Management and Conservation



Implications of Goat Eradication on the Survivorship of the Galapagos Hawk

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ABSTRACT Non-native mammals cause ecological disasters in island ecosystems and their eradication is usually considered beneficial to native biodiversity. Goats (*Capra hircus*) were introduced to Santiago Island, Galapagos, Ecuador, in the early 1800s, and their numbers increased to about 100,000 by 1970. A goat eradication campaign initiated in 2002 was successful, eliminating the last individuals in 2006. To evaluate the effects of goat eradication, between 1998 and 2010 we studied the Galapagos hawk (Buteo galapagoensis) population on Santiago Island before, during, and after eradication. We used a 12-year data set in a capture mark-recapture analysis to estimate the apparent survivorship of territorial adults in 33 breeding territories, and a 5-year data set to estimate the population sizes of the floater (non-territorial) fraction of the population. Juvenile floaters showed a drastic decline starting in 2006 and continuing in 2007, 2008, and 2010, which we attribute to the completion of goat eradication in 2006, and subsequent habitat changes. We found a significant decline in adult survivorship after the goat eradication program. Additionally, group size positively affected adult survivorship in this cooperatively polyandrous raptor, presumably reflecting the benefit of shared defense and offspring provisioning during harsher conditions. The changes in the hawk population after goat eradication are an example of unforeseen consequences of a restoration program, and we hypothesize that these changes are adjustments towards a new equilibrium under the current ecosystem characteristics and capacity. © 2012 The Wildlife Society.

KEY WORDS eradication program, floaters, Galapagos Islands, herbivores, introduced species, survivorship, tropical raptor.

Introduced species are one of the major causes of biodiversity loss (Courchamp et al. 2003). Restoration programs that included the eradication of introduced species are widespread, with more than 600 islands worldwide cleared of one or more introduced species by late 2005, and other efforts underway (Krajick 2005). However, unforeseen negative consequences might complicate eradication programs aiming to conserve native species and the ecological restoration of altered habitat. These occur most often when the introduced species have replaced native species in the local ecology (Zavaleta et al. 2001), especially in simple non-redundant ecosystems (Courchamp et al. 2003). A recent example, the removal of introduced pigs (Sus domestica) from the Channel Islands off California, resulted in recently arrived golden eagles (Aquila chrysaetos) prey-switching to the endemic island fox (Urocyon littoralis; Courchamp et al. 2003,

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Collins et al. 2009). On Sarigan Island, part of the Marianas Islands, the eradication of feral goats (*Capra hircus*) and pigs led to a significant recovery of native plants and forest, but also a proliferation of the introduced vine *Operculina ventricosa* (Kessler 2002). These examples show that with time, introduced species can become an integral part of an ecosystem and removing them may have unintended consequences (Zavaleta et al. 2001).

Goats were introduced to the Galapagos Archipelago in the early 1800s by seamen; they colonized most of the major islands, leading to major changes in the ecosystem. On Santiago, goats became the major herbivore after the extinction of land iguanas (*Conolophus subcristatus*) and the near extinction of giant tortoises (*Geochelone nigra*). The herbivory of goats turned the natural thick shrubby vegetation into more open habitat (Campbell and Donlan 2005, Lavoie et al. 2007), which was favorable for the hunting strategy of *Buteo* hawks (Ferguson-Lees and Christie 2001). As part of a continuous effort by the Galapagos National Park and the Charles Darwin Foundation, major goat eradication activities throughout the Archipelago began in 2002 and culminated in early 2006 (Lavoie et al. 2007, Cruz et al. 2009).

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Hunting peaked in March–May 2002, November 2003, and March 2004 (Cruz et al. 2009). Hunters left goat carcasses where they fell, which provided an abundance of an easy-access food source for other animals and may have changed the predator carrying capacity of the ecosystem during that time. Following eradication, a remarkable recovery of the vegetation community and some bird populations, such as the endemic Galapagos rail (*Laterallus spilonotus*) followed goat eradication (Donlan et al. 2007, Lavoie et al. 2007, Cruz et al. 2009).

