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Galapagos Hawk: Demographic and Social Effects in a Changing Environment

Jose Luis Rivera
University of Missouri-St. Louis, jose.rivera@umsl.edu

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Jose Luis Rivera
Licenciado, Ciencias Biologicas, Pontificia Universidad Catolica del
Ecuador, 2007

**Galapagos Hawk: Demographic and Social Effects in a Changing
Environment**

Master of Science in Biology with an emphasis in Ecology

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<u>Advisory Committee</u>

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Patricia Parker, Ph.D
Chairperson

Robert Ricklefs, Ph.D

Zuleyma Tang-Martinez, Ph.D

Abstract

The Galapagos Hawk (*Buteo galapagoensis*) is endemic to the Galapagos Islands, where it is the top predator and only resident diurnal raptor. On most islands, Galapagos hawks form polyandrous breeding groups with one female with up to eight males. Before entering a breeding group, individuals spend 3-4 years as non-breeding floaters.

I studied the hawks on Santiago Island, where introduced goats had been recently eradicated, leading to drastic changes in the ecology of the island. Using mark-recapture procedures, we assessed the size of the juvenile component of the population over time. In addition, using software MARK with a 12-year demographic database on this population to model annual survivorship of breeding adults. I also used this database as well as current observations to describe natal dispersal patterns and patterns of floater sociality. The population size of the floater fraction of the population declined at the end of the goat eradication program, with an apparent disappearance in 2007 and 2008, and an apparent recovery in 2009. Territorial adult survivorship probability is a function of sex, body size, territory vegetation type and breeding group size per year, but the relative importance of these factors changes between years. The lowest annual adult survivorship through the 12 years monitored was 2005-2006, the final year that the goats were eradicated. In the component focusing on juvenile behavior, I found that individuals do tend to disperse to territories neighboring their natal territories ($p < 0.05$), but they showed no statistical preference for territories with similar vegetation ($p > 0.05$).

Individuals in the four-year juvenile period do not form stable coalitions with particular individuals even though they are often highly aggregated.

The eradication of goats from Santiago Island had an effect on the Hawk's population; further monitoring is needed to better understand possible long term effects still to be seen and better understand the relationship of survivorship estimates with possible unaccounted variables such as prey abundance.

Key words: natal dispersal, polyandry, raptor, sociality, survivorship.

General Introduction

The Galapagos Hawk (*Buteo galapagoensis*) is the only diurnal resident raptor of the Archipelago. It is endemic to the islands and is a true cooperative polyandrous breeder (Faaborg *et al.*, 1995). It has an opportunistic and diverse diet that ranges from grasshoppers to iguanas and scavenging. After fledging, young hawks spend 3-4 years as non-breeding "floaters" without a territory, and it is thought that they wander all over the island during this time. After reaching adulthood they may enter to a group in order to breed. Group size can vary greatly from just pairs as on Espanola to a group consisting of a female with up to 8 males (DeLay *et al.* 1996).

The Santiago Island population has been monitored annually since 1998, focusing in two study areas: James Bay and Sullivan Bay. James Bay has around 23 identified territories located in the northwestern part of the island; Sullivan bay is located in the eastern part of Santiago and has 8 territories identified.

As in most of the other islands in the Galapagos, Santiago Island has introduced species, one of which, feral goats (*Capra hircus*), drove major changes in the ecosystem of the island. They turned the thick shrubby vegetation into open habitat with some scarce trees. The Isabela Project conducted by the Galapagos National Park and the Charles Darwin Foundation, succeeded in the eradication of the goats from the island of Santiago, finishing in 2006 (Campbell & Donlan, 2005; Lavoie et al., 2007; Cruz et al., 2009). Since then a remarkable recovery in the vegetation cover has been observed.

This long monitoring and the overlap with the Isabela Project made it possible to ask several questions that are organized here in two chapters.

The First Chapter refers to an analysis of the natal dispersal patterns and sociality as juveniles of the Galapagos Hawk, using probabilistic theory to detect behaviors significantly different from random.

The Second Chapter is about using capture-mark-recapture (CMR) models to: estimate floater population sizes and to model adult survivorship as a function of sex, vegetation type on the territory, body size and group size per year.

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Chapter One

Natal dispersal and sociality of the floater population of the Galapagos Hawk in the Island of Santiago.

Jose Luis Rivera[1], Hernan Vargas[2] and Patricia Parker[1]

[1]University of Missouri-St. Louis. One University Boulevard. St. Louis, MO 63121-4400.

[2]The Peregrine Fund. 5668 West Flying Hawk Lane. Boise, Idaho 83709.

ABSTRACT

The Galapagos Hawk is the only diurnal resident raptor in the Galapagos Archipelago, where it exhibits a cooperatively polyandrous mating system. Before sexual maturity, individuals spend 3-4 years as non-territorial floaters. Individuals in this age group are highly gregarious on the island of Santiago, but otherwise their biology is poorly understood. Here we use probabilistic theory to examine patterns in natal dispersal and to ask whether they appear to develop social affiliations with particular individuals during their juvenile years. Using data collected from a banded population of 25 territorial groups between 1998 and 2009, we found that natal dispersal is more likely to be to territories adjacent to natal territories than expected by chance, and is not significantly

related to the specific type of vegetation of the territory. We found no evidence

of social affiliations among particular juveniles; they move aggregated in large

groups, but not in more stable coalitions among particular individuals. We think

these behaviors are ways of dealing with the difficulties of being a floater and the

changing conditions of the Galapagos Islands.

Key words: coalitions, floater, natal dispersal, raptor.

INTRODUCTION

Natal dispersal can be defined as the permanent movement of an

individual from its place of birth to the place where it reproduces (Greenwood

and Harvey, 1982; Ronce, 2007). These patterns of movements are crucial for

the genetic structure of the population, gene flow and colonization. Dispersal by

juvenile raptors has been widely studied in temperate zones (e.g. Ferrer and

Harte, 1997; Newton and Rothery, 2000; Real and Manosa 2001; Forero et al.,

2002) finding different patterns related to age (Forero et al., 2002), habitat

characteristics (Suarez et al., 2000; Kauffman et al., 2004), sex (Whitfield et al.,

2009), brood size and sociality (Kenward et al., 2001) and breeding density

(Struwe-Juhl and Grunkhorn, 2007). Common factors affecting juvenile

movements and nest site selection were habitat quality and seasonal weather, a

factor significantly different in the tropics. To the best of our knowledge, very

few studies on natal dispersal have been done on tropical raptors (e.g. van Balen,

1998; Rafanomezantsoa et al., 2002; Nijman and van Balen, 2003); those few

studies found that habitat quality is the major factor determining natal dispersal patterns. In general, birds selectively choose habitats after dispersing (Cody, 1985), and their preferences maybe genetically determined, or the other alternative is that habitat preferences are acquired during development (Gruenberg and Liesler, 1990; Teuschl et al., 1998), so the natal place of a chick can determine what it will look for as a breeding adult.

The Galapagos Hawk (*Buteo galapagoensis*) is the only diurnal resident raptor of the Galapagos Archipelago. It is endemic to the islands and is a cooperatively polyandrous breeder (Faaborg *et al*., 1995; Parker 2009a). After fledging, young hawks spend 3-4 years as non-breeding "floaters" without a territory. After reaching adulthood they may attempt to enter a group in order to breed.   Group size varies from just pairs as on Espanola Island to a group consisting of a female with up to 8 males (DeLay *et al.* 1996). The study of Galapagos Hawk began with the work by de Vries (1973, 1975), a collaborative study of their unusual cooperative polyandry (Faaborg *et al.* 1980; Faaborg and Patterson 1981; Faaborg and Bednarz 1990), and genetic confirmation of polyandry came with the work by Faaborg *et al.* (1995). Other studies with this species include about the morphological differences among islands (Bollmer *et al.* 2003), the genetic differentiation among island populations (Bollmer *et al.* 2005), and what we can infer about their ancestral colonization and history of colonization of various islands from the hawks themselves (Bollmer *et al.* 2006)

and from their parasites (Whiteman *et al.* 2007). But the "floater" period of their lives is still poorly known.

Our second question focuses on the sociality of individuals in this period as floaters. Floater individuals are important for the persistence of raptor populations (Penteriani et al., 2005). Galapagos hawks are highly social animals as adults (Faaborg et al., 1995) and it is common to see large aggregations of floaters on the island of Santiago (de Vries, 1975). The floater fraction of the population is made up mainly by juveniles of different ages. Association patterns between related individuals and movements in "coalitions" have been documented for black vultures (Rabenold, 1986; Parker et al., 1995), Egyptian vultures (Margalida and Boudet, 2003) and marginally in long-eared owls (Galeotti et al., 1997). To the best of our knowledge this is the first study that address this question in a neotropical raptor. We were interested in this characteristic because being social as a floater could enhance survivorship of juveniles, by helping to overwhelm defenses by territorial adults; it is possible that coalitions formed as juveniles may persist until adulthood and breeding group formation.

Juveniles are the "pipeline" source for breeding adults, so understanding this period of time it is crucial to understand the dynamics of any population. The natal dispersal patterns and the preferences of juveniles that may be related to natal habitat characteristics can affect species distribution and chances of

colonization (Tonnis, et al., 2005), a major factor in an island ecosystem such as the Galapagos Archipelago. The particular breeding system, cooperative polyandry, of the Galapagos hawk makes it a remarkably interesting system to study breeding system evolution, and to examine the nature of sociality in the juvenile age class. In this paper we use probabilistic theory to examine whether the long "floating" period of juveniles ends in a breeding position near the natal territory, and to test if the observed groups of juveniles are composed of more stable coalitions or are just opportunistic aggregations.

