11-3-2006

Avian seed dispersers of the invasive *Rubus niveus* (Rosaceae) in the Galapagos Islands, Ecuador

Monica C. Soria
University of Missouri-St. Louis, monica-soria@hotmail.com

Recommended Citation

Soria, Monica C., "Avian seed dispersers of the invasive *Rubus niveus* (Rosaceae) in the Galapagos Islands, Ecuador" (2006). *Theses*. 12.
https://irl.umsl.edu/thesis/12

Avian seed dispersers of the invasive *Rubus niveus* (Rosaceae) in Santa Cruz Island, Galapagos, Ecuador

Monica Cecilia Soria Carvajal

A thesis submitted to the Graduate School at the University of Missouri-St. Louis in partial fulfillment of the requirements for the degree of Master of Science in Biology

December, 2006

Advisory Committee

Patricia Parker, PhD.
Advisor

Bette Loiselle, PhD.
Committee

Patrick Osborne, PhD.
Committee

ACKNOWLEDGEMENTS

First and foremost, I thank God because “in Him all the things are done.” I am entirely thankful to my family for their support and love I have always received, particularly to my Mother who has always encouraged me to pursue my dreams. I owe to my family the privilege to live in a special place like the Galapagos Archipelago. With their example, they have taught me to love, respect and contribute with the best I have to the conservation of the Islands and for that I am immensely thankful.

I especially thank Dr. Patricia Parker and Dr. Bette Loiselle for providing valuable advice during this project. I also want to thank Dr. Patrick Osborne for his guidance since the first day I arrived at school and his key comments during writing. Dr. Patricia Parker always gave me her unconditional support and advice and for which I am very grateful. I want to thank Professor Douglas Smith for statistical advice. The Galapagos National Park provided permits for the study, transportation and access to laboratory facilities and I particularly want to acknowledge Wacho Tapia, Dr. Virna Cedenio, Ruth Boada and Rene Valle. The Charles Darwin Research Station provided meteorological data and field assistance. In particular I thank Dr. Alan Tye, Chris Buddenhagen and Solanda Rea for their support.

I wish to acknowledge the Loiselle’s and Parker’s Labs in particular Kimberly Holbrook, Renata Durães, Daniel Cadena, Jennifer Bollmer, Diego Santiago-Alarcon, Andrea Loayza, Cintia Cornelius and Caroline Duffie for their valuable comments and engaging discussions. Finally I thank Dr. Walter Durka (UFZ) for providing general advice and Kathy Upton for her assistance in the greenhouse at University of Missouri-St. Louis.

This project was financed through a fellowship from The Christensen Fund Program in Plant Conservation through the Whitney R. Harris World Ecology Center and by the E. Desmond Lee Collaborative to whom I will be always grateful.

Avian seed dispersers of the invasive *Rubus niveus* (Rosaceae) in Santa Cruz Island, Galapagos, Ecuador.

ABSTRACT

The foraging behavior of bird assemblages at *Rubus niveus* was determined over two seasons in the agricultural zone of Santa Cruz Island, Galápagos in order to identify effective seed dispersers of the species and understand the factors that aid invasion of fleshy fruited weeds. A total of seven bird species were observed feeding on *R. niveus* fruits. In both seasons, the small ground finch (*Geospiza fuliginosa),* the introduced smooth-billed ani (*Crotophaga ani)* and the small tree finch (*Camarhynchus parvulus*) were the most common visitors. Mean number of seeds removed per visit was higher for anis than for *Geospiza* and *Camarhynchus*. Finches fed on pulp and juice of ripe fruit and predate seeds. Anis swallowed entire fruits, suggesting that they handle seeds more effectively than finches. Additionally, 57% of seeds recovered from anis' feces were viable using a 2,3,5-triphenyl tetrazolium chloride test. Forty-four percent of those seeds germinated in a greenhouse experiment from May to October. In contrast, finches rarely passed viable seeds of *R. niveus*. Effective seed dispersal may be an important factor contributing to the rapid naturalization and invasion of *R. niveus* since its introduction on Santa Cruz 20 years ago, and represents one potential mechanism by which this species may be dispersed to adjacent islands.

TABLE OF CONTENTS

Avian seed dispersers of the invasive *Rubus niveus* (Rosaceae) in Santa Cruz Island, Galapagos, Ecuador.

LIST OF TABLES AND FIGURES

INTRODUCTION

Islands are particularly vulnerable to biological invasions owing to evolution in isolation, unsaturated niche occupancy, poor competitive abilities and restricted distributional ranges of their organisms (Loope and Muller-Dombois, 1989; Muller-Dombois and Loope, 1990). In the Galápagos Islands, the number of introduced species is higher than the number of native species: 700 reported in 2006 (Buddenhagen & Jewell, 2006) versus 604 indigenous taxa (60 of them uncertainly native) (Adsersen, 1989, 1990). Three endemic species are now recognized as extinct and several species are highly threatened (Mauchamp *et al*. 1998; Schofield, 1989; Snell *et al.* 2002). Of the 175 endemic plant species, 10% are on the brink of extinction, 15% are in serious population decline and 40% are vulnerable to extinction (Snell *et al*. 2002; Tye, 2002).

At least 100 plant species have escaped cultivation on the Galapagos Islands, becoming nuisances in natural ecosystems (in Buddenhagen and Jewell, 2006). Long distance dispersal of weeds has been aided by humans in many areas of the world (Cousens and Mortimer, 1995). Invasive species arrived on the Galapagos Islands with the arrival of the first humans. The Islands were visited occasionally by pirates and buccaneers during the late sixteenth to the nineteen century (Larrea, 1956; Jackson, 1993). Goats and donkeys have been introduced by this means (Schofield, 1989) but rats and other mammals may have also been introduced by humans. The first resident (an Irishman probably marooned on Floreana) planted the first vegetables in 1807 (Slevin, 1959; Jackson, 1993), and since then many species have been introduced and planted in the agricultural zones of inhabited islands from where they have escaped cultivation. The number of visitors to the Galapagos National Park has increased from approximately 10,000 in 1979 to approximately 100,000 in 2005, and currently the annual immigration rate is 6% resulting in a local human population of 27,000 in 2005.

Rubus niveus (Thunb.), Hill Raspberry, is a native thorny shrub of Southeast Asia, Indonesia and the Philippines (Flora of Taiwan, 2003). Since its introduction to the Galapagos Archipelago in 1983 it has become a major threat to moist ecosystems (Fig. 1, 2). The major areas of infestation (foci) are found in the agricultural zones of the four inhabited islands (San Cristóbal, Santa Cruz, Isabela, Floreana) and Santiago (Lawesson and Ortiz; 1990; Juan Cháves (GNP) *pers. comm*. 2000; Saul Robalino (GNP) *pers. comm.* 2005; Felipe Cruz (CDRS) *pers. comm*. 2000). It has naturalized into natural ecosystems, threatening several native communities such as *Scalesia pedunculata, Miconia robinsoniana, Pteridium aquillinum-Jaegeria gracilis*.

Seed dispersal often is a key process during establishment, naturalization and invasion of weeds (Cousens and Mortimer, 1995). Seed dispersal facilitates invasion by forming new infestation foci. Similarly, the rate and pattern of invasion will depend on the mechanism(s) of dispersal. Birds have been recognized as the main dispersers of fleshy-fruited plants, moving seeds from places of human introduction to natural ecosystems (naturalization) (Richardson *et al*. 2000). For example, the range expansion for 25% of 199 weeds was attributed mainly to seed dispersal by birds and to a lesser extent by mammals (14%) and ants (1%) (the remaining 60% have no adaptations for animal dispersal or their dispersal mechanisms are unknown) (Cronk and Fuller, 1995, in Richardson *et al*. 2000). The members of the genus *Rubus* are dispersed by a wide range of taxa in both their native habitat and non-native range. Infructescences are composed of multiple drupelets with small seeds and red, fleshy pericarps which make them palatable for specialized and non-specialized bird species (Snow, 1981). In south-east Alaska, *R. spectabilis* is dispersed by brown bears *Ursus arctos* (Traveset *et al.* 2001). In south-central Spain, *R. ulmifolius* is dispersed by several passerine species (Jordano, 1982). In Australia, *R. procerus* (*R. discolor*) is dispersed by emus *Dromaius novaehollandiae* and foxes *Vulpes vulpes* (Brunner *et al*. 1976). On Reunion Island, *R. alceifolius* is dispersed by another invasive species, the red-whiskered bulbul *Pycnonotus jocosus* (Mandon-Dalger *et al.* 2004).

While endozoochory may favor long-distance dispersal of several *Rubus* species, other biological traits associated with this genus increase their invasive ability as well. Invasive *Rubus* spp. have higher photosynthetic rates than non-invasive ones (MacDowell, 2002). Sexual reproduction is facultative and asexual reproduction is effected through cloning from single branches and apomixis (seed formation without fertilization) (Nybom, 1988). Moreover, in the Galapagos Islands, *R. niveus* fruits are produced continuously throughout the year with large seed banks (ca. 22,800 seeds/m^2 in highly infested areas) with high germination rates (81% in buried seeds after nine months and no seed predators have been identified for this species) (Landázuri, 2002).

Some dispersers may be more effective than others, making them more important for the process of invasion. Seed dispersal effectiveness has been defined as the contribution that a disperser makes to plant reproduction (Schupp, 1993). The number of seeds that a disperser carries away from the plant is a function of the number of visits, number of seeds handled per visit, and beak and gut treatment of the seeds. Seed shadows depend on gut retention time and the movement of the disperser. Seed germination and seedling survival depend on habitat suitability (or microsite) and competition from other plants following seed germination. The number of visits that a disperser makes to the plant may be influenced by several factors such as abundance of the disperser, fruit availability and attractiveness, time of the day or season and may vary along the distributional range of the species.

