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THE DIET OF THE GALAPAGOS HAWK (*BUTEO GALAPAGOENSIS*) BEFORE AND AFTER GOAT ERADICATION

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ABSTRACT.— Eradication is often the preferred method of invasive species management on islands; however, its consequences may affect native communities. Feral goats (*Capra hircus*), donkeys (*Equus asinus*), and pigs (*Sus scrofa*) were eradicated from Santiago Island in the Galapagos Archipelago by 2005. Because feral goats were the dominant herbivores on Santiago Island until their eradication, we examined the consequences of goat eradication on the diet of territorial Galapagos Hawks (*Buteo galapagoensis*) through a comparative study of observations of prey deliveries to nests before (1999–2000) and after (2010–2011) eradication. We predicted that vegetation recovery after eradication would limit the hawks' hunting success of terrestrial prey and they would therefore switch to predominantly arboreal prey. We did not observe the predicted switch from terrestrial to arboreal prey in the diet; on the contrary, after goat eradication, hawks delivered significantly fewer arboreal prey items. However, introduced black rats (*Rattus rattus*) represented a significantly greater proportion of the hawks' diet after eradication, particularly in moderate to dense vegetation (arid and transition habitats), replacing other prey items. Overall, 73% of total prey biomass delivered after eradication consisted of introduced rats, compared to only 20% before eradication. This study documents the complex interaction of predators and introduced prey, even in relatively simple ecosystems.

KEY WORDS: *Galapagos Hawk*; Buteo galapagoensis; *black rat*; Rattus rattus; *diet*; *introduced species*; *restoration ecology*.

DIETA DE *BUTEO GALAPAGOENSIS* ANTES Y DESPUÉS DE LA ERRADICACIÓN DE *CAPRA HIRCUS*

RESUMEN.—La erradicación es, a menudo, el método preferido para el manejo de especies invasoras en islas. Sin embargo, sus consecuencias pueden tener efectos secundarios en las comunidades nativas. En 2005 se completó la erradicación de cabras (*Capra hircus*), burros (*Equus asinus*) y cerdos (*Sus scrofa*) en la isla Santiago, Archipiélago de Galápagos. Considerando que las cabras asilvestradas eran los herbívoros dominantes en la isla Santiago hasta su erradicación, investigamos las consecuencias de esta medida en la alimentación de *Buteo galapagoensis* comparando su dieta antes (1999–2000) y después (2010–2011) de la erradicación en base a observaciones de aportes de presas en el nido. Predecimos que la recuperación de la vegetación después de la erradicación limitaría el éxito de caza de *B. galapagoensis* sobre las presas terrestres y que comenzaría a cazar presas predominantemente arbóreas. No observamos el cambio predicho en la dieta de presas terrestres a arbóreas; al contrario, después de la erradicación hubo una disminución en la cantidad de presas arbóreas entregadas a los pichones en el nido. Las ratas introducidas (*Rattus rattus*) representaron una proporción significativa de la dieta de *B. galapagoensis* después de la

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erradicación, particularmente en zonas de vegetación moderadamente densa (zona árida) y muy densa (zona de transición), reemplazando a los otros tipos de presas. En general, el 73% de la biomasa total de presas aportadas en los nidos después de la erradicación fueron ratas introducidas, comparado con solo un 20% antes de la erradicación. Este estudio documenta la complejidad de las interacciones entre depredadores y sus presas, incluso en ecosistemas relativamente simples.

[Traducción de los autores editada]

Isolated island communities have been a major target of global conservation efforts due to their high concentration of endemic biodiversity and anthropogenic threats, including invasive species. Eradication is often the preferred method of invasive species management on islands and has been effective in restoring local habitats and their biodiversity (Donlan and Wilcox 2008). Nevertheless, when introduced species have displaced native species and replaced their function in the community, their removal can have unforeseen negative effects on native populations that have adapted to their presence (Zavaleta et al. 2001). It is thus of great importance for future management action to document the outcomes of such eradications.

The Galapagos Islands have been subjected to many biological invasions. Goats (*Capra hircus*) were introduced on Santiago Island in the early 1900s and reached a population size of approximately 100,000 individuals by the 1970s (Calvopiña and deVries 1975). In addition, large populations of feral pigs (*Sus scrofa*) and feral donkeys (*Equus asinus*) roamed the island from 1875 until their recent eradications (Cruz et al. 2004, Carrion et al. 2007). Whereas endemic species such as the Galapagos giant tortoise (*Chelonoidis darwini*) and the land iguana (*Conolophus subcristatus*) were decimated in part due to competition with goats and predation by pigs (MacFarland et al. 1974), it is likely that some native species benefited from the environment created by over a century of ungulate grazing.

In 2006, Santiago Island (585 km^2) was declared the world's largest island from which goats had been successfully eradicated (Cruz et al. 2009). By then, pigs and donkeys had also been eradicated (Cruz et al. 2004, Carrion et al. 2007). As goats were the dominant herbivore on Santiago, their eradication resulted in a remarkable recovery of vegetation. For example, native stickleaf (*Mentzelia aspera*), wartclub (*Commicarpus tuberosus*) and other herbs and bushes have spread swiftly throughout James Bay (Fig. 1) creating a tall, dense, and sticky groundcover (Fig. 2). Introduced plant species similarly experienced a release from foraging pressure; the introduced Chinese Senna (*Senna obtusifolia*) now covers large areas of previously unvegetated ground at James Bay (Fig. 2c, d).