METHODS

Study site

The study was conducted on Santiago Island (Fig. 1). The island is located in the center of the archipelago. Its highest point is 907m and has 585 Km^2, one of the largest of the islands not inhabited by humans (Jackson, 1993). Since 1998 hawk territories have been identified focusing in two sites, James Bay (n=25 territories) and Sullivan Bay (n=8). Groups of floaters are common in the James Bay site and this paper will focus on this area. James Bay is located in the northwestern part of the island of Santiago. The James Bay study area is relatively heavily vegetated with the following distinct zones: a distinguishable arid zone, characterized for having sparse vegetation dominated by palo santo trees (*Bursera graveolens),* various shrubs, Opuntia cactus and seasonal herbaceous plants; a transition zone with abundant shrubby and seasonal herbaceous vegetation particularly "pegadilla" (*Pisonia floribunda*) and various

tree species as guayabillo (*Psidium galapageium*) and muyuyo (*Cordia lutea*); and in the south-western part of the James Bay study area, there are open lava flows, constituted primarily by pahoe-hoe lava with scarce vegetation. Galapagos hawk territories can be found in all three vegetation types (Figure 1); because of the differences between vegetation types we consider them an important factor for our questions.

Every year juveniles and adults have been caught to take morphological measurements and blood samples (used in previous and in different ongoing studies) and have been banded with a color and aluminum bands with unique numbers, making possible individual identification. The hawks are caught with noose of rope or using a bal-chatri trap with a rat as bait. Since 1998, 660 hawks (270 adults and 390 juveniles, 110 banded as nestlings/fledglings) have been captured and banded on Santiago Island.

Natal Dispersal

Most juveniles are banded after fledging, so in this analysis we used only individuals that were banded as nestlings/fledglings on natal territories and then known to enter a territorial group years later (n=13); each individual was considered as an independent repetition. We asked if juveniles disperse as adults to territories neighboring their natal territories (despite they fact that they may have moved extensively during their nonterritorial years). For each nest from which we had data, we classified the number of territories in our study area as neighboring territories (immediately adjacent to the natal territory) and

non-neighboring territories (those at least one territory away from the natal territory inside the study area). To compare with the random chance of an individual settling in the neighboring or non-neighboring territory we calculated the number of neighboring territories and the number of non-neighboring territories for each nest in the study area and then a global mean that we used to calculate random probabilities of an individual entering either category of territory (weighted by the number of neighboring or non neighboring territories), assuming all territories are equally accessible to each individual. We used a chi-squared test to compare the number observed entering adjacent territories to the number expected by chance.

We also asked if each juvenile for which we had natal and first breeding territories settled in a territory with the same vegetation type as its natal territory. To analyze this, we used a discrete vegetation type classification of each territory, with three types: arid zone, transition zone and lava field (territories close or surrounded by lava fields). We proceeded in a similar manner as for the tests for dispersal to neighboring territories; we calculated a random chance of entering a territory in each vegetation type based on the relative abundances of territories of different vegetation types, assuming all are equally accessible to each individual, and then used a chi-square test to compare that expected value with the one observed. To calculate random expectation for location and vegetation for each disperser, we assumed it would not settle in its natal territory. Thus expectations differed slightly among dispersers, depending

on the number of neighboring territories and the vegetation type of the natal territory.

Coalitions

Since 2005 we established baiting sites in the Espumilla site (Parker 2009b). The baiting sites are located in open areas where we put meat for several consecutive days (5-14) in the summer months to attract floater individuals. We conduct censuses every 30 min for at least 8 hours per day in the area surrounding the bait, recording the identities of all the banded individuals present and the number and age class of banded and unbanded hawks.

Using the information from the baiting sites, we calculated a mean visit time and its 95% confidence interval, and used the lower confidence interval as a standard time measure of association. We calculated the association per each dyad of individuals, counting as seen together on a given day, when both individuals were at the baiting site at least the standard time of association. In case this definition of association was too strict, we also calculated the random probability of seeing together two individuals based simply on their presence/absence in a baiting site on any given day. For calculating the random probability of seeing each dyad of individuals we calculated the probability of seeing each individual, based on the frequency of their presence at the baiting sites, and then multiplied the probabilities of the individuals in each dyad (based on Zar, 1999). We then compared these two expected values to the observed value using a chi-squared test.

RESULTS

Natal Dispersal

For each of the 13 individuals used in this analysis, natal territory and

first adult breeding territory are listed in Table 1, with their sex (determined by

their morphology, based on Bollmer et al., 2003), year when each fledgling was

banded, the first year when they were seen as territorial adults, the number of

neighboring territories and the number of territories with the same vegetation

type. These numbers are useful to understand the pattern and the statistical

significance found; for example, most individuals born in the arid zone entered a

territory in the arid zone, which might be thought to suggest a preference for

this vegetation type. But considering that 11 out of 24 available territories are in

the arid zone (and X in transition zone and Y in lava zone), it is more likely that

an individual born in the arid zone enter a territory in the same vegetation type.

Figure 1 is the map of our study area, showing the location of the different

territories, and showing the different vegetation types (arid, transition, and lava

field) with different colors.

For the chi-square that compared the preference of entering as adult a

neighboring territory to its natal one, we found significant differences ($X^2 =$

3.992, df =1, p<0.05) from random expectation, with the biggest deviation from

the expected value found in the number of hawks entering neighboring

territories. Natal dispersal in Galapagos hawks is more likely to be to territories

adjacent to natal territories than expected by chance.

We did not find a significant (X^2=8.439, df=5 p>0.05) relationship between vegetation zones of the natal territory and breeding territory across the 13 individuals for which both locations were known. Our sample has males far more represented than females (males = 11; females =2) so it was not possible to consider sex as a factor to analyze natal dispersal.

Coalitions

For the analysis of associated movement of floaters, we did not find significant overall associations for any of the years (2005, X^2= 19.5, df=44; 2006, X^2= 1.775, df=5; 2009, X^2=150, df=209). We could not perform the analysis for 2007 and 2008 because of the absence of juveniles on the scans of those years (details on this period are published elsewhere). We were concerned about biasing our results of coalition formation by being too strict in our definition of "together" by using the restrictions explained in the methods section, so we conducted a similar analysis without any restriction and still found no significant differences (2005, X^2= 3.92, df=44; 2006, X2= 3.075, df=5; 2009, X^2=22.9, df=209) from random association in any year.

DISCUSSION

Natal Dispersal

The juveniles of Galapagos Hawk have apparently high mortality, with return rates every year of <10% (details published elsewhere); even when more than 100 hawks have been banded at their natal territory only 13 were later

seen as territorial adults in our study area. The distance that can be effectively

monitored by foot limits the size of the study area. So our results may have the

bias of lack of data in the dispersal patterns beyond the study area limits.

Through studies of genetic structure (Bollmer et al. 2005) we know that there is

gene flow across the island. So juveniles disperse further than our study area.

According to our results, we can say that hawks do tend to disperse to territories

neighboring their natal territories, but considering the breeding system, social

characteristics must have an important role in determining the actual chances

for a hawk to enter into a group, and that may often lead to greater dispersal

distances that would explain the continuous gene flow across the island. Finding

significance (p<0.05) for a preference towards entering as adult a neighboring

territory to its natal one can be related to familiarity of the habitat and efficiency

in hunting in that type of habitat, similar to the report by Kauffman (2004).

However, in this case the test concerning habitat preference was not significant

(p=0.134). We can speculate that the attraction of neighboring territories may be

because of familiarity with hunting opportunities, or familiarity with the

individuals in neighboring territorial groups. Other characteristics, such as

group size, phase of the breeding cycle and territory quality, may be related to

the chance of an individual entering into a group. It is difficult to speculate

further since the actual mechanism by which young adults join territorial groups

remains unknown.

Sex may be an important factor in the dispersal patterns of the hawks, but

because our sample we could not test for it. The breeding system imposes very

different challenges for males and for females; males can enter into a territory increasing the group size but without needing to displace a former male, and since there can be several males per territory there are more chances for floater males to become breeding adults. In the case of females, they have to displace the territorial female, and since there is only one female per territory the chances of a female floater of becoming a breeding territorial are fewer. So we can speculate that females would have to disperse farther looking for an opportunity of becoming a breeding adult; further monitoring of the population and banding of nestlings/fledglings is needed to better understand possible differences in pressure for dispersal related to sex.

Coalitions

According to our results, juvenile hawks, even if found in groups, do not move in more stable cohesive coalitions. But still this pattern of aggregation would be advantageous for the individuals, related to overwhelming territorial defenses or hunting efficiency. Parker et al. (1995) and Margalida and Bouret (2003) found these coalitions formed among relatives in black vultures and Egyptian vultures, respectively. In the case of the Galapagos hawk, that lays two (rarely three) eggs and successful nests commonly fledge only one, it is likely that hawks cannot recognize previously fledged individuals, so advantages related to kin selection are unlikely in our system. So even when hawks form close stable associations as adults, they can move aggregated as juveniles but not in close association with other individuals, just taking advantage of the effect

that numbers can have (e.g. overwhelming territorial defense to gain access to food). This also shows a tendency even as juveniles to gregariousness and tolerance to the presence of other conspecifics, which foretells their later tendency to form stable groups as breeding adults. Again, the mechanism of group formation and individual choice for group admission remains unknown.

In this paper we gave some insights to the mostly unknown years as floaters of the Galapagos hawk. According to our results Galapagos hawks tend to disperse to territories neighboring their natal ones, but a larger sample size and more monitoring in the rest of the island are needed to test this pattern and possible differences between sexes. Even though the floater hawks frequently aggregate in large groups, they do not seem to move in more stable close coalitions, so advantages of aggregation are likely related just to the advantages of group membership and not to alliances with particular individuals.

The changing and challenging conditions in the Galapagos Islands may select for behaviors or characteristics that help to cope with them; becoming a breeding adult in a territory neighboring its natal territory may have the advantage of knowing the environment or the members of at least one neighboring territory (its natal group), and maybe the discrete vegetation classification is not enough to detect more specific features that may be the attractive features of a given habitat. Differences in relative abundances of prey species and possible differences in diet between territories are likely, but studies on this are needed. The exact mechanism of floaters becoming breeding

territorials remains unknown. One possibility is that floaters end up entering neighboring territories due to familiarity with those hawks, but we need to understand how hawks recognize each other and how a group "chooses" to accept a new male or female in the territory. The strong bias in our sample in relation to sex (11 males and 2 females) may give important cues of sex related dispersal patterns. As fledglings, around the same number of females and males were banded, so this bias maybe explained either by high female mortality, which is not seen in the baiting sites census, or with differences in dispersal pressures. Due to the breeding system, and given that there is only one spot for a female per breeding group, females in some cases should have to disperse further in order to find a breeding territory. Bollmer et al. (2005) found that there is continuous gene flow between James Bay and Sullivan Bay, which supports the idea that individuals form these sites disperse to the rest of the islands; but a bigger sample size and further monitoring is needed.

