The Role of the White-Winged Guan (Penelope albipennis) in Seed Dispersal and Predation in Tumbesian Dry Forest, Peru

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The white-winged guan (Penelope albipennis, Cracidae), thought extinct until 1979, today numbers <300 individuals. We investigated the role of the guans in seed dispersal and predation dynamics by recording seed germination from fecal samples of wild birds during the dry-season (May–December 2010). This study was conducted at Chaparri Ecological Preserve, in the critically endangered Tumbesian ecosystem on the western slope of the Andes. Field observations show that this bird is a frugivore; Cordia lutea (Boraginaceae) was the primary fruit consumed of the eight species of seeds collected from droppings. Collected seeds were sown in pots under nursery conditions and monitored for germination. Germination rates of passed seeds for Cordia lutea were compared to those that had been collected from a control group of trees. Germination was significantly different between fecal and control seeds, suggesting the plant germinated better after passing through the guans alimentary tract. The identification of flower structures, and digested seeds in feces show that guans can be effective fruit and flower predators. This study provides further information regarding the diet for conservation of the white-winged guan and suggests the bird may aid seed germination in some instances and may act as a predator in others.

KEYWORDS white-winged guan (Penelope albipennis), Cracidae, seed dispersal, Cordia lutea, Pithecellobium, Solanum betaceum, Tumbesian dry forest, Peru, biodiversity

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INTRODUCTION

It is widely accepted that many frugivorous birds are effective transporters of seeds (Mcatee, 1947). Furthermore, plant reproductive strategies are often adapted to dispersal by frugivorous birds (Howe & Smallwood, 1982). Germination is enhanced because scarification and chemical washing of the seed coat occurs in the digestive system of the bird without destroying the seed itself (Krefting & Roe, 1949). Stomach acids make the seed coat thinner, enabling the radical to penetrate the seed coat more easily (Traveset, Riera, & Mas, 2001) and the seed can be passively dispersed from the parent tree. Many birds have been shown to be effective seed predators, digesting both fruit and seed. Cracids such as Salvin’s curassow (Mitu salvini) are effective seed predators (Yumoto, 1999). Another study found that endozoochory was the dominant animal dispersal strategy of plants in the Tumbesian dry forest (Jara-Guerrero, De la Cruz, & Mendez, 2011).

The white-winged guan (Penelope albipennis) is a critically endangered species (International Union for the Conservation of Nature [IUCN], 2012) endemic to the critically endangered Tumbesian dry forest (Olson & Dinerstein 2002; Angulo-Pratolongo, Diaz-Montes, Williams, & Cancino, 2006). Located on the western slope of the Peruvian Andes between 300–1,100 masl, the Tumbesian region has a 25% endemism rate among vascular plants, and contains 45 species of endemic birds, of which 14 are considered threatened (Stattersfield, Crosby, Long, & Wege, 1998). The Tumbesian region is noted for its dry forest along the Pacific coast and adjacent to the cold Humboldt Current that creates strong wet and dry seasons (Best & Kessler, 1995).

Penelope albipennis was thought to be extinct prior to 1977 (Williams, 1980). Upon rediscovery, this species morphological characteristics were compared with other congeners to determine their systematic position (Eley, 1982). Since then, captive breeding programs and conservation efforts have been working to increase numbers to stock preserves established in the Tumbesian dry forest. A reintroduction program exists that has actively bolstered the wild population since 2000 (Angulo-Pratolongo, 2004). The most recent population estimate is ~300 individuals including some wild-reared chicks whose parents were captive-bred and reintroduced (Angulo-Pratolongo, 2008).

Penelope albipennis moves along valleys and riparian gallery forests during the dry season (March–November) because it prefers flowering and fruiting evergreen trees and shrubs along dry riverbeds. In the wet season, P. albipennis moves into the surrounding hillsides as vegetation leaves-out and flowers and fruits become present. The diet of the guan includes leaves, fruits, flowers, seeds, and spouts (Lerner-Martinez, Ceroni-Stuva, & Gonzalez-Romo, 2003). The most recently published list of food items showed 40 species of plants consumed by P. albipennis (Lerner-Martinez
et al., 2003), with 20 species common in their diet (Angulo-Pratolongo et al., 2006, Ortiz-Tejada & Diaz-Montes, 1997).

The objective of this study is to determine the role *P. albipennis* plays in seed dispersal and predation. The working hypothesis is that *P. albipennis* is an effective seed disperser, and germination rates increase when passed through the alimentary tract of the bird.