In the Galapagos Islands, little is known about the most effective dispersers that may favor invasion of many fleshy fruited weeds. *Rubus* constitutes a good model to study seed dispersal by birds, owing to its fruit characteristics and generalized dispersal systems. The species became naturalized immediately following its introduction (no lag phase) suggesting effective seed dispersal. It was first planted on one farm on San Cristóbal in 1983 and rapidly became invasive in surrounding areas and natural ecosystems (Lawesson and Ortiz, 1990). Dispersal among inhabited islands was initially aided by humans (not sure for Santiago Island) and birds (and other vectors) are probably seed dispersers. On Santa Cruz Island, viable seeds of *R. niveus* have been found in feces of a mist-netted ani and a Galapagos flycatcher (*Myiarchus magnirostris*) (Guerrero, 2002). Experiments on gut treatments with Galapagos mockingbirds (*Nesomimus parvulus*), small ground finches (*Geospiza fuliginosa*) and medium ground finches (*G. fortis*) have shown that mockingbirds are more effective dispersers than finches (species chosen for the experiment were based on ease of capture) (Buddenhagen and Jewell, 2006).

The aim of this paper is to identify effective seed dispersers of *R. niveus* in the agricultural zones of Santa Cruz that may aid invasion of other areas by delivering viable seeds and creating new infestation foci. Specific objectives are: (1) to identify the avian foraging assemblage of *R. niveus* and feeding behavior of the visitors in the agricultural zone of Santa Cruz; (2) to determine visitation reliability of dispersers across the seasons; and (3) to determine the effectiveness among dispersers based on number of visits, number of seeds handled and seed viability after gut passage.

METHODS

The study site

Santa Cruz Island is one of the oldest, largest and most biologically diverse islands, though it is highly altered by human activities and invasive species (Snell *et al*. 2002). It is located at $0^0$37’S, $90^0$21’W, has an area of 98,555 hectares and its nearest large neighbour is Isabela, 27.6 km distant (Snell *et al*. 1996). Five main vegetation zones have been described by Wiggins and Porter (1971) (littoral, arid, humid, fern-sedge and pampas zones) and 15 native vegetation communities by Hamann (1981) (Fig. 1). The humid zone (118 km^2), once dominated by *Scalesia pedunculata* (Asteraceae), begins at 180 m above sea level on the southerly slopes and in places, extends up to 400-550 m. It has been calculated that 75% of the humid zone has been transformed to agriculture and this has promoted the population growth of invasive species (Snell *et al*. 2002). Invasive species have escaped cultivation and threaten many natural ecosystems on the Islands.

The birds

Twenty six native species of land birds have been recorded on Santa Cruz Island. Nine species of Darwin's finches present on the Island belong to five genera (*Geospiza, Camarhynchus, Cactospiza*, *Certhidea*, *Platispiza*) and are distributed through all vegetation zones (Grant, 1986) though *Certhidea* may inhabit particularly the humid zone of the Island (Lack, 1945; Tebbich *et al.* 2003). Ground finches (*Geospiza*) are mainly seed eaters, and tree finches (*Camarhynchus, Cactospiza* and *Certhidea*) are mainly insectivorous. Beak morphology (length, depth, width and curvature) is associated with feeding habits and food type, and beak size is associated with the size of the food consumed (Bowman, 1961; Grant, 1986). Deep beaks such as those of the small, medium and large ground finches (*Geospiza fuliginosa, G. fortis, G. magnirostris*) are called "base crushing", suitable for cracking seeds. Long pointed beaks such as those of the warbler finch (*Certhidea olivacea*) and the woodpecker finch (*Cactospiza pallida*) are specialized for probing vegetation for insects. Beaks with curved upper and lower mandibles, "tip biting beaks" such as those of the small and large tree finches (*Camarhynchus parvulus, C. psittacula*) are specialized to feed on insects. The vegetarian finch (*P. crassirostris*), with a stubby bill, is a form intermediate between base crushing and tip biting beaks (Grant, 1986). Among tree finches, *C. parvulus* and the vegetarian finch *P. crassirostris* include an important proportion of plant material in their diets (Grant, 1986; Tebbich *et al*. 2003). For example, it has been calculated that in the wet season, 45% of the diet of the small tree finch are comprised of nectar, fruit, seeds and leaves in the *Scalesia* forest of Santa Cruz (increasing fruit consumption in the dry season). Similarly, in the arid zone, they feed on equal proportions of insects and plant material in the wet season (increasing feeding on flowers in the dry season).

All birds were identified to species level following Grant (1986) and Castro and Phillips (1996) and as *Geospiza* sp. or *Camarhynchus* sp. when identification to species was not possible among the ground or the small and large tree finches.

The smooth-billed ani was probably introduced to the Galapagos Islands by farmers to control tick infections in cattle (Grant and de Vries, 1993). They feed mainly on insects (Rosenberg *et al*. 1990) though seeds of invasive plant species have been found in feces of mist-netted individuals (Guerrero, 2002). Anis inhabit mainly the agricultural zones of populated islands (Jara and DeVries, 1995) but have also dispersed to pristine islands such as Fernandina, Pinta, Marchena and Darwin. The species was first reported in the agricultural zone of Isabela Island in 1962, on Santa Cruz in 1966 and on Santiago in 1967 (Grant and de Vries, 1993). They became common and dispersed to pristine islands after the intense rains caused by El Niño in 1982-83 (Rosenberg *et al*. 1990; Grant and de Vries, 1993). In the 1980's the population of anis in the agricultural zone of Santa Cruz was estimated at 4,800 birds (Rosenberg *et al*. 1990).

The plant

Rubus niveus was probably introduced to mainland Ecuador via Africa and Central America and from there to the Galapagos. It was introduced to Kenya in 1947, to Florida in 1948 and Puerto Rico in 1955 (Morton, 1987) (Fig. 2). *Rubus niveus* is a scrambling shrub ca. 2 m high, with whitish or red stems and hooked prickles up to 7 mm long, compound leaves, 5-7 ovate-elliptic leaflets, alternate, oddly pinnate, margins serrate. Flowers are in terminal panicles, pinkish purple, 4-5 cm long with 5 petals and many stamens. Fruit is an aggregate compound (infructescence), with fleshy drupelets, red to reddish black, ca. 1 cm diameter (McMullen, 1999). The species also is invasive in Hawaii (Starr *et al*. 2003).

Foraging assemblage and feeding behavior

Six study sites were established in highly infested areas of the agricultural zone of Santa Cruz (Santa Rosa), 300-400 m above sea level with coordinates $0^0$38’49’’S, $90^0$24’37’’W (Fig. 1). A study site consisted of a mono-specific clone (clone) of *R. niveus* with an area of 200-250 m^2 and vegetation height of 2.44 m (SD = ±0.42), located 1-2 km apart and no more than 50 m from adjacent *Rubus* stands. Because my presence disturbed the feeding activity of the anis, a blind was built near each study site. Feeding observations were conducted without influencing the behavior of the birds. In the second field season, two of the sites were replaced and four of them were the same as the first field season. All observations were conducted using binoculars, with or without a field assistant.

Observations were conducted during July-August 2005 and January 2006 corresponding to the cold-garúa season and the beginning of the warm-wet season respectively. During August 2005, 129.20 mm of precipitation were recorded at the meteorological station of the Charles Darwin Research Station (194 m above sea level), while in January 2006, only 6.40 mm of rain were recorded. Mean temperatures in the cold-garúa and warm-wet seasons were 20.9^0 C and 24.3^0 C respectively. In both seasons, two different clones were observed per day, one in the morning and one in the afternoon. Observation effort in all clones in the first and second field seasons were 10 days (87 hours) and 12 days (97 hours) respectively. Morning sessions started between 06:00-08:00h to 13:00h and in the afternoon, sessions lasted from 14:00-15:00h to 18:00h. Variation in starting time was due to constraints in transportation and access to two of the clones when cattle were released. In both seasons, the mean time of observation hours was 8 hours/day.

Foraging activity of the visitors was assessed using focal animal sampling and visitation rate based on the number of visits for a specific time interval. Focal animal sampling was performed for 50 minutes every hour during all observation sessions. Each focal bird was followed from its moment of arrival at the clone, and all of its activities were recorded and timed until its departure. If more than one individual visited the clone one was chosen randomly, but if a common and a rare species arrived, then the rare one was chosen over the common one. When one focal animal departed, the next bird arriving was chosen as the next focal animal.

Activities were classified as follows: feeding on ripe, unripe and dry fruits of *R. niveus* or other resources such as nectar or insects, searching or being stationary. Seed-handling techniques for the *Geospiza* were assessed based on Grant (1986) who describe them mainly as seed predators. But since other fruit handling types were observed, categories described by Levey (1987), Moermond and Denslow (1985) for frugivores were also considered: gulpers are those that swallow fruits and biters are those that feed mainly on pulp and can eventually pass viable seeds (particularly small ones) (Levey, 1987).

Visitation time was the total time a bird spent in the clone from its arrival until its departure. If a bird arrived and then disappeared into the clone, the observation time was stopped unless the bird reappeared in the next few seconds. Only complete visits were used to calculate visitation time though it was not possible to identify if the same individual made repeated visits.

Kolmogorov-Smirnov (D) and Shapiro-Wilk (S) tests were use to assess normality of the data and Levene's test to evaluate the homogeneity of the variances (Field, 2005). Analyses were performed with four species in both seasons. Visitation time of species with sample sizes <7 (*Certhidea olivacea*, *Dendroica petechia* and *Myiarchus magnirostris*) were pooled in one category and compared with the other four species. And since four sites were observed in both seasons, the analysis included individuals observed only at those sites to test differences between seasons. In both seasons, data were normal for *G. fortis* and *D. petechia*). Visitation time was not normal for some species ($p<0.05$). Some were significantly and positively skewed ($Z_{\text{skewness}} = > 3.29$, $p<0.01$) and kurtosis was not normal ($Z_{\text{kurtosis}} = >3.29$, $p<0.01$). Data became normally distributed (both seasons) and variances homogeneous after log transformation. Similarly, visitation time at some clones was not normal after the data were transformed but variances were homogeneous in all sites in both seasons. Mean time per species and sites are reported in Tables 5 and 6.

Two-way ANOVAS (one for each season) were run to test if visitation time was influenced by sites and species. A two-way ANOVA was also performed to test for differences in visitation time between seasons (sites were pooled because there was no site effect). Hochberg's GT2 test was used for pair-wise comparisons within a season.

The test was used because the data have unequal samples sizes but homogenous variances.