We assume that floaters move more or less freely over the island, and some opportunistic data support that idea (Parker et al., unpublished data) but we need more information on movement patterns of floaters, to analyze differences between sexes, and range relate to age. This information would help to better understand natal dispersal patterns and association with other individuals. The fact that we did not find formation of stable coalitions between juveniles differs from adult behavior, when they form a cohesive stable breeding group; we need to understand what triggers this change, and understand the mechanism of becoming territorial will help in this respect.

Further monitoring is needed to understand the floater years of this raptor species and its population dynamics. Thanks to the fact that this species is found in the relatively simple and well protected environment of the Galapagos Islands, together with extensive monitoring, the Galapagos hawk can become a useful model for the conservation and management of other tropical raptors. We recommend efforts are made to maintain monitoring and studying this endemic species.

LITERATURE CITED

Amstrup, S., McDonald, T. and Manly, B. 2005. Handbook of Capture-Recapture Analysis. Princeton University Press. New Jersey, USA.

Berger DD, Mueller HC. 1959. The bal-chatri: a trap for birds of prey. Bird-Banding 30:18–26.

Bollmer, J.L., Whiteman, N., Cannon, M., Bednarz, J., DeVries, T. and Parker, P.. 2005. Population genetics of the Galápagos Hawk (*Buteo galapagoensis*): Genetic monomorphism within isolated populations. Auk 122:1210-1224.

Bollmer, J.L., Sanchez, T., Donaghy Cannon, M., Sanchez, D., Cannon, B., Bednarz, J., DeVries, T., Struve, M. and Parker, P. 2003. Variation in morphology and

mating system among island populations of Galápagos Hawks. The Condor 105:428-438.

Bollmer, J., Kimball, C., Whiteman, N., Sarasola, J. and Parker, P. 2006. Phylogeography of the Galápagos Hawk: a recent arrival to the Galápagos Islands. Molecular Phylogenetics and Evolution 39:237-247.

Campbell, K, Donlan, C. 2005. Feral goat eradications on islands. Conservation Biology 19: 1362-1374.

Cody, M.L. 1985. Habitat selection in birds. Academic Press, New York, New York, USA.

Cruz F, Carrion V, Campbell KJ, Lavoie C, Donlan CJ. 2009. Bio-economics of large-scale eradication of feral goats from Santiago Island, Galápagos. *J Wild Manage* 73:191–200

de Vries, Tj. 1973. The Galápagos hawk, an eco-geographical study with special reference to its systematic position. Ph.D. dissertation, Vrije University, Amsterdam.

de Vries, Tj. 1975. The breeding biology of the Galápagos hawk, *Buteo galapagoensis*. Le Gerfaut 65:29-57.

DeLay, L.S., J. Faaborg, J. Naranjo, S.M. Paz, Tj de Vries, P.G. Parker. 1996. Paternal care in the cooperatively polyandrous Galápagos Hawk. Condor 98:300-311.

Faaborg, J., and C. B. Patterson. 1981. The characteristics and occurrence of cooperative polyandry. Ibis 123:477-484.

Faaborg, J., and J. C. Bednarz. 1990. Galapagos and Harris' hawks: divergent causes of sociality in two raptors. Pages 359-383 *in* Cooperative Breeding in Birds: Long Term Studies of Ecology and Behavior (P. Stacey and W. Koenig, Eds.). Cambridge University Press, Cambridge.

Faaborg, J., P.G. Parker, L. DeLay, T. de Vries, J.C. Bednarz, S.M. Paz, J. Naranjo, T.A. Waite. 1995. Confirmation of cooperative polyandry in the Galapagos Hawk (*Buteo galapagoensis*) using DNA fingerprinting. Behav. Ecology and Sociobiology 36:83-90.

Faaborg, J., Tj. de Vries, C. B. Patterson, and C. R. Griffin. 1980. Preliminary observations on the occurrence and evolution of polyandry in the Galápagos hawk (*Buteo galapagoensis*). Auk 97:581-590.

Greenwood, P. and Harvey, P. 1982. The Natal and Breeding Dispersal of Birds. Annual Review of Ecology and Systematics 13:1-21.

Gruenberger, S. and Leisler, B. 1990. Innate and learned components in the habitat selection of coal tits *Parus ater*. J. fuer Ornith. 131, 460–464.

Hull, JM, WK Savage, JL Bollmer, RT Kimball, PG Parker, NK Whiteman, HB Ernest. 2008. On the origins of a Galapagos archipelago lineage: An examination of phenotypic differentiation and mitochondrial paraphyly. Biol. J. Linnean Soc. 95:779-789.

Jackson MH. 1993. Galápagos: a Natural History. Canada: University of Calgary Press.

Kenward R.E, Marcström V, Karlbom M 1999 Demographic estimates from radio-tagging: models of age-specific survival and breeding in the goshawk. *J. Anim. Ecol.* 68:1020–1033

Kenward, R., Walls, K. and Hodder, K. 2001. Life Path Analysis: Scaling Indicates Priming Effects of Social and Habitat Factors on Dispersal Distances. Journal of Animal Ecology 70:1-13.

Kirk, D.A. And C. Hyslop. 1998. Population status and recent trends in Canadianraptors: A review. Biological Conservation 83:91-118.

Margalida, A. and Boudet, J. 2003. Dynamics and temporal variation in age structure at a communal roost of Egyptian vultures (neophronpercnopterus) in Northeastern Spain. Journal of Raptor Research 37:252-256.

Newton, I . 2001 . Causes and consequences of breeding dispersal in the Sparrowhawk *Accipiter nisus* . Ardea 89:143-154.

Nijman, V. and van Balen, S. 2003. Wandering stars: age-related habitat use and dispersal of Javan Hawk-eagles *(Spizaetus bartelsi)*. Journal of Ornithology 144:451-458.

Parker, P., Waite, T. and Decker, M. 1995. Kinship and association in communally roosting black vultures. Animal behaviour 49:395-401.

Parker, P.G. 2009a. A most unusual hawk: One mother and several fathers. Pp. 130-137 in (Tui de Roi, ed.). Galapagos: Preserving Darwin's Legasy. Firefly Books, Ontario.

Parker, PG 2009b. 2005-2009 Survey of Galapagos Hawks (*Buteo galapagoensis*) on Islas Santiago and Espanola, Galapagos, Ecuador. Report to the Galapagos National Park. 19 pp.

Sandercock B. 2006. Estimation of demographic parameters from live-encounter data: a summary review. J. Wildlife Manage. 70:1504–1520

Struwe-Juhl, B. and T. Grünkorn. 2007. Results of colour-ringing White-tailed Sea Eagles Haliaeetus albicilla in Schleswig-Holstein: site fidelity, movements, dispersal, age of first breeding, age structure and breeding of siblings. *Vogelwelt* 128:117–129.

Teuschl, Y., Taborsky, B. and Taborsky, M. 1998. How do cuckoos find their host? The role of habitat imprinting. Anim. Behav. 56, 1425–1433.

Thiollay JM. 1993. Response of a raptor community to shrinking area and degradation of tropical rainforest in the south Ghats (India). *Ecography* 16:97–110

Tonnis, B., Grant, P. Grant, R. and Petren, K. 2005. Habitat selection and ecological speciation in Galápagos warbler finches (Certhidea olivacea and Certhidea fusca). Proc. R. Soc. B272:819-826

Whiteman, NK, RT Kimball, PG Parker. 2007. Co-phylogeography and comparative population genetics of the Galápagos Hawk and three co-occurring ectoparasite species: Natural history shapes population histories within a parasite community. Molecular Ecology 16:4759-4773.

Whitfield, P. et al. 2009. Juvenile Dispersal of White-Tailed Eagles in Western Scotland. Journal of Raptor Research 43:110-120.

Zar, J. 1999. Biostatistical Analysis. 4th Edition. Simon & Shuster, Upper Saddle River, New Jersey, USA.

TABLES

Table 1. Summary of individuals used in study of natal dispersal patterns. There
are listed the individuals with its respective sex (M=male, F=female); year
where the individual was banded as fledgling or nestling, and its natal
territory; the year when each individual was first seen as territorial and in
which territory it first joined a breeding group. The number of immediate
neighboring territories and territories with the same vegetation type
inside the study area are listed. An asterisk next to the number means that
the individual either entered one of the immediate neighboring territories,
or entered a territory with the same vegetation type.

| Ind	Sex	Year	Natal Territory	Year	Breeding Territory	Neighbors		Same Vegetation	
1	M	2001	GUA	2006	GUL	3		8	
2	M	2002	PER	2006	GUL	3	*	11	*
3	M	2002	VAL	2006	GUL	5		11	*
4	M	2002	PER	2006	GUL	3	*	11	*
5	M	2002	CO2	2008	GUL	4		11	*
6	M	2001	LEJ	2006	LAG	3		3	
7	M	2002	ESP	2009	LEJ	3	*	3	*
8	M	2001	GUA	2006	MID	3	*	8	*
9	M	2001	LAV	2009	VAL	3		3	
10	F	2001	SHL	2004	CO1	4		8	
11	F	2002	CO1	2006	GUL	6	*	11	*
12	M	2000	GUA	2009	LEJ	3		8	
13	M	2003	YOG	2008	VAL	4		11	*