**METHODS**

**Study Site**

The 11,346-ha Zona Reservada de Laquipampa in the Tumbesan dry forest (EBA 045, Stattersfield et al., 1998) was established in 1982 for the preservation, conservation, and scientific investigation of *P. albipennis* and other species of fauna and flora (Ortiz-Tejada & Diaz Montes, 1997, Flanagan & Angulo-Pratolongo, 2002). Tree and shrub species in the families Celestraceae, Solanaceae, and Fabaceae are common in this topography of valleys and dry riverbeds, although most of the original forest vegetation has been destroyed from overgrazing.

There are approximately 24 species of fruiting plants representing 19 genera and 12 families, with *Cordia lutea* (Boraginaceae) the dominant species (Linares-Palomino & Ponce-Alvarez, 2009). Additional plants include *Ludwigia* sp., *Solanum betaceum* Cav., *Pithecelobium multiflorum* Kunth., *Muntingia calabura* L., and *Cestrum auriculatum* L. Species reported by guides to as consumed by guans but not observed during the study include *Bursera graveolens* Kunth. and *Quararibea cordata* syn. *Matisia cordata* Humb. & Bonpl.

**Field and Lab Protocol**

Fieldwork included collection of fecal samples, observations on guan group size and behavior, and composition and structure of guan habitat. Guan feces were collected by direct observation of defecation site. Floral and fruiting structures within feces were identified with a hand lens (10 ×). A spotting scope (Nikon Fieldscope 4–20 × 60 mm; Nikon Inc., Melville, NY, USA) and binoculars (Nikon Monarch 10 × 42) were used to observe birds. Observations recorded included bird activity, feeding preferences, vocalizations, endozoochory, and head-twitching (Flieg & Dooley, 1972).

Fecal material was collected and placed in 0.25 L of water for 24 hr to create a suspension. Fecal samples were strained (<1 mm) and seeds and other vegetative parts were taken from the strainer, identified, and counted. Seed size and shape of *C. lutea* and *S. betaceum*, seed coats of *Pithecelobium* sp., and endosperm of *C. auriculatum* were matched with fruits of the same species from a reference collection. Two criteria for positive identification
were: (a) the plant was fruiting in the ecosystem, and (b) the seed matched physical characteristics of the related plant.

Processing the feces took place at a nursery consisting of a 6 m × 3 m netted area that served to protect seeds and seedlings from seed predators and herbivores. Seeds were sown in fecal groups in pots that were labeled and catalogued. Pots were perforated at the base to allow water flow. Soil was heat-sterilized for 12 hr at 100°F (37.8°C) and then washed to remove contaminants. Pots were filled with soil 2 cm from the rim, and then seeds were placed in the potted soil. The seeds were covered with one additional cm of soil and then lightly compressed, ensuring good soil-seed contact. Pots were monitored and germination was recorded daily for 6 months. Sevin insecticide was used to prevent insect predation.

Control seeds were planted as groups from a single fruit of the parent plant. Control seeds were not cleaned by fruit maceration for species such as C. lutea, nor were arils removed for Pithecellobium; M. calabura was planted as a macerated berry to mimic fruit fall from the tree. Control groups were planted in the same nursery and received equal amounts of water and sunlight as fecal groups. Each control fruit was chosen for ripeness and easy removal from the parent plant.

Data Analysis

Data were collected during the dry season (May–December 2010). Data parameters collected include whether or not a seed germinated, and days until germination. Percentages were calculated for all fecal components including anthers, styles, peduncles, seed coats, seeds, and digested vegetable matter.

Minitab 16 statistical software (Minitab Inc., 2010) was used to evaluate data using a two sample T-test to examine differences between days until germination between fecal and control groups. A test for two-proportions (95% CI) was used to examine the effect of guan ingestion on seed germination. A linear regression was used to examine the predictor of the quantity of seed present in feces and the natural log of percent makeup.

RESULTS

Cordia lutea

C. lutea has an egg-shaped, oblong fruit that is approximately 1 cm in length, allowing the guan to easily consume the fruit. The exocarp is thin, the mesocarp is sticky, and the endocarp houses a single seed. The fruit is born in clusters on the apices of branches making presentation for feeding a goal of the species. Using a linear regression of C. lutea quantity in fecal material and
FIGURE 1 Linear regression plotting quantity versus natural log of percent *C. lutea* in feces. A higher $R^2$ value is obtained with a natural log transformation of the data.

the natural log of percent seeds in feces indicated high predictive capacity ($R^2 = 61.6\%$; Figure 1).