A recent study of Galapagos Hawks (*Buteo galapagoensis*) on Santiago Island, between 1998 and 2010, documented reduced survivorship of territorial adult hawks after goat eradication (Rivera-Parra et al. 2012). This sudden decline in the population of adult hawks may have been associated with changes in vegetation structure and its influence on the hawks' hunting success. Some *Buteo* species, such as the Galapagos Hawk, often prefer areas of low vegetation cover with available tree perches for foraging (Bechard 1982, Leyhe and Ritchison 2004). By clearing large areas of vegetation cover (Calvopiña and deVries 1975), goats likely enhanced the Galapagos Hawks' hunting success.

The Galapagos Hawk population is divided into territorial adult and non-territorial immature and adult birds (deVries 1975). Territorial groups consist of a polyandrous female that mates with up to eight unrelated male group members (Faaborg et al. 1995, Bollmer et al. 2003). Hawk groups are highly territorial (deVries 1975), fairly stable, and can hold the same territories for many years (Donaghy-Cannon 2001). Their territories encompass the entire area where they breed and forage and they do not move easily to other territories. Hawks nest throughout the year with a peak in reproductive activity in June–July and another slight peak in November–December. When feral goats were present on Santiago Island, the hawks' diet consisted of a variety of terrestrial animals including endemic racer snakes (*Alsophis* spp.), lava lizards (*Microlophus albemarlensis*), centipedes (S*colopendra galapagoensis)*, introduced black rats (*Rattus rattus*), house mice (*Mus musculus*) and goat carrion. Arboreal prey included Galapagos Doves (*Zenaida galapagoensis*), Galapagos Mockingbirds (*Mimus parvulus*), and Darwin's finches (*Geospiza* spp. and *Camarhynchus* spp.). Other prey included seabirds, Pacific green sea turtle neonates (*Chelonia mydas*) and large painted locusts (*Schistocerca melanocera*; Donaghy-Cannon 2001).

Cases of prey switching are known to follow after eradications of introduced species (Copson and Whinam 2001, Collins et al. 2009). Although most *Buteos* specialize on terrestrial prey, particularly

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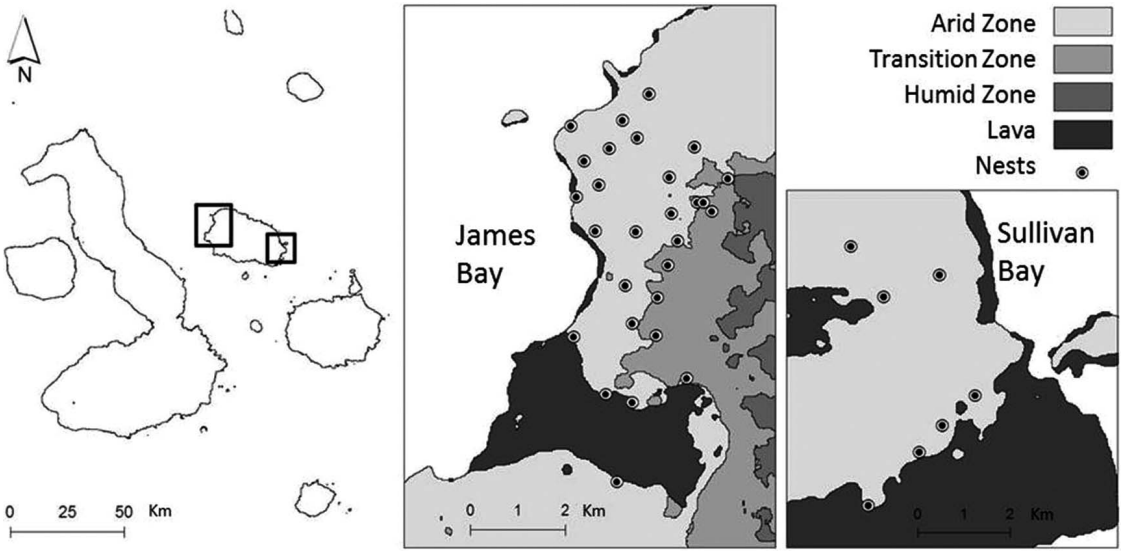


Figure 1. Major habitat types of Santiago Island and location of nests (in 2010 and 2011, encircled black dots) at James Bay (left) and Sullivan Bay (right) study sites. (The humid zone falls outside the study area but it is included for illustrative purposes.)

rodents, birds have been identified as good alternative prey (Graham et al. 1995, Reif et al. 2001). Moreover, for Common Buzzards (*Buteo buteo*) in Poland, there appears to be a relationship between vegetation type and the percentage of birds in their diet during the breeding season; buzzards breeding in forest areas consumed more birds than those breeding close to open areas (Jedrzejewski et al. 1994). Furthermore, adult Galapagos Hawks are highly territorial and sedentary. Thus, we considered that hawks would respond to changes in prey availability with prey-switching, rather than changing the location of foraging grounds to areas outside their territories.

We used a statistical approach to determine if periods before and after eradication (considered treatments in this analysis) could explain observed variation in the composition of prey items delivered to nests by Galapagos Hawks. We predicted that as vegetation cover increased, terrestrial prey such as rodents, reptiles, and invertebrates would become less accessible (i.e., more difficult to hunt) and hawks would turn to arboreal prey such as land birds that are likely to be hunted on top of the vegetation. In addition, we expected prey composition in the diet to differ between territories that included large areas of unvegetated lava and those located in the arid and transition zones where vegetation is progressively denser. We hypothesized that as terrestrial prey became less accessible in the more densely vegetated areas, arboreal prey would become more frequent in the hawks' diet relative to the unvegetated lava habitat.