The Galapagos hawk (Buteo galapagoensis) is the only diurnal resident raptor of the Archipelago and is considered a threatened species because of its small population size, limited range, and low genetic variability (Bollmer et al. 2005, BirdLife International 2009). This hawk species has an opportunistic and diverse diet that ranges from grasshoppers to iguanas and carrion (de Vries 1973, 1975). The Galapagos hawk exhibits cooperative polyandry (Faaborg et al. 1995, Parker 2009), in which a group of unrelated adult males defends a territory year-round (where they hunt), sharing copulation privileges with the territory's single female occupant, and collectively protecting and providing for offspring (Faaborg and Patterson 1981). Group size on Santiago ranges from pairs to groups of up to 8 males (mode = 2-3 males/group) with a single female (Bollmer et al. 2003). After fledging, a juvenile hawk will spend 3-4 years as a non-breeding floater without a territory, wandering over the island (P. G. Parker, University of Missouri-St. Louis, personal observation). When an opportunity arises, a hawk joins a territorial adult breeding group, but the process by which a hawk enters a group remains unknown.

We studied the response of the Galapagos hawk to goat eradication on Santiago, where we have continuous data from 1998 to 2010. Although goats have been eradicated from other Galapagos islands (Marchena, Pinta Espanola, and Santa Fe; Lavoie et al. 2007), evaluating the effects of goat eradication on the hawk population was not possible because no long-term (before and after eradication) data were available to evaluate effects on those islands. We took advantage of this natural experiment to analyze the impact of intrinsic and environmental factors (vegetation), interacting with the polyandrous breeding system, on the apparent survivorship of the Galapagos hawk. More specifically, we tested for the contribution of sex, territorial group size, body size, and vegetation structure to apparent survivorship of adult hawks before, during, and after eradication. We analyzed population sizes of the floater fraction of the population (mostly consisting of juveniles), to determine whether changes in abundance were related to the goat eradication.

STUDY AREA

We focused our study on the Galapagos hawk population of Santiago, an uninhabited 585-km² island located in the center of the archipelago with a peak elevation of 907 m (Jackson 1993). Since 1998, hawk territories have been studied at 2 sites on Santiago: James Bay, located in the north-

western part of the island, and Sullivan Bay, located on the eastern coast of Santiago (Fig. 1). A barren, young pahoehoe lava flow and large tracts of a-a lava dominate the Sullivan study site, where the hawks inhabit small volcanic cones dotted with sparse xerophytic vegetation. In contrast, the James Bay study site contains 3 distinct vegetation zones: 1) the arid coastal zone, characterized by vegetation dominated by palo santo trees (Bursera graveolens), various shrubs, Opuntia cactus and seasonal herbaceous plants; 2) the transition zone, with abundant shrubby and seasonal herbaceous vegetation, particularly pegadilla (Mentzella aspera) and various tree species such as guayabillo (Psidium galapageium) and muyuyo (Cordia lutea); and 3) open lava flows, constituted primarily by pahoe-hoe lava with patches of vegetation resembling the Sullivan Bay area. Galapagos hawk territories occurred in all 3 vegetation types (Fig. 1).

METHODS

Field Methods

We captured hawks with a noose pole or a bal-chatri trap (Berger and Mueller 1959). We banded each individual with an anodized aluminum band with a unique combination of letters, numbers, and color (Acraft, Alberta, Canada) and an unanodized aluminum band bearing a unique alphanumeric code on the other leg. We recorded 8 morphometric measurements: foreclaw, hallux, body mass, wing, tail, cranium, bill depth, anterior nares to culmen tip, and culmen width (see Bollmer et al. 2003 for details). We performed a principal components analysis (PCA) with all morphometric measurements (SPSS 17.0; SPSS, Inc., Chicago, IL), and used the coordinates in PC1 to index body size (based on Bollmer et al. 2003). We also used morphometric measurements to determine the sex of individuals. Bollmer et al. (2003) described the sexual dimorphism of this species and the ranges of the measurements for each sex, with wing, weight, and foreclaw distinguishing between the sexes. We determined age class based on molting patterns and plumage coloration (juveniles are lighter than adults). We collected a small blood sample from the brachial vein to be used in other concurrent projects. All the procedures conformed to animal welfare standards (UMSL protocol 09-06-07).

Each year between 1998 and 2009, we conducted censuses of territorial (adult) hawks during the peak of the breeding season in June–July. We visited all identified territories as many times as needed to be sure all the individuals were counted; each territory was visited at least twice. During each census, we recorded which individuals were present as members of each territory, changed bands if they were illegible, recorded breeding activity, and banded fledglings and unbanded adults. The birds were tolerant of observers and we were usually able to read bands from a distance of <10 m.