Visitation rate per hour was calculated by recording all birds visiting the study site for ten minutes every hour during all observation sessions (scan intervals). A total of 17 hours were observed at all sites (6) per season. Number of visits per hour per season was calculated by dividing the total number of visits by the total number of observation hours. Visitation frequency of the species was also calculated based on species occurrence (presence and absence) in each ten minute observation period and then dividing the total number of presences by the total number of observed intervals in each season (103 and 101 respectively). Data were analyzed for the six and the four common study sites separately.

Seed dispersal effectiveness

Dispersal effectiveness was determined for each species based on the calculated number of visits in 12 hours (daylight), mean number of seeds removed per visit, and the proportion of viable seeds after gut treatment (Schupp, 1993). Effectiveness = (quantity) x (quality); where quantity equals number of visits multiplied by number of seeds handled per visit and the quality equals the proportion of viable seeds after gut passage.

Fruit handling is defined here as the action of extracting flesh and seeds, swallowing entire fruits or crushing seeds (mainly dry and unripe fruits). Proportion of seeds per fruit type (ripe, unripe and dry) was calculated based on a calculated number of seeds handled. Mean number of seeds handled in ripe fruits was calculated from the number of fruits (or parts) consumed. Mean number of seeds per infructescence was based on 12 ripe infructescences collected in the study areas which were weighed and seeds counted using a microscope. When parts of a fruit were removed or ripped out, number of seeds handled was calculated based on the estimated proportion of fruit removed. Mean number of seeds handled per visit for unripe and dry fruits was based on the total number of pecks per visit (here it is assumed that one seed is removed per peck since they carefully remove seeds and crush them).

Seed removal among species were compared among three species in the first field season (*G. fuliginosa, Anis* and *G. fortis*) and among four species in the second field season (*C. parvulus* included). Comparisons were carried out with data of the four common study sites in both seasons to examine seasonal effects. To detect the effect of study sites and species on fruit removal, the non-parametric Kruskal-Wallis test (X^2) was used. Kruskal-Wallis was chosen instead of ANOVA because after data were log transformed, normality and homogeneity of variances varied among species, seasons and sites. For example, in the first field season, data were normal for all sites but homogeneity of variances was violated ($p<0.05$). In the second field season, fruit removal of *G. fuliginosa* was not normal but variances were homogeneous ($p>0.05$). Pair-wise comparisons of species and genera were performed using non-parametric multiple comparisons with unequal sample sizes (Q) (Zar, 1999).

Gut treatment was assessed from the proportion of viable seeds of *R. niveus* recovered from feces of anis and small and medium ground finches. Viability of seeds was assessed on 96 out of 216 seeds collected in three fecal samples of anis feces using 2,3,5- triphenyl-tetrazolium chloride (TTC) and seeds were planted in the greenhouse at the University of Missouri-St. Louis where germination was observed from February to

October 2006. Droppings with seeds were collected in January 2006 on filter paper and stored in plastic bags at 4° C (except when traveling) and brought to the U.S. for analysis. Tetrazolium chloride is a non-toxic salt, soluble in water, which reacts with the hydrogenase secreted during cell respiration, causing TTC to turn cells pinkish-red if they are respiring (Busso *et al.* 2005). Test procedures were based on Grabe (1970); seeds were hydrated for 24 hours prior to the test in order to activate respiration enzymes. Seeds were cut longitudinally, soaked in TTC solution (1%) and incubated overnight at 37° C. Next day, embryo and parts were examined; only those colored were classified as viable (Appendix 1).

Germination tests in the greenhouse were conducted from February to October 2006; 48 seeds recovered from anis' feces collected in January 2006 were planted in pots (18 cm diameter x 12 cm depth) with garden soil (ca. 10 seeds per pot). Additionally, 152 control seeds, collected at the study sites in January 2006 (without pulp) were planted to compare germination between seeds recovered from anis' feces and those collected directly from fruits.

The proportion of viable seeds of *R. niveus* after gut treatment of finch species was calculated based on experiments conducted in 2003 by Buddenhagen and Jewell (2006) with *G. fuliginosa* and *G. fortis*. They carried out fourteen feeding trials with five captive small-ground finches and 17 trials with six-medium ground finches. Amount of fruit offered per trial varied, from 2-5 infructescences for both species. At the end of all experiments, only one viable seed was found in feces of *G. fuliginosa* and no seeds in feces of *G. fortis*. Therefore the proportion of viable seeds passed for *G. fuliginosa* was based on an estimation of the number of seeds handled per mean weight of fruit consumed per trial and proportion of viable seeds recovered in feces. On average *G. fuliginosa* consumed 0.85 g (SD = ±0.48) of fruit per trial which is equivalent of 0.57 of a fruit (mean weight per infructescence = 1.48 g). This value (0.57) was multiplied by the mean number of seeds per infructescence (79, SD= ±7) and by the number of trials giving a result of 630 seeds potentially handled. Since one seed passed was viable, 0.002 was the proportion of viable seeds passed for the species (Chris Buddenhagen and Kelly Jewell, *pers. comm.*, August 30, 2006).

Gut treatment based on Buddenhagen and Jewell (2006) for *G. fuliginosa* were also used for the large ground finch *Geospiza magnirostris*, tree finches *Camarhynchus* and woodpecker finch *Cactospiza pallida* (since experiments with these species are not available). Though *Camarhynchus* and *C. pallida* are mainly insectivorous, they were observed handling fruits of *R. niveus* in ways similar to that of *Geospiza*. Additionally, 17 fecal samples of *G. fuliginosa* were collected during this study and examined for seeds. Samples were collected near a small waterfall where finches would stand on a wire fence before and after their baths, and would leave droppings while preening.

RESULTS

Foraging assemblage and feeding behavior at R. niveus

Thirteen species of land birds visited the clones in the two field seasons (Table 1). A total of 376 visits were observed in the cold-garúa season and 660 during the warm-wet season during focal animal sampling. Commonly observed species in both seasons were *G. fuliginosa, C. ani, C. parvulus* and *G. fortis*. A total of 209 visits and 429 visits were recorded in 17 hours in the cold-garúa and warm-wet seasons resulting in a mean visitation rate of 12 visits/ hour and 25 visits/ hour in each season respectively (Table 2). Anis, *Geospiza* and *Camarhynchus* were also the most commonly represented groups in all observation intervals (Table 3).

When data of the four clones are pooled, *Geospiza fuliginosa*, *C. ani* and *C. parvulus* made 64%, 13% and 10% of the total visits (respectively). Similarly, in the second field season, the three species made 82%, 7% and 6% of the total visits.

Six finch species, *C. ani* and rats (*Rattus rattus*) were observed feeding on *R. niveus* fruits. Finch species that fed on ripe, unripe, dry fruits and nectar were *G. fuliginosa, G. fortis, G. magnirostris, C. parvulus, C. psittacula, C. pallida* (ripe fruits only) and possibly the vegetarian finch *P. crassirostris*. In a feeding visit, 75-100% of all seeds handled were from ripe fruits though they also included seeds of ripe and unripe fruits (Table 4). Rats were observed feeding on ripe fruits and taking them underneath the clone (burrows) though these events were rather infrequent (during 184 observation-hours only three events were observed).

Species observed feeding on insects along the branches were the warbler finch *C. olivacea*, *D. petechia*, *M. magnirostris* and the vermillion flycatcher (*Pyrocephalus rubinus*). In the cold-garúa season, the *C. olivacea* was observed extracting larvae (unidentified) from decomposing *R. niveus* fruits. In the second field (warm-wet) season, a dark-billed cuckoo (*Coccyzus melacorphylus*) was observed entering the clone sporadically to hunt Lepidoptera. In both seasons, a solitary *N. parvulus* was seen on several occasions feeding always on the ground but not in the clones.

Foraging for fruits and nectar were the most commonly recorded activities. When all activities (both seasons) are pooled, 66.4% of observations are from feeding on fruits, 21.2% on nectar (*R. niveus* flowers), 3.2% on insects and the remaining were indirectly associated with feeding (Table 1). When activities are partitioned between seasons, the greater frequency of fruit feeding activity was registered during the warm-wet season (86%) (Fig. 3a, b). Three fruit handling types were observed among species. Anis swallowed entire ripe fruits passing seeds after gut treatment and thereby acted as true seed dispersers. In contrast, finches pecked at ripe fruits, ingesting fruit piecemeal, but pecked and crushed seeds from unripe and dry fruits. This pattern seems consistent for all ground and tree finch species observed in this study. When extracting the pulp of ripe fruits, finches extract the soft part, leaving the bulk of seeds on the plant; seeds eventually fall to the ground. Seeds that are ingested are later spat out while removing the first bits of pulp or while drinking juice. Seeds are ejected by head shakes after pecking and by wiping the sides of their beaks on the perch. The fruit may be detached from the plant while feeding. When detached, it is held by the feet or beak and moved as pulp is extracted. When most of the juice has been removed the birds move to another ripe fruit or switch to dry, unripe fruits or nectar. On a few occasions finches were observed to move fruits from one branch to another or to fly short distances from the study site to the ground.

When feeding on unripe and dry fruits, finches hold seeds in the beak for a few seconds while they are crushed. Seeds were crushed and bits were observed falling from the beak. For unripe fruits, the testa is left on the leaves and sometimes opened into two halves and the embryo and parts extracted.

Visitation time

Mean visitation time for the anis was 3.25 minutes (SE = $\underline{+}0.38$) during the cold-garúa and 1.94 minutes (SE = $\underline{+}0.30$) during the warm-wet season (Table 5). If the time is partitioned, anis spent more time stationary than feeding during a visit. Average visitation time for the finches ranged from 0.55 to a maximum of 3.99 minutes in the first field season and from 1 to 2.48 minutes in the second field season.

Visitation time among species was different in the first field season but not in the second one ($F_{4,\,326} = 3.72$, $p \leq 0.05$; $F_{4,\,248} = 2.48$, $p > 0.05$). Visitation time of the species was not different among the clones in both seasons ($F_{3,\,326} = 0.35$, $p > 0.05$; $F_{3,\,248} = 1.48$, $p > 0.05$). Similarly, no interaction effect of species-sites was detected in both seasons ($F_{12,\,326} = 1.15$, $p > 0.05$; $F_{11,\,248} = 1.15$, $p > 0.05$). Pair-wise comparisons among species within the first season show that *C. ani* had higher visitation time than *G. fuliginosa* and time was significantly higher for other small insectivores such as *C. olivacea*, *D. petechia*, *M. magnirostris* ($p \leq 0.05$) (Fig. 4).