We also examined the abundance in the diet of one of the remaining introduced vertebrates, the black rat, given that it is an important prey species for hawks. Black rats are food-limited (Clark 1980); thus, the rapid recovery of vegetation may have provided more food resources and allowed their population size to increase. For hawks, a larger rat population could compensate for the additional difficulty of hunting in dense vegetation; hence, we also measured changes in rat abundance because capture data from a previous study were available (Levenstein 2008). In this study, we documented the shifts in prey deliveries of the endemic Galapagos Hawk and report on numbers of the invasive black rats before and after eradication.

METHODS

Study Area. We conducted our work at two study sites established on Santiago: James Bay and Sullivan Bay (Fig. 1). As hawks mainly forage and nest in the transition and arid zones and on lava fields, we considered these the primary nesting habitat types within

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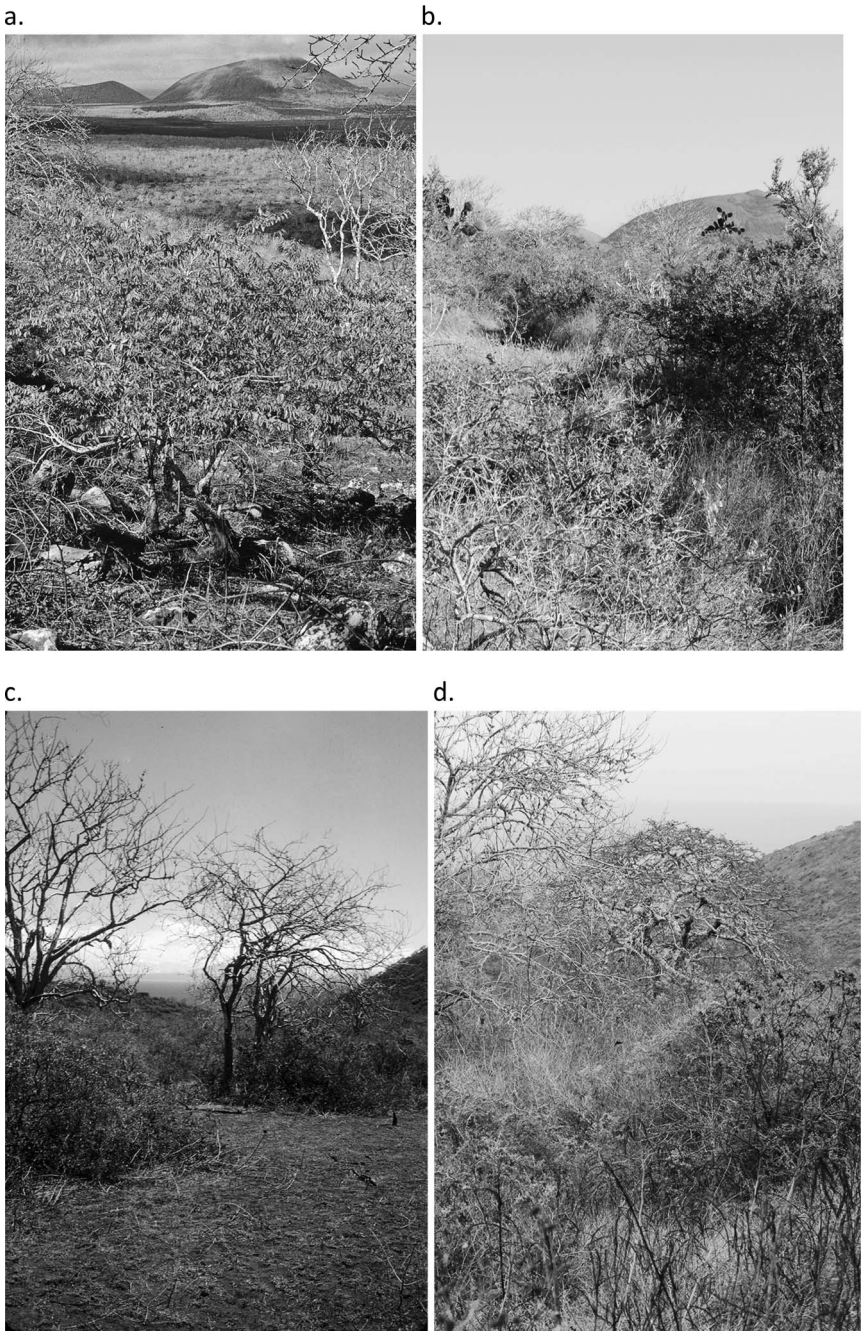


Figure 2. Main habitat zones on Santiago study areas. Arid zone habitat overlooking James Bay (a) before and (b) after eradication; transition zone habitat (c) before and (d) after eradication with Cerro Cowan in background to the right; and lava habitat at Sullivan Bay (e) before and (f) after eradication. (Photographs before eradication, 1999–2000, were provided by Donaghy-Cannon; photographs after eradication, 2010–2011, provided by Jaramillo.)

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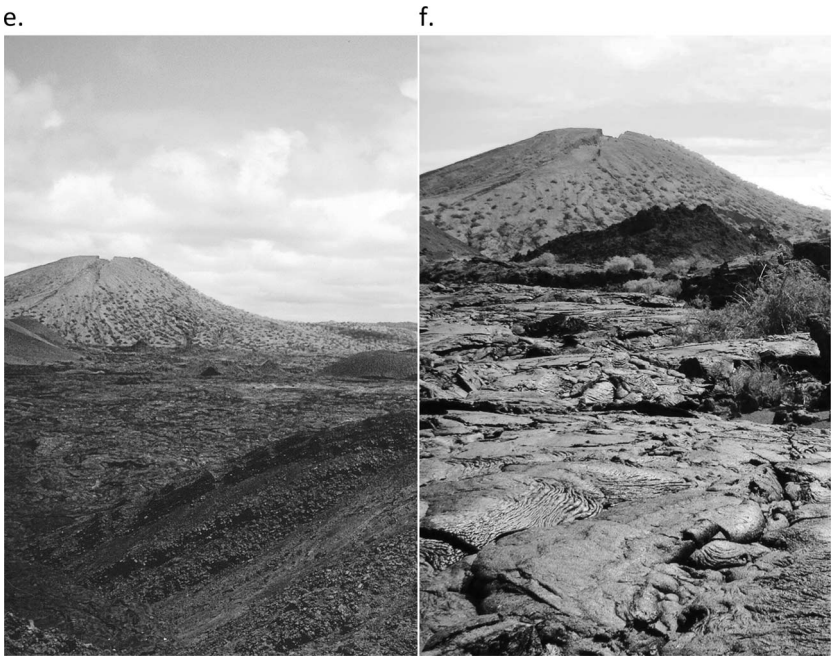


Figure 2. Continued

our study area. The arid zone (Fig. 2a, b) is dominated by prickly pear cactus (*Opuntia echios*) and deciduous plants including incense trees (*Bursera graveolens*). Common trees in the transition zone (Fig. 2c, d) are incense trees, yellow cordia (*Cordia lutea*) and Galapagos guava (*Psidium galapageium*), as well as shrubs and herbs such as glorybower (*Clerodendrum molle*) and wartclub. Large parts of our study areas included basaltic lava fields (Fig. 2e, f) with scarce vegetation consisting mainly of lava cactus (*Brachycereus nesioticus*), thorn shrub (*Scutia spicata*) and Stewart's scalesia (*Scalesia stewartii*).

Prey Deliveries. We conducted focal observations of prey deliveries at nests with nestlings present. We set up an observation post at a distance (20–80 m) that allowed us to observe nestlings and accurately identify prey without disturbing adults. We recorded prey deliveries using 10–60 × telescopes, and 10 × and 12 × binoculars and identified prey items to species level. Nests were observed approximately 9 hr per d, between 0700 and 1700 H, depending on walking distance from the camping site to the observation post. Nestlings were observed at all nestling phases due to the restricted period available for observations; however, nestling age was included in the models to account for possible effects.

Donaghy-Cannon (2001) recorded diet before eradication for a total of 1059 hr of observation at 19 nesting attempts, from June through August of 1999 and 2000 (Appendix). We compared this data set to diet observations after eradication with a total of 1051 hr at 18 nests, from June through December 2010 and June through August 2011. Although after-eradication observations included months (September–December 2010) not represented in the data set before eradication, the composition of prey deliveries at nests did not differ much from those of the same habitat type earlier that year (June–August 2010; 3.5% difference for arid habitat and 8.7% difference for transition habitat). We considered observer bias to be minimal because methods before and after eradication were largely the same, prey species were promptly identified at nests, and we used genus, not species, in the analyses.

Territory Classification. We estimated territory boundaries by georeferencing detailed maps from Donaghy-Cannon (2001) with ArcMap 10 (Environmental Systems Research Institute Inc.). Donaghy-Cannon delineated territory boundaries by assessing territorial birds' behavior toward other hawks and to an intruding Osprey (*Pandion haliaetus*) kite model. Ospreys are occasional visitors to the archipelago and elicit a territorial response from Galapagos Hawks. We found hawks in the same territories in 2010–2011, often using the same nesting sites. We used territory boundaries to assess territory topography and assigned

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territories to different habitat types. We classified territories that included large areas of lava as lava habitat type and other territories as arid or transition habitat based on the elevation where we observed a shift in vegetation characteristics. In 2011, estimates of percent vegetation cover were 15% for lava, 26% for arid, and 41% for transition zone territories, based on mean fraction of vegetation cover (FVC) of hawk territories derived from NDVI (Normalized Difference Vegetation Index) values of a fine-resolution IKONOS satellite image taken on 27 July 2011. FVC, commonly used in vegetation monitoring with remote sensing, determines the fraction of a single pixel that is covered by vegetation. We used a Digital Elevation Model obtained from the Charles Darwin Foundation to orthorectify the image. We adjusted the image values (DN) based on acquisition date, sun elevation, and IKONOS sensor properties in ArcMap 10.1. Fraction of vegetation was obtained with the power function of scaled NDVI values (Baret et al. 1995).

Data Analysis. Our primary prediction was that the hawks' diet would have a higher frequency of arboreal prey and a lower frequency of terrestrial prey following goat eradication. 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 their relative average fresh weights (e.g., one mouse = 10 g = 1 prey unit, one rat = 100 g = 10 prey units). We considered lizards, centipedes, rats, mice, and snakes as terrestrial prey, and finches, doves, mockingbirds, and other birds as arboreal prey. We observed each nest for an average of 55.7 ± 6.9 (SD) hr before eradication and 58.4 ± 7.1 (SD) hr after eradication. We standardized all nest observation periods to 60 hr.

To investigate differences in prey deliveries between treatments before and after eradication, we constructed Generalized Linear Mixed Models (GLMMs), using the "glmmADMB" package (Fournier et al. 2012, Skaug et al. 2012) in R (ver. 2.15). For prey delivery models we included only unique territories to avoid pseudoreplication (n before eradication: four lava, four arid, and five transition; n after eradication: five lava, five arid, and three transition). The response variables were prey mass, in units, in each territory for both terrestrial and arboreal prey assuming a negative binomial distribution and using a log-link function. Year was a random nested variable in all models to account for variation within treatments (before and after eradication). Treatment and habitat type (lava, arid, and transition) were fixed categorical variables. Because years before goat eradication were drier on average (1999–2000, 0.5 ± 1.7 mm/mo) than years after eradication (2010–2011, 1.6 ± 6 mm/mo) we included precipitation in our models, to account for its possible effect on the abundance of prey populations. We considered that a measure of precipitation in the 6 mo prior to data collection was representative of environmental conditions that influenced prey abundance, hence prey availability, during the time of observations. We obtained precipitation data from the Charles Darwin Foundation (2012) meteorological database. We also included brood size, nestling age, and number of males in a territory during nestling provisioning as variables subjected to model selection, to explain variation in prey deliveries. We used the same approach to construct a model to investigate changes in the frequency of rats delivered to nests, where rat frequency was used as the response variable.

We used model selection to identify the models that best described variation in diet based on corrected Akaike Information Criteria (AIC_c) and ΔAIC_c values (Hurvich and Tsai 1989, Burnham and Anderson 2004), and variable significance. We assessed the level of support for model i using the ΔAIC_c value and we considered models with Δi values ≤ 2 to have substantial evidence (Burnham and Anderson 2004). We interpreted the strongly supported models' output and determined category and variable significance using an alpha value of 0.05; we used the Bonferroni method to correct for multiple comparisons. We also compared the total log-transformed frequency (number of prey items in each category in our data set) and biomass (avg. prey weight * frequency) of prey delivered at nests before and after eradication with a t-test to investigate discrepancies in the total number of prey items recorded before and after goat removal (569 and 275 respectively, $n = 26$ nests). We report measurements in the Results as mean prey frequency/biomass ±SE.

Black Rat Abundance. To detect any changes in black rat numbers, we captured rats after eradication (April–September 2010–2011; M. Jaramillo unpubl. data) using Levenstein's (2008) methodology to enable comparisons with rat captures before eradication (May–August 2002–2004; Levenstein 2008, $n = 2880$ trap-nights, 24 territories). We set up 4 × 5 grids of Tomahawk live traps to sample rat abundance. In 2010–2011, we placed two traps at each of 20 stations located 20 m apart and checked the traps on three consecutive nights at each of 20 hawk territories ($n = 2400$ trap-nights). We placed the capture grids ca. 200 m away from hawk nests within each territory in a random direction. We applied a spot of ink (Sharpie marker) to

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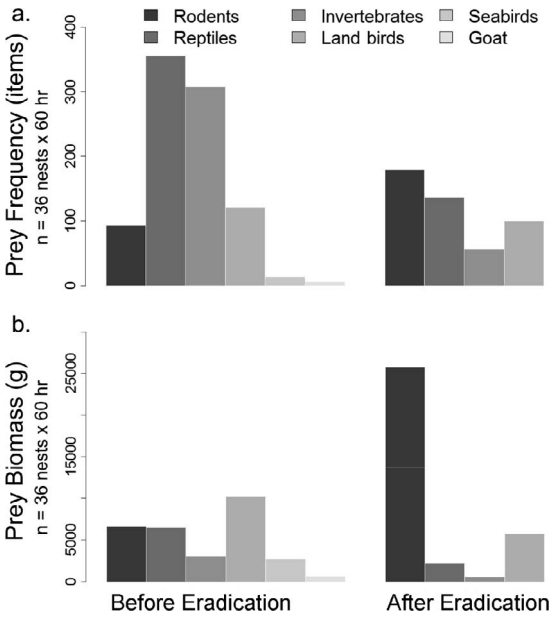


Figure 3. Prey frequency (a) and biomass (b) of total prey items in each prey category delivered during 60 hr of observation at each nest (n = 36 nests) before and after goat eradication.

rats to avoid double-counting individuals. We used rat captures as a measure of rat abundance generalized over the entire area or each habitat type.

We modeled rat capture numbers for treatments before and after eradication using GLMMs and employed a negative binomial distribution with a log-link function. Treatment and habitat type were fixed effects and year was a random variable in all models. Territory was included as a random effect to account for repeated observations throughout the years. We included precipitation in our models for its possible effect on the numbers of rats and also included number of male hawks in a territory, as the amount of primary prey available on territories has been found to be positively correlated with male group size (Levenstein 2008). These variables were subjected to model selection based on AIC_c values and ΔAIC_c in the candidate model sets. We report measurements in the Results as mean rat captures ± SE.

RESULTS

Donaghy-Cannon (2001) recorded a total of 947 prey items delivered before eradication (Fig. 3a). At that time, 54% of total prey biomass consisted of terrestrial prey (rodents, invertebrates and reptiles), whereas 34% consisted of arboreal prey (land birds). After eradication we recorded 481 prey deliveries (Fig. 3b). Of these, 83% of total prey biomass consisted of terrestrial prey, whereas only 17% consisted of arboreal prey. Furthermore, 73% of prey biomass delivered after eradication consisted of black rats compared to only 20% of total biomass across the study areas before eradication. Mean frequency of total prey deliveries before eradication was higher than after eradication (43.8 ± 6.8 vs. 21.15 ± 3 prey items/nest/60 hr respectively, $t = 3.4$, $P < 0.01$, $n = 26$). However, total prey biomass delivered was lower before than after eradication (1215.5 ± 144.9 vs. 1936.9 ± 233.6 g/nest/60 hr respectively, $t = -2.5$, $P < 0.05$, $n = 26$).

The amount (in units) of terrestrial prey delivered to Galapagos Hawk nests was best explained by models containing habitat type, and habitat type and treatment (before and after eradication, Table 1). Although there were more terrestrial prey units delivered after goat eradication (154 ± 30.2 prey units/nest/60 hr) than before (80.4 ± 16.9 prey units/nest/60 hr), this difference was not statistically significant ($P > 0.05$, Fig. 4a). The number of deliveries of terrestrial prey in lava habitat was lower (50.4 ± 12 prey units/nest/60 hr) than in both arid and transition habitats (157.4 ± 32.9; 147 ± 35.8 prey units/nest/60 hr, respectively; adjusted $P < 0.01$), but did not differ between arid and transition (adjusted $P > 0.05$, Fig. 4a).

The amount (in units) of arboreal prey delivered was best described by models containing habitat type and treatment, and habitat type, treatment, and their interaction (Table 1). There were fewer arboreal prey delivered after eradication (38.1 ± 14.5 prey units/nest/60 hr) than before eradication (45.9 ± 14.6 prey units/nest/60 hr; $P < 0.05$; Fig. 4b). Overall, there were more arboreal prey delivered in lava (80.3 ± 17.7 prey units/nest/60 hr) than in arid and transition habitats (19 ± 14.5; 24.6 ± 12.3 prey units/nest/60 hr, respectively; adjusted $P < 0.05$), but arid and transition habitats did not differ (adjusted $P > 0.05$). Arboreal prey deliveries in lava were greater than in arid and transition habitats after eradication (93 ± 20.1; 5.2 ± 2.1; 1.3 ± 1.3 prey units/nest/60 hr, respectively; $P < 0.01$) but not before eradication (64.5 ± 32.4; 36.3 ± 32.7; 38.6 ± 17.2 prey units/nest/60 hr, respectively; adjusted $P > 0.05$; Fig. 4b).

The best descriptor variables for the number of black rats delivered by hawks to the nests were

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Table 1. AIC_c values for the set of GLMMs performed to explain variation in Galapagos Hawks' prey deliveries to nests. Strongly supported models are shown in bold. Response variables were units of prey delivered: terrestrial prey (TP), arboreal prey (AP), and rat frequency (R). Predictor variables were: habitat (h), treatment before and after eradication (treat), nestling age (a), brood size (bs), precipitation (prec) and no. males (nm). Yr is a random factor included in all models.

MODEL CATEGORY	MODEL	AIC_{CI}	$\Delta AICc_i$	ω_i	k
Terrestrial prey (TP)	**TP { h (yr)}**	**299.832**	**0**	**0.630**	**5**
	TP { h + treat (yr) }	**301.127**	**1.295**	**0.330**	**6**
	TP { h * treat (yr)}	305.665	5.833	0.034	8
	TP { h * treat + prec (yr)}	309.176	9.344	0.006	9
	TP { h * treat + prec + bs (yr)}	314.249	14.417	0.000	10
	TP { h * treat + prec + bs + a (yr)}	320.193	20.361	0.000	11
	TP { h * treat + prec + bs + a + nm (yr)}	327.240	27.408	0.000	12
Arboreal prey (AP)	**AP { h + treat (yr)}**	**237.907**	**0**	**0.614**	**6**
	AP { h * treat (yr)}	**239.259**	**1.352**	**0.312**	**8**
	AP { h * treat + bs (yr)}	242.312	4.405	0.068	9
	AP { h * treat + bs + prec (yr)}	247.275	9.368	0.006	10
	AP { h * treat + bs + prec + a (yr)}	253.463	15.556	0.000	11
	AP { h * treat + bs + prec + a + nm (yr)}	260.606	22.699	0.000	12
Rat prey (R)	**R { h + treat** (yr)**}**	**131.542**	**0**	**0.847**	**6**
	R { h * treat (yr)}	135.379	3.837	0.124	8
	R { h * treat + a (yr)}	138.603	7.061	0.025	9
	R { h * treat + a + bs (yr)}	142.444	10.902	0.004	10
	R { h * treat + a + bs + prec (yr)}	148.204	16.662	0.000	11
	R { h * treat + a + bs + prec + nm (yr)}	155.099	23.557	0.000	12

habitat and treatment (Table 1). Deliveries of rats increased between the periods before and after eradication (1.6 ± 0.6; 8 ± 1.7 rats/nest/60 hr, respectively, $P < 0.05$, Fig. 5). Overall, there were significantly fewer rats delivered to nests in the lava (1.6 ± 0.5 rats/nest/60 hr) compared to arid and transition habitats (7 ± 2.2; 5.9 ± 2.2 rats/nest/60 hr, respectively, adjusted $P < 0.01$), but rat deliveries in arid and transition habitats did not differ (adjusted $P > 0.05$, Fig. 5).

The number of rat captures was best predicted by habitat type and precipitation (Table 2). We captured significantly more rats in transition than in the arid habitat territories (28.5 ± 1.7; 19.1 ± 2.1 captures/territory, respectively, adjusted $P < 0.05$). Rat captures did not differ between lava (20.7 ± 2.3 captures/territory) and transition (28.5 ± 1.2 captures/territory, adjusted $P > 0.05$), or between lava and arid habitats (19.1 ± 2.1 captures/territory, adjusted $P > 0.05$, Fig. 6). The model showed a significant positive relationship between the number of rat captures and precipitation (estimate ± SE = 0.01 ± 0.0023, $Z = 4.43$, $P < 0.01$), with years after eradication (2010–2011) being wetter on average (1.6 ± 6 mm/mo) than years before eradication (2002–2004, 0.85 mm/mo ± 3.8)

DISCUSSION

We found that treatment (whether goats were present or not) did play a role in explaining variation in the diet of Galapagos Hawks. Introduced black rats became the most important prey for hawks after goat eradication, particularly in territories with moderate to dense vegetation (arid and transition habitats); rats represented 73% of total prey biomass delivered after eradication compared to only 20% before eradication. Habitat type was also important for understanding the changes in diet composition and frequency.

We did not observe the predicted switch from terrestrial to arboreal prey in the diet of the Galapagos Hawk. Prior to eradication, deliveries of arboreal and terrestrial prey did not differ among the three habitat types. Following goat eradication, hawks delivered significantly fewer arboreal prey and deliveries of terrestrial prey did not change significantly overall. However, we recorded more terrestrial prey and fewer arboreal prey delivered in arid and transition habitats than in lava (Fig. 4). This may be an indication that terrestrial prey were more cost-effective in dense vegetation, in terms of hunting effort, than arboreal prey.

Our major finding is that, after goat eradication, introduced rats represented a more substantial

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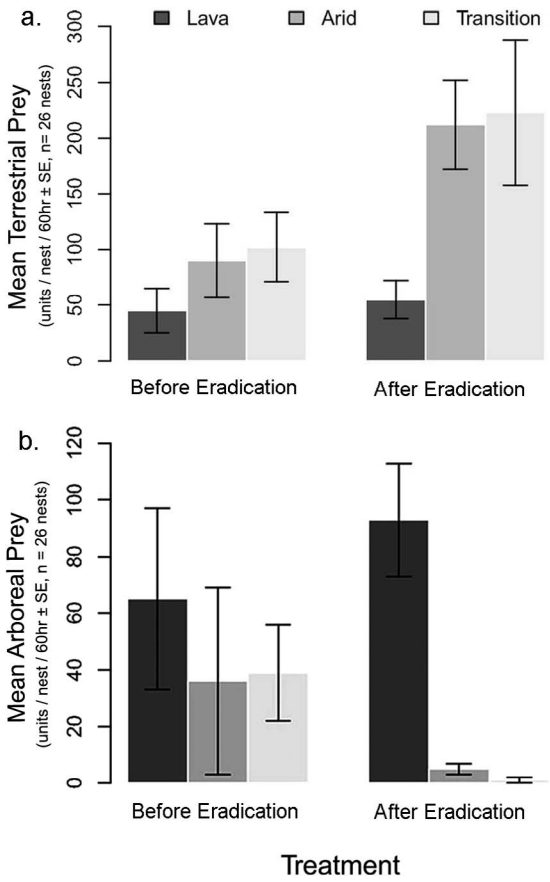


Figure 4. Mean number of units of (a) terrestrial prey and (b) arboreal prey delivered during 60 hr of observation at each nest (n = 26 nests) in the three habitat types before and after eradication of goats, with standard error bars.

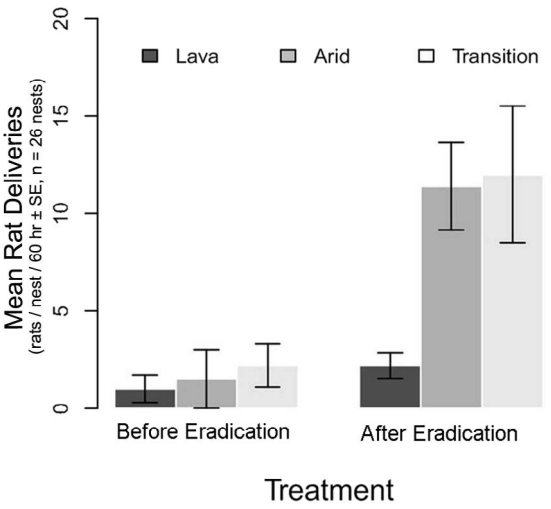


Figure 5. Mean rat deliveries during 60 hr of observation at each nest (n = 26 nests), in the three habitat types before and after eradication of goats, with standard error bars.

portion of the hawks' diet (Fig. 3). Despite the positive correlation between the number of rats we captured and precipitation, with years after eradication being wetter on average than years before eradication, our trapping study did not reveal an increase in the abundance of rats after goat removal (Table 2, Fig. 6). The number of rats captured did not decrease either, despite the prevalence of rats in the hawks' diet. Additional research on rat population dynamics and hawk foraging ecology will be needed to better understand the degree to which hawk predation may affect rat populations on this island.

Although the total frequency of prey deliveries decreased after eradication, the total prey biomass increased. This increase in total biomass, while hawk numbers were decreasing (Rivera-Parra et al. 2012), may seem puzzling. However, the higher biomass value is related to the higher fresh weight of rats that were more frequent in the hawks' diet after eradication (Fig. 3, 5). Rather than switching from terrestrial to arboreal prey, the change in diet was species-specific, as hawks delivered more rats to the nests after goat eradication. In the transition zone in particular, the deliveries were almost exclusively black rats (Fig. 4a, b). It was striking how much the frequency of rats increased in deliveries after eradication (Fig. 5), despite the increase in vegetative ground cover. Some rats may be captured on trees, as black rats are known to be agile climbers (Key and Woods 1996, Phillips et al. 2007). We did not observe successful hunting attempts by hawks in dense undercover; however, we did observe black rat feces on Galapagos guava tree branches in the transition zone. Rats may be preferred by hawks because they provide the highest energy gain (at least in terms of biomass) relative to the higher costs of hunting in dense vegetation.

Although it was surprising that the main prey item in the diet of the only endemic raptor of the archipelago after eradication was an introduced rodent, rats are not an entirely new prey item in the diet of Galapagos Hawks. Before the introduction of black rats, the endemic rat of Santiago (*Nesoryzomys swarthi*) was likely widespread and an important part of the

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Table 2. AIC_c values for the set GLMMs performed for rat captures. Strongly supported models are shown in bold. Number of rat captures (C) is the response variable. Predictor variables are: precipitation (prec), habitat (h) and treatment before and after eradication (treat). Territory (terr) and yr are random factors included in all models.

RAT CAPTURES (C) MODEL	AIC_C	ΔAIC_C	Ω_I	K
C { prec + h (terr, yr)}	**304.446**	**0**	**0.610**	**7**
C { prec + h + treat (terr, yr) }	306.519	2.073	0.216	8
C { prec + h * treat (terr, yr) }	307.281	2.835	0.148	10
C { prec + h * treat + nm (terr, yr) }	310.784	6.338	0.026	11

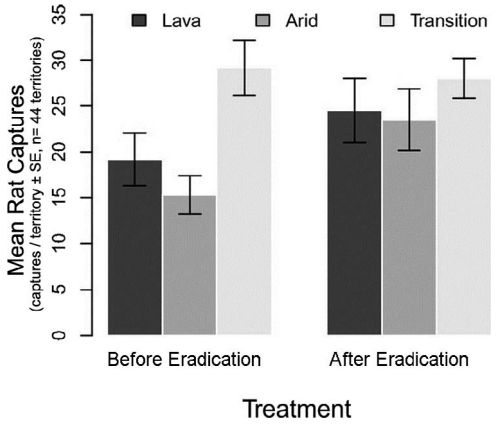


Figure 6. Mean number of rats captured per territory (n = 5280 trap-nights, 44 territories) in the three habitat types before and after eradication of goats, with standard error bars.

hawk's diet. Until recently, *N. swarthi* was thought to be extinct; however, a small population remains in the arid north-central coast of Santiago, outside our study area (Harris and Macdonald 2007). In this area, *N. swarthi* might still be included in the hawk's diet.

This study was based on observational data obtained from adult hawk prey deliveries at nests. However, in accordance with Levenstein (2008) and based on our own observations in the field, we suggest that the diet of adults was similar to that delivered to nestlings. Thus, we consider prey deliveries at nests to be representative of the territorial hawks' diet during the breeding season. We did not investigate how goat eradication may have changed the diet of nonbreeding adults and immature hawks due to the difficulty of observing this highly mobile portion of the population. However, goat carcasses left on site during the eradication campaigns provided an abundance of food resources to nonbreeding adults and immature hawks that rapidly congregated around the carcasses, whereas only a small proportion of the prey delivered to nests by territorial adults before eradication consisted of goat carrion (Fig. 3).

Overall, we observed a significant change in the diet composition of territorial Galapagos Hawks, largely represented by an increase in delivery of introduced black rats and a decrease in consumption of arboreal prey, which we attribute to goat eradication and the subsequent vegetation recovery. The differences in vegetation cover between habitats have been increasing since the eradication of goats (Fig. 2a–d), and changes in diet composition after eradication appear to be related to these differences. More rats were delivered in moderate to densely vegetated habitat than before eradication and more birds were delivered in lava habitat after eradication.

This study was possible due to the availability of diet observations at nests from before goat eradication and we were able to follow the same methodology to compare diet after eradication. We examined the differences in composition of prey deliveries before and after eradication and linked these differences to vegetation changes by comparing across habitats with different types of vegetation. It is also possible that there were other sources of variation (e.g., resources available to prey species, less food competition caused by mortality of juveniles and nonbreeders) that we did not measure and that may have been operating simultaneously. However, the recovery of vegetation has been so rapid that any other sources of variation would probably be linked, directly or indirectly, to dominant changes in vegetation.

We recommend that future studies to document the outcomes of eradication are designed alongside eradication plans to include necessary data from before and after eradication, and control populations if possible. Assessments of the effect of introduced species eradication on the ecology of raptors should consider interactions between predators and prey and include an evaluation of prey populations and characteristics of the surrounding vegetation. The Galapagos Hawk monitoring project has allowed identification of changes in diet (this study) and demography (Rivera-Parra et al. 2012), following the eradication of goats, thus demonstrating the importance of long-term monitoring.

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