Of 97 seeds in the control group only 9 germinated, and of 65 seeds in the fecal group 20 germinated (Figure 2). The proportion of seeds that germinated in the control group (9.3%) was smaller than the fecal group (30.8%), suggesting higher germination rates are attained when the seeds pass through the guan’s alimentary tract. In a two-sample $T$-test assuming unequal variances, days to germination between fecal and control groups was not significant ($\alpha = .05, p = .387$; Figure 3).

The mean number of *C. lutea* seeds found in each fecal sample was 3.4 (median = 3, $r = 1–9$) and germinated 25–137 days after planting (mean = 63.7, median = 43). The mean number of control group *C. lutea* seeds was 8.8 (median = 12, $r = 2–15$) and germinated 32–115 days (mean = 76.3, median = 92 days). Using a test for two-proportions (95% CI), seeds in the fecal group had a higher frequency of germination than the control group ($\alpha = .05, p < .001$; Figure 2).

Experimental samples had some predictive capacity as *C. lutea* showed increased germination rates when compared to control groups. *Pithecellobium sp.*, *S. betaceum*, *M. calabura*, and an unidentified species of legume phyтомorph were also found in guan feces but were excluded from dispersal analyses because they did not germinate.

Predated Species

Seven species of plants were identified in fecal samples from intact seeds or reproductive structures (Table 1). Seed not passed intact through the
FIGURE 2 The proportions of seeds that germinated (G) versus those that did not (N) is higher in the fecal group. A significant difference is shown between the groups.

FIGURE 3 Days to germination medians are shown by a vertical line in each box for both control and fecal groups; the mean in each group is expressed as a circular cross. Q1 and Q3 are below and above the median, respectively, whiskers represent minimums and maximums and there were no outliers. There is no significant difference between these groups.

digestive system of the guan were used nutritionally. *Solanum betaceum* was identified from intact seed in the feces. Seed coats of *Pitbecellobium sp.* and endosperm of *C. auriculatum* were also found in the feces. Although *M. calabura* was eaten by guans no viable seeds were detected in the feces. *Swartzia obscura* was not sexually mature at the time of consumption.
Table 1 Plant Species and Their Parts Consumed by Guan

<table>
<thead>
<tr>
<th>Species</th>
<th>Leaves</th>
<th>Flowers</th>
<th>Fruits</th>
<th>Buds</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bursera graveolens</td>
<td>Vo</td>
<td>—</td>
<td>Vo</td>
<td>—</td>
</tr>
<tr>
<td>Cestrum auriculatum</td>
<td>Vo</td>
<td>Vo</td>
<td>F, P</td>
<td>Vo</td>
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<tr>
<td>Cordia lutea</td>
<td>Vo</td>
<td>Vo</td>
<td>F, I</td>
<td>F</td>
</tr>
<tr>
<td>Fuchsia sp.</td>
<td>—</td>
<td>Vo</td>
<td>F, P</td>
<td>Vo</td>
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<tr>
<td>Ludwigia sp.</td>
<td>Vo</td>
<td>Vo</td>
<td>—</td>
<td>Vo</td>
</tr>
<tr>
<td>Muntingia calabura</td>
<td>Vo</td>
<td>—</td>
<td>F, P</td>
<td>—</td>
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<tr>
<td>Unidentified legume phytomorph</td>
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<tr>
<td>Pithecellobium sp.</td>
<td>—</td>
<td>Vo</td>
<td>F, P</td>
<td>Vo</td>
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<tr>
<td>Psismum sp.</td>
<td>Vo</td>
<td>F</td>
<td>—</td>
<td>Vo</td>
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<tr>
<td>Quararibea cordata</td>
<td>—</td>
<td>Vo</td>
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<td>Vo</td>
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<tr>
<td>Solanum betaceum</td>
<td>—</td>
<td>—</td>
<td>F, P</td>
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<tr>
<td>Swartzia obscura</td>
<td>—</td>
<td>—</td>
<td>F, P</td>
<td>—</td>
</tr>
</tbody>
</table>

Note. F = found in feces, I = intact seed, P = predated seed, Vo = visual observation in the field; “—” = not present.

The unidentified legume phytomorph had a distinctively white hilum and a hard seed coat with evidence of predation prior to consumption. Although Bursera graveolens and Quararibea cordata seeds were not found in feces, they were consumed by the guans during the fruiting season (J. Vallejos Santa Cruz, personal communication, June 2010).

DISCUSSION

The diet of *P. albipennis* has been documented (Ortiz-Tejada & Diaz-Montes, 1997; Lerner-Martinez et al., 2003; Martos, Scarpati, Rojas, & Delgado, 2009) but the dietary list has been amended by this report to include the following: Fuchsia sp., Psismum sp., Quararibea cordata, Solanum betaceum, and Swartzia obscura.