When a two-way ANOVA is run to detect effects of species and season, the results suggest that visitation time depended neither on species ($F_{4,\,603} = 1.04$, $p > 0.05$) nor on seasons ($F_{1,\,603} = 0.002$, $p > 0.05$); but species adjust their visitation times according to seasons ($F_{4,\,603} = 3.22$, $p \leq 0.05$) (Fig. 4).

Number of seeds handled per species

Number of seeds handled (fruit consumption) per species was higher for the anis than for the finches in both seasons. Anis removed on average 3.4 (SD = $\pm$ 2) fruits per visit in the cold-garúa season and 3 (SD = $\pm$ 1.6) in the warm-wet season (Table 6). In the first field season they removed between 0.5 -10 fruits and in the second field season they removed between 1-7 fruits. In the first field season, finches handled 1.5 - 2.7 fruits per visit with similar results in the second field season (1 – 2.1 fruits). On one occasion a large ground finch handled 3.5 fruits.

Kruskal-Wallis test showed that fruit removal was not different among clones in any of the seasons, $X^2 = 7.09$, df = 3, $p > 0.05$; $X^2 = 7.03$, df = 3, $p > 0.05$). But instead, fruit removal depended on species in both seasons ($X^2 = 27.76$, df = 2, $p \leq 0.05$; $X^2 = 10.42$, $p \leq 0.05$).

Non-parametric multiple comparisons with unequal sample sizes among the three species in the first season and among the four species in the second field seasons show significant differences between anis and the small ground finch, Q = 5.57, df = 3, $p \leq 0.05$; Q = 2.84, df = 4, $p \leq 0.05$. No differences were found for any other species combinations in both seasons. Significant differences in seed removal were found when data were pooled and comparisons between *Geospiza* and *Crotophaga* were performed in the first field season, Q (2) = 35, $p \leq 0.05$ (Fig. 5). Similarly, among *Crotophaga* and *Geospiza* (Q (3) = 2.41, $p \leq 0.05$) and *Crotophaga* and *Camarhynchus* (Q (3) = 2.84, $p \leq 0.05$) in the second field season (Fig. 6). No differences on fruit removal were found between *Geospiza* and *Camarhynchus* in the second field season, Q (3) = 0.11, $p > 0.05$.

Gut treatment

Anis feces collected in the field contained entire seeds with undamaged embryos, radicals and cotyledons. A total of 216 seeds were recovered from three fecal samples of smooth-billed anis. Viability tests using 2,3,5-tetrazolium showed a viability of 57% after passing through the anis' gut. Forty four percent of the 48 seeds collected from anis feces and 53% of the control seeds germinated in the greenhouse from May to October 2006 and after three months of being planted.

Based on proportion of viable seeds found in anis' feces and proportion of seeds passed by the small and medium ground finches (Buddenhagen and Jewell, 2006), an index of dispersal effectiveness was calculated to compare importance of seed dispersal among species. Anis are the most effective dispersers in this study (Table 7). Anis disperse 97% of the total viable seeds in the system while finches only 3%. While *G. fuliginosa* is an important seed remover, seeds dropped or wiped on branches are probably not effectively dispersed resulting in cero fitness for the plant. *Crotophaga ani* in the other hand is a more effective disperser because it ingests and delivers undamaged seeds. It also consumes more fruit during the cold-garúa season than during the warm-wet season though rain may impede its movements. Since no seeds were found in feces of the *G. fortis* (Buddenhagen and Jewell, 2006), this species has the lowest index value among the remaining species. No seeds were found in the 17 fecal samples of *G. fuliginosa* finch collected in the field.

DISCUSSION

Rubus niveus constitutes a food resource for at least six species of Darwin's finches and the invasive smooth-billed ani. Among the finches, *G. fuliginosa and C. parvulus* were the most reliable visitors but are not the most important dispersers of *Rubus.* Finches feed mainly on nectar, pulp and juice of ripe fruits and crush seeds of ripe and unripe seeds. Buddenhagen and Jewell (2006) in their study of gut treatment of seeds of *Rubus* and other invasive species with *G. fuliginosa* and *G. fortis* demonstrated that they rarely pass entire seeds. In the field, finches discard seeds and ingest mainly pulp probably as a strategy to maximize the ingestion of available nutrients and reduce the cost of crushing seeds and may constitute a novel feeding technique adopted to exploit this new and abundant resource.

Finches deliver intact seeds after pulp extraction near to the parent plant contributing to the seed bank from which seeds may be dispersed by other means. Seeds can be carried by water draining clones, particularly during El Niño and if soil is moved by people among farms. Cattle and other livestock can also move seeds if they become attached to their feet in mud. Seed dispersal among islands aided by finches is very unlikely owing to the small proportion of seeds passed intact and rare movement of birds between islands (Grant, 1986). However, if seeds are ingested deposition distance will depend on the movement of the birds over the next 15-20 minutes (Buddenhagen and Jewell, 2006). All these physiological traits make the finches ineffective dispersers of *Rubus* seeds.

Anis, on the other hand, are both important visitors and fruit removers and are more effective than finches because they ingest entire fruits and pass at least 57% of the seeds in viable condition. Moreover, the theory of dispersal effectiveness suggests that large birds may be better dispersers than small birds because of their capacity of ingesting more fruit (Levey, 1997). Anis are larger than most of the native birds such as finches, Galapagos doves (*Zenaida galapagoensis*), *N. parvulus* and rails (*Lateralus spilonotus*). Similarly, seeds that are ingested may travel greater distances and have greater probabilities of survival than those that are delivered near to parent plant. Seed retention times of the anis remain to be studied but it may be longer than finches. *Rubus* seeds were retained for 85 minutes in the guts of *N. parvulus*, another omnivorous species. It is possible that anis can fly from Santa Cruz to Santiago in that period of time and thereby deliver viable seeds. Since anis move among islands, seeds can also be transported from Santa Cruz to Santiago and from Santiago or other islands. All these physiological and biological traits make anis important seed dispersers of *Rubus*.

Anis are known as mainly omnivorous (Quinn and Startek-Foote, 2000). They feed on insects and fruits such as figs (*Ficus* spp.) in Brazil (Shanahan *et al.* 2001). A sister species, *Crotophaga sulcirostris*, feeds on ripe drupes of *Bursera simaruba* in Costa Rica (Scott and Martin, 1984). Past adaptations and feeding habits may explain association of anis with *Rubus* which constitute a novel association of two invasive species in the Galápagos Islands.

Seed viability after gut passage through anis in this study is estimated at 57% with 44% of germination. Up to October 2006, 53% of the control seeds also germinated. Landázuri (2002) found higher germination in buried seeds after nine months. Since seeds continue germinating in the greenhouse these percentages may be higher. The similar rates of germination between seeds ingested by anis and controls may indicate that anis do not damage seeds since both germinated almost at the same time.

Rubus invasion has serious future implications for the conservation of native plant communities and native avifauna. *Rubus* fruits, rich in carbohydrates and water (in Jordano, 1982), may be an important food resource for native species all year round. Beak size and morphology in finches is proportional to the size and type of food they eat (Grant, 1986). Fluctuations in abundance of small and large seeds owing to climatic conditions have changed gene frequencies of beak size on Daphne (Grant, 1986; Grant and Grant, 2006). Moreover, in years of extreme drought when large seeds of *Tribulus cistoides* become scarce populations of *G. magnirostris* and *G. fortis* decline. On Marchena, *G. difficilis* feeds particularly on nectar of *Walteria ovata* and these birds have sharper beaks than their congeners on other islands.

High visitation frequencies of some species may be the results of high population abundance. In this study, *G. fuliginosa, C. ani and C parvulus and C. fortis* were the most common visitors in both seasons. These species were also the most commonly captured birds using mist-nets near my study areas in 2005 in a health survey (Patricia Parker *unpublished data*): *G. fuliginosa* comprised 58% of the total captures (312 birds); *G. fortis* 19%, *D. petechia* 12% and *C. parvulus* 5%. The remaining 5% comprised *N. parvuls, C. olivacea, C. pallida, Myiarchus magnirostris, C. psittacula, P. crassirostris and Z. galapagoensis*. These data do not provide actual abundances of the species but indicate the relative number of *G. fuliginosa* to other species. Only two anis were captured in this study; but this is not surprising, knowing that anis avoid both nets and humans.

Other species not quantified in this study may also disperse *Rubus* seeds. Rats were observed feeding on ripe fruits and may be important fruit removers during the night and are known to disperse seeds of endemic plants in Santa Cruz (Clark, 1981). Other native birds, such as the *M. magnirostris* (Guerrero, 2002) and *N. parvulus* may also disperse seeds (Buddenhagen and Jewell, 2006). Nevertheless, *M. magnirostris* and *N. parvulus* may not be important dispersers of *R. niveus* when compared with anis, because of their low visitation rates and feeding habits (mainly on insects). *Nesomimus* are also less likely to be good dispersers in other islands such as San Cristobal because they occur in very low numbers. A similar situation occurs on Floreana where they are extinct owing to habitat alteration and introduced species. They may be important dispersers in natural or less altered habitats if they co-occur with *Rubus* such as in Santiago and Isabela Islands. But seed dispersal among islands aided by *N. parvulus* is unlikely because genetic population studies have shown that individuals rarely move among islands (Jennifer Bollmer, *pers. comm.*).

Doves and rails are known to disperse seeds in other systems and it will be important to investigate their effectiveness as dispersers within the Archipelago. Genetic studies of various populations of Galapagos doves have shown that they move among islands (Santiago-Alarcon *et al.* 2006) and this makes them potentially important as seed dispersers. Predators such as hawks and owls have been suggested as potential dispersers of native species (Porter, 1983) and may also be dispersers of *R. niveus* if they prey on rats, finches or anis that contain seeds in their guts. Seeds of native species have been found in owl regurgitation pellets in Daphne that fed on rats and finches on Santa Cruz (Grant *et al*. 1975). Galapagos hawks do not breed on Santa Cruz anymore but juveniles disperse (sporadically) to Santa Cruz and from there to other islands (Bollmer *et al*. 2006). Two species of bats are also present on the islands though they are thought to be mainly insectivorous (Whitaker and McCracken, 2001).

