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RESEARCH ARTICLES

RAPID SEAFLOOR MAPPING OF THE NORTHERN GALAPAGOS ISLANDS, DARWIN AND WOLF

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SUMMARY

Darwin and Wolf are the most remote of the Galapagos islands and are famous for their remarkable pelagic and benthic marine species abundance and diversity. However, little is known about their surrounding bathymetry. Rapid surveys were carried out in 2008 and 2009 to collect geo-referenced depth soundings down to 100 m around both islands, as a step towards a better understanding of their habitat and species distribution. Five spatial interpolation methods were tested on the data, to find the most accurate. The Triangular Irregular Network (TIN) was the best interpolator for these data sets with the fewest interpolation errors, and was then used to create contour and three-dimensional maps of the seafloor topography of both islands. Darwin has a bigger insular platform with gentle submarine slopes whereas Wolf has very steep slopes with a smaller platform.

RESUMEN

Mapeo rápido del fondo submarino de las islas del norte de Galápagos, Darwin y Wolf. Darwin y Wolf son las islas más remotas del Archipiélago de Galápagos. Son famosas debido a la alta biodiversidad marina de especies pelágicas y bentónicas. Sin embargo, ningún estudio ha levantado información sobre su batimetría. Se realizó una serie de sondeos rápidos en 2008 y 2009 para coleccionar información geo-referenciada de hasta 100 m de profundidad alrededor de ambas islas, para mejorar el entendimiento de la distribución de especies y hábitats. Cinco métodos de interpolación espacial fueron probados sobre los datos para encontrar el más preciso. La Red de Triangulación Irregular (TIN, por sus siglas en inglés) fue el mejor, generando los valores de error más bajos, y fue el usado para generar mapas de contorno y de tres dimensiones de la topografía del fondo submarino de ambas islas. La plataforma insular de Darwin es mucho mayor y con pendientes más suaves que la de Wolf, que presenta pendientes muy fuertes y menor plataforma.

INTRODUCTION

Mapping the seafloor is a key step towards understanding the bio-geological dynamics of marine environments. Horizontal circulation of water interacting with geological features often results in complex marine current interactions (including upwellings) that shape the environmental conditions and thus the biodiversity and community distribution of pelagic and benthic ecosystems (Hamner & Hauri 1981, Witman & Smith 2001, Genin 2004). Nevertheless, producing seafloor maps is not straightforward since it typically requires the use of expensive specialized equipment, including side-scan and multi-beam sonar, which often involve costly ship time, sophisticated processing equipment and skilled operators. There have been few applications of such high technology in shallow waters.

In Galapagos, seafloor mapping was initiated in the 1940s by the U.S. Navy under the command of the U.S. Defense Mapping Agency (DMA 1944–85). They carried out many expeditions and produced the first charts for Galapagos. Since then, several attempts have been made to review and update the information available (INOCAR 1985–2000, Michaud et al. 2006, <<http://www.pmel.noaa.gov/vents/staff/chadwick/galapagos.html>> consulted July 2009). Even though the spatial scale achieved is moderately good and covers most of the archipelago, many areas remain either incorrectly characterized or entirely lack soundings.

This is the case for Darwin and Wolf Islands, the most northwesterly islands in the Galapagos Marine Reserve (GMR). Their bathymetry has not previously been mapped and is inaccurately represented on many of the digital nautical charts used today (e.g. 2008 MapSource

by Garmin® and 2009 Google Maps by Google®). The most accurate maps of their coastlines were based on satellite imagery and field data (The Nature Conservancy-CLIRSEN 2006), yet some errors still exist in island shapes, caused primarily by misrepresentation of shadows as land.

GPS-Sonar log data are often used for bathymetric mapping of lagoons and rivers, and are relatively cheap to collect and analyze. There are several statistical and non-statistical methods, called spatial interpolators, developed to interpolate between point data and predict unknown values from measured ones (Issaks & Srivastava 1989, Collins 1995). Spatial interpolators differ principally in their method: each is suitable for certain types of data and will produce different levels of accuracy in different situations (Johnston 2002, Sterling 2003). The present study compares the accuracy of five common spatial interpolators in order to produce bathymetric maps of both islands. In addition, several errors found in the coastlines of both islands are corrected, and estimations on depth area are provided as tools for future sub-tidal habitat coverage analysis.

METHODS

Study site

Darwin and Wolf Islands represent the northerly limits of the Galapagos Archipelago (Fig. 1). These oceanic islands are the eroded tops of two larger, extinct volcanoes that

rose from seafloor depths of more than 2000 m (McBirney & Williams 1969). Both islands are part of the Wolf–Darwin Lineament (WDL), a two million year-old bathymetric feature that includes several seamounts north and south of both islands (Harpp & Geist 2002). The WDL may have originated from the interaction between the 91°W transform fault along the Galapagos Spreading Centre and the horizontal migration of the Galapagos mantle plume (Harpp & Geist 2002).

Darwin, the northernmost island, is a semi-rectangular flat-topped edifice rising 170 m above sea level, at 1.673°N, 91.989°W. Wolf is a boomerang shaped island 255 m high, approximately 2.5 km long and 500 m wide, at 1.383°N, 91.822°W (McBirney & Williams 1969). Darwin presents two small reefs and two islets, the most extensive being Darwin's Arch on its southeast coast. Wolf has three small islets on its south and northern sides.

Data collection

Tracks were performed around Darwin and Wolf Islands on three field expeditions in July and November 2008 and March 2009. Depth and geographic coordinates were recorded using a Lowrance GPS-Sonar (model LMS-525 c-df) set in a fibreglass vessel 8.2 m long and 2.45 m wide, powered by two Mercury 75HP outboard engines. The vessel followed tracks perpendicular and parallel to the shoreline, only changing the planned course where strong swells were present (Fig. 2). Data were collected to a depth limit of 120–130 m at an average speed of 3 m.s⁻¹ with a sampling interval of 1 record per s.

Data preparation

Sonar log and GPS data were exported using the free software Sonar Viewer® (from Lowrance Co.). The depth data were stored in feet and then transformed to meters at 3.28 ft = 1 m. Because the GPS data were recorded in Mercator projection (datum WGS 84), a conversion was performed from the Mercator WGS 84 projection to the NAD83 Geographic coordinate system using the formulae in Schaefer *et al.* (2008), as follows:

$$\text{Latitude} = \text{RadtoDeg} \cdot (2 \cdot \arctan(\exp(Y/\text{SemiMinor}))) - \pi/2$$

$$\text{Longitude} = \frac{X \cdot \text{RadtoDeg}}{\text{SemiMinor}}$$

Where: the constants $\text{RadtoDeg} = 57.2957795132$ and $\text{SemiMinor} = 6356752.3142$; X is Lowrance position X in Mercator WGS84 and Y is Lowrance position Y in Mercator WGS 84. The resulting data were imported into ArcGIS® 9.3 software to display the depth data geo-spatially and to convert them into WGS 84.

Using field observations, aerial photography, using 2009 Google Earth® satellite imagery and LANDSAT 7 images (<<http://landsat.gsfc.nasa.gov/images/find.html>> consulted December 2008) and older maps (The Nature Conservancy-CLIRSEN 2006), new maps of the

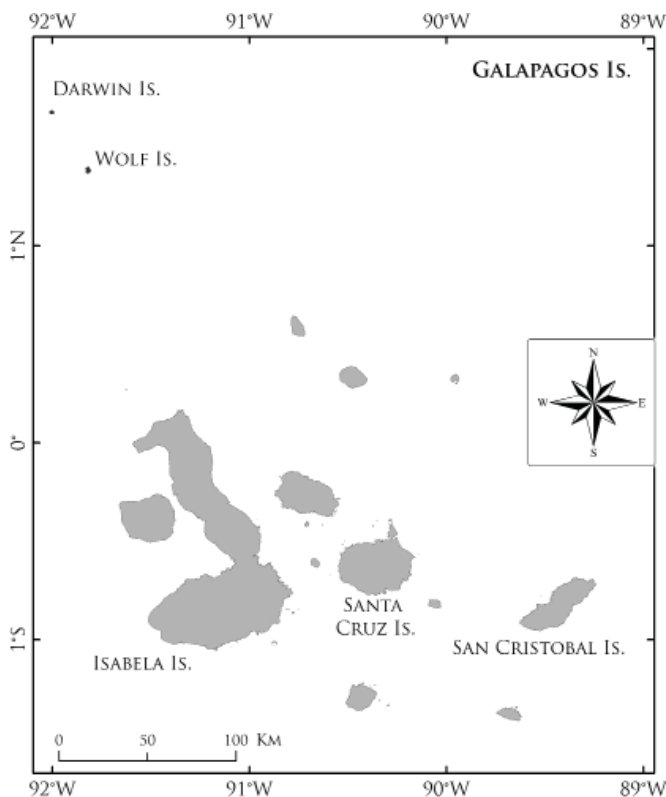


Figure 1. Location of Darwin and Wolf Islands in the Galapagos Archipelago.

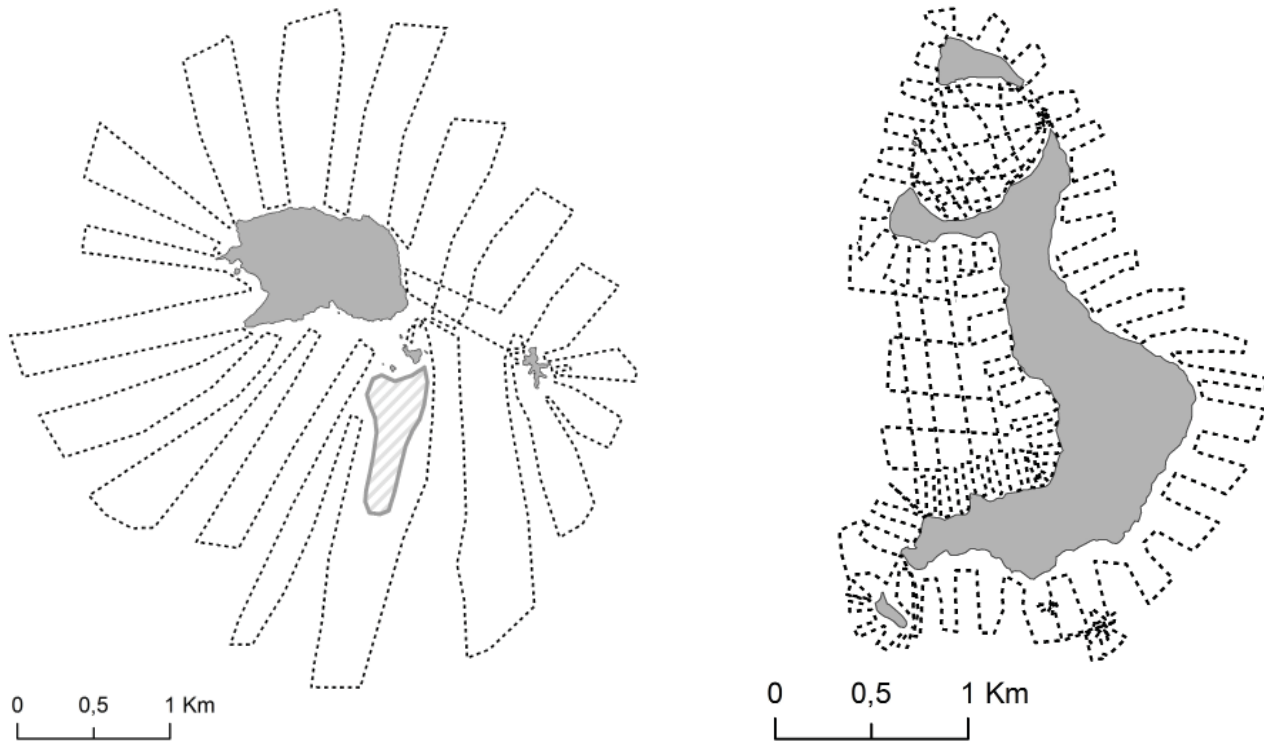


Figure 2. Data collection tracks for depth sounding around Darwin Island (left) and Wolf Island (right). Grey striped area on the map of Darwin represents the unsampled area.