This study confirms that *P. albipennis* predates the seeds of several species and only disperses C. lutea. This is similar to the findings of Yumoto (1999) where seeds of only one viable species were dispersed by *Mitu salvini*. Howe and Smallwood (1982) suggested escape, colonization, and direct dispersal pathways are used by plants. To test this hypothesis other species of animals would need to be included in the study to identify the exact pathways that plants are using in dispersal other than *P. albipennis*. Spectacled bears (*Tremarctos ornatus*) are also present in the ecosystem, and although they have not previously been identified as seed dispersers their feces contain seeds (e.g., Cordea lutea) of unknown parental origin (LAB personal observation). More rigorous scarification of the seed may occur from passage through the gut of spectacled bears as opposed to *P. albipennis*. This scarification may make a difference in water permeating.
the seed coat, promoting more rapid germination. Looking at the viability and germination rates of seeds passed by spectacled bears may reveal another unique ecological pathway (cf. Peyton, 1980). By comparison, North American black bears (*Ursus americanus*) are effective predators of certain seeds in xeric highland forest in Arizona (DMB unpublished data).

Analysis shows no significant difference for the period between consumption events and days to germination. However, there is apparently a commensalsitic symbiotic relationship where *C. lutea* frequency of germination increases as a result of consumption by the guan. The seed’s embryo is stimulated as a result of passage through the guan’s alimentary tract. The lack of differences in *C. lutea* germination rates between fecal and control groups may be due to embryonic development rates, seed coat inhibitors, or water intake ability. Alternatively it is possible that inhibitors were removed from the seed coat in both groups but scarification was not present to encourage water intake in the control group.

Seeds that were destroyed *in vitro* were used for nutrients by the guan. Reproductive organs of *Cestrum auriculatum*, *Fuchsia* sp., *Muntingia calbaura*, and *Pithecellobium* sp. were all observed to be consumed and destroyed by the guan. While seeds in this group were predated in the surrounding exocarp, mesocarp, and endocarp, these fruits also provide nutrients in the form of sugars, starches, and lipids. The unidentified legume phytomorph, *Solanum betaceum* and *Swartzia obscura*, were not observed to be consumed but were found in the feces of the guan.

*Ludwigia* sp. was consumed by the guan. This herbaceous plant had fruits that were coated with sticky peltate glands tipped with resin to aid adhering to animals for phoretic dispersal. This epizoochorous method of transport was observed on guans at Chaparri once during the study.

Other seeds such as *Pithecellobium* sp. are borne in a leguminous pod that dehisces along a septum and presents black seeds with a red placenta while on the tree. Red and black presentation is known to attract birds (Willison & Whelan, 1990). In this case, however, the presentation does not seem to warrant dispersal by *P. albipes*. Other species of birds in the forest may transport this seed, however.

*Solanum betaceum* seeds passed through the bird physically undamaged but germination did not take place in either fecal or control groups, suggesting that seed viability was affected even though they were not used as nutrients by the guan. Control group fruits chosen for germination were ripe but did not abscise from the parent plant; they were extracted and planted because they were detected in feces. Seeds collected from feces are likely to have been consumed as whole fruits born on parent plants. While these fruits and seeds were selected to be compared, they were likely neither choice edibles nor viable seeds. These fruits were produced post wet-season and probably did not develop properly since the study took place during
the dry season. The persistence of the fruit on the plant suggests these seeds were likely undeveloped when feeding occurred.

More detailed studies are needed. For example, spatial tracking experiments need to be accomplished to determine dispersal distance by the guan. Additionally, while this study documented events during the dry season, further investigations should target the wet season to determine whether seeds and vegetation exhibit characteristics different from the dry season (e.g., dormancy).

As land managers work to increase guan populations, some considerations render themselves as a result of this study. *Cordia lutea* is being dispersed by the guan and likely needs little support in the landscape; this species is being dispersed by the guan and experiences improved germination after consumption. Other plants whose fruits are being predated by the guan will likely need support in the ecosystem in the form of propagation and establishment by land managers. To support guan populations as an ecosystem strategy, vegetation management considerations can be inferred. The predation of high nutrient choice edibles by the guan and other animals limits their reproduction in the landscape. Similarly, these same species provide nutrients for survival and reproduction of a species that is imperiled. A strategy that promotes vegetation management and establishment of plant populations that includes species such as *C. lutea* whose dispersal is facilitated by the guan should be considered as a means to support the ecosystem vegetation, as well as the available nutrients for the guan.

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