FIGURES
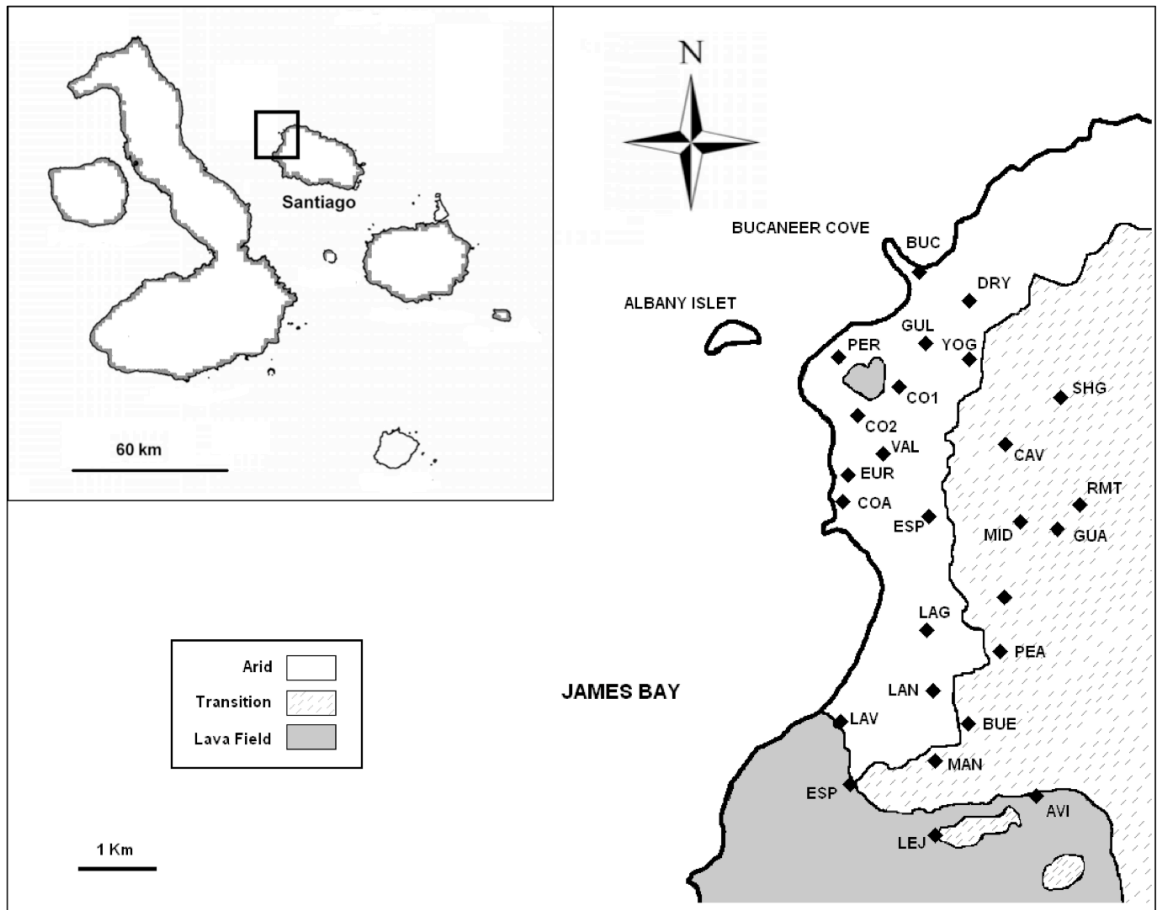
Figure 1. Map of the Study Area. Our study area is located in the north western side of the Santiago Island. Diamonds indicate locations of the 26 nests/territories of our study area with its name code next to it; and schematized the different vegetation zones (1) Arid, (2) Transition, and (3) Lava Field.

Chapter Two

Survivorship in the Galapagos hawk: Demographic and social effects in a changing environment

Jose Luis Rivera[1], Ken Levenstein[3], PNG Person[4], Hernan Vargas[2] and Patricia Parker[1]

[1]University of Missouri-St. Louis. One University Boulevard. St. Louis, MO 63121-4400.

[2]The Peregrine Fund. 5668 West Flying Hawk Lane. Boise, Idaho 83709.

[3] Ken's Intitution

[4] Parque Nacional Galapagos

ABSTRACT

The Galapagos Hawk (*Buteo galapagoensis*) is an endemic raptor of the Galapagos Archipelago, where it is the only diurnal resident bird of prey. On the island of Santiago the hawk resides in monogamous pairs and polyandrous groups in breeding territories maintained throughout the year. We used a 12-year data set in a capture-mark-recapture approach 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. We used program MARK to evaluate the effect on adult survivorship of sex, body size, polyandrous group size per year, and vegetation zone of the

territory. The best model included all the above parameters with different

intercepts per year, with group size per year having the greatest contribution;

this indicates that breeding system has a significant effect on adult survivorship.

The differences between years (shown by having models with yearly intercepts)

might be related to other variables, such as variation in prey abundance,

individual prey preferences, or to effects of goat eradication and vegetation

recovery afterwards, that we could not detect with the discrete vegetation

classification used. Juvenile floaters showed a drastic decline in 2007 and 2008

which we attribute to the eradication of feral goats in 2006 and subsequent

habitat changes.

Key words: apparent survivorship, capture-mark-recapture model, floaters,

Galapagos Islands, tropical raptor.

INTRODUCTION

The Galapagos Hawk (*Buteo galapagoensis*) is the only diurnal resident raptor of

the Archipelago. It is endemic to the islands and is a true cooperative

polyandrous breeder (Faaborg et al. 1995; Parker, 2009), in which a group of

unrelated adult males defends a territory year-round, sharing copulation

privileges with the territory's single female occupant, participating in incubation,

and collectively protecting and providing for the offspring (Faaborg and

Patterson 1981). The polyandrous group size varies from a single male paired

with a female to a group of up to eight males with a single female (DeLay et al.

1996). The dominant mating system varies among islands: on Espanola there are only pairs, whereas in Santiago island there is diverse group composition, from pairs to groups of a female with up to eight males, with a mean of 2-3 males per group (Bollmer et al. 2003). This hawk species has an opportunistic and diverse diet that ranges from grasshoppers to iguanas and scavenging (de Vries 1973, 1975). After fledging, a juvenile hawk will spend 3-4 years as a non-breeding "floater" without a territory, and it is thought that they wander all over the island during this time. After adulthood they may enter a group in order to breed, but some birds in adult plumage remain with the cohort of subadult juveniles; the process by which a hawk enters a group remains unknown.

This unusual breeding system has awakened the interest of previous researchers that tried to understand its effects on the population and individual level. Faaborg (1986) found that in short term polyandrous males have a disadvantage in reproductive success compared with monogamous males; Faaborg and Bednarz (1990), in search of an explanation for a system that may not offer clear breeding advantages, proposed that polyandrous males may have increased survivorship.

Faaborg (1986) estimated annual adult survivorship as >0.90, without considering sex or group size as factors, and with a small sample size (N=18). This is higher than estimates made for other raptors (e.g., 0.75 in Northern Goshawks: Reynolds et al. 2004; 0.544 for first-year birds, 0.60 for second-year and 0.80 for older birds in peregrine falcons: Craig et al. 2004).

In this study we focus on the Galapagos hawk population from the island of Santiago, of size 585 Km^2 located in the center of the archipelago and highest point at 907m (Jackson, 1993). Since 1998 hawk territories have been studied in two study sites on Santiago. James Bay has 25 identified territories located in the northwestern part of the island (Figure 1). Sullivan Bay is located the eastern coast of Santiago and has 8 territories identified (Figure 1). The Sullivan study area is dominated by a barren, young pahoe-hoe lava flow, with some parts of a-a lava, where the hawks inhabit small volcanic cones containing sparse vegetation. In contrast, James Bay is relatively heavily vegetated with a distinguishable arid zone and transition zone where nests are located. A small part of the James Bay study area consists of the James Bay lava flow, a more open habitat with "islands" of vegetation resembling the Sullivan Bay area. From previous studies we know that there is gene flow between the study areas (Bollmer et al., 2005).

As in most of the other islands in Galapagos, Santiago has introduced species. Seamen released goats (*Capra hircus*) in the early 1800s so that they could later harvest them as a source of fresh meat, and the goats led to major changes in the ecosystem, turning thick shrubby vegetation into open habitat with some scarce trees (Campbell and Donlan, 2005; Lavoie et al. 2007). Project Isabela, conducted by the Galapagos National Park and the Charles Darwin Foundation, succeeded in eradicating the goats from the island of Santiago, finishing in 2006 (Lavoie et al. 2007; Cruz et al. 2009). Since then a remarkable recovery in the vegetation cover has been observed.

We were interested in investigating which factors may be influencing the survivorship probability of the Galapagos hawk, taking into account their breeding system and the ecological changes subsequent to the eradication of goats from the Santiago Island. Specifically, we were interested in the contributions of sex, vegetation type of territory, and group size to differences in survivorship, and whether there were detectable changes in those effects in relation to the eradication of goats. Complementary to this analysis of the territorial adults, we were interested in the population sizes of the floater fraction of the population, since they are important for the persistence of the population (Penteriani et al. 2005). In addition, the number of juveniles seeking breeding positions may be a factor influencing territorial group sizes, by contributing to stress related to territory defense and sex ratio-related effects on apparent survivorship probability.

METHODS

The hawks were caught with a noose pole, or with a bal-chatri trap (Berger & Mueller, 1959). From each individual we recorded eight morphometric measurements: foreclaw, hallux, body mass, wing, tail, cranium, bill depth, and culmen (see Bollmer et al. 2003 for details). In addition, sex was determined for each individual by size of particular morphometric measurements, since Galapagos hawks are sexually dimorphic (Bollmer et al. 2003), and age class was determined based on molting patterns and color (juveniles are lighter than

adults). Finally, we collected a small blood samples from the brachial vein (to be used in other concurrent projects).

Each individual was banded with an aluminum band with a unique combination of letters, numbers and color (made by Acraft, Alberta Canada) and a regular aluminum band with a unique alphanumeric code was put in the other leg. The color bands are easy to read, so resighting can be confidently conducted.

Beginning in 1998 we conducted censuses during june-july in all the identified territories that increased during the first years of study until the current 33 identified territories (James Bay N=25, Sullivan Bay N=8). The annual census has been done during the summer months (during the peak of the breeding season), and consisted of recording which individuals were present as members of each territory, changing bands if they were getting too old to be read, recording breeding activity, and banding fledglings and unbanded adults. To study the floater, non-breeding fraction of the population, since 2005 we established two baiting sites at the James Bay study area. These baiting sites are open areas where we put meat in order to attract juveniles, and we record which individuals are seen and the numbers of banded and unbanded hawks. We have capture/resighting histories for each individual, and proportions of banded vs. unbanded floaters at baiting sites; these data are suitable for analysis using CMR models.