Starting in 2005, we operated 2 baiting sites at the James Bay study area (Fig. 1) to study the floater (non-breeding) fraction of the population. These baiting sites were located in open areas where the bait (goat meat) was easily visible. We conducted censuses for 5–14 consecutive days in June–July from 2005 through 2010. During each day at each site for

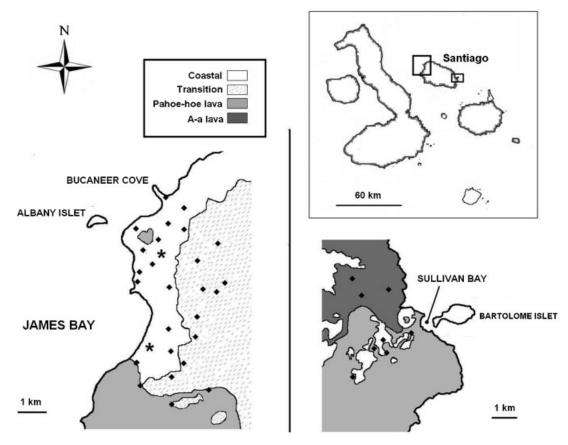


Figure 1. Study area where we investigated population responses of Galapagos hawks to goat eradication, 1998–2010. Vegetation types in each study site, within the Island of Santiago, are represented in different colors. Diamonds show nest locations; and the stars represent the 2 baiting sites in the James Bay site.

≥8 hours, we scanned the baited area every 30 minutes, counted the number of banded and unbanded birds of juvenile and adult age classes, and recorded the identity of all banded birds.

Analysis

We compiled capture-resight histories across years for territorial individuals and floaters, and proportions of banded versus unbanded floaters at baiting sites, to analyze survivorship using capture-mark-recapture (CMR) models. We divided our analysis into 2 groups: territorial adults and floaters, because of the differences in life history during these phases of their lives and the different approaches required to monitor them. Because of the marked decline in the floater population, we were unable to use the same analytical approaches on the 2 age classes of the population. The low recapture-resight rates (<10%) for floaters in censuses at baiting sites left us unable to produce reliable and unbiased estimates of survivorship in the nonterritorial (floater) component of the population, so we only reported changes in estimated population sizes per year for this age class.

We used the Cormack–Jolly–Seber (CJS) model for open populations (Cormack 1964, Jolly 1965, Seber 1965) including individual covariates to estimate apparent survivorship of adult hawks and understand the relative contributions of the different tested factors. We included sex, body size index

(PC1 from the PCA), vegetation zone where the territory was located (coastal, transition, or lava) and territorial group size (number of adults) as covariates. To test specifically for changes in survivorship linked to the eradication of goats from the island, we chose 3 different years when we predicted there would be changes in survivorship. We tested for changes related to goat eradication just after the beginning of the eradication program (2003), after the eradication of most of the goat population (2005; Cruz et al. 2009), and at the end of the eradication program (2006). We also tested a 2 cutting point model, to test for differences before (before 2002), during (2002–2006), and after (2006) the eradication program. We constructed 3 models to test for the effects of El Niño Southern Oscillation (ENSO) on the survivorship of adult hawks: 1) based on ENSO indices (National Oceanographic Atmospheric Administration, 2011); 2) based on observed ENSO events, with 1998 being the last conspicuous ENSO event; and 3) using yearly precipitation records (Charles Darwin Foundation 2011) as a proxy for what is considered the most significant ENSO-related climatic variation in land ecosystems.

We analyzed the capture histories of territorial adults using Program MARK (White and Burnham 1999, Cooch and White 2007) and used Akaike's Information Criterion (AIC; Akaike 1973, 1974) to select the model that best fit the data. We tested 30 models (Table 1) to understand which variables significantly contributed to changes in survivorship

Table 1. Tested models to evaluate survivorship of adult Galapagos hawks on Santiago, 1998–2010. We modeled survivorship (phi), recapture probability (p), and factors potentially affecting these estimates. We present the number of parameters (K), Akaike weight (w_i), the change in Akaike's Information Criterion based on quasi-likelihood corrected for small sample size ($\Delta QAIC_i$), model likelihood, and deviance as a measure of fit (QDeviance) for each model.