Management implications

Dispersal associations may be explained from the perspective of mutualisms where both the plant and the dispersers benefit. Mutualisms among weeds and seed dispersers have favored invasions in many parts of the world (Richardson *et al*. 2000). Therefore, anis and *Rubus,* two invasive species in the Galapagos Islands, may benefit from each other. Integrated management of both species is recommended to control further invasion of the species to other islands. Increase in abundance of *R. niveus* may favor dispersal by increasing fruit production and fruit removal. Jordano (1982) found correlation between fruit production and fruit removal of *R. ulmifolius*.

Effective management of *Rubus* will require not only reducing seed production but also fruit quality and controlling its main disperser, the anis. Preference for fleshy fruited weeds over native ones has been reported in systems where native species are scarce or absent (Richardson *et al.* 2000). Since finches feed on *Rubus,* its elimination needs to be accompanied by ecological restoration and landscape management where native species are re-introduced to the agricultural zone. A census of endemic bird species in the populated islands is also recommended in order to evaluate their conservation status and prevent further extinctions.

It will be necessary to reduce to zero the probability that people move *Rubus* among islands. Quarantine regulations are very strict and prohibit seed and animal movement within the Archipelago but education campaigns and regulations for the control of *Rubus* infestations in the agricultural zones are urgently needed. Farms highly infested with *Rubus* are seed banks from where seeds may disperse to pristine islands aided by anis and other birds. Providing funds to farmers who can not afford the control of extensive infested areas is highly recommended.

CONCLUSIONS

Effective gut treatment (viable seeds after gut passage), high visitation rates and number of seeds handled explain why the smooth-billed ani is a more effective disperser of *Rubus* seeds than finches. Ground finches (*Geospiza*) have higher visitation rates than anis but they ingest fewer seeds (though they may eventually pass some). Moreover, anis move to pristine islands, implying that viable seeds could be delivered there.

Other endemic species such as small insectivorous and omnivorous birds may play a minor role in dispersing *R. niveus* because of their low visitation rates and feeding habits.

CITED REFERENCES

Adsersen, H. 1989. The rare plants of the Galápagos Islands and their conservation. *Biol. Conserv. 47(1):49-77.*

Adsersen, H. 1990. Intra-archipaelago distribution patterns of vascular plants in the Galápagos. *Monogr. Syst. Bot. Missouri Bot. Gard. 32:201-210.*

Bollmer, J. L., R. T. Kimball, N. K.Whiteman, J. H. Sarasola, and P. G. Parker. 2006. Phylogeography of the Galapagos hawk (*Buteo galapagoensis*): A recent arrival to the Galapagos Islands. *Molecular Phylogenetics and Evolution 39(1):237-247.*

Bowman, R. I. 1961. Morphological differentiation and adaptation in the Galápagos finches. *University of California Publications in Zoology 58:1-302.*

Brunner, H., Harris, R.V., and R.L. Aor. 1976. A note on the dispersal of seeds of blackberry (*Rubus procerus* P.J. Muell.) by foxes and emus. *Weed Research 16:171-173.*

Buddenhagen, C., and K. J. Jewell. 2006. Invasive plant seed viability after processing by some endemic Galapagos birds. *Ornitologia Neotropical 17:73-80.*

Busso, C. A., M. Mazzola, and M. L. Perryman. 2005. Seed germination and viability of Wyoming sagebrush in northern Nevada. *Interciencia 30(10):631-637.*

Castro, I., and A. Phillips. 1996. A guide to the birds of the Galapagos Islands. Princeton University Press, New Jersey, USA.

Clark, D. A. 1981. Foraging patterns of black rats across a desert-montane forest gradient in the Galápagos Islands. *Biotropica 13(3):182-194.*

Cousens, R., and M. Mortimer, 1995. Dynamics of weed populations. Cambridge University Press, Cambridge, UK.

Cronk, Q. B., and J. L. Fuller. 1995. Plant invaders: the threat to natural ecosystems. Chapman and Hall, London, UK.

Field, A. P. 2005. Discovering statistics using SPSS, 2nd. edition. Sage Publications, London, UK.

Flora of Taiwan. 2003. 2nd. edition, Vol. VI, Department of Botany National Taiwan Univ. Taipei, Taiwan.

Grabe D. F. (ed.) 1970. Tetrazolium testing handbook for agricultural seeds. Contribution No. 29 to the handbook on seed testing. The Association of Official Seed Analysts, Las Cruces, New Mexico, USA.

Grant, P. R. 1986. Ecology and evolution of Darwin’s finches. Princeton University Press, New Jersey, USA.

Grant, P. R., J. N. M. Smith, B. R. Grant, I. J. Abbott, and L. K. Abbott. 1975. Finch numbers, owl predation and plant dispersal on Isla Daphne Major, Galápagos. *Oecologia 19(3):239-258.*

Grant, P.R., and T. De Vries. 1993. The unnatural colonization of Galapagos by smooth-billed anis (*Crotophaga ani*). *Noticias de Galápagos 52:21-23.*

Grant, P. R., and R. Grant. 2006. Evolution of character displacement in Darwin’s finches. *Science 313:224-226*

Guerrero, A. M. 2002. El rol de las aves en el proceso de dispersión de semillas de plantas nativas e introducidas en Santa Cruz, Galápagos [The role of birds on the dispersal of native and introduced species in Santa Cruz, Galápagos]. Unpublished Doctoral thesis. Univ. Central del Ecuador, Quito, Ecuador.

Hamann, O. 1981. Plant communities of the Galápagos Islands. *Dansk Botanisk Arkiv 34(2):1-163*

Jackson, M. H. 1993. Galápagos: A natural history. University of Calgary Press, Calgary, Canada.

Jara, M. E., and J. De Vries. 1995. Distribución y abundancia del Garrapatero *Crotophaga ani* en las Islas Galápagos, Ecuador. *Revista de la Pontificia Universidad Católica del Ecuador 23(59):121-169.*

Jordano, P. 1982. Migrant birds are the main dispersers of blackberries in southern Spain. *Oikos 38(2):183:193.*

Lack, D. 1945. The Galápagos finches (Geospizinea): A study in variation. *Occasional Papers of the California Academy of Science 21:1-159.*

Landázuri, O. D. 2002. Distribución, fenología reproductiva y dinámica del banco de semillas de mora (*Rubus niveus* Thunb.*)* en la parte alta de la isla Santa Cruz, Galápagos [Distribution, reproductive phenology and seed bank of blackberry (*Rubus niveus* Thunb.) in the hihglands of Santa Cruz, Galápagos]. Unpublised Doctoral thesis. Univ. Central del Ecuador, Quito, Ecuador.

Larrea, C. M. 1956. El Archipiélago de Galápagos durante los siglos XVII Y XVIII. Piratas y corsarios. La pesca de la ballena: [The Galápagos Islands in the 17th and 18th centuries. Pirates and privateers. Whaling. *Boletín de la Academia Nacional de la Historia, Ecuador 36(88):195-208.*

Lawesson, J. E., and L. Ortiz. 1990. Plantas introducidas a las Islas Galápagos. *Monogr. Syst. Bot. Missouri Bot. Gard. 32:201-210.*

Levey, D. J. 1987. Seed size and fruit-handling techniques of avian frugivores. *The American Naturalist 129 (4):471-485.*

Loope, L. L., and D. Mueller-Dombois. 1989. Characteristics of invaded islands, p. 257–80. In: Drake, J.A., *et al*., (eds.), Ecology of biological invasions: a global synthesis. John Wiley and Sons, Chichester, UK.

MacDowell, S. C. 2002. Photosynthetic characteristics of invasive and noninvasive species of *Rubus* (Rosaceae). *American Journal of Botany 89(9):1431–1438.*

Mandon-Dalger, I., P. Clergeau, J. Tassin, J. N. Riviére, and S. Gatti. 2004. Relationships between alien plants and alien bird species on Reunion Island. *Journal of Tropical Ecology 20:635-642.*

Mauchamp, A., I. Aldaz, E. Ortiz, and H. Valdebenito. 1998. Threatened species, a re-evaluation of the status of eight endemic plants of the Galapagos. *Biodiversity and Conservation 7(1):97-107.*

McMullen, C. 1999. Flowering plants of the Galapagos. Cornell University Press, Ithaca, New York, USA.

Moermond, T. C., and J. C. Denslow. 1985. Neotropical avian frugivores, patterns of behavior, morphology and nutrition, with consequences for fruit selection. In: Buckley F.G., M.S. Foster, E.S. Morton, R.S. Ridgley, and F.E. Buckley, (eds.). Neotropical ornithology, *Ornith. Mong.* 36: 865-897.

Morton, J. F. (ed.). 1987. Mysore raspberry. In: Fruits of warm climates. Flair Books Miami, Florida, USA.

Muller-Dombois D., and L.L. Loope. 1990. Some unique ecological aspects of oceanic islands ecosystems, In: Lawesson, J.E., O. Hamann, G. Rogers, G. Reck, and H. Ochoa, (eds.). Botanical Research and Management in Galapagos. *Monog. Syst. Bot. Missouri. Bot. Gard. 32:21-27.*

Nybom, H. 1988. Apomixis versus sexuality in blackberries (*Rubus* subgen. *Rubus,* Rosaceae). *Plant Syst. Evol. 160:207-18.*

Porter, M. D. 1983. Vascular plants of the Galapagos: origins and dispersal. In: R. I Bowman, M. B. Berson and A. E. Leviton, (eds.), Patterns of evolution in

Galapagos organisms (pp. 33-96). (AAA) American Association for the Advancement of Science, San Francisco, California, USA.

Quinn, J. S., and J. M. Startek-Foote. 2000. Smooth-billed Ani (*Crotophaga ani*). In: The Birds of North America, No. 539, A. Poole and F. Gill (eds.), The Birds of North America, Inc., Philadelphia, Pennsylvania, USA.