Floater Population size estimates

Since 2005 we established baiting sites in the James Bay area. We conducted

censuses for 5-14 consecutive days in the summer months. We conducted

censuses every 30min for at least 8 hours per day in the area surrounding the

bait, recording the number and identities of all banded individuals present and

the number of unbanded hawks of each age class (juvenile and adult).

In order to estimate the population size of the floater fraction of the

Galapagos hawk population, we used the census data from the baiting sites at the

James Bay area. We calculated the proportion of banded vs. unbanded

individuals, taking care to exclude the territorial individuals that visit the baiting

sites and followed Armstrup et al. (2005) to estimate population sizes per year.

Survivorship Analysis

Advances in mathematical theory to analyze capture-mark-recapture

(CMR) datasets, such as the Jolly-Seber and Cormack-Jolly-Seber models for

open populations (Cormack 1964, Jolly 1965, Seber 1965), together with the

development of software for conducting this intensive analysis, such as program

MARK (White & Burnham 1999; Cooch & White 2007), provided the opportunity

to obtain more reliable estimates of survivorship, including the contributions of

different factors or covariates (Anderson and Burnham1999; Sandercock 2006).

We used sex, body size, vegetation type where the territory is found (arid,

transition, and lava field) and group size per year as covariates.

The estimated survivorship refers to the probability of an individual surviving from one year to the next or not leaving the study area. In other words, we cannot know if an individual is dead or just left the study area; therefore, the estimated survivorship is not the real survivorship and is commonly referred as apparent survivorship (Amstrup et al., 2005).

We used a Jolly-Seber model to estimate the floater population size (Amstrup et al. 2005); and the data were limited in a manner that left us unable to conduct survivorship estimates in this fraction of the population because extremely low recapture/resighting rates (<10%) which would produce unreliable and possibly biased estimates due to low recapture probabilities. The census data (CMR data) were analyzed using the program MARK (Cooch & White,2007), and Akaike's Information Criterion (AIC; Akaike 1973, 1974) was used to select the model that best fit the data.

Fourteen models were tested (Table 1); these models were chosen based on their biological meaning, plus one null model for comparison. The null model was defined as a constant survivorship and recapture probability over all the years of study, without any distinction based on sex or vegetation type of the territory, and without any covariates as group size or body size. The other models are logical combinations of the factors of interest: sex, body size, group size per year, vegetation type of the territory, and variation between years, chosen to understand the influence of each variable and possible interactions between them. To obtain the body size index we performed a PCA with all the morphometric measurements taken, and used the coordinates in PC1 as a

measure of differences in body size between individuals (based on Bollmer et al. 2003). PCA was done in SPSS 17.0.

As noted by Armstrup 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 equal probability of surviving a given time interval; (3) bands/marks are not lost or overlooked, and the individual ID 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.

Since our study species is a cooperative breeder, we were concerned with the first, second, and sixth assumptions, since hawks that belong to the same territorial group may face the same conditions and therefore lack independence; therefore, using program RELEASE we performed a goodness of fit test and calculated a ĉ index, for correction in case of data overdispersion, and therefore we used QAIC, that is an approximation based in the Quasi-likelihood theory of the AIC (Anderson et al. 1994) for the final model selection and further inferences.

RESULTS

The Galapagos Hawks are remarkably tame and curious, which facilitated the process of capture which was reflected in a considerable sample size for the

territorial adults (N=198 banded during 12 years) and made possible reliable

band reading which was one of the assumptions of the Cormack-Jolly-Seber

model.

In the case of juveniles/floaters, the baiting sites proved to be a good method to

attract them and estimate population sizes. From 1998 to 2009, a total of 390

juveniles were banded, but their resighting was very low, less than 10%. This

may be related to high mortality or high emigration rate from the study area.

This low resighting probability made survivorship estimates unreliable.

However, the structure of our data permitted us to estimate local population

sizes.

Population Estimates

During two years, 2007 and 2008, we found no juveniles at the baiting

sites. This complicated our original ideas of relating group size in territorials

with floater population sizes. Even so, we were able to estimate population sizes

for 2005, 2006 and 2009, but with only three points we were not able to relate

this factor with adult survivorship or group size.

We saw a decline in size of the nonterritorial component of the

population between 2005 and 2006 (Figure 2) from 130 ± 34.885 (95% CI)

floaters in 2005, to 79 ± 10.76(95%) CI in 2006, to the apparent disappearance

of this fraction of the population during 2007 and 2008. In 2009 our estimates

were 165 ± 15.64 (95% CI), even higher that for 2005. At that time we found a

small number of previously banded individuals that had not been observed

during 2007 or 2008; this showed that even when we did not see any floaters

during those years, some were still alive. However, during 2009, except for 12

previously banded hawks, the rest were recently fledged individuals, suggesting

that there was a severe restriction in number of juveniles surviving through the

years 2007 and 2008.

Survivorship Modeling

Among the 14 models tested, the one that best fit the data was the most

general model that included all the factors: sex, body size, vegetation type, and

group size per year. We were interested to see if the relative importance of the

variables changed between years, and we tested this with two models, one with

a common intercept for all years and one with an intercept for each year. The

model with yearly intercept fitted the data best (lower deviance) and had the

lowest QAIC (Table 1). The variation in QAIC between the two models was

6.1846, and a Likelihood Ratio test between these two models supported that

the best model was the one with different yearly intercepts (Chi square = 48.78;

df=17; p=0.0001).

The weight of the QAIC (wQAIC in Table 1) was used to estimate the

relative importance of each variable, following the recommendations by

Burnham and Anderson (2002). This index is a relative measurement of the fit of

the model, specific to the set of tested models, so it can not be extrapolated to

other models out of this set, but is a useful tool to compare how much the

addition or removal of a variable affects the fit of the model. We found that the

most important variable was variation between years (model with different intercepts was the best model in the set, and had a difference of 0.90889). The next important variable was group size per year. The rest of the factors were far less important. Sex did not show high importance, contrary to our predictions, nor did body size. The type of vegetation was important for the resighting probability. Table 2 shows the signs of the Beta coefficients of the best fit model (including all variables and yearly intercepts); this illustrates the variation between years in the relationship of survivorship and the tested variables.

   In Figure 3 the survivorship estimates and 95% CI obtained from program MARK can be observed. Figure 3.A compares the adult males and females from territories in the arid, transition and near lava vegetation types. For comparison we divided them by sex in Figure 3.B for females and Figure 3.C for males. For the first period of time, 1998-1999, there are no data for males nor females of the transition zone because we had not found any nests/territories in that vegetation area at that time. The oscillations in mean survivorship per sex and per vegetation type are remarkable, even when most of them are not significantly different. Interesting changes are the decline in females from the arid zone in the 2003-2004 period, one year after the beginning of the goat eradication campaign, and again a decline in the survivorship of females from the arid zone, and females from the territories near the lava fields in the period 2005-2006, around the time when the eradication campaign was finishing, and in 2007-2008, two years after completing goat removal. Males experienced a decline in apparent survivorship in the 2007-2008

year for the males in the arid zone, and an overall decline in the 2008-2009

period for the males of all vegetation zones. At the end of the study period, it is

not possible to separate the capture probability from the survivorship

probability, since further information is not available for this analysis (for

further details review Armstrup et al., 2005); so this last period of time will not

be considered for the discussion.

DISCUSSION

To the best of our knowledge this is one of the first studies using this type

of approach to estimate the apparent survivorship of a tropical *Buteo*. This

species is endemic to the Galapagos Islands and considered endangered because

of their small population sizes and low genetic variability (Bollmer et al. 2005

BirdLife International 2009), and because of their unusual breeding system,

cooperative polyandry, together with the ecological restoration program, Isabela

Project, that took place during our monitoring years. This approach allowed us

to analyze how the polyandrous breeding system may be related to advantages

in survivorship and how an ecological restoration program that seeks to restore

a degraded ecosystem to its original condition can also have an impact on the

native fauna. Unfortunately, in order to separate these two effects, it would have

probably been better to have several more years of data before the eradication

program to establish a baseline in order to assess the impact of the restoration

program on the Galapagos Hawk.

We decided to divide our analysis into two groups: territorial adults and floaters, due to the differences in life history during those periods of their lives. We were very interested in analyzing changes in survivorship during the last years of the goat eradication campaign (Isabela project), but significantly low return rates in the floaters made this analysis unreliable, so our conclusions for this group are based just on the population estimates since 2005. During 2005-2006, a tendency to decline in population size can be seen (Figure 2), until in 2007 and 2008, when we did not see any floaters. In general, non-territorial 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). Aggregation would give them the chance of overwhelming the attacks and harassment of territorial adults and gaining access to resources (e.g., goat carcasses, or bait at our baiting sites). The number of juveniles surviving 2007-2008 was probably small enough that they were not able to overwhelm the territorial defenses, and did not approach to the baiting sites. This might explain our failure to detect them during 2007 and 2008, but we saw some of them in 2009, when large numbers of floaters (mostly hatchlings of the year) were present. Therefore, our juvenile population estimates of zero during 2007 and 2008 were underestimates, possibly due to the limitations of our method to account for social interactions between floaters and territorial hawks. Because of the lack of data before the beginning of the eradication program we cannot show conclusive evidence supporting the theory of the eradication of goats as a factor changing the population dynamics of the

floater fraction of the population. However, prior to our formal censuses of

juveniles 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. We conclude that

the decline in the floater population beginning at the end of the eradication

program and persisting for two years must be related to that eradication, but the

exact mechanism is still to be determined. One of the possibilities that we ruled

out was lead poisoning; we conducted tests for lead (Parker et al., unpublished

data) without finding any evidence of abnormal levels. So we believe the

explanation must be in the population dynamics, possibly related to artificially

inflated floater numbers during the years when the goat-induced openness of

the habitat facilitated their foraging followed by years of goat eradication during

which an estimated 100,000 goat carcasses were left on Santiago to be

scavenged. The sudden decline of the floater population followed the removal of

what may have been a major feeding resource.   Further monitoring is needed to

understand the possible effects of the drastic decline in floater population during

2007 and 2008, considering that floaters are the "pipeline" for replacing

breeding adults in territorial groups. These possible effects can constitute a long

term effect of goat eradication still to be seen.