No.	Model ^a	K	w_i	$\Delta QAIC_c$	Model likelihood	QDeviance
1	phi(g ₂₀₀₅) p(v, s)	33	0.43	0	1	705.80
2	phi(g _{before 2002 and after 2006}) p(v, s)	33	0.23	1.29	0.53	707.08
3	phi(gs, g ₂₀₀₆) p(v, s)	37	0.17	1.80	0.41	698.97
4	phi(gs, g ₂₀₀₅) p(v, s)	35	0.09	3.09	0.21	704.59
5	phi(g ₂₀₀₆) p(v, s)	33	0.05	4.39	0.11	710.19
6	phi(g ₂₀₀₄) p(v, s)	34	0.01	7.39	0.02	711.04
7	phi(gs) p(v, s)	50	0.01	7.87	0.02	676.48
8	phi(g ₂₀₀₃) p(v, s)	34	0	9.70	0.01	713.35
9	$phi(gs, g_{2004}) p(v, s)$	37	0	10.20	0.01	707.37
10	phi(ENSO ₁₉₉₈) p(v, s)	34	0	11.61	0	715.26
11	phi(ENSO _{summer}) p(v, s)	34	0	11.63	0	715.28
12	phi(v, s, b, gs) p(v, s)	110	0	12.46	0	537.86
13	phi(ENSO _{precip}) p(v, s)	35	0	13.14	0	787.37
14	phi(gs, g ₂₀₀₃) p(v, s)	38	0	13.61	0	708.61
15	phi(gs) p(t)	29	0	23.16	0	737.52
16	phi(b, v, gs) p(t, s, v)	95	0	29.86	0	592.92
17	phi(v, b, gs) p(v)	86	0	31.04	0	616.09
18	phi(s, b, gs) p(0)	57	0	34.80	0	687.68
19	phi(s, b, gs) p(s)	63	0	35.96	0	675.17
20	phi(s) p(t)	32	0	36.93	0	744.87
21	phi(s, b) p(t)	47	0	39.82	0	715.09
22	phi(s, v, gs) p(t, s, v)	99	0	40.86	0	594.01
23	phi(s) p(s)	42	0	48.49	0	734.77
24	phi(v, gs) p(t)	60	0	51.25	0	697.32
25	phi(v) p(0)	42	0	60.09	0	746.37
26	phi(v) p(v)	61	0	63.85	0	707.64
27	phi(0) p(0)	2	0	64.32	0	834.53
28	phi(g, s, v, gs) p(s, v)	39	0	76.45	0	769.28
29	phi(b, v, gs) p(s, v)	78	0	81.74	0	685.95
30	phi(t) p(t)	122	0	162.77	0	657.06

a b, body size; g, goats and the year tested for changes in survivorship; gs, group size; s, sex; v, vegetation type of the territory: coastal, transition, or lava field; ENSO, El Niño Southern Oscillation Multivariate Index (MEI); t, yearly variation; 0, constant over time.

of territorial adults. We created models to test each of the variables (body size, group size, sex, vegetation type, ENSO, and goat eradication) of interest, the synergies and interactions between them, and a null model for comparison. We defined the null model as exhibiting constant survivorship and recapture probability over all years.

As noted by Amstrup et al. (2005) the assumptions made for the use of the CJS model are: 1) capture probability is equal for every animal at a given time in the population; 2) every animal in the population has an equal probability of surviving a given time interval; 3) bands or marks are not lost or overlooked, and the individual identification is correctly recorded; 4) sampling periods are effectively instantaneous, so no migration or deaths occur; 5) emigration from the area is permanent; and 6) survival and capture probabilities are independent between individuals. As our study species is a cooperative breeder, we were concerned with the first, second, and sixth assumptions, because hawks that belong to the same territorial group may face the same conditions and thus lack independence; therefore, using program RELEASE (Burnham et al. 1987), we performed a goodness of fit test and calculated a ĉ index, for correction in case of data overdispersion. We used QAIC, an approximation based on the quasi-likelihood theory of AIC (Anderson et al. 1994, Anderson and Burnham 1999, Burnham and

Anderson 2002), for the final model selection and further inferences.

We used bait station census data to estimate the population size of the floater fraction of the Galapagos hawk population. Of the total number of individuals visiting the bait, we calculated the proportion of banded individuals every 30 minutes, taking care to exclude any local territorial adults. We divided the number of different banded individuals resighted during the multi-day bait scans by this proportion to estimate floater population sizes per year (Amstrup et al. 2005). We used a closed population model because of genetic evidence of population isolation (Bollmer et al. 2005) and the assumption that our sampling period was short enough to be effectively instantaneous, without significant migration, mortality, or recruitment. We tested for the effect of ENSO using a correlation analysis of our population estimates with yearly precipitation records from the Archipelago (Charles Darwin Foundation 2011).

RESULTS

In 12 years, we banded 198 territorial adult hawks at both study areas. Initially, in 1998, we identified 8 territories and with further exploration reached 33 identified territories by 2000 (James Bay N=25, Sullivan Bay N=8). From 1998 to 2010, we banded 390 juveniles.