Richardson, D. M., N. Allsopp, C. M. D'Antonio, S. J. Milton, and M. Rejmánek, 2000. Plant invasion; the role of mutualisms. *Biol. Rev. 75:65-93.*

Rosenberg, D.K., M.H. Wilson, and F. Cruz. 1990. The distribution and abundance of the Smooth-billed ani *Crotophaga ani* (L.) in the Galapagos Islands, Ecuador. *Biol. Conserv. 51:113-123.*

Santiago-Alarcón, D., S. M. Tanksley, and P. G. Parker. 2006. Morphological variation and genetic structure of Galapagos Dove (*Zenaida galapagoensis*) populations: Issues in conservation for the Galapagos bird fauna. *Wilson Journal of Ornithology 118(2):194-207.*

Schofield, E. K. 1989. Effects of introduced plants and animals on island vegetation: examples from the Galápagos archipelago. *Conservation Biology 3(3):227-237*.

Schupp, E. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetatio 107/108:15-29.*

Scott, P. E., and R. F. Martin, 1984. Avian consumers of *Bursera, Ficus* and *Ehretia* fruit in Yucatan. *Biotropica 16(4):319-323.*

Shanahan, M., S. Samson, S. G. Compton, and R. Corlett. 2001. Fig-eating by vertebrate frugivores: A global review. *Biol. Rev*. 76:529- 572.

Slevin, J. R. 1959. The Galápagos Islands. A history of their exploration. *Occasional Papers of the California Academy of Sciences 25:1-150.*

Snell, H. L., P.A. Stone, and H.L. Snell. 1996. A summary of geographical characteristics of the Galápagos Islands. *Journal of Biogeography 23:619-624.*

Snell, H. L, A. Tye, C.E. Causton, and R. Bensted-Smith. 2002. Current status of and threats to the terrestrial biodiversity of Galápagos, In: R.A. Bensted–Smith, (ed.), Biodiversity vision for the Galápagos Islands (pp. 30-47), Charles Darwin Foundation and World Wildlife Fund, Pto. Ayora, Galápagos, Ecuador.

Snow, D. W. 1981. Frugivorous birds and their food plants: A world survey. *Biotropica 13(1):1-14.*

Starr, F., K. Starr, and L. L. Loope. 2003. *Rubus niveus f. a.,* Hill or mysore raspberry, Rosaceae (Report), (USGS-BRD) United States Biological Survey - Biological Resources Division, Haleakala Field Station, Maui, Hawaii, USA.

Tebbich, S., M. Taborsky, B. Fessl, M. Dvorak, and H. Winkler. 2003. Feeding behavior of four arboreal Darwin’s finches: adaptations to spatial and seasonal variability. *The Condor 106:95-105.*

Traveset, A., T. Bermejo and M. Willson, 2001. Effect of manure composition on seedling emergence and growth of two common shrub species of Southeast Alaska. *Plant Ecology 155:29-34.*

Tye, A. 2002. Revision of the threat status of the endemic flora of Galápagos. In: Informe Galápagos No. 6. Fundación Natura y el Fundo Mundial para la Naturaleza, Quito, Ecuador.

Whitaker, J. O., and G. F. McCracken. 2001. Food and ectoparasites of bats on the Galapagos Islands. *Acta Chiropterologica 3(1):6369.*

Wiggins, I. L and D. M. Porter. 1971. Flora of the Galápagos Islands. Stanford Univ. Press, Stanford, California, USA.

Zar, J. 1999. Biostatistical analysis, 4th. edition, Prentice Hall, New Jersey, USA.

Table 1. Frequencies of the foraging activities of birds registered in the study sites of *Rubus niveus* (Rosaceae) in the agricultural zone of Santa Cruz, Galápagos during the cold-garúa season (1) and the warm-wet season (2).

		Activities					
Species	Season	Fruit	Nectar	Insects	Search/ Stationary	Partially Hidden	Total
Crotophaga ani	1	65				14	79
Crotophaga ani	2	12				22	34
Geospiza fuliginosa	1	63	159		11		233
Geospiza fuliginosa	2	469	27		24		520
Geospiza fortis	1	16	3				19
Geospiza fortis	2	17	6				23
Geospiza magnirostris	1		1				1
Geospiza magnirostris	2	2					2
Geospiza sp.	1	1	2				3
Geospiza sp.	2	12			2	2	16
Camarhynchus parvulus	1	1	13	1	2		17
Camarhynchus parvulus	2	16	5		7		28
Camarhynchus psittacula	2	1					1
Camarhynchus sp.	1		2		1		3
Camarhynchus sp.	2	9			1		10
Cactospiza pallida	1	1					1
Cactospiza pallida	2	1					1
Certhidea olivacea	1		1	7	1		9
Certhidea olivacea	2			2	2		4
Myiarchis magnirostris	1			2	2		4
Myiarchis magnirostris	2			10	2		12
Coccyzus melacorphylus	2			2			2
Dendroica petechia	1		1	4			5
Dendroica petechia	2			4	2	1	7
Pyrocephalus rubinus	1			1			1
Laterallus spilonotus	1						1
Total		687	219	33	57	39	1036
%		66.4	21.2	3.1	5.5	3.8	100

Table 2. Visitation frequency of birds in 17 observation hours (per season) at *R. niveus* study sites in the agricultural zone of Santa Cruz.

	cold-garúa		warm-wet	
Species	N	%	N	%
Geospiza fuliginosa	131	62	364	84
Crotophaga ani	29	14	21	5
Camarhynchus parvulus	21	10	20	5
Certhidea olivacea	9	4	1	0
Dendroica petechia	8	4	4	1
Geospiza fortis	4	2	7	2
Cactospiza pallida	3	1	0	0
Geospiza	2	1	7	2
Myiarchus magnirostris	2	1	5	1
Laterallus spilonotus	1	0	0	0
Geospiza magnirostris	0	0	0	0
Camarhynchus psittacula	0	0	1	0
Camarhynchus	0	0	1	0
Total	210	100	431	100
Hours of observation	17		17	
Visits/hour	12		25	

Table 3. Species visitation frequency per site based on species occurrence (presences) during all 10 minute observation periods (OP).

Site	OP	Ani	GF	GFo	G	CPa	CPs	C	CPl	CO	MM	DP	LS	Total
cold-garúa														
1	19	5	12			2				3	1	1		24
2	21	2	10			3			2	1		3		21
3	21	5	12	3	4	4				1		1	1	31
4	11	2	8	1		3						1		15
5	15	3	2	1	1	1				2				10
6	16	1	4							1	1	2		9
Total	103	18	48	5	5	13	0	0	2	8	2	8	1	110
Warm- wet														
1	15		16											16
2	17	2	17	3		4		1				1		28
3	18	1	17	2	2	3					1			26
4	18		16		2	4								22
7	17		14		1	1	1					1		18
8	16	5		1	1	6						1		14
Total	101	8	80	6	6	18	1	1	0	0	1	3	0	124

Ani: *Crotophaga ani;* **GF:** *Geospiza fuliginosa;* **GFo,** *G. fortis;* **G***; Geospiza*; **CPa:** *Camarhynchus parvulus;* **CPs:** *C. psittacula*; **C:** *Camarhynchus*; **CPl:** *Cactospiza pallida*; **CO:** *Certhidea olivacea*; **MM:** *Myiarchus magnirostris*; **DP:** *Dendroica petechia*; **LS:** *Laterallus spilonotus*.

Table 4. Proportion of seeds consumed per visit based on fruit type (ripe, dry and unripe) during the cold-garúa and the warm-wet seasons.

	cold-garúa			warm-wet		
Species	Ripe	Dry	Unripe	Ripe	Dry	Unripe
Geospiza fuliginosa	0.85	0.12	0.02	0.93	0.06	0.01
Crotophaga ani	1			1		
Camarhynchus parvulus	1			0.98	0.02	
Geospiza fortis	0.75	0.12	0.12	0.78	0.11	0.11
Cactospiza pallida	1			1		
Geospiza magnirostris				0.94	0.06	
Camarhynchus psittacula					1	

Table 5. Mean visitation time (in minutes) and standard error (SE) for species and study sites (*Rubus* clones) in the cold-garúa and warm-wet seasons (only complete records recorded during focal animal sampling). Only those clones sampled in both seasons are shown.

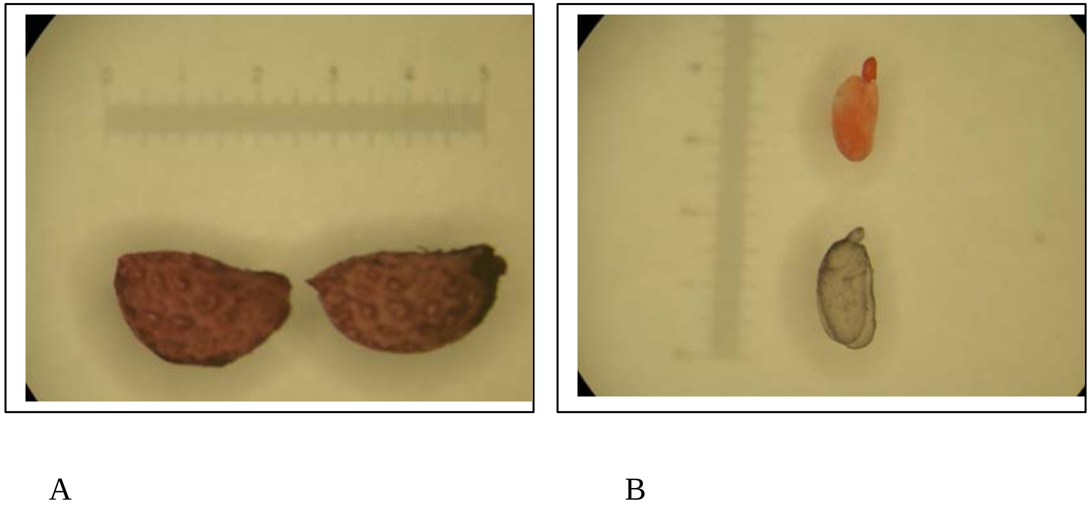
Species	Sites				Mean total	SE
Cold-garúa	1	2	3	4		
Crotophaga ani	2.41	4.52	3.58	1.97	3.25	0.38
Geospiza fuliginosa	2.26	1.49	1.51	2.14	1.78	0.14
Geospiza fortis	5.60	1.78	4.43	3.98	3.99	0.92
Camarhynchus parvulus	1.61	6.15	1.60	0.66	1.7	0.43
Certhidea olivacea	2.30	1.97		1.21	1.94	0.66
Dendroica petechia	0.54	0.56			0.55	0.1
Myiarchus magnirostris	0.17	1.18	0.63		0.65	0.24
Mean Total	2.34	2.18	2.12	2.06		
SE	0.26	0.33	0.24	0.25		
warm-wet						
Crotophaga ani	2.12	2.23	0.83		1.94	0.3
Geospiza fuliginosa	2.25	1.98	2.33	2.68	2.33	0.14
Geospiza fortis	1.68	3.18	2.50	3.66	2.48	0.67
Camarhynchus parvulus	1.84	1.78	2.23	2.70	1.87	0.34
Dendroica petechia	0.07	0.38		1.77	1	0.76
Myiarchus magnirostris	2.15	4.50	0.08	0.70	1.98	0.62
Mean Total	2.13	1.99	2.22	2.65		
SE	0.22	0.19	0.24	0.26		

Table 6. Mean number of seeds handled, standard error (SE) and an approximate number of fruits handled per visit in the study sites in the cold-garúa and warm-wet seasons.

Species	Sites				Total	SE	Fruits
	1	2	3	4			
Geospiza fuliginosa	178	53	146	117	117	20	1.48
Crotophaga ani	233	252	329	238	270	19	3.41
Geospiza fortis	105	91	247	364	217	80	2.74
Mean total	214	162	286	191			
SE	20	24	36	54			
Fruits	2.70	2.04	3.61	2.41			
Warm-wet							
Geospiza fuliginosa	189	141	143	199	169	10	2.14
Crotophaga ani	264	317	119		244	34	3.08
Camarhynchus parvulus	79	171	158	79	144	23	1.82
Geospiza fortis	101		52	79	80	24	1.01
Mean total	189	152	136	194			
SE	22	16	14	16			
Fruits	2.38	1.91	1.71	2.45			

Table 7. Index of dispersal effectiveness of the species calculated based on the approximate number of visits in 12 hours (day), mean number of seeds handled per visit (ripe fruits only) and proportion of viable seeds after gut treatment.

Species	Season	N	Mean seeds	Viable seeds	Index	Scaled index
Geospiza fuliginosa	cold-garúa	92	117	0.002	21.528	0.00
Geospiza fuliginosa	warm-wet	257	169	0.002	86.866	0.02
Crotophaga ani	cold-garúa	20	270	0.57	3078	0.58
Crotophaga ani	warm- wet	15	244	0.57	2086.2	0.39
Camarhynchus parvulus	cold-garúa	21	183	0.002	7.686	0.00
Camarhynchus parvulus	warm- wet	14	144	0.002	4.032	0.00
Geospiza fortis	cold-garúa	2	217	0	0	0.00
Geospiza fortis	warm- wet	1	80	0	0	0.00
Cactospiza pallida	cold-garúa	2	143	0.002	0.572	0.00
Cactospiza pallida	warm- wet	1	79	0.002	0.158	0.00
Geospiza magnirostris	warm- wet	1	277	0.002	0.554	0.00
Geospiza	warm- wet	1	193	0.002	0.386	0.00
Camarhynchus	warm- wet	1	89	0.002	0.178	0.00
Total		428	2248	1.16	5286.16	1.00



Appendix 1. *Rubus niveus* seeds collected from *Crotophaga Crotophaga ani* droppings (A). Viable (colored) and not viable seed after testing with 2,3,5-triphenyl tetrazolium chloride (B).

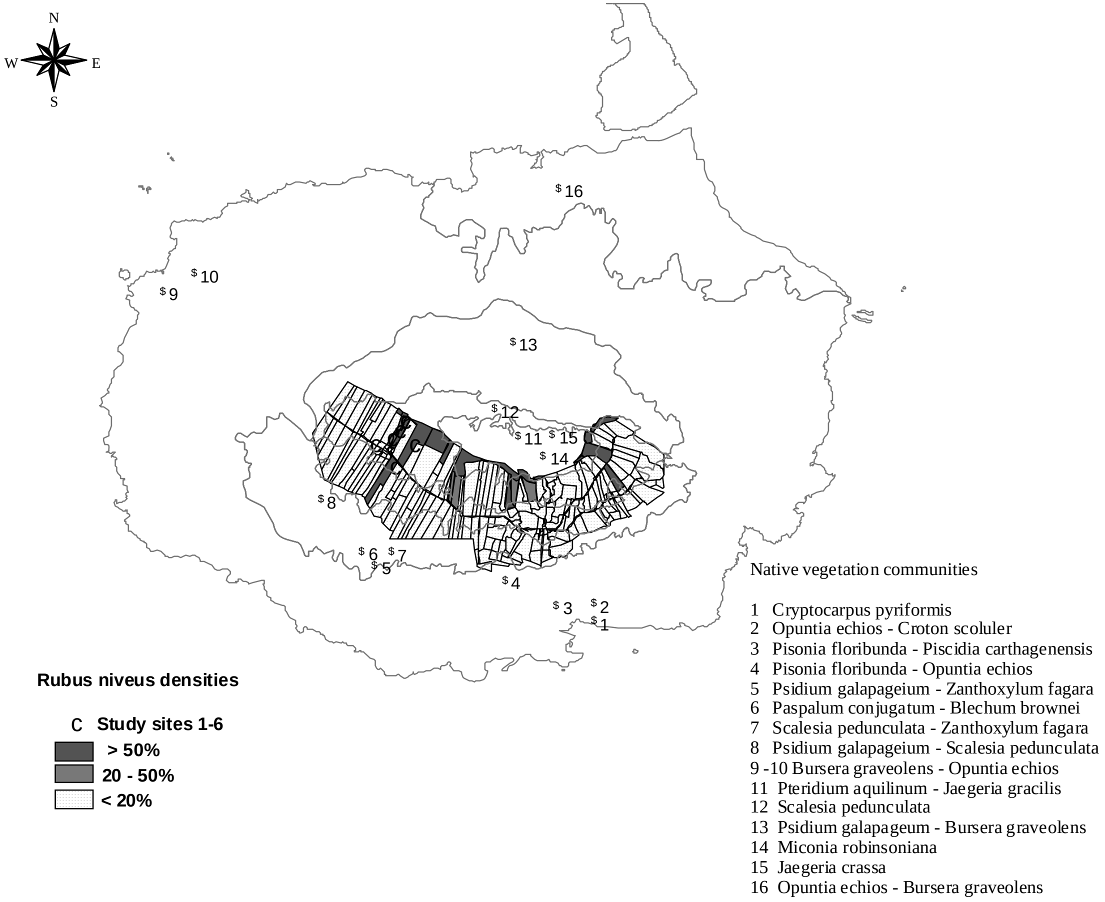


Fig. 1 Map of Santa Cruz Island, study sites in the agricultural zone and native vegetation communities identified by Hamann (1981). Areas in dark, medium dark and white represent different densities of *Rubus niveus* (Base map: Galapagos National Park).

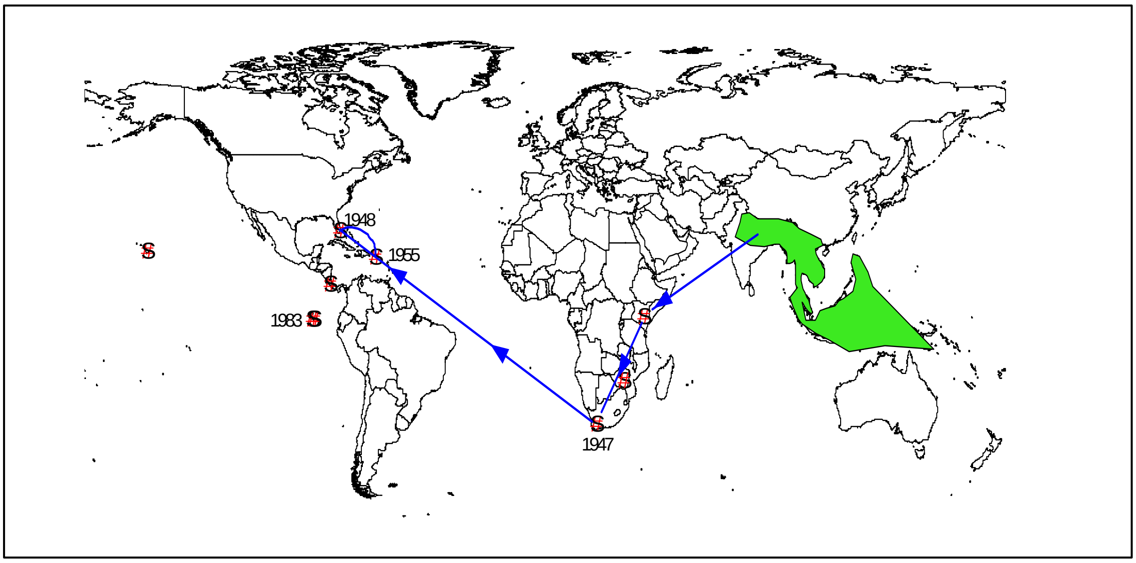


Fig. 2 Native range of *Rubus niveus* in Asia and Indonesia (colored areas) and dates of introduction to Africa and America (based on Morton, 1987). The species was first reported in the agricultural zone of San Cristobal Island, Galapagos in 1983 and since then it has dispersed to other islands.