Our survivorship estimates (Figure 3) on average are consistent with the

simplest estimate made by Faaborg (1986), and reflect one of the highest annual

survivorship estimates reported for a raptor (Klavitter et al. 2003, Craig et al. 2004, Millsap et al. 2004, Reynolds et al. 2004). This may be related to the fact that this species is sedentary, and does not go through a migration process that other studied raptors do, besides being a polyandrous breeder, which is thought to benefit survivorship. According to the models, the variable that was the most important for apparent survivorship of the hawks was group size (Compare wQAICc in Table 1). This in some ways agrees with Faaborg and Bednarz (1990) that affirmed that individuals in bigger groups should have the advantage of higher survivorship. But the relationship between survivorship and group size changed between years and between vegetation types (Table 2), based on the fact that the best model included different intercepts between years. So there is no "optimum" group size and it is not true that polyandrous males have higher survivorship. But it seems logical that being part of a group would be an effective way of dealing with the changing environment of the islands. This gives support for the idea of the evolution of polyandry to be able to deal with uncertain conditions. The mechanism by which the group size is determined, in other words, how the hawks "choose" which males and how many will form each group, is still unknown. One anecdotal observation (Parker, personal observation) suggests that a new male experiences a period where he hunts and provides for the offspring, even when the female may be very aggressive towards him. But we have few additional insights into this mechanism. Further behavioral studies are needed to understand this aspect of this breeding system.

The fact that the hawks, females and males, from the transition zone had more stable, and on average higher survivorship than the hawks from the other vegetation types (Table 3), was at first surprising to us. The transition zone is a highly vegetated area, with thorny bushes and tall seasonal grasses, which would provide challenges to hunting for a *Buteo* hawk. But it is possible that this higher apparent survivorship may be related to how much competition occurs over territories in different habitat zones. In this case, lower survivorship can be explained in the territories where more hawks are trying to enter, because of its higher quality, like the arid zone or near the lava fields; both of the habitats with higher apparent turnover are more open and more suitable for the hunting strategy of a *Buteo* hawk, leaving the transition zone as a marginal habitat, where few hawks live. Another way of understanding the apparent survivorship estimated by CMR model is that apparent survivorship can be thought of as turnover rate in each territory. High quality territories may have higher pressure by floaters to enter the breeding group, increasing the turnover rate of the territory and therefore lowering apparent survivorship. So the fact of finding higher and more stable apparent survivorship in the transition zone may be related to low territory quality or territory demand; insights into the group formation mechanism would help us to understand how the quality of the territory and the demand of becoming a breeding territorial adult affects turnover rate and its relationship with the different vegetation zones.

Finding that the effect of the different factors varies between years seems consistent with the high seasonality observed in Galapagos. Related to the El

Nino Southern Oscillation (ENSO), research in other endemic species of the archipelago like penguins (*Spheniscus mendiculus*; Vargas et al. 2006), Darwin's finches (*Geospiza* spp; Grant et al. 2000) and lava lizards (*Microlophus* spp; Jordan and Snell 2000) have shown the impact that different weather conditions, particularly rainfall, can have on the ecology of the islands and the population of the species that inhabit them. So if the populations of Galapagos hawk prey species (e.g. lizards, grasshoppers) and vegetation are affected by the ENSO or yearly differences in rainfall, this will affect the Galapagos hawk populations through a trophic cascade. But further studies of annual relative prey abundances are needed to test this hypothesis, not just in ENSO years, but general seasonal and annual variations. It is also likely that different individuals have different prey preferences, as a way of "niche partitioning" within groups to avoid intra-group competition, so variations in a specific prey population may affect distinctively each individual, but this hypothesis of within group prey preference remains to be tested.

We chose to analyze vegetation under a discrete classification of the major features of each type, considering: (1) arid zone the more open habitat with sparse vegetation; (2) transition zone with more abundant seasonal vegetation, more humidity and found at higher elevation; (3) and territories dominated by the lava flows found in our study area; this was a proxy to measure the effect of goat removal, since the vegetation recovery after goat eradication has been most conspicuous in the transition zone (personal observation). Therefore, if goat eradication negatively impacted survivorship by

impeding hunting, we predicted the greatest impact in the transition zone. But since our models indicate an undetermined effect with a temporal component, it is possible that annual variation in vegetation cover itself can be such a factor. So a finer analysis of vegetation variation and composition within territories may help us to interpret the evidence from the models. We can say that the eradication of goats did not have a significant impact on the survivorship of the territorial adults of the Galapagos hawk, as we can not find clear patterns that can relate adult survival to goat eradication. But it is very suggestive that the lowest survivorship estimate during our study was in the period between 2005-2006, at the end of the eradication program (Table 3). But not having a strong, clear pattern does not mean the goat eradication did not have an impact on the Galapagos hawk population in the Santiago Island; survivorship may not be the adequate response variable to analyze the effect of goat eradication on the territorial adults, since we expect that being older, more experienced and owning a permanent area to hunt they will be able to deal with changing conditions. One of the traits that we consider can be better response variable to measure the effect of ecological changes instead of adult survivorship, is reproductive success, which can link the patterns found in the population sizes of floaters with our finding in adult survivorship. The lack of data on breeding success during the years of our study means that we cannot relate the extremely low numbers of floaters during 2007 and 2008 to low breeding success by the territorial adults, related to ecological changes driven by the restoration program, but is a very likely explanation for the observed pattern.

Invasive species are a major conservation concern everywhere, which has led us to start with the eradication of these species and ecological restoration programs. But in cases where the introduced species have been in the ecosystem for long enough time, these species became an integral part of the community, so restoration programs motivated to conserve the native fauna can have an unanticipated negative impact on those species. Our study has shown evidence that the eradication of goats from Santiago has had a negative effect on the Galapagos hawk population, severely reducing the floater population sizes after the completion of the eradication. But this does not mean the project was negative for the species; this may mean the whole ecosystem is adjusting to a new equilibrium after losing its major herbivore for the last 200 years, and the numbers of Galapagos hawks are adjusting to the current capacity of the ecosystem. We recommend the population of the Galapagos hawk in the Santiago Island be further monitored to better understand how the island ecosystem with its current features are shaping the Galapagos hawk population, and factors as relative prey abundance, diet preference, vegetation recovery patterns and differences between territories, and reproductive success between vegetation zones be documented as valuable information for the understanding of this endemic and endangered island raptor.

ACKNOWLEDGMENTS

LITERATURE CITED

Akaike H. 1973. Information theory and an extension of the maximum likelihood principle. In: Petrov BN, Csaki F, editors. International Symposium on Information Theory. 2nd ed. Budapest, Hungary. p. 267–281

Akaike, H. 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control 19: 716–723

Amstrup, S., McDonald, T. and Manly, B. 2005. Handbook of Capture-Recapture Analysis. Princeton University Press. New Jersey, USA

Anderson, D. and Burnham, K. 1999. General strategies for the analysis of ringing data. Bird Study 46(sup):S261-S270.

Anderson, D. R., Burnham, K. P. and White, G. C. 1994. AIC model selection in overdispersed capture-recapture data. Ecology 75 1780-1793

Berger DD, Mueller HC. 1959. The bal-chatri: a trap for birds of prey. Bird-Banding 30:18–26

Bollmer, J.L., N.K. Whiteman, M.D. Cannon, J.C. Bednarz, Tj. DeVries, P.G. Parker. 2005. Population genetics of the Galápagos Hawk (*Buteo galapagoensis*): Genetic monomorphism within isolated populations. Auk 122:1210-1224

Bollmer, J.L., T. Sanchez, M.M. Donaghy Cannon, D. Sanchez, B. Cannon, J.C. Bednarz, Tj. DeVries, M.S. Struve, P.G. Parker. 2003. Variation in morphology and mating system among island populations of Galápagos Hawks. The Condor 105:428-438

Burnham KP, Anderson DR. 2002. Model Selection and Inference: a Practical Information Theoretic Approach. New York: Springer-Verlag

BirdLife International (2009) Species factsheet: *Buteo galapagoensis*. Downloaded from http://www.birdlife.org on 2/4/2010

Campbell, K, C.J. Donlan. 2005. Feral goat eradications on islands. Conservation
        Biology 19: 1362-1374

Cooch E, White GC. [online]. 2007. Program Mark: a gentle introduction. 7th ed.
        <http://www.phidot.org/software/mark/docs/mark_book/> (10 April
        2009)

Cormack RM. 1964. Estimates of survival from the sighting of marked animals.
        Biometrika 51:429–438

Craig, G., White, G. and Enderson, J. 2004. Survival, recruitment, and rate of
        population change of the Peregrine Falcon population in Colorado. J.
        Wildlife Manage. 68:1032–1038

Cruz, F., Carrion, V., Campbell, K. et al. 2009. Bio-economics of large-scale
        eradication of feral goats from Santiago Island, Galapagos. J Wildlilife
        Management 73:191 200.

de Vries, Tj. 1973. The Galápagos hawk, an eco-geographical study with special
        reference to its systematic position. Ph.D. dissertation, Vrije University,
        Amsterdam

de Vries, Tj. 1975. The breeding biology of the Galápagos hawk, *Buteo
        galapagoensis*. Le Gerfaut 65:29-57

DeLay, L.S., J. Faaborg, J. Naranjo, S.M. Paz, Tj de Vries, P.G. Parker. 1996.
        Paternal care in the cooperatively polyandrous Galápagos Hawk. Condor
        98:300-311

Faaborg J, Bednarz JC. 1990. Galápagos and Harris' hawks: divergent causes of
        sociality in two raptors. In: Stacey, P. B., and Koenig, W. D., editors.
        Cooperative Breeding in Birds: Long Term Studies of Ecology and
        Behavior. Cambridge: Cambridge University Press. P. 359–383

Faaborg J, Parker PG, DeLay L, de Vries Tj, Bednarz JC, Paz SM, Naranjo J, Waite
        TA. 1995. Confirmation of cooperative polyandry in the Galápagos Hawk
        (*Buteo galapagoensis).* Behav. Ecol. Sociobiol. 36:83–90

Faaborg J, Patterson CB. 1981. The characteristics and occurrence of cooperative
        polyandry. Ibis 123:474–484

Faaborg J. 1986. Reproductive success and survivorship of the Galápagos Hawk
        (*Buteo galapagoensis*): potential costs and benefits of cooperative
        polyandry. Ibis 128:337–347

Grant, P., Grant, R., Keller, L. and Petren, K. 2000. Effects of El Nino events on
        Darwin's finch productivity. Ecology 81:2442–2457

Jackson MH. 1993. Galápagos: a Natural History. Canada: University of Calgary
        Press.