Adult Survivorship

Among the 29 models tested, 5 best fit the data (Table 1) and were statistically indistinguishable (likelihood ratio test was not significant). Two of these assumed a difference in survivorship directly related to the eradication of goats, 1 using 2005 as the cutting point (when most of the goats had been eradicated) and the other using 2006 (at the end of the eradication program). The other 2 models included the presence-absence of goats, same as above, but also included the size of the territorial group per year. The last model included the effect of the eradication program directly, dividing changes in survivorship before, during, and after the eradication program (before 2002 and after 2006). Parameters included in these models were consistent and we concluded that a significant decline in adult hawk survivorship could be directly related to the eradication of goats from the island of Santiago (Tables 1 and 2). Groups with a female and ≥4 males had about 10% greater survivorship than groups with fewer males. The difference in survival increased after the goat eradiction. The 95% confidence intervals obtained from Program MARK revealed a noticeable increase in variation after the cutting point for goat eradication (Table 2).

Population Estimates of Floaters

We conducted censuses at baiting sites annually between 2005 and 2010, but in 2007, 2008, and 2010, we found no floaters at the 2 locations (or elsewhere on the island; Fig. 2).

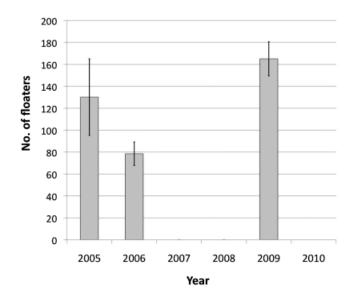


Figure 2. Population size estimates for floater Galapagos hawks based on the Cormack–Jolly–Seber model including proportions of banded and unbanded floaters observed at baiting sites in the James Bay study site between 2005 and 2010. Error bars correspond to 95% confidence intervals. Goat eradication was completed in 2006.

We were, however, able to estimate population sizes for the non-territorial component of the population in 2005, 2006, and 2009.

We recorded a decline in floater population size between 2005 and 2006 (Fig. 2) from 130 \pm 34.885 (95% CI) floaters

Table 2. Survivorship estimates for adult Galapagos Hawks on Santiago, 1998–2010 for the best 5 fitted models. Lower and upper 95% confidence intervals are included.

Model ^a	Time period	Estimate	Lower 95% CI	Upper 95% CI
phi(g ₂₀₀₅) p(v, s)	Before 2005	0.94	0.91	0.96
1 0-1111	After 2005	0.84	0.77	0.89
phi(gbefore 2002 and after 2006) p(v, s)	Before 2002	0.95	0.89	0.98
1 000000 2002 800 8000 2000, 1 (, , ,	During eradication (2002–2006)	0.92	0.88	0.94
	After 2006	0.74	0.63	0.83
phi(gs, g ₂₀₀₆) p(v, s)	1998–1999	0.92	0.81	0.97
1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	1999-2000	0.93	0.90	0.95
	2000-2001	0.93	0.90	0.95
	2001–2002	0.93	0.90	0.95
	2002-2003	0.93	0.90	0.96
	2003-2004	0.93	0.90	0.95
	2004–2005	0.93	0.90	0.96
	2005-2006	0.93	0.90	0.95
	2006-2007	0.93	0.79	0.98
	2007–2008	0.92	0.79	0.98
	2008-2009	0.85	0.72	0.93
phi(gs, g ₂₀₀₅) p(v, s)	1998–1999	0.90	0.75	0.96
1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	1999–2000	0.93	0.90	0.95
	2000-2001	0.93	0.90	0.95
	2001-2002	0.94	0.90	0.95
	2002-2003	0.94	0.91	0.96
	2003-2004	0.94	0.91	0.96
	2004–2005	0.94	0.91	0.96
	2005-2006	0.84	0.77	0.89
	2006-2007	0.84	0.77	0.89
	2007–2008	0.84	0.76	0.89
	2008-2009	0.84	0.74	0.90
phi(g ₂₀₀₆) p(v, s)	Before 2006	0.93	0.91	0.95
1 0	After 2006	0.78	0.70	0.85

^a phi, survivorship; p, recapture probability; g, goats and the year tested for changes in survivorship; gs, group size; s, sex; v, vegetation type of the territory: coastal, transition, or lava field.

in 2005 to 79 ± 10.76 (95% CI) in 2006. In 2009, our estimate was 165 ± 15.64 (95% CI), even greater than that for 2005. At that time, we found a small number of previously banded individuals that had not been observed during 2007 or 2008. Therefore, even though we did not see any floaters during those years, some were still alive. However, during 2009, except for 12 previously banded hawks, observed floaters were recently fledged individuals as judged by plumage, suggesting a severe reduction in number of juveniles surviving through the years 2007 and 2008. In the summer of 2010, again, we observed no floaters. The correlation analysis between population estimates of floaters and yearly precipitation was not significant $(r^2 = 0.38, P > 0.05)$.

DISCUSSION

Our objective was to test if the goat eradication had any impact on Galapagos hawk survivorship and population size. We documented a decline in the floater population size of the Galapagos hawk on Santiago Island after goat eradication. For the territorial adults, we observed a decline in survivorship that coincided approximately with the eradication program, but the exact details and cause behind this decline remain unknown.

The 5 models that best fit the data consistently showed a detectable and significant effect of the eradication of goats on the apparent survivorship of the territorial adult Galapagos hawks on Santiago Island. The 2 models that included only presence-absence of goats, show significant differences preand post goat eradication. These 2 models indicate a change in the dynamics of the adult fraction of the population, but having such a binary estimation is not very informative regarding future trends. Competing models including territorial group size per year, afford further insights into possible future trends. The declining trend observed in our models emphasizes the need of further monitoring.

Our study demonstrates that the eradication of goats from Santiago precipitated declines in the survivorship of breeding hawks. We included other factors as part of our analysis, such as vegetation type, body size, sex, and ENSO because we were interested in understanding the factors influencing survival. However, none of these factors provided significant insights into the mechanisms underlying this decline. The most explanatory models were those with different cut-offs at the end of the eradication program or before and after the eradication program, indicating that the effect was not instantaneous. This lag time supports the interpretation that these changes were related to changes in vegetation (not detected by our discrete and constant vegetation classification).

We directly tested the effect of ENSO in models 10, 11, and 13, finding no significant contribution of this variable or relationship to survivorship changes. Even so, the weather in the islands is heavily influenced by ENSO and these changes in weather conditions mainly rainfall, affect populations of other endemic species such as penguins (*Spheniscus mendiculus*; Vargas et al. 2006), Darwin's finches (*Geospiza* spp; Grant et al. 2000) and lava lizards (*Microlophus* spp; Jordan

and Snell 2002). We can not rule out the possibility of ENSO affecting territorial Galapagos hawk survivorship through a trophic cascade. Further research on the feeding ecology of the hawks, together with whole ecosystem monitoring are needed to better understand the trophic network of the Archipelago and its relationship with ENSO.

The polyandrous breeding system has been shown to have an effect on Galapagos hawk survivorship (Levenstein 2008). Males in larger groups have relatively higher survivorship than non-territorial males and males in small groups. Our models suggest a differential effect of territorial group size when presumably the conditions on the island were harsher (increase in shrubby vegetation after goat eradication). Beginning with the first studies on the Galapagos hawk (de Vries 1973, 1975), the primary hypothesis for the evolution of polyandry was related to coping with limited resources (either food or proper breeding sites) and changing conditions. Our study contributes evidence supporting the influence of the territorial group size on hawk survivorship during ecosystem changes, such as those produced by the eradication program. But further research is required to specifically understand the limiting factors for the population and the exact relationship of territorial group size with other contributing factors such as vegetation, climate, and social interactions.

For the floater fraction of the population, we documented a decline during 2005-2006 (Fig. 2), and in 2007, 2008, and 2010 we did not see any floaters. The number of juveniles surviving 2007-2008 may have been so few that they did not achieve the critical mass necessary to overcome the defenses of territorial adults, and thus stayed away from the baiting sites. This might explain our failure to detect them during 2007 and 2008, even though we observed some of the survivors in 2009, when larger numbers of floaters (mostly hatchlings of the year) were present. In other species, nonterritorial birds or floaters are harassed by territorial birds (Smith and Arcese 1989), have a more difficult time finding food (Studds and Marra 2005), and often suffer from lower survivorship (Stutchbury 1994). Our population estimates of juveniles are snapshots in time and are restricted to the population size found on the island during our census. Our 2009 data might have been an artifact of the timing of our visit just after the young birds fledged. The lack of observed floaters in 2010 indicates that even when adults are raising their broods to fledging, those fledglings may not be surviving afterwards.

Because of the lack of comparable data before the beginning of the eradication program, we cannot demonstrate conclusively that the eradication of goats was a causative factor driving the decline of the floater fraction of the population. However, before our formal annual censuses of juveniles began in 2005, we opportunistically caught and banded at least 20 juveniles in every year between 1998 and 2004 on Santiago in visits of similar duration to those between 2005 and 2009. This suggests that their apparent absence in 2007 and 2008, when we were specifically attempting to quantify their presence, represented a sudden and drastic change for that age class. This evidence,

together with lack of support of a correlation between floater population sizes and precipitation (as proxy for ENSO), leads us to conclude that the decline in the floater population is related to goat eradication. We found no evidence of abnormal levels of lead in our blood samples (P. Parker, unpublished data), ruling out lead poisoning as a possible contributor to the decline. We suggest the explanation must be in the population dynamics. Prior to goat eradication, a more open habitat (created by the goats) and then an abundant feeding resource in the goat carcasses, may have inflated the floater population numbers. The sudden decline of the floater population followed the elimination of what may have been a major food resource and concomitant closing up of the vegetation structure. Another possibility is increased dispersal to other islands. Bollmer et al. (2005) found almost no gene flow among hawk populations, but maybe under the current conditions juvenile hawks are dispersing farther than usual. Monitoring of hawk populations across the archipelago to find banded individuals, together with new genetic studies may help to test this possibility. Moreover, further monitoring is needed to understand the possible long-term population effects of the drastic decline in floater population during 2007 and 2008, considering that floaters are responsible for replacing breeding adults in territorial groups.

MANAGEMENT IMPLICATIONS

Our study has shown evidence that the eradication of goats from Santiago has had a strong effect on the Galapagos hawk population, severely reducing the floater population size and survivorship of the territorial adults. Even so, the net impacts to the suite of native and endemic species present should be considered. Most species appear to have benefited from the goat eradication (Donlan et al. 2007; V. Carrion, Galapagos National Park Service, personal observation). Further, our conclusions are not meant to imply that the eradication was negative for the ecosystem or for the Galapagos hawk. Instead, the ecosystem may be adjusting to a new equilibrium after losing its major herbivore for the last 200 years. The numbers of Galapagos hawks might be adjusting to the current carrying capacity of the ecosystem. Other management decisions such as re-introductions of extirpated herbivores and native herbivore population management could be valuable in reinitiating ecosystem processes, such as seed dispersal and natural herbivory. Further monitoring should enable us to understand the exact mechanism by which goat eradication affected the hawk population, and allow us to analyze its adjustments to changes in the island's ecological dynamics.

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LITERATURE CITED

- Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267–281 *in* B. N. Petrov and F. Csaki, editors. International Symposium on Information Theory. Budapest, Hungary.
- Akaike, H. 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control 19:716–723.
- Amstrup, S., T. McDonald, and B. Manly. 2005. Handbook of capture-recapture analysis. Princeton University Press, Princeton, New Jersey, USA.
- Anderson, D., and K. Burnham. 1999. General strategies for the analysis of ringing data. Bird Study 46(sup):S261–S270.
- Anderson, D. R., K. P. Burnham, and G. C. White. 1994. AIC model selection in overdispersed capture-recapture data. Ecology 75:1780– 1793.
- Berger, D. D., and H. C. Mueller. 1959. The bal-chatri: a trap for birds of prey. Bird Banding 30:18–26.
- BirdLife International, 2009. Species factsheet: *Buteo galapagoensis*. http://www.birdlife.org>. Accessed 2 Apr 2010.
- Bollmer, J. L., T. Sanchez, M. Donaghy-Cannon, D. Sanchez, B. Cannon, J. C. Bednarz, T. DeVries, M. S. Struve, and P. G. Parker. 2003. Variation in morphology and mating system among island populations of Galápagos hawks. Condor 105:428–438.
- Bollmer, J. L., N. K. Whiteman, M. D. Cannon, J. C. Bednarz, T. DeVries, and P. G. Parker. 2005. Population genetics of the Galápagos hawk (*Buteo galapagoensis*): genetic monomorphism within isolated populations. Auk 122:1210–1224.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and inference: a practical information theoretic approach. Springer-Verlag, New York, New York, USA.
- Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock. 1987. Design and analysis methods for fish survival experiments based on release-recapture. American Fisheries Society Monograph 5.
- Campbell, K., and J. C. Donlan. 2005. Feral goat eradications on islands. Conservation Biology 19:1362–1374.
- Collins, P. W., B. C. Latta, and G. W. Roemer. 2009. Does the order of invasive species removal matter? The case of the eagle and the pig. PLoS ONE 4:e7005.
- Cooch, E., and G. C. White. 2007. Program Mark: a gentle introduction. Seventh edition. http://www.phidot.org/software/mark/docs/mark_book/>. Accessed 10 Apr 2009.
- Cormack, R. M. 1964. Estimates of survival from the sighting of marked animals. Biometrika 51:429–438.
- Courchamp, F., J.-L. Chapuis, and M. Pascal. 2003. Mammal invaders on islands: impact, control, and control impact. Biological Reviews 78:347–383
- Charles Darwin Foundation. 2011. Charles Darwin Foundation Climate Database. http://www.darwinfoundation.org/datazone/climate/. Accessed 5 Dec 2011.
- Cruz, F., V. Carrion, K. Campbell, C. Lavoie, and C. Donlan. 2009. Bioeconomics of large-scale eradication of feral goats from Santiago Island, Galapagos. Journal of Wildlife Management 73:191–200.
- de Vries, T. 1973. The Galápagos hawk, an eco-geographical study with special reference to its systematic position. Dissertation. Vrije University, Amsterdam, Netherlands.
- de Vries, T. 1975. The breeding biology of the Galápagos hawk, *Buteo galapagoensis*. Le Gerfaut 65:29–57.
- Donlan, J. C., K. Campbell, W. Cabrera, C. Lavoie, V. Carrion, and F. Cruz. 2007. Recovery of the Galápagos rail (*Laterallus spilonotus*) following the removal of invasive mammals. Biological Conservation 138:520–524.

- Faaborg, J., P. G. Parker, L. DeLay, T. de Vries, J. C. Bednarz, S. M. Paz, J. Naranjo, and T. A. Waite. 1995. Confirmation of cooperative polyandry in the Galápagos hawk (*Buteo galapagoensis*). Behavioral Ecology and Sociobiology 36:83–90.
- Faaborg, J., and C. B. Patterson. 1981. The characteristics and occurrence of cooperative polyandry. Ibis 123:474–484.
- Ferguson-Lees, J., and D. A. Christie. 2001. Raptors of the world. Christopher Helm, London, United Kingdom.
- Grant, P., R. Grant, L. Keller, and K. Petren. 2000. Effects of El Nino events on Darwin's finch productivity. Ecology 81:2442–2457.
- Jackson, M. H. 1993. Galápagos: a natural history. University of Calgary Press, Calgary, Canada.
- Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration—stochastic model. Biometrika 52:225– 247
- Jordan, M. A., and H. L. Snell. 2002. Life history trade-offs and phenotypic plasticity in the reproduction of Galapagos lava lizards (*Microlophus delanonis*). Oecologia 130:44–52.
- Kessler, C. C. 2002. Eradication of feral goats and pigs and consequences for other biota on Sarigan Island, Commonwealth of the Northern Mariana Islands. Pages 132–140 in C. R. Veitch and M. N. Clout, editors. Turning the tide: the eradication of invasive species. IUCN SSC Invasive Species Specialist Group, Gland, Switzerland and Cambridge, United Kingdom.
- Krajick, K. 2005. Winning the war against island invaders. Science 310: 1410–1413.
- Lavoie, C., F. Cruz, V. Carrion, K. Campbell, C. Donlan, S. Harcourt, and M. Moya. 2007. The thematic atlas of project Isabela. Charles Darwin Foundation and the Galapagos National Park Service, Puerto Ayora, Ecuador

- Levenstein, K. M. 2008. Reproductive ecology of the cooperatively polyandrous Galápagos hawk on Santiago Island, Galápagos. Dissertation, Arkansas State University, Jonesboro, USA.
- National Oceanographic Atmospheric Administration. 2011. Multivariate ENSO Index (MEI) Database. http://www.esrl.noaa.gov/psd/enso/mei/table.html . Accessed 6 Dec 2011.
- Parker, P. G. 2009. A most unusual hawk: one mother and several fathers. Pages 130–137 *in* T. de Roy, editor. Galapagos: preserving Darwin's legacy. Firefly Books, Ontario, Canada.
- Seber, G. A. 1965. A note on the multiple recapture census. Biometrika 52:249–259.
- Smith, J., and P. Arcese. 1989. How fit are floaters? Consequences of alternative territorial behaviors in a nonmigratory sparrow. American Naturalist 133:830–845.
- Studds, C., and P. Marra. 2005. Nonbreeding habitat occupancy and population processes: an upgrade experiment with a migratory bird. Ecology 86:2380–2385.
- Stutchbury, B. 1994. Competition for winter territories in a Neotropical migrant: the role of age, sex, and color. Auk 111:63–69.
- Vargas, H., S. Harrison, S. Rea, and D. Macdonald. 2006. Biological effects of El Niño on the Galápagos penguin. Biological Conservation 127:107–114
- White, G., and K. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46(sup):S120–S138.
- Zavaleta, E. S., R. Hobbs, and H. A. Mooney. 2001. Maximizing the benefits of eradication: why invasive species removal should be viewed in whole-ecosystem context. Trends in Ecology & Evolution 16:454–459.

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