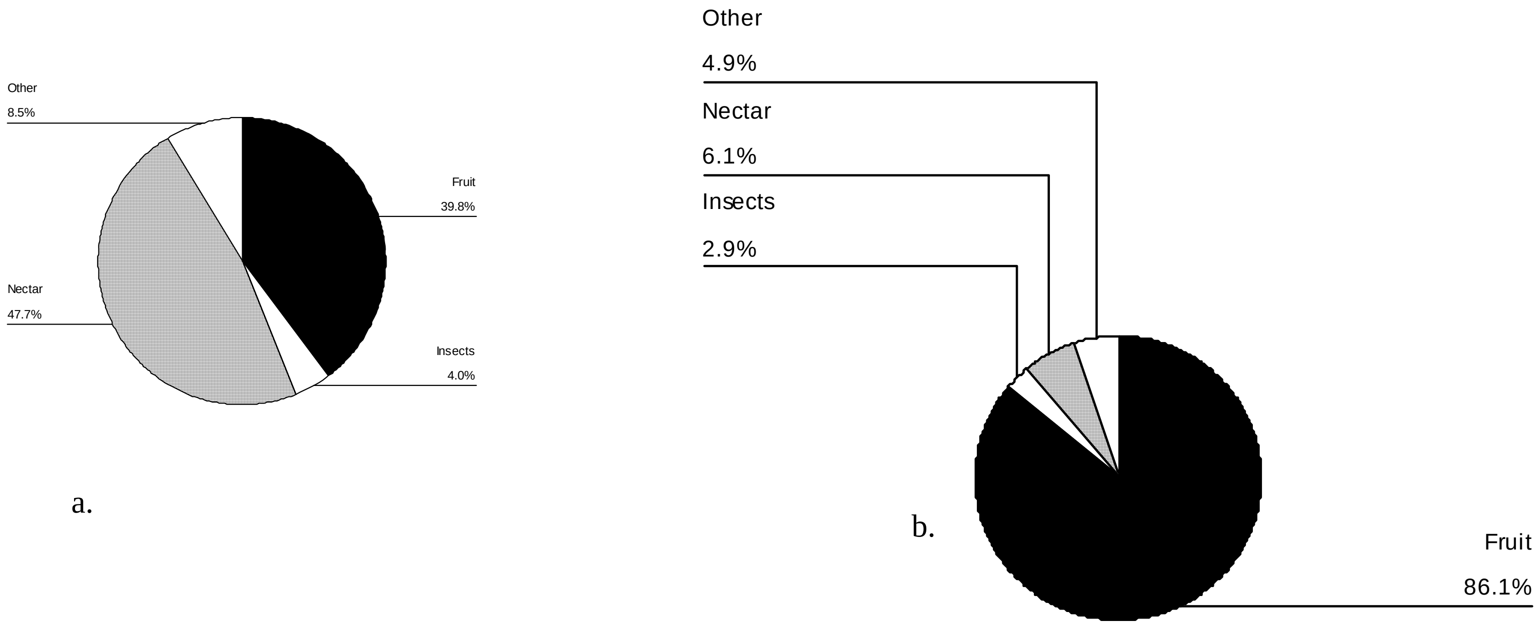


Fig. 3 Foraging activities of the birds at *Rubus niveus* registered in the cold-garúa (A) and hot-rainy seasons (B).

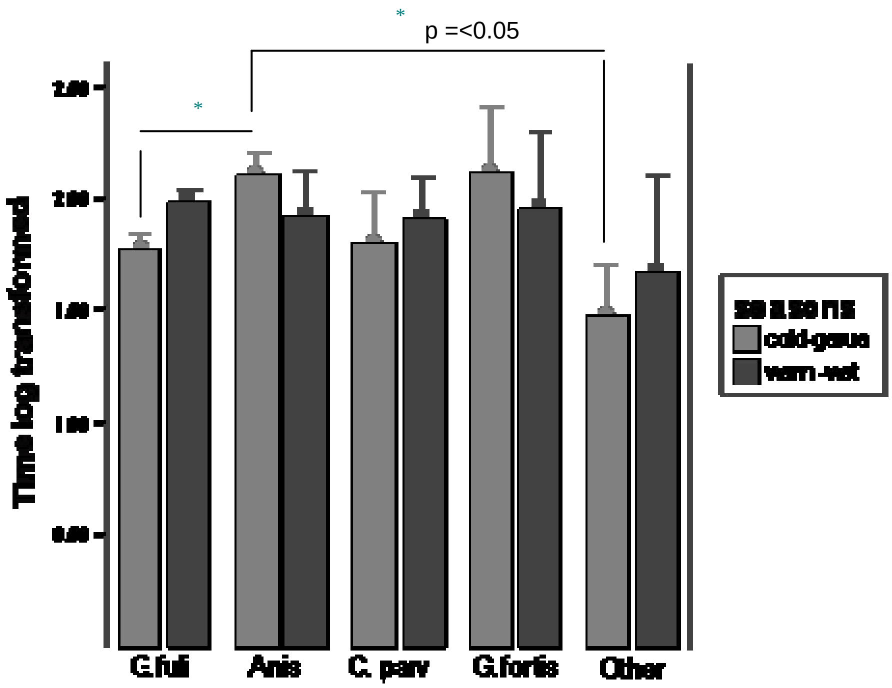


Fig. 4 Mean number of visitation time of the birds and standard error of the mean (95% CI) in the cold-garúa and warm-wet seasons. Asterisks and lines show significant differences among species.

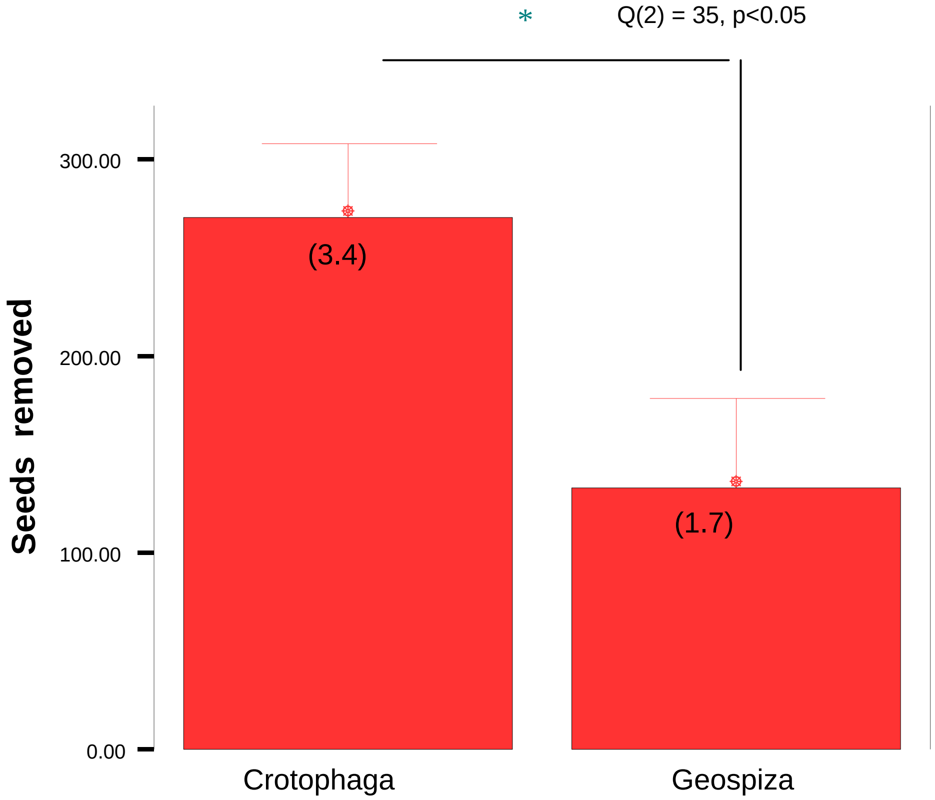


Fig. 5 Bars represent the mean number of *R. niveus* seeds (fruits) removed by *Crotophaga ani* and *Geospiza* species during the cold-garúa season. Error bars represent the standart error of the mean.

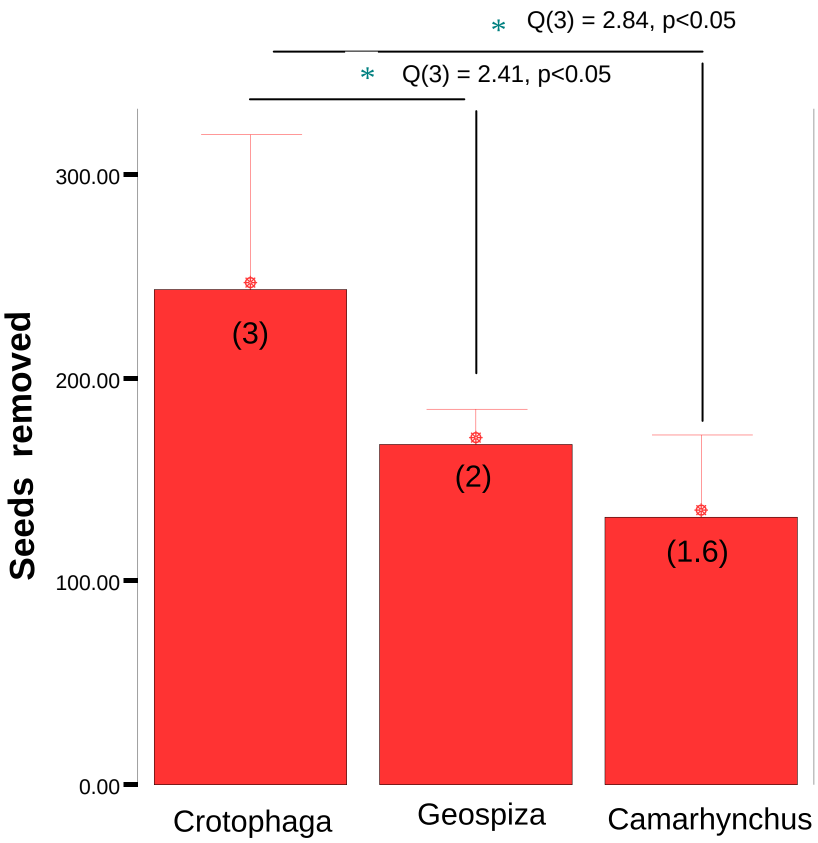


Fig. 6 Bars represent the mean number of *R. niveus* seeds removed (fruits) by *Crotophaga ani*, *Geospiza* and *Camarhynchus* during the warm-wet season. Error bars represent the standard error of the mean.