Jolly GM. 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.

Klavitter, J., Marzluff, J. and Vekasy, M. 2003. Abundance and demography of the
        Hawaiian hawk: is delisting warrented? J. Wildlife Management 67:165-
        176.

Lavoie, C., Cruz, F., Carrion, V., Campbell, K., Donlan, C., Harcourt, S. and Moya, M. 2007. The thematic atlas of project Isabela. Puerto Ayora, Ecuador, Charles Darwin Foundation and the Galapagos National Park Service.

Millsap B, Breen T, McConnell E, Steffer T, Phillips L, Douglass N, Taylor S. 2004. J. Wildlife Manage. 68:1018–1031

Parker, P.G. 2009a. A most unusual hawk: One mother and several fathers. Pp. 130-137 in (Tui de Roi, ed.). Galapagos: Preserving Darwin's Legasy. Firefly Books, Ontario.

Parker, P.G. 2009b. 2009 report – I believe this is cited.

Penteriani, V., Otalora, F. and Ferrer, M. 2005. Floater survival affects population persistence. The role of prey availability and environmental stochasticity. Oikos 108:523-534.

Reynolds RT, White GC, Joy SM, Mannan RW. 2004. Effects of radio transmitters on Northern Goshawks: do tailmounts lower survival of breeding males? J. Wildlife Manage. 68:25–32.

Sandercock B. 2006. Estimation of demographic parameters from live-encounter data: a summary review. J. Wildlife Manage. 70:1504–1520

Seber GAF. 1965. A note on the multiple recapture census. Biometrika 52:249–259.

Smith, J. and Arcese, P. 1989. How fit are floaters? Consequences of alternative territorial behaviors in a nonmigratory sparrow. American Naturalist 133:830-845.

Studds, C., Marra, P. 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., Harrison, S., Rea, S. and Macdonald, D. 2006. Biological effects of El Niño on the Galápagos penguin. Biological Conservation 127:107–114.

White, G. and Burnham, K. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study Suppl. 46:120–138

TABLES

Table 1. Tested Models. Phi stands for survivorship, p stands for recapture probability and the factors are in the parenthesis. The factors are bs = body size, s = sex, v = vegetation type, gs = group size. QAIC is an approximation to the AIC (Akaike's Information Criterion; Akaike, 1974) based on Quasi Likelihood theory, and corrected with a c-hat 0f 1.5990. Delta QAIC are the differences in QAIC with the best model, and wQAIC is the relative weight of each model. Also the Likelihood of the model, and the number of parameters that were estimated can be seen, and the deviance as a measure of fit.

Model	QAICc	Delta QAICc	wQAICc	Model Likelihood	Num. Par	QDeviance
phi(v, s, b, gs) and p(v, s) year intercept	786.6589	-	0,95211	1	110	537.8277
phi(v, s, b, gs) and p(v,s) common intercept	792.8435	6.1846	0,04322	0,04540	93	586.6073
phi(gs) and p(t)	797.3446	10.6857	0,00455	0,00480	29	737.4696
phi(v, b, gs) and p(v)	805.3030	18.5741	0,00009	0,00010	86	616.0501
phi(s, b, gs) and p(0)	808.9865	22.3276	0,00001	0,00000	57	687.6398
phi(s, b, gs) and p(s)	810.1481	23.4892	0,00001	0,00000	63	675.1279
{phi(male-female) and p(t)}	811.1095	24.4506	0,00000	0,00000	32	744.8262
phi(s, b) and p(t)	814.0038	27.3449	0,00000	0,00000	47	715.0455
phi(s) and p(s)	822.6710	36.0121	0,00000	0,00000	42	734.7235
phi(v, gs) and p(t)	825.4383	38.7794	0,00000	0,00000	60	697.2777
phi(v) and p(0)	834.2728	47.6139	0,00000	0,00000	42	746.3253
phi(v) and p(v)	838.0367	51.3778	0,00000	0,00000	61	707.5948
phi(0) and p(0)	838.4931	51.8342	0,00000	0,00000	2	834.4805
phi(t) and p(t)	936.9601	150.3012	0,00000	0,00000	122	857.0176

Table 2. Signs of Beta coefficients of the best-fitted model. The sign of the beta coefficient of the model indicates the direction of the relationship: e.g. a positive sign in body size indicates that larger birds had higher survivorship, and in the case of a negative sign would mean that larger birds had lower survivorship.

		1998-1999	1999-2000	2000-2001	2001-2002	2002-2003	2003-2004	2004-2005	2005-2006	2006-2007	2007-2008	2008-2009
Male Arid	Intercept	+	+	+	-	+	+	+	+	-	-	+
	Body Size	-	-	+	-	+	-	+	+	-	-	-
	Group Size	+	+	-	+	+	+	-	+	+	+	-
Male Trans	Intercept	-	+	+	-	+	+	-	+	+	+	-
	Body Size	-	-	-	+	-	-	-	+	-	+	-
	Group Size	-	+	+	+	+	+	+	-	+	+	+
Male Lava	Intercept	+	+	+	+	+	-	-	+	+	-	-
	Body Size	-	-	+	+	-	+	-	+	+	-	+
	Group Size	+	+	+	+	-	+	+	-	-	+	+
Female Arid	Intercept	+	-	-	-	+	+	+	+	-	+	+
	Body Size	+	+	+	+	+	-	+	-	+	-	+
	Group Size	+	-	-	+	+	-	+	+	+	-	-
Female Trans	Intercept	-	-	-	-	+	-	+	+	-	-	+
	Body Size	-	+	-	+	-	+	+	+	-	-	+
	Group Size	-	+	+	+	+	+	+	-	+	-	+
Female Lava	Intercept	-	+	-	+	+	+	-	-	+	+	+
	Body Size	-	+	+	+	-	+	+	+	-	-	+
	Group Size	+	-	+	-	-	+	+	+	-	+	+

Table 3. Survivorship Estimates obtained from program MARK using the best fitted model. 95% CI is included. Values of 1 or 0 are the result of approximation.

|	1998-1999	1999-2000	2000-2001	2001-2002	2002-2003	2003-2004	2004-2005	2005-2006	2006-2007	2007-2008	2008-2009
female arid	1 ±0	1 ±0	0.927 ±0.037	0.891 ±0.109	1 ±0	0.732 ±0.059	1 ±0	0.822 ±0.046	0.891 ±0.037	1 ±0	1±0
female lava	1 ±0	1 ±0	0.902 ±0.048	0.837 ±0.025	0.909 ±0.037	1±0	0.846 ±0.097	0.597 ±0.077	1±0	0.714 ±0.119	1 ±0
female transition	-	0.500 ±0	1 ±0	1 ±0	0.887 ±0.062	1 ±0	1 ±0	1 ±0	1 ±0	1 ±0	1 ±0
male arid	1 ±0	1 ±0	0.952 ±0.062	0.920 ±0.025	0.917 ±0.022	1 ±0	1 ±0	0.886 ±0.025	1 ±0	0.643 ±0.049	0.901 ±0.055
male lava	1 ±0	1 ±0	0.932 ±0.038	0.897 ±0.025	1 ±0	0.931 ±0.028	1 ±0	0.877 ±0.024	0.938 ±0.041	1 ±0	0.880 ±0.070
male transition	-	1 ±0	1 ±0	1 ±0	1 ±0	1 ±0	0.846 ±0.086	0.939 ±0.073	1 ±0	1 ±0	0.722 ±0.170
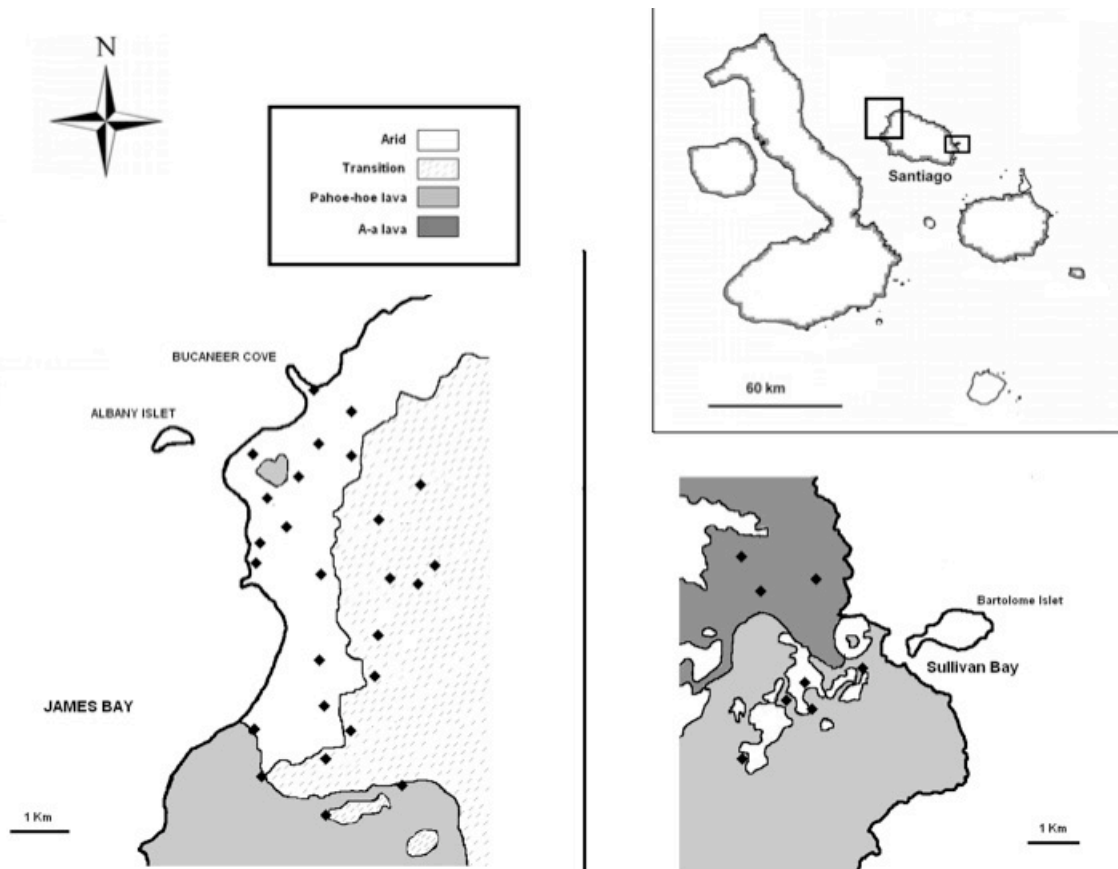
Figure 1. Map of the study areas. Using colors there are represented the different vegetation types in each study area within the Island of Santiago. The diamonds in each map represent identified nests.
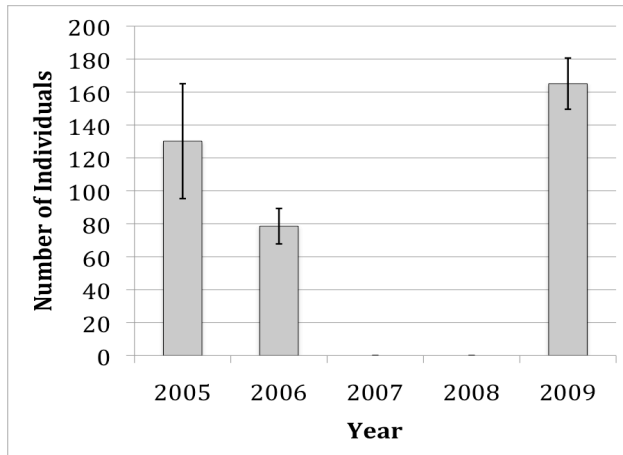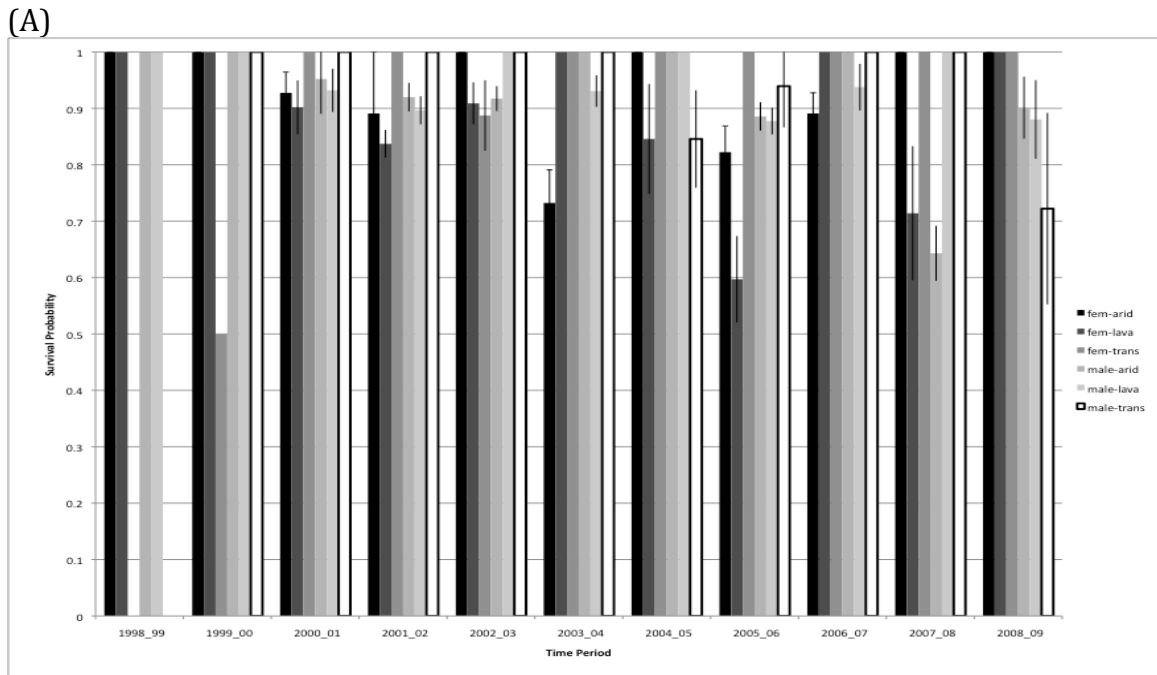
Figure 2. Floater population estimates per year. Result of use of Jolly-Seber models based on proportions of banded vs. un-banded floater individual seen at baiting sites in the James Bay study area. Error bars correspond to 95% Confidence Interval.
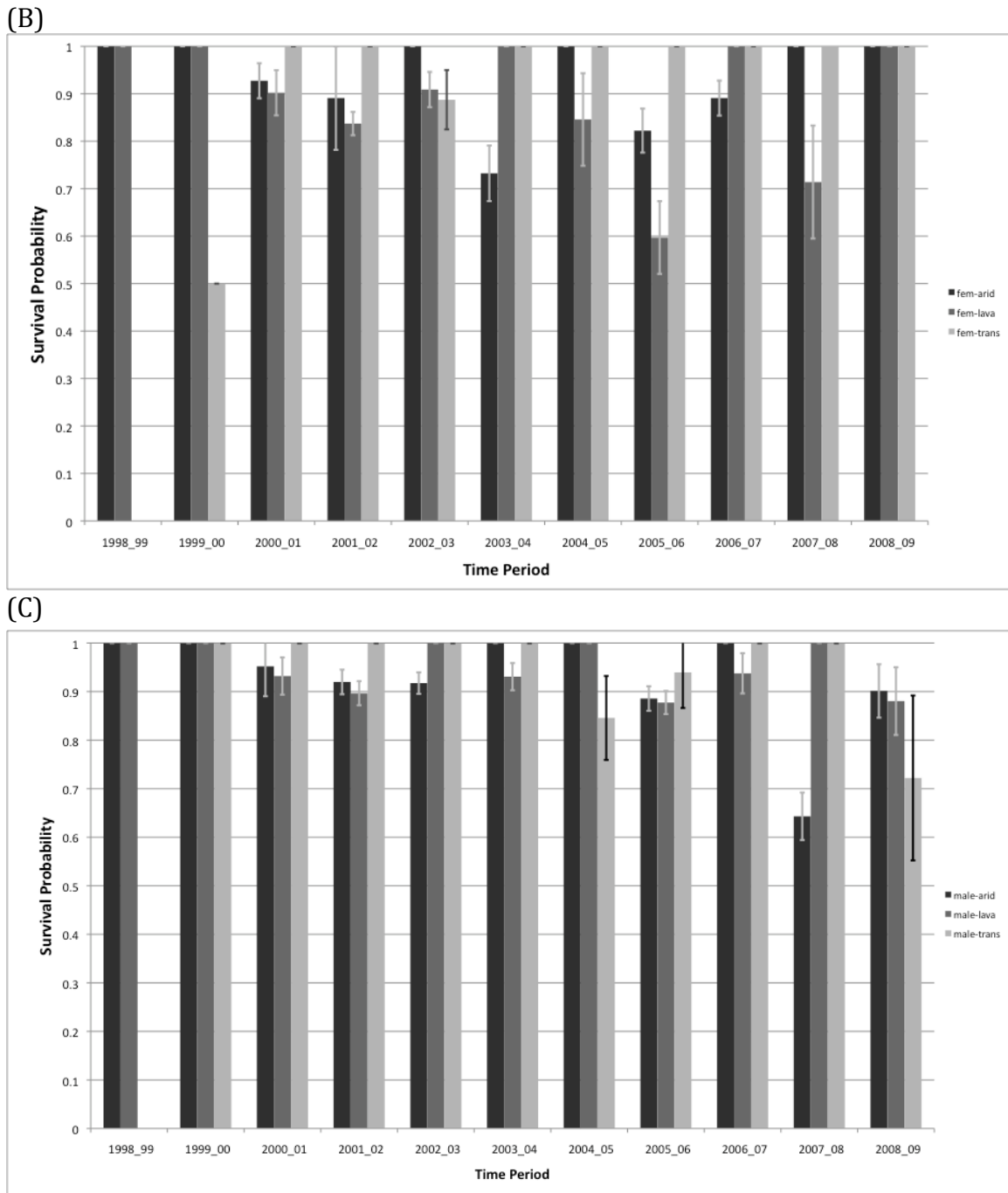
(A)

(B)

(C)

Figure 3. Survivorship Estimates obtained from program MARK using the best fitted model. Error bars correspond to the 95% CI of the estimate. (A) Comparison of the 6 tested groups: females from the arid zone, females from the transition zone, females from near the lava fields, males from the arid zone, males from the transition zone and males from near lava fields. For facilitating comparison the former figure was subset in (B) females from the different vegetation zones; and (C) males from the different vegetation zones.

General Conclusions

The breeding system of the hawks impose different challenges by sex; this is reflected in possible sex related natal dispersal patterns and in relative higher survivorship for males.

The changing environmental conditions in the Archipelago affect the life history of the hawks, evidenced in apparent preferences in natal dispersal patterns and in survivorship variation between years.

The eradication of goats had an impact on the hawk population, that can be evidenced in lower survivorship in adults (2005-2006) decline of juveniles in 2007 and 2008 long term effects still to be seen. Maybe these changes are adjustments towards a new equilibrium.

Maybe territorial adult survivorship was not the best response variable to measure the impact of goat removal, so even when some evidence of impact is seen, a variable that might have shown stronger evidence is breeding success and juvenile survivorship during those years.

Further monitoring is needed to understand long term effects of goat eradication. The transition zone and the persistence or abandonment of those territories may give insights on habitat quality and possible nesting habitat limitation and breeding system evolution.

Monitoring on relative prey abundance (and some other factors still to be analyzed) is needed to understand the changes in relative importance between factors between years.

Introduced species eradication programs may have negative impacts on native populations, especially when the introduced species have been there for a long period of time or become keystone in the community function. So these programs have to consider these impacts and try to mitigate them.