Darwin and Wolf coastlines were developed in order to correct errors detected in the old maps. The new coastline developed for Darwin differs primarily in the position and size of Darwin's Arch and the south reef. Both features were considerably under-sized and slightly misplaced in earlier maps (Fig. 3). Similarly, at Wolf Island, shadow effects misrepresented some coastline features on Wolf itself and on Banana and Elephant islets (Fig. 4).

Finally, using these new coastlines, boundary files were created and merged with the depth data to prevent erroneous interpolations.

Spatial analysis

Five interpolation methods were tested to produce contour interval maps. Interpolators used were: 1) triangular



Figure 3. Comparison between the previous mapped coastline (black dashed lines: The Nature Conservancy-CLIRSEN 2006) and the revised coastline determined here (grey areas) of Darwin Island.



Figure 4. Comparison between the previous mapped coastline (black dashed lines: The Nature Conservancy-CLIRSEN 2006) and the revised coastline determined here (grey areas) of Wolf Island.

irregular network (TIN); 2) inverse distance weighting (IDW); 3) spline; 4) ordinary kriging; and 5) universal kriging.

TIN is a vector-based geometrical interpolation technique that constructs by triangulation a set of vertices (points). Each vertex is connected with a series of edges to form a network of triangles. There are different methods of interpolation to form these triangles, but the most commonly applied is the Delaunay triangulation method, which produces triangles that are as close to equilateral as possible (Issaks & Srivastava 1989).

IDW is an interpolation method in which values at unsampled areas are calculated from known points using a weight function in a search neighbourhood. Points closer to the interpolated area have more influence than points further away (Johnston 2002). IDW is one of the simpler interpolation techniques in that it does not require pre-modelling (Tomczak 1998).

The Spline method attempts to fit a surface through each observation of a dataset while also minimizing the total curvature of a surface (Davis 1986, Cressi 1993). Splines are well suited for calculating surfaces from a large set of points on gently sloping surfaces (Sterling 2003).

Kriging is a geostatistical interpolation technique which quantifies the spatial autocorrelation among measured points to generate surfaces that incorporate the statistical properties of the measured data and that include the error or uncertainty, as an indicator of how good the final predictions are (Issaks & Srivastava, 1989). Kriging builds these estimates using a semivariogram, which measures the spatial correlation between two points (Lam 1983). Weights are then given to points that have similar directional influence and distance. Kriging is typically applied when dependence between sample values decreases as the distance between observations increases. This is called ordinary kriging. However, if there is a general trend in data values, kriging can be adapted to accommodate such a trend. This routine is called universal kriging (Issaks & Srivastava 1989).

Performance of these spatial interpolators was tested using the Root Mean Square Error (RMSE) and Median Absolute Deviation (MAD) analysis. According to the Federal Geographic Data Committee (<www.fgdc.gov/standards/projects/FGDC-standardsprojects/accuracy/part3/chapter3> consulted 5 July 2008) the RMSE is the most accepted test for quantifying interpolation accuracy. It quantifies the validity of a predictive model by calculating the differences between observed and estimated data from the contour plot as follows:

$$\text{RMSE} = \sqrt{\sum \frac{(Z_i - Z_t)^2}{n}}$$

where Z_i is the interpolated depth of a test point, Z_t is its true depth and n is the number of test points (<<http://erg.usgs.gov/isb/pubs/factsheets/fs04000.html>> consulted 22 May 2007).

MAD is a robust statistical parameter used to cross-validate the performance of an interpolation method by assessing the absolute variance of the interpolated surface (Golden Software 2009). It is calculated by computing the data's median value, subtracting the median value from each point value, taking the absolute value of the difference and calculating their median. RMSE and MAD calculations were made using Surfer 9® (Demo Version) software.

Contours, area and volume

Contour maps were created based on the best interpolator method. In addition, digital elevation models (DEM) were generated for calculating the insular platform volume for Darwin and Wolf. Insular platform is defined as the sampled area between 0 and 100 m depth around each island. Area estimations were also calculated for the total and for the planar depth interval planar area (every 10 m). Planar area is defined as the area of a three-dimensional feature projected in a two-dimensional plane). These two estimations were then used for estimating an approximated volume of the water mass over the insular platform of both islands. Area and volume calculations were done using ArcGIS 9.3® software and cross-validated with an additional routine available in Surfer 9® (Demo Version) software.

RESULTS

Spatial analysis

Calculations of the RMSE showed TIN, IDW and Spline interpolations to perform better than kriging, contrary to our expectation (Table 1). TIN was most consistent in its accuracy for both islands, showing lower RMSE (1.86 m for Darwin; 0.9 m for Wolf) and the lowest MAD values (0.09 for Darwin; 0.14 Wolf). IDW error value was the lowest for the Darwin dataset (RMSE = 1.64) but its variance was higher in comparison to TIN (0.16). Spline had equal lowest RMSE values for one dataset (Wolf), but not lower than TIN.

Bathymetric models

The resulting bathymetric maps for both islands reveal different seafloor shapes at 100 m (Fig. 5). Darwin's platform reveals a large shield volcano underlying the island and surrounding reefs, extending over 1 km from

Table 1. RMSE and MAD calculations for five interpolation methods. All values are in meters.

Method	Darwin		Wolf	
	RMSE	MAD	RMSE	MAD
IDW	1.65	0.16	3.15	0.32
TIN	1.86	0.09	0.92	0.14
Spline	3.66	0.12	1.38	0.26
Ordinary Kriging	3.17	0.33	5.55	0.35
Universal Kriging	3.05	0.28	3.10	0.33

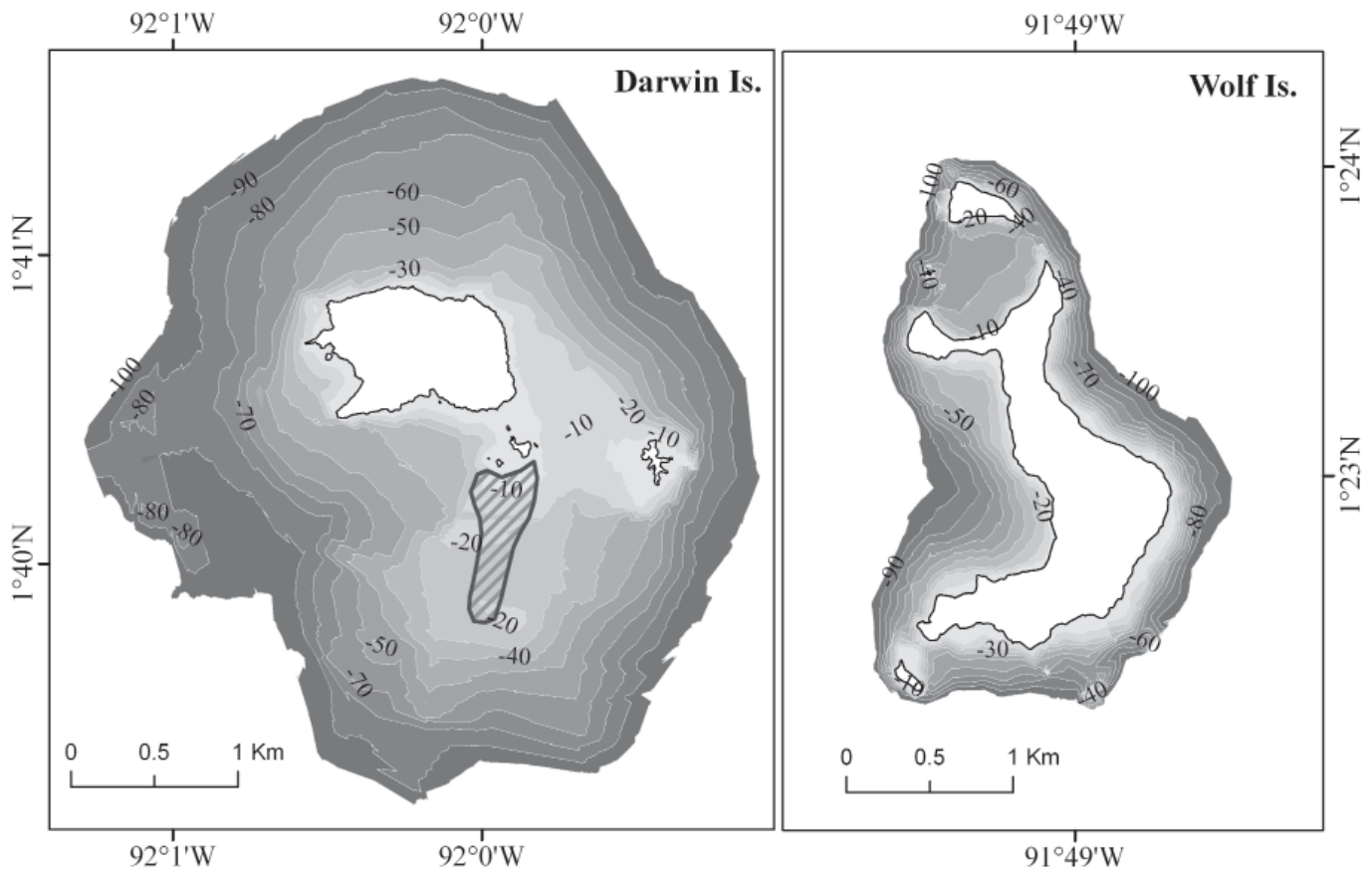


Figure 5. Contour maps of insular platform shield of Darwin and Wolf from 0 to 100 m depth. Dashed area on Darwin represents the unsampled area.

the coast all round. The rapid increase in depth off the eastern face of Darwin's Arch is quite different from the more gradual slope off the rest of the island (Fig. 6). Darwin's insular platform has an estimated volume of nearly 500 Mm³, with a planar area covering around 11.7 Mm² (Table 2). We estimate the amount of water covering the platform to be nearly 665 Mm³.

Wolf's insular shield was observed to be narrower and smaller than Darwin's, extending < 1 km away from land in all directions. The slope of its seafloor is more abrupt, with depths rapidly increasing away from land, apparently following the shapes of the island's sub-aerial cliffs. Soundings also captured two reefs south of the main island, the first called "La Draga" and the second as yet unnamed (Fig. 7). The estimated volume for Wolf's insular platform is approximately 280 Mm³ and its planar surface area around 4.1 Mm² (Table 3).

DISCUSSION

Coastline corrections

The new coastlines developed through this assessment differ considerably from maps of Darwin and Wolf produced by The Nature Conservancy-CLIRSEN (2006). Those previous versions were produced using aerial photography with limited ground-truthing. Most errors

found were shadows areas over the sea that were mistakenly considered to be part of the land mass. Our new maps represent the integration of aerial photography,

Table 2. Area and volume estimations for Darwin's insular platform (0–100 m depth) based on the TIN interpolation method.

Site	Depth interval	Area (m ²)
Arch	exposed land	15,210
	0 to -10	107,904
Darwin	exposed land	661,051
	0 to -10	335,037
Darwin exposed rock	exposed land	69
Southern reef	exposed land	8,063
Stack	exposed land	1,087
Entire platform	-10 to -20	825,755
	-20 to -30	786,297
	-30 to -40	756,944
	-40 to -50	1,003,598
	-50 to -60	1,077,676
	-60 to -70	1,240,455
	-70 to -80	1,156,711
	-80 to -90	1,910,900
	-90 to -100	1,832,088
Darwin platform total area		11,718,843
Darwin platform total volume (m ³)		505,946,204
Water mass volume (m ³)		665,938,119

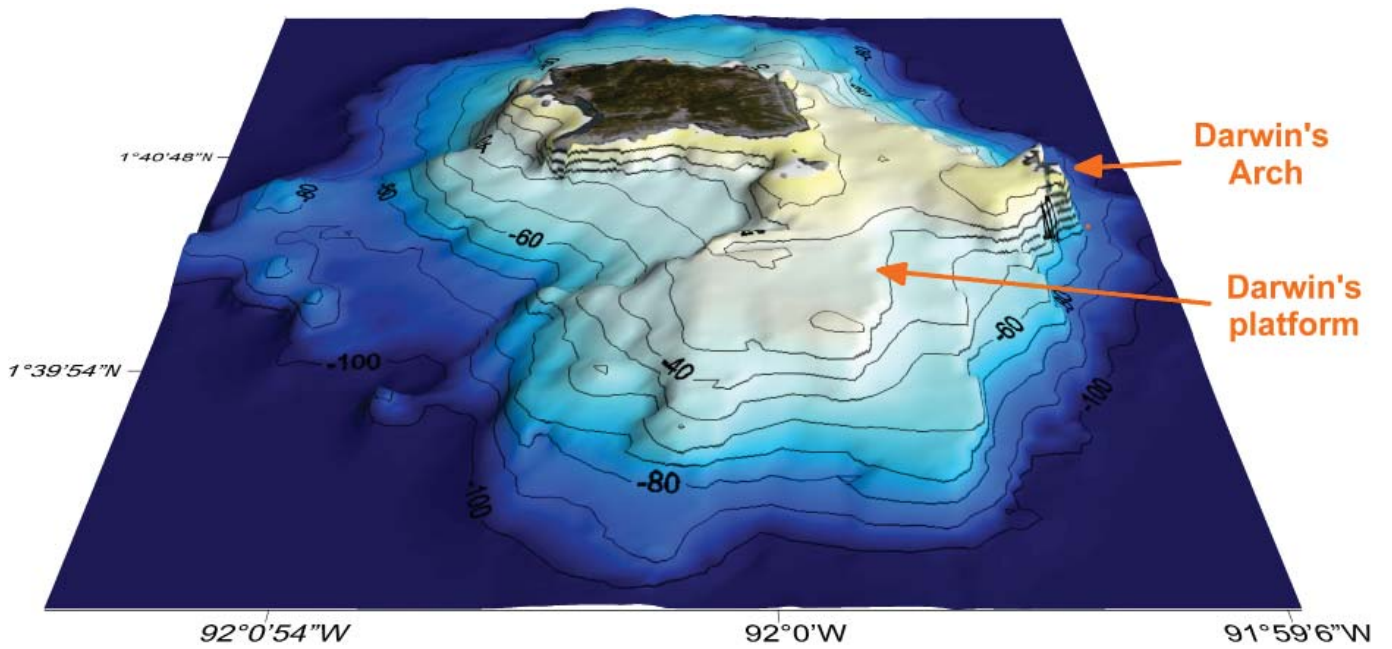


Figure 6. Three-dimensional view of Darwin and its platform from a smoothed TIN interpolation. Depth is exaggerated 3.8 times for illustrative purposes.

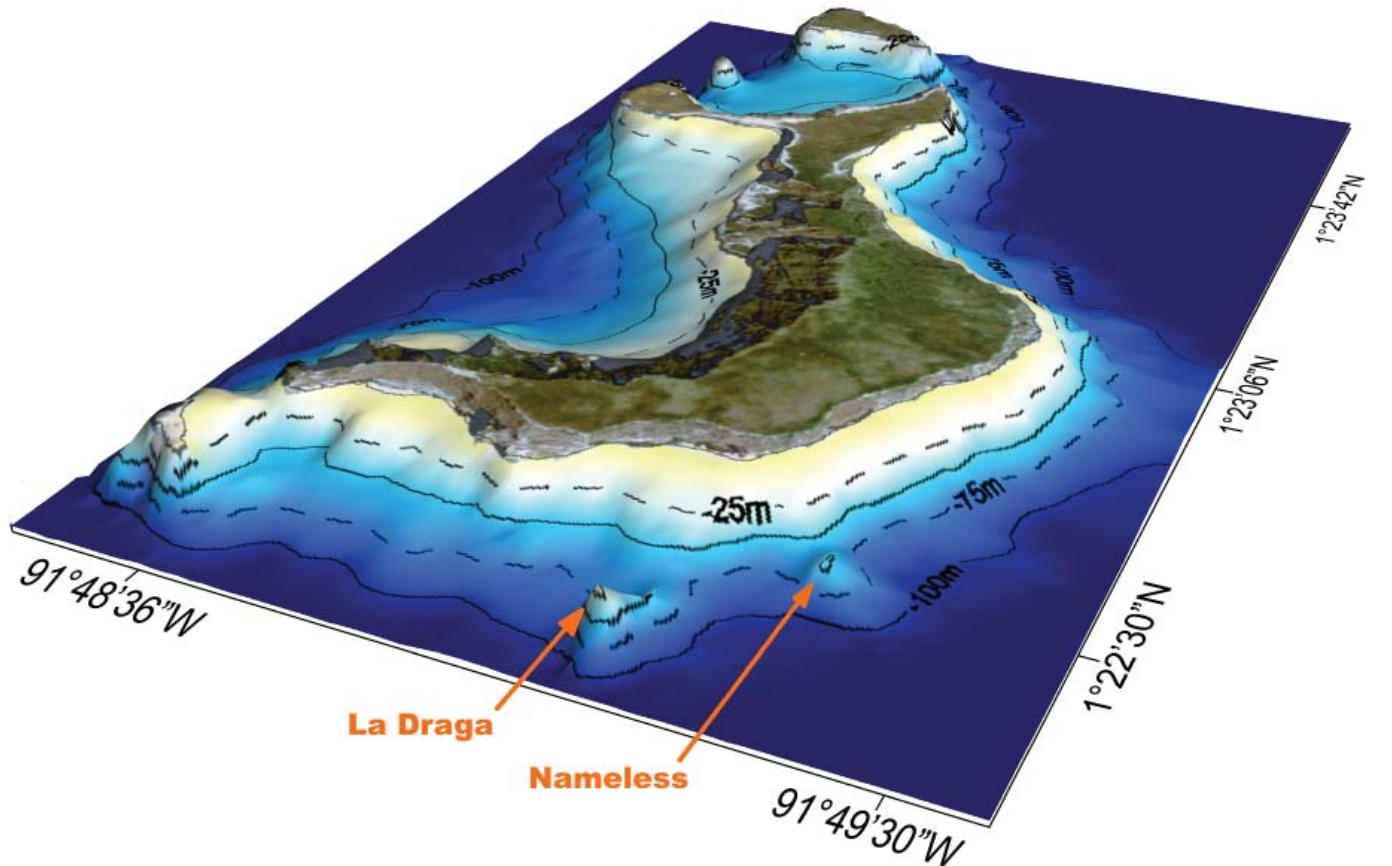


Figure 7. Three-dimensional view of Wolf, showing La Draga and Nameless reefs, from a smoothed TIN interpolation. Depth is exaggerated 3.8 times for illustrative purposes.

Table 3. Area and volume estimations for Wolf's insular platform (0 to 100 m depth) based on the TIN interpolation method.

Site	Depth interval	Area (m ²)
Banana	exposed land	62,100
	0 to -10	9,040
	-10 to -20	8,830
	-20 to -30	9,330
	-30 to -40	11,100
La Draga reef	-40 to -50	34,600
	-10 to -20	1,460
	-20 to -30	763
	-30 to -40	1,172
	-40 to -50	1,809
Elephant	-50 to -60	4,940
	exposed land	11,000
	0 to -10	18,700
Exposed pinnacle	-10 to -20	9,960
	exposed land	346
	0 to -10	1,390
	-10 to -20	763
	-20 to -30	825
Nameless reef	-30 to -40	969
	-40 to -50	4,430
	-40 to -50	520
Wolf	-50 to -60	2,870
	exposed land	1,230,000
	0 to -10	271,000
Wolf-Elephant	-10 to -20	209,000
	-20 to -30	197,000
	-30 to -40	250,000
Wolf-Elephant-Banana-Exposed pinnacle	-40 to -50	337,000
	-50 to -60	410,000
Entire platform	-60 to -70	327,000
Entire platform	-70 to -80	333,000
Entire platform	-80 to -90	382,000
Wolf platform total planar area		4,142,917
Wolf platform total volume (m ³)		279,182,502
Water mass volume (m ³)		135,109,160

satellite imagery and field observations. Although a differential GPS could be used in the future to achieve a more accurate coastline, the many inaccessible cliffs around the islands may continue to cause problems. Shorelines of both islands are mainly cliffs that reach more than 100 m above sea level in some places.

Spatial analysis

Kriging interpolation methods are usually considered to be the best, as they use quantifiable error and uncertainty to estimate un-sampled areas (Issaks & Srivastava 1989). Nevertheless, both kriging methods produced higher RMSE and MAD values in comparison to IDW, Spline and TIN. This situation might be produced by the particularities of the sampling tracks. IDW is an exact interpolator when no smoothing factor is used, but has a tendency to create "bull's-eye" contour maps around outlier sample points, with extreme values surrounded by

several concentric circles (Sterling 2003). Abrupt changes between data points are thus easily misrepresented by this interpolator, as was observed in test contour maps of Darwin, for which reason IDW was not assessed further. In the case of Spline, its error and variance values were good, but not lower than those of TIN. Indeed, RMSE and MAD values calculated for Wolf with TIN were very low (< 1 m of error and 0.14 of variance). TIN interpolations performed better than any other method for both data sets. It produced the smallest error and absolute variance, which means that it generated the least uncertainty in predicting the values in the un-sampled areas. As a result, contour maps and area calculations were produced using TIN.

Bathymetric models

The present bathymetric maps provide a good start for Darwin and Wolf islands, although some areas could be improved by additional soundings. In the south part of Darwin, a large, shallow platform extension was mapped less accurately than other areas. The rough swell usually present over this area hampered navigation, yet results from the few tracks available provide a good general perspective. On Wolf, small pinnacles along the east border of the crater are not visible due to the inaccuracy of the interpolation method and equipment limitations. Smoothing methods were used over TIN interpolations for both islands in order to diminish the noise produced by the rugged rocky bottom, but this also precluded the possibility of producing a detailed view of some small but potentially important features. Present output cannot therefore be used for navigation purposes, as more soundings are needed to represent all near-surface features properly. Nevertheless, the use of these sampling and interpolation techniques presents several advantages over some others, including: the ability to produce a rapid image of the seafloor without the use of specialized software (sampling took *c.* 5 h per island); a cheap technique compared to other methods; mapping of shallow areas where bigger vessels cannot navigate and thus acquisition of bathymetric data very close to shoreline areas of biological importance.

The present results have greatly improved the resolution of the topography of both islands, changing even the perception of their relative size. Darwin was thought to be the smaller, but its insular platform is actually about twice that of Wolf. Darwin therefore has a wider seafloor area exposed to currents and light, which could produce a greater biomass of benthic and reef species. Area and volume estimations provide a first insight on the island mass and the water mass covering both platforms, which could help in marine life density estimations. Depth should be taken as an approximation of the actual profile, as tidal variation and sampling method could affect estimates. No data were collected on tidal height variation, so the results are not corrected for this.

The next task will be to link this bathymetric information to other oceanographic variables in order to

understand biodiversity patterns on and around the islands. Concentrations of zooplankton and fish around seamounts are often driven principally by the interactions of seafloor topography with ocean currents (Genin 2004). Darwin and Wolf host the largest coral reefs in the GMR (Vera & Banks 2009) and harbour fish and apex predator aggregations associated with strong currents on their southeast faces (Hearn *et al.* 2010). We anticipate that the new bathymetric data will help to understand these biological phenomena better.

The new data provide a significant improvement in resolution of seafloor bathymetry. Nevertheless, the mapping needs to be extended to deeper areas. The new data will complement further side-scan sonar surveys in order to achieve a greater resolution for benthic habitat maps and subsequent use in ecological, biological, and geological studies. Final bathymetric contour maps will be available at <www.migramar.org> and <www.darwinfoundation.org>.

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STATUS OF TWO SPECIES OF TILEFISH, *CAULOLATILUS PRINCEPS* (JENYNS) AND *C. HUBBSI* DOOLEY, ORIGINALLY DESCRIBED FROM THE GALAPAGOS ISLANDS

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SUMMARY

We re-examine the characters and character states used to differentiate *Caulolatilus hubbsi* from *C. princeps* and find that they are continuously variable, subjective, arbitrary and non-informative. We conclude that *C. hubbsi* is a junior synonym of *C. princeps*.

RESUMEN

Estado de dos especies de blanquillo, *Caulolatilus princeps* (Jenyns) y *C. hubbsi* Dooley, descritas originalmente de las Islas Galápagos. Re-examinamos los caracteres y sus estados usados para diferenciar *Caulolatilus hubbsi* de *C. princeps* y encontramos que son continuamente variables, subjetivos, arbitrarios y no-informativos. Concluimos que *C. hubbsi* es un sinónimo posterior de *C. princeps*.

INTRODUCTION

Three species of tilefishes (family Malacanthidae) are reported to occur at the Galapagos Archipelago: Pacific Golden-eyed Tilefish *Caulolatilus affinis* Gill, 1865; Enigmatic Tilefish *C. hubbsi* Dooley, 1978 and Ocean Whitefish *C. princeps* (Jenyns, 1840; as *Latilus princeps*). Two of these species have their type locality at these islands. *C. princeps* was collected during the voyage of HMS Beagle at Chatham Island (= San Cristóbal) (Fig. 1). *C. hubbsi* has

a type locality of Charles Island (= Floreana). We review here the validity of *C. hubbsi*.

Caulolatilus hubbsi has had an unsettled history. Described in 1978 (Fig. 2), its geographic range was given as "... from California and the Gulf of California southward to the Galapagos Islands and Callao, Peru." The species was not included by Robins *et al.* (1980), except as an appendix note stating "the recently described *C. hubbsi* ... is considered a synonym of *C. princeps*." However, Marino & Dooley (1982) responded that "*C. hubbsi* should

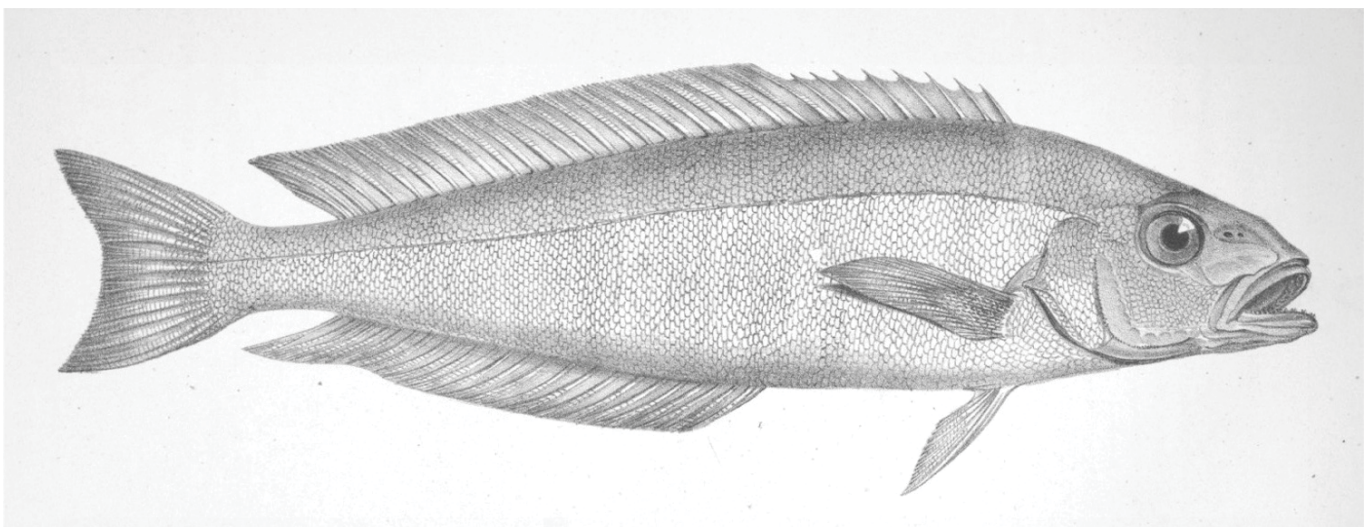


Figure 1. Holotype of *Caulolatilus princeps* from Chatham Island. From Jenyns (1840), drawing by W. Hawkins, reproduced with permission from J. van Wyhe (ed.) *The Complete Work of Charles Darwin Online* (<http://darwin-online.org.uk/>).

be considered valid for the reasons stated in the original description (Dooley, 1978) and the myological differences cited here, or until objective reasons to the contrary are presented." In response to this, the American Fisheries Society-American Society of Ichthyologists and Herpetologists Committee on Names of Fishes corresponded with a number of California ichthyologists maintaining faunal lists for the state as well as the Eastern Pacific, including L.J. Dempster, W.I. Follett, C.L. Hubbs, R.J. Lavenberg, R.N. Lea and others. These researchers, for the most part, concluded that recognition of the species was problematic. Grove & Lavenberg (1997) treated *C. hubbsi* as a synonym of *C. princeps* "Because of the overlap in number of pored lateral-line scales (100–110 in *C. hubbsi*; 99–115 in *C. princeps*) and other similarities in morphometrics". Nelson *et al.* (2004) treated *C. hubbsi* as valid although controversial.

Dooley (1978) used three main characters to diagnose *C. hubbsi*, distinguishing it from *C. princeps*: mouth large with thick fleshy lips, jaws extending back to under the middle of the pupil, as opposed to the small gape and jaws extending only to under the anterior orbital rim in *C. princeps*, and nearly truncate tail, versus emarginate tail in *C. princeps*. He also suggested that *C. hubbsi* had a more rounded profile and slightly deeper body. However, when he presented meristic values for dorsal fin elements, anal fin elements, first arch gill rakers and pored lateral line scales, for all nine species of *Caulolatilus* included in his revision, in all cases but one, the values for *C. hubbsi* fell within the range of *C. princeps*. In the case of dorsal soft rays *C. hubbsi* had a count of one less than the lower limit for *C. princeps* (23–27 for *C. hubbsi* and 24–27 for *C. princeps*). In three of the above character sets modal values were the same for both species.



Figure 2. Head of holotype of *Caulolatilus hubbsi* (USNM 41421). Note position of end of maxilla relative to vertical through anterior edge of pupil. Photograph by Sandra Raredon, Smithsonian Institution, Division of Fishes.

Only one larval type has been identified for *Caulolatilus* from the eastern Pacific to date (W. Watson, pers. comm.), and Moser (1996) gave a description of the larva of only *C. princeps*. There is no information on larval types of *C. affinis* or *C. hubbsi*.

In the comparative myological study by Marino & Dooley (1982), *C. princeps* and *C. hubbsi* are defined within the same subdivision (A3â) of the adductor mandibulae complex and the difference between them is one unit on a scale of 1–6 (*C. hubbsi* 5; *C. princeps* 6), based on examination of only seven specimens of *C. hubbsi* and one specimen of *C. princeps*. This character state is founded on the relative degree of muscle complexity and is inherently subjective. It is our contention that this difference is too fine to support species distinction given that minor variation within a species is to be expected.

METHODS

We examined specimens, photographs and illustrations of all of the type material of both species and a majority of other specimens listed by Dooley (1978), as well as other specimens of *C. princeps*, including specimens from the following institutions: Natural History Museum of Los Angeles County (LACM); Museum of Comparative Zoology, Harvard University (MCZ); United States National Museum, Smithsonian Institution (USNM).

We analyzed each of the three main characters or character states identified above. Lips were ranked into three categories: slightly fleshy, moderately fleshy and thickly fleshy. The shape of the caudal fin was examined to determine general profile. The position of the maxilla in relation to the orbit was measured with a vertical line from the posterior edge of the maxilla and expressed as a percentage of orbital diameter. If the vertical overlapped the orbit it had a positive value and when the vertical was anterior to the orbit it took a negative value.

RESULTS AND DISCUSSION

Fleshy lips

Of the eight paratypes of *C. hubbsi* (all catalogued at LACM under number 8836-3) only two specimens qualified as *hubbsi* type (thick fleshy lips). Four additional specimens from the same collection (all numbered LACM 8836-14) but apparently not examined by Dooley, included two specimens with moderately fleshy lips and two with lips slightly fleshy. LACM 3644 in Dooley (1978), comprises two specimens listed as non-type material, now re-catalogued as LACM 33721-1; these have moderately fleshy lips. LACM 3207 of Dooley (1978) (1 non-type; now re-catalogued as LACM 33720-1) had lips slightly fleshy. MCZ 25725 and MCZ 26798 were considered slightly fleshy and thickly fleshy, respectively. It is our conclusion in evaluating this character state for *C. hubbsi* and *C. princeps* that fleshiness of lips is highly variable, subjective, and not informative.

Shape of caudal fin

We found that all specimens examined, of both *C. hubbsi* and *C. princeps*, had concave (= emarginate) caudal fins which varied from slightly concave to obviously concave and the degree of concavity was not notably different between the two nominal taxa. No specimens with truly truncate caudal fins were encountered. We conclude that degree of concavity of the caudal fin is a variable and non-informative character for these taxa.

Relationship of position of maxilla to orbit

Regarding this character, in the diagnosis for *C. hubbsi* Dooley (1978) specified "jaws extending posteriorly to under middle of pupil (gape small and jaws extending only to under anterior orbital rim in *princeps*)". We did not find any individual of *C. hubbsi* whose jaws extend posteriorly to under the middle of the pupil. The maxilla of the holotype (USNM 41421, Fig. 2) reaches a vertical under the forward part of the pupil (0.24 orbit diameter, where 0.50 orbit diameter would signify that the end of the maxilla reached a vertical through the middle of the pupil). Based on this character, five of the eight *C. hubbsi* paratypes at LACM would qualify as *C. princeps* (0.00 to 0.20) and the remaining three as intermediate (0.21 to 0.26). The other paratypes of *C. hubbsi* (USNM 50091 and 53476) had scores of 0.24 and 0.26, respectively, and additional specimens examined (LACM 3207 in Dooley 1978, now re-catalogued as 33720-1; LACM 3644, now 33721-1; MCZ 25752; MCZ 26798; USNM 77616) have a range of -0.16 to 0.24. Thus, of all the *C. hubbsi* material that we examined, the range of scores for maxilla position to orbit was -0.16 to 0.26. We conclude that position of the end of the maxilla relative to the orbit varies intra-specifically and does not serve as a differentiating character.

CONCLUSION

The characters proposed to distinguish *Caulolatilus hubbsi* as a species are for the most part subjective and highly variable or can be attributed to variation within a single species. *Caulolatilus hubbsi* Dooley is therefore a junior synonym of *Caulolatilus princeps* (Jenyns).

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We thank Richard H. Rosenblatt (Scripps Institution of Oceanography), John E. McCosker (California Academy of Sciences), and Christine Thacker and Jeffrey A. Seigel (LACM) for their valuable comments on various stages of this paper. Jeff Williams and Sandra Raredon provided digital images and information on type material of *C. hubbsi* at USNM. Karsten Hartel and Andrew Williston provided digital images and information on *Caulolatilus* housed at MCZ.

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THE SPIDER *THERIDION MELANOSTICTUM* (ARANEAE, THERIDIIDAE), A RECENT INTRODUCTION TO GALAPAGOS?

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SUMMARY

The theridiid spider *Theridion melanostictum* O. Pickard-Cambridge 1876 is reported as a possible recent introduction to Galapagos, having been found only in samples from Santa Cruz island collected from 2010 onwards.

RESUMEN

La araña *Theridion melanostictum* (Araneae, Theridiidae), ¿una reciente introducción en Galápagos? La araña *Theridion melanostictum* O. Pickard-Cambridge 1876 es reportada como una posible reciente introducción en Galápagos, ya que ha sido encontrada solo en muestras de la isla Santa Cruz colectadas desde 2010 en adelante.

INTRODUCTION

The spider fauna of the Galapagos archipelago has been well studied. A first synthesis of all collections between Darwin's visit in 1835 and N. and J. Leleup's in 1964–5 was given by Roth & Craig (1970). The islands were later sampled between 1968 and 1980 by S. Riechert and W.G. Reader, whose material was only recently studied (2010–11) by one of us (LB), who also sampled all major islands with his Belgian team from 1982 to 2010. Other important sampling was done in the same period (1985–96) by the Canadian team of S. Peck, and in the urban and agricultural zones of the inhabited islands between 2003 and 2006 by the Charles Darwin Research Station. An analysis of all these data was given by Baert (2013). In total, 700 localities scattered over the whole archipelago and from the coast up to the highest summits have been sampled, including the remote islands of Wolf and Darwin. The most intensively sampled island by far is Santa Cruz, with its large urban and agricultural zones.

We report here an additional species which probably represents a new introduction to Galapagos.

METHODS

On analyzing spider samples collected by NW by means of beating vegetation in the Santa Cruz agricultural zone above El Chato and at the Caseta Occidente in 2011 and 2012, a number of small theridiid spiders were found which appeared to represent a species not before found on Santa Cruz. Two males were collected in a field with many Avocado *Persea americana* trees

(probably an old plantation: 0°38'S, 90°25'W) near the El Chato ranch, along the road running south from Santa Rosa towards the El Chato reserve area at c. 370 m altitude, on 4 Apr 2011. Twelve males, ten females and one subadult male were collected in a young coffee plantation (0°42'S, 90°21'W; plants up to 2.5 m tall) along the west side of the road to Caseta Occidente at 156 m alt., on 13 Apr 2012.

Theridion males are quite easy to identify but females are not. We therefore re-examined two theridiid females collected by F. Hendrickx in a mangrove stand in front of the cemetery of Puerto Ayora (0°44'33"S, 90°18'35"W) on 31 Jan 2010, which could not be identified at that time.

Specimens were examined and measured with a Wild M5 stereomicroscope, and drawn and photographed using a Wild M10 stereomicroscope. The female genitalia were cleared in a methylsalicylate solution.

RESULTS

All the specimens were identified by JVK as belonging to the cosmopolitan species *Theridion melanostictum* O. Pickard-Cambridge 1876. The following description is based on the Galapagos specimens. Total length: males 2.2–2.6 mm, females 2.4–2.8 mm. Cephalothorax creamy coloured with blackish borders and median longitudinal black stripe; sternum creamy, variably suffused with black; abdomen creamy, the dorsum with broad median white leaf-shaped pattern, sides with white and greyish dots and venter with median black dot; legs creamy, articulations variably suffused with black. The left male palp and the female epigyne are depicted in Figs 1 and 2.

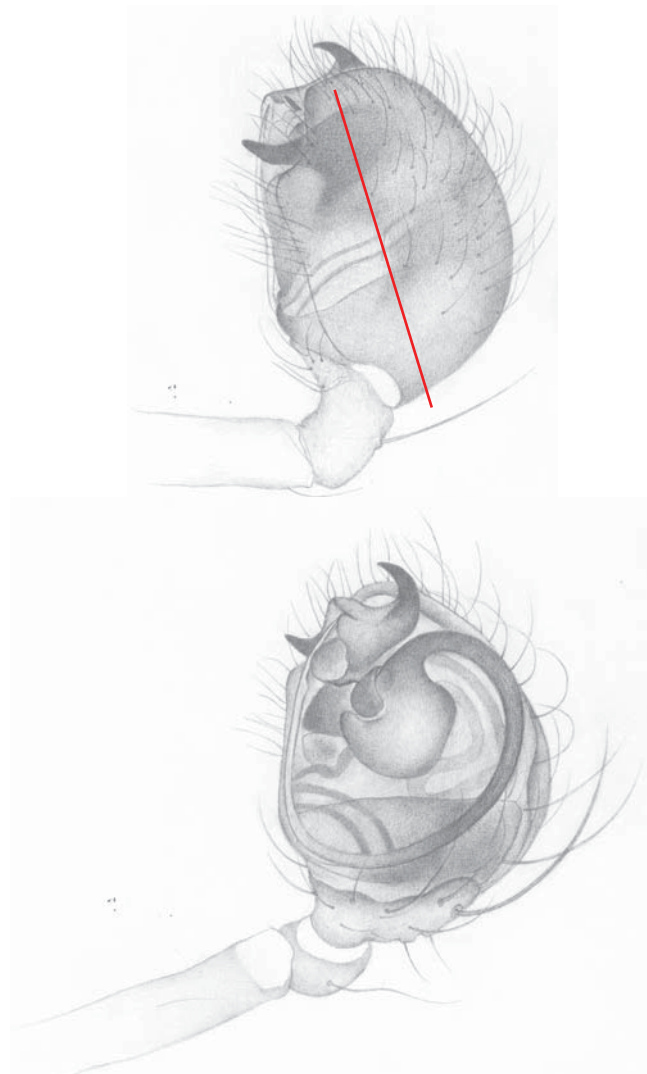


Figure 1. Male left palp: above, lateral view; below, ventral view. Length of cymbium (red line) 0.52 mm.

DISCUSSION

Given that *T. melanostictum* was not caught during the numerous intensive collections done before 2010 in the same vegetation zones and that the spider fauna of Santa Cruz is one of the best inventoried of the archipelago, the fact that this cosmopolitan species (Canary Islands, Mediterranean, Aldabra, Seychelles, China, Japan, Polynesia, North America, Hispaniola: Le Peru 2011, <<http://research.amnh.org/entomology/spiders/catalog>> consulted 9 Dec 2013) was found for the first time in the urban zone near the port of Puerto Ayora and later on in large numbers of both sexes in the agricultural zone of the island, strongly suggests that it was brought recently to the islands by man and that it quickly spread to the higher agricultural zone.

Theridiid spiders construct irregular space-webs known as cobwebs or gumfoot webs, with threads radiating in different directions. Prey, often ants, is overpowered in a wrap-bite attack involving sticky silk. Nothing is

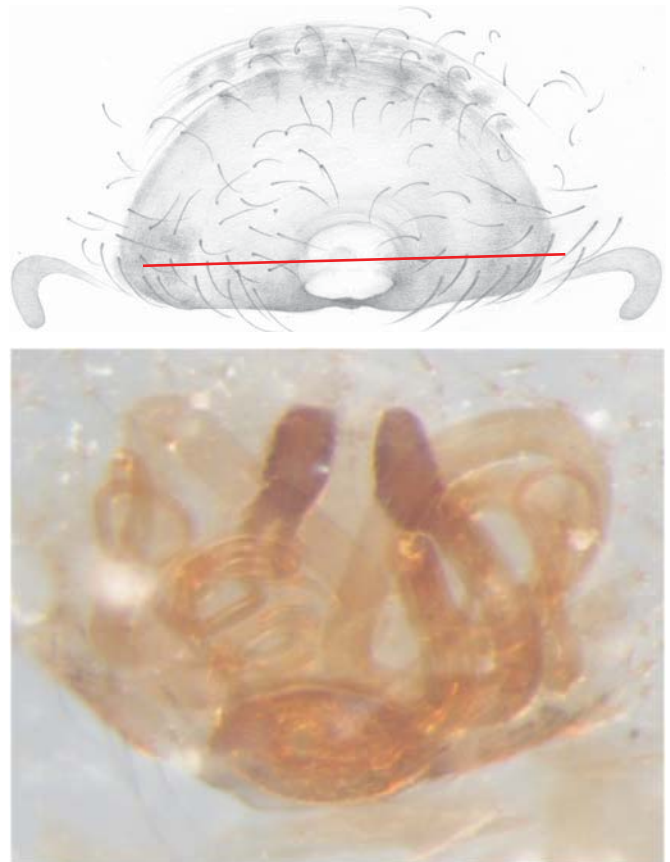


Figure 2. Epigynum: above, ventral view; below, vulva, ventral view. Width of epigastral fold (red line) 0.87 mm.

known of the likely impact of this species on the native invertebrate fauna.

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THE BIOLOGY OF AN ISOLATED POPULATION OF THE AMERICAN FLAMINGO *PHOENICOPTERUS RUBER* IN THE GALAPAGOS ISLANDS

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SUMMARY

A genetically and morphologically divergent population of *c.* 500 American Flamingos, isolated from the parental Caribbean stock of *Phoenicopterus ruber*, occurs in the Galapagos archipelago. Based primarily on data from a 3-year study, we provide the first description of the feeding and breeding biology of this population. Galapagos provides a suitable habitat comprising lagoons on a number of islands, among which the flamingos travel in response to food and nest site availability. We identify putative food items. The occurrence and quantity of some food species was associated with the chlorosity of lagoon water, as was the distribution of flamingos. The flamingos bred opportunistically at five lagoons on four islands, sometimes simultaneously on more than one island. Group display usually involved ≤ 20 birds, and colonies contained as few as three nests. Laying occurred during nine months of the year, mainly August–January, coinciding with the coastal drier season and low lagoon water levels. On average *c.* 30 % of all adults incubated clutches each year, producing 0.37 fledglings per clutch. Recruitment is probably sufficient to sustain the population, which has been stable over at least *c.* 45 years, and is probably limited by suitable habitat. Moulting to flightlessness was recorded among adults. We review potential dangers to this unique population and suggest conservation measures.

RESUMEN

Biología de una población aislada del Flamingo americano *Phoenicopterus ruber* en las Islas Galápagos. Una población morfológica y genéticamente divergente de *c.* 500 Flamingos americanos, aislada de la población originaria de *Phoenicopterus ruber* del Caribe, se encuentra en el archipiélago de Galápagos. Basándonos sobre todo en los datos provenientes de un estudio de tres años, presentamos la primera descripción de la biología de la alimentación y reproducción de esta población. Galápagos provee un hábitat apropiado que consiste de lagunas en varias islas, entre las cuales los flamingos viajan según la disponibilidad de alimento y sitios de anidación. Identificamos supuestos elementos alimenticios. La presencia y cantidad de algunas especies de alimento fueron relacionadas con la clorosidad del agua de las lagunas y con la distribución de los flamingos. Mediando las condiciones, los flamingos anidaron en cinco lagunas de cuatro islas, a veces simultáneamente en más de una isla. El despliegue en grupo a menudo involucró ≤ 20 aves, y las colonias podían ser de solamente tres nidos. Hubo puesta de huevos durante nueve meses del año, sobre todo de agosto a enero, coincidiendo con la estación costera más seca y con bajos niveles de agua en las lagunas. En promedio *c.* 30 % de los adultos incubaron nidadas cada año, produciendo 0.37 volantones por nidada. El reclutamiento probablemente es suficiente para sostener la población, la cual se ha mantenido estable por al menos *c.* 45 años, y probablemente es limitada por la disponibilidad de hábitat adecuado. Se observó en adultos la muda que imposibilita el vuelo. Analizamos amenazas potenciales a esta población única y sugerimos medidas para su conservación.

INTRODUCTION

The Galapagos archipelago (0°N, 90°W) supports a small population of the American Flamingo *Phoenicopterus ruber*, some 1500 km from its parental stock which is currently found in the Caribbean, Mexico, Colombia and Venezuela (Espinoza *et al.* 2000, Baldassarre & Arengo 2000, <<http://www.flamingoresources.org/fsg.htm>> consulted 27 Dec 2013). Microsatellite and mitochondrial DNA sequence data, and skeletal and egg measurements, showed that

the Galapagos population differs genetically and morphologically from that in the Caribbean (Frias-Soler *et al.* 2014), consistent with its reproductive isolation.

The age of the Galapagos population is unknown, though a genetic distance estimate suggests that the archipelago was colonized about 70,000 to 350,000 years ago by flamingos from the Caribbean (Frias-Soler *et al.* 2014). Flamingos were recorded in one of the earliest accounts of Galapagos, in the log of Captain Cowley's 1684 voyage (Salvin 1876), and they have been consistently

reported since. They are recorded over a c. 20,000 km² area that includes at least 37 beach, inland or volcanic crater lagoons, all within c. 2 km of the coast, at 24 locations on six of the major islands in the archipelago (Fig. 1). All lagoons where they occur fall within a circle of radius c. 100 km, and each lagoon is within c. 50 km of its nearest neighbouring lagoon. The population is stable, ranging from 371 to 696 birds in censuses conducted from 1967 to 2010 (Gordillo 1973, Tindle & Tindle 1977, Harcourt 1982, Valle & Coulter 1987, Vargas *et al.* 2008, unpublished annual census reports of the Charles Darwin Research Station (CDRS) 1981–2009, Jiménez-Uzcátegui & Naranjo 2010), in which (usually) simultaneous counts were made at most lagoons where flamingos primarily occur. Lower counts were associated with incomplete coverage. During this period, flamingos have bred on Isabela Island (three lagoons), Santiago (three), Floreana (one), Bainbridge (one) and Rábida (one).

While *P. ruber* throughout its range is listed as Least Concern on the IUCN Red List (<<http://www.iucnredlist.org>> consulted 11 Dec 2013), the population in Galapagos was considered Endangered by Granizo (2002) and Jiménez-Uzcátegui *et al.* (2007), because of its small size.

Unlike its populations in the Caribbean region (Rooth 1965, Ottenwalder *et al.* 1990, Espinoza *et al.* 2000), little is known of the biology of the American Flamingo in Galapagos apart from census information and an association of flamingo distribution with rainfall and lagoon water level: flamingo abundance was lower at lagoons when water levels were above their seasonal means (Vargas *et al.* 2008). The objectives of the present study were to describe the feeding ecology, breeding biology and population dynamics of the Galapagos birds, particularly in regard to their isolation from the ancestral

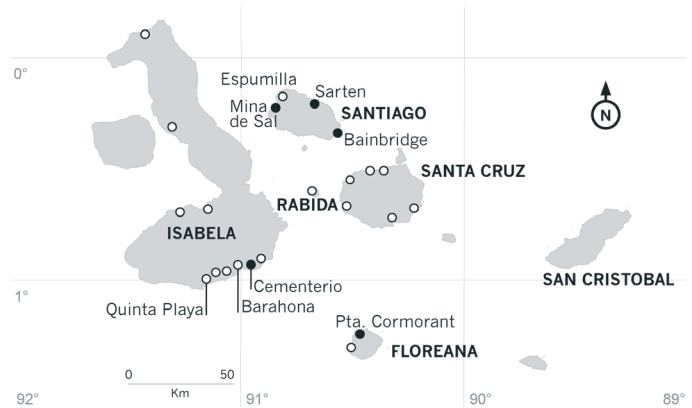


Figure 1. Occurrence of American Flamingos in Galapagos. Circles denote approximate locations of lagoons where flamingos have been regularly or occasionally seen. Solid circles denote lagoons where breeding occurred during 1970–9. Lagoons considered in the present study are named. Island names are in upper case (Bainbridge is on an islet off Santiago).

stock. The outcome is relevant to the management of this evolutionarily divergent population.

METHODS

Study Sites

The study focused on eight lagoons (Table 1, Fig. 1) which supported 70–90% of the total Galapagos flamingo population during a 37-month study period (June 1976 to June 1979). These lagoons contain all the major sites at which flamingos are known to have bred in the archipelago (Harris 1973, Jiménez-Uzcátegui & Naranjo 2010). During the study period no nests were recorded at other lagoons examined.

Table 1. Characteristics of the main study lagoons during the study period.

Island	Lagoon	Coordinates	Length x representative width (m)	Lagoon type	Features ¹	Water level fluctuation	Flamingo stock
Isabela	Cementerio	0°57'13"S, 90°59'11"W	1702 x 689	Behind beach	Occasional flooding at spring tides. Tidal seepage.	Much	Itinerant
	Quinta Playa	1°0'14"S, 91°4'53"W	1102 x 259	Behind beach	Occasional flooding at spring tides. Tidal seepage.	Little	Permanent
	Barahona	0°59'16"S, 91°02'09"W	283 x 123	Behind beach	Inward tidal overspill. Tidal seepage.	Much	Unknown
Santiago	Sartén	0°13'5"S, 90°36'48"W	520 x 147	In lava field, c. 0.5 km inland	Tidal seepage.	Little	Permanent
	Mina de Sal	0°14'27"S, 90°50'14"W	295 x 269	Crater lake, c. 1 km inland	Much evaporation. Large rain catchment. Seawater seepage. Solar lake effect.	Much	Itinerant
	Espumilla	0°12'0"S, 90°49'41"W	353 x 101	Behind beach	Tidal overspill and seepage. Large rain catchment.	Much	Itinerant
Bainbridge 3	Bainbridge	0°21'6"S, 90°33'58"W	Crater lake	Evaporation. Large rain catchment. Seawater seepage? Solar lake effect.	Much	Itinerant	
Floreana	Punta Cormorant	1°13'36"S, 90°25'38"W	519 x 272	Behind beach	Inward tidal overspill. Tidal seepage.	Little	Almost permanent

¹Solar lake effect is stratification of lagoon water according to chlorosity and temperature.

One to five visits of one day or less were made to seven of the study lagoons (not Barahona) each month over the study period; Barahona was visited monthly from Jan 1976 to Apr 1977. In addition, monthly visits were made to Cementerio lagoon over 13 years (1968–80). Less frequent visits to a further nine lagoons where flamingos have been recorded (Fig. 1) were made as transport allowed. A further ten lagoons were visited once during the study period. At each visit, the number of adult and juvenile birds was recorded and any active nests and their contents recorded. Lagoon water and mud samples were collected. The water level was measured at Cementerio lagoon during 1970–9.

Extended visits were made to five of the study lagoons during breeding (Table 2), when a team of 2–3 observers continuously monitored individual nests from vantage points within 3–20 m of the colonies, between 6h00 and 18h00 (approximately dawn to dusk) for 134 days and from 18h00 and 6h00 for 40 moonlit nights, totalling c. 14,500 nest-hours of observation. The locations of nests were mapped and data collected on nesting and parenting. The generally open aspect and small size of the lagoons allowed simultaneous observation of the activities of adult flamingos not directly engaged in nesting (the “flock”). Data from the flock were obtained on feeding behaviour, displays and copulation. A flock was defined as a group of ≥ 10 individuals within 20 m of each other.

Lagoon ecology

Water level in the lagoons was determined by a number of factors (Table 1). Water level at Cementerio lagoon was measured monthly to the nearest cm using a permanently located 0–150 cm rule. In other lagoons, water level was estimated as “high”, “medium” or “low” by the same observer (RWT) who was familiar with the lagoons.

Water samples (c. 200 ml) were collected from Quinta Playa and Espumilla lagoons monthly over 16 months during 1976–8 and from Mina de Sal, Punta Cormorant and Sartén lagoons opportunistically over 30 months during 1976–8, at 2–5 locations per lagoon. Chlorosity (g of chloride and chloride equivalents per litre) was determined by the method of Strickland & Parsons (1972), using International Association for Physical Sciences of the Ocean (IAPSO) sea water as standard (chlorosity 19.38 Cl/l). Salinity = $1.807 \times \text{chlorosity}/\text{density}$. Chlorosity is suggested as the preferred measure during mixing of fresh and salt water (Head 1985), as occurred in some lagoons.

Mud samples (c. 250 ml) were collected from beneath the lagoon water into a graduated container and strained through a 0.5 mm mesh. The retentates were dried at 60–80°C for 72 h and weighed (i). Organic matter was oxidized off by burning twice with absolute ethanol, followed by heating on a hotplate for 3 h, and the sample re-weighed (ii). Percent organic matter was determined as (ii)/(i) $\times 100$.

To determine identity and concentration of organisms in lagoon water, five sweeps of water in the lagoon were

Table 2. Extended observation periods at breeding lagoons.

Lagoon	Observation periods	Stage of breeding cycle
Cementerio	17 Oct to 18 Nov 1976	Display, eggs, chicks 1–30 days
	17–24 Dec 1976	Chicks c. 60 days
	4–16 Dec 1978	Eggs, chicks c. 5–90 days
Quinta Playa	25–28 Aug 1976	Display
	7–16 Dec 1978	Display
Sartén	27 Jan to 10 Feb 1977	Chicks c. 20–60 days
	10–20 Mar 1977	Chicks c. 75–90 days
	3–19 Dec 1977	Display, chicks c. 1–8 days
	20 Jan to 8 Feb 1978	Chicks c. 15–45 days
Mina de Sal	22 Mar to 5 Apr 1978	Chicks c. 90 days
	6–25 Jan 1977	Display, eggs, chicks c. 1–8 days
	20–22 Dec 1977	Display, eggs, chicks c. 2–12 days
Punta Cormorant	15–25 Feb 1978	Eggs, chicks c. 30 days
	13–14 May 1979	Display, eggs
Punta Cormorant	14–19 Mar 1979	Display, eggs
	28–31 Mar 1979	Eggs, chicks c. 1–10 days

made at least 5 cm above the lagoon bottom, using a plankton net of 0.1 mm mesh with a 25 cm diameter mouth (each sweep being previously calibrated to pass c. 2 l of water). Organisms were retrieved from the net and resuspended in 10 ml of 10 % formaldehyde in seawater. Mud samples were collected from 2–5 locations per lagoon by straining c. 250 ml mud taken from the top 5 cm of substratum through a 0.5 mm sieve. Eighteen 1-ml samples of strained mud from the sieve were bottled with 2 ml of 10 % formaldehyde in seawater. For identification of organisms in mud, 0.25 ml of the sample in formalin was diluted with 2 ml water.

Water, mud and aquatic organisms sampled from lagoons were returned to the laboratory within at most three days of collection for analysis of water chlorosity, identification of organisms in water and mud, and determination of mud organic content.

Organisms were identified and counted by binocular (10x objective) or monocular (10x eyepiece, 10x or 40x objective) microscopy depending on organism size. Samples were analyzed in duplicate, and mean values recorded. Some organisms were sent to the Smithsonian Institution, Washington DC (U.S.A.) for confirmation of identity. The occurrence in lagoon water of two predominant potential food items, the brine shrimp *Artemia salina* and the hemipteran *Trichocorixa reticulata* (Tindle & Tindle 1978), was used as a measure of food availability. *A. salina* is associated with a chlorosity of >30 Cl/l, while *T. reticulata* is associated with chlorosity <15 Cl/l (Davis 1966, Daintith 1996, Tripp & Collazo 2003).

Flamingo biology

Flock sizes and the numbers of adults (“grey” birds were considered sub-adult) in the flocks engaged in feeding and other behaviour (resting, preening, aggressive encounters,

alarm posture, flying, copulation, comfort movements; the birds engaged in nesting activities were excluded from this analysis) were recorded at Mina de Sal and Sartén lagoons at 20-min. intervals during the period 5h30–17h30 on 16 days at each lagoon during Jan–Feb 1977 and 1978. Food was abundant at each lagoon during these periods. Data for each hour period were recorded at least 32 times over the 16 days. In addition, data on the number of flamingos engaged in nocturnal feeding were collected over four nights (17h30–5h30) during these months at each lagoon. Data were expressed as the mean percentage of the flamingos in the flock involved in feeding and other activities during four 6-h time blocks covering the 24-h cycle (17h30–23h30, 23h30–5h30, 5h30–11h30, 11h30–17h30). The timing, location and number of birds involved in group display (Rooth 1965, Studer-Thiersch 1974, 2000, Kahl 1975) were recorded.

Inter-nest distances were measured centre-to-centre at newly vacated colonies (Sartén, $n = 42$ nests; Cementerio, $n = 48$; Mina de Sal, $n = 14$; Bainbridge, $n = 4$). Distances separating groups of nests were measured as the distance between the nearest nests per group. Data were pooled and the mean inter-nest distance was used to calculate the density of nests per m^2 . Only nest mounds used that season were recorded.

Nest contents (egg or chick) were noted. The length and greatest width of eggs which had rolled from nests or were abandoned because of colony flooding, at Cementerio, Sartén, Mina de Sal and Bainbridge lagoons, were measured using callipers. Chick age was determined from time of hatching (where known) or estimated from chick size, plumage characteristics, bill shape, and colour of leg skin (Johnson & Cézilly 2007). The small size of the colonies allowed recognition of individual parent birds by reference to nest, individual plumage colour and pattern, and bill markings. The sex of individual parents was determined by body size (males were almost invariably larger) and/or call (males had a deeper vocalization). In most cases, after leaving the nest at age 7–11 days to join the nearby crèches, individual chicks could be recognized by their body size relative to other chicks within the crèche (owing to asynchronous hatching) or by reference to their parents when being fed.

The timing of arrival and departure of parents at the nest was recorded. Where it was not possible to determine exact durations of nest site attendance (because of arrivals or departures when the colony was not being observed), minimum and maximum durations were derived by recording the sex of the parent in residence when observations resumed. The timing and duration of feeds given to the offspring (grouped as age 1–3, 4–9, 10–11, 12–30, 31–60, 61–90, 91–105 days) at the nest and in the crèche were recorded.

Synchronous moult of flight feathers was determined by the inability of flocks of flamingos to take flight and by the visible absence or partial re-growth of flight feathers of individual birds.

Twenty-two flightless adult flamingos and ten c. 2-month old chicks were banded with site-specific coloured plastic rings at Sartén and Cementerio lagoons during Jan–Mar 1978. Seventeen flightless adults were banded at Quinta Playa lagoon in Dec 1978. Banded birds were re-sighted with binoculars. Inter-lagoon and inter-island travel was demonstrated by re-sightings of banded birds, by parent birds leaving nesting lagoons to feed at lagoons elsewhere, by juvenile dispersal and by gut contents.

Statistics

Data are expressed as means \pm SD. A surrogate Poisson generalized linear model was used to compare breeding outcomes (fledglings per clutch). Because expected values were sometimes small (< 5), the analyses were verified using a Pearson's chi-square contingency table analysis with P values calculated by Monte Carlo simulation (Hope 1968). These tests were also used to compare the number of attentive periods at the nest, and the number of feeds given to offspring by paired male and female parents. The frequency of nest building by male and female partners was compared using a paired two-tailed t-test. Minimum/maximum durations of attentive periods were grouped into four classes (in all cases the minimum and maximum derived period for each observation both fell into the same class) and compared using the log-likelihood (LogLik) ratio statistic, while exact durations of attentive periods at the nest by males and females were compared using a two-tailed Mann-Whitney U-test. Data from members of the same pair were not included in comparison of exact durations of attentive periods.

RESULTS

Distribution

Punta Cormorant, Quinta Playa and Sartén lagoons supported flocks for all or most of the year, while Mina de Sal, Cementerio and Espumilla lagoons supported itinerant flocks of usually < 30 flamingos (Fig. 2). The largest flocks (100–350 birds) occurred at Quinta Playa.

Lagoon water chlorosity, the abundance of food items, and flamingo numbers were related. At Espumilla, two blooms of *A. salina* occurred in the latter parts of 1976 and 1977, coinciding with high chlorosity of lagoon water (Fig. 3). The blooms were separated by a period of lower chlorosity during which the concentration of *A. salina* fell considerably, or was entirely absent. For part of this low-chlorosity period, a bloom of *T. reticulata* occurred (Fig. 3). The flamingo population size fluctuated extensively, with larger numbers following *A. salina* blooms (Fig. 3), and an absence of flamingos (during July–September) following a near absence of both *A. salina* and *T. reticulata*. At Quinta Playa, chlorosity remained stable at < 30 Cl/l, a population of *T. reticulata* persisted throughout the 15-month period, and the flamingo population size remained relatively stable (Fig. 3).

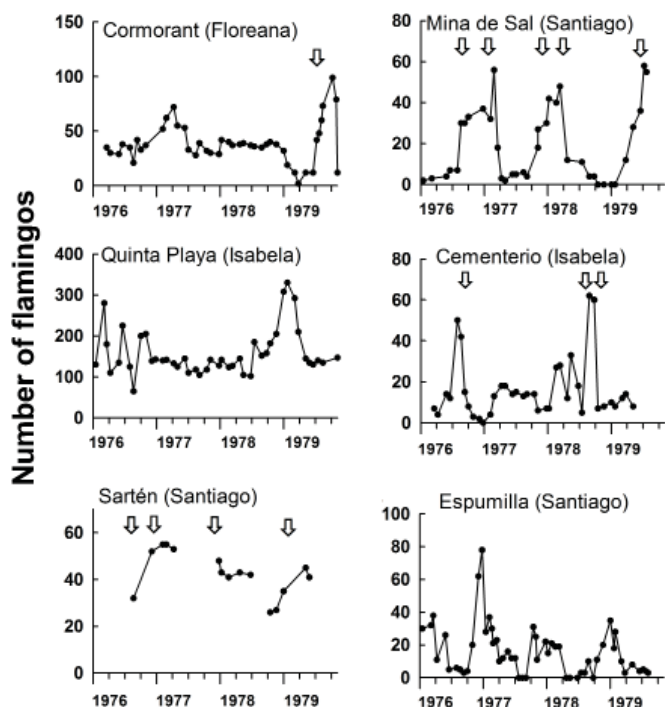


Figure 2. Distribution and egg laying peaks (arrows) of Galapagos flamingos in six study lagoons during 1976–9. Data from Quinta Playa and Cementerio lagoons are monthly counts. Data from other lagoons are highest counts of 2–5 counts per month, except where there was a difference of >15 birds between highest and lowest counts for any one month, when both highest and lowest counts are plotted. Gaps of > 1 month occurred in visits to Sartén in 1977 and 1978, but local fisherman reported that flamingos were always present.

Chlorosity at Mina de Sal varied widely, with corresponding fluctuations in the concentration of *A. salina* and *T. reticulata* and in flamingo numbers: the highest flamingo counts coincided with periods of higher *A. salina* concentrations (Fig. 3), and when both *A. salina* and *T. reticulata* were scarce or absent flamingos were also absent (Aug 1978). In contrast, at Sartén and Punta Cormorant lagoons chlorosity was consistently < 30 CL/l with little fluctuation, populations of *T. reticulata* were consistently recorded, *A. salina* was absent and flamingo populations fluctuated considerably less (Fig 3). These two lagoons provided a more consistent potential food supply than at Mina de Sal, where food supply fluctuated in both composition and concentration (Fig. 3).

A. salina was present in four out of 15 lagoons examined and *T. reticulata* in 13 of them. Other putative food items were frequently recorded (Table 3). Mud containing algal debris, bacteria, seeds, plant and animal remains occurred in varying amounts on the floor of all lagoons, and varied in organic content: single samples from Quinta Playa, Barahona, Cementerio and Punta Cormorant lagoons contained 9.8%, 45.9%, 26.2% and 5.5% organic material respectively. Water samples taken from the ten lagoons visited only one once during the study period ranged widely in chlorosity from 5.2 to 46.6 Cl/l.

Lagoon water levels and flamingo numbers were also related. Records over a 9-year period at Cementerio lagoon show that flamingos accumulated with falling water level in eight of the nine years (not 1977), with breeding occurring on islets exposed by falling water level in five or six years (Fig. 4). This lagoon experiences a quasi-annual cycle of water level due to the ‘rainy’ season (c. Dec–Jun); it is also affected by tidal seepage and periodic breaching

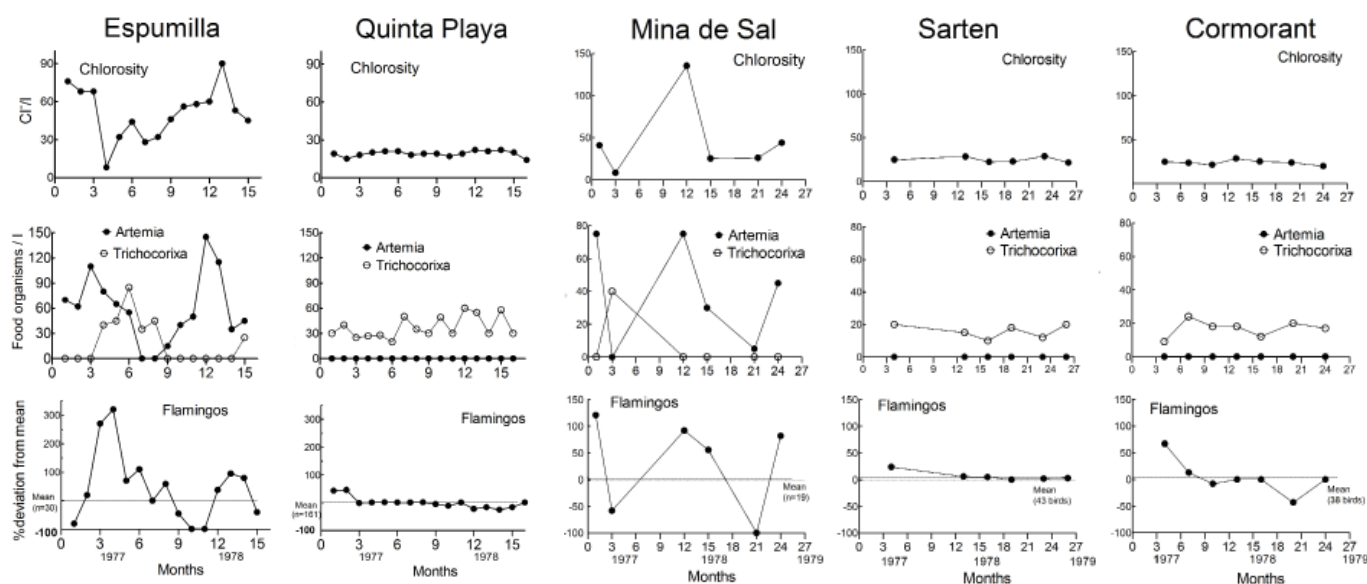


Figure 3. Fluctuation in the abundance of Galapagos flamingos relative to chlorosity of lagoon water and concentrations of *Artemia salina* and *Trichocorixa reticulata* at five lagoons: Espumilla, Quinta Playa (Oct 1976 to Dec 1978), Mina de Sal, Sartén, and Punta Cormorant (Oct 1976 to Dec 1979). The horizontal lines in the lower graphs indicate the mean numbers of flamingos at each lagoon over the duration of observations (n = 15 or 27 months).

Table 3. Potential food items of flamingos, in water and mud samples from Galapagos lagoons.

Food item	Typical amounts
Water	
<i>Artemia salina</i>	30–100/l
<i>Trichocorixa reticulata</i> (instar:adult ratio varied from 0:1 to 25:1)	5–30/l
Mud	
Copepoda (cyclopoid and harpacticoid)	1350 ± 1060/l*
Ostracoda	155,000 ± 145,876/l*
Brachyuran zooea and megalopa larvae	≥ 10 per sample
<i>Palaemonetes</i> sp. (Malacostraca) nymphs	≥ 10 per sample
<i>Enochrus</i> sp (Coleoptera) larvae and adults	< 10 per sample
<i>Ochthebius</i> sp. (Coleoptera)	< 10 per sample
<i>Dytiscus</i> sp. (Coleoptera) larvae	< 10 per sample
<i>Dasyhelea</i> sp. (Diptera) larvae and pupae	< 10 per sample
<i>Scatella</i> sp. (Diptera) pupae	< 10 per sample
Filamentous and globular algae	≥ 10 per sample
Diatoms	≥ 10 per sample

*n = 32 (16 monthly samples from each of Quinta Playa and Barahona).

by extreme high tides. Lower water level occurs during c. Jul–Nov. This lagoon provides a poor feeding environment for flamingos because of periodic explosive populations of invertebrate- and detritus-eating euryhaline marine fish (*Chanos* sp. and *Mugil* sp.) trapped in the lagoon as juveniles. No *A. salina* and few *T. reticulata* ($5.1 \pm 0.8/l$, n = 30) and few other food organisms were recorded over a 15-month period in 1978–9. Nearly all birds at Cementerio nested, and breeding birds travelled to feed at lagoons elsewhere. Potential feeding lagoons are within 20 km of the Cementerio colony, so a round-trip journey flying at 40–50 km per hour (Bruderer & Boldt 2001) would take ≤ 1 h.

Movement

Four adult birds banded at Sartén lagoon were re-sighted at Espumilla (c. 24 km distant), one was re-sighted at Mina de Sal (c. 25 km), and one at Punta Cormorant (c. 113 km), 16, 15 and 0.5 months later, respectively. A male sighted at Sartén, identifiable by a neck deformity, was recorded 0.5 months later at Mina de Sal. Juvenile flamingos were recorded in several lagoons on southern Isabela in 1976, and at Punta Cormorant lagoon in 1977, even though no breeding occurred on these islands in the current or preceding year. The crop of a freshly dead flamingo at Cementerio contained abundant green olivine crystals (magnesium iron silicate), which occur in the mud at Punta Cormorant lagoon but not at lagoons on Isabela Island. These observations indicate that travel among lagoons and islands was common.

Activity budget

During daylight hours (5h30–17h30) feeding (Table 4), resting and preening (not shown) were the major activities in which adult flamingos in the non-breeding

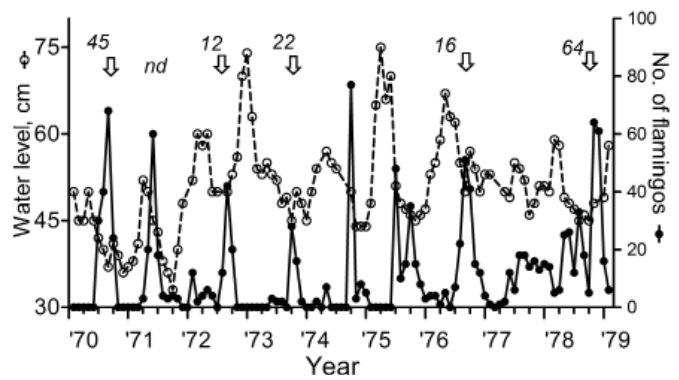


Figure 4. Numbers of flamingos and lagoon water level at Cementerio lagoon. Breeding attempts are indicated by arrows with the number of occupied nests per attempt. It is not known whether breeding occurred in 1971, indicated as “nd”; no breeding occurred in 1974, 1975 and 1977.

flock engaged. Other activities (see Methods) contributed < 8% of the activity budget. At both Sartén lagoon (where the predominant potential food-item was *T. reticulata*) and Mina de Sal lagoon (predominant potential food-item, *A. salina*) on average c. 40 % of the activity budget during daylight hours was taken up with feeding; feeding activity increased at night, particularly at Sartén (Table 4).

Breeding

Group displays involved a mean of 12 birds (range 4–22, n = 30 display bouts) and occurred in all months except June and July, with most observed during the peak months of egg-laying. Display bouts were recