number of observations: total=44, =5, =22
Random effect variance(s):
  year  (Intercept)    0.044121
  territory  (Intercept)    0.052431

Negative binomial dispersion parameter: 21.679 (std. err.: 13.024)
Log-likelihood: -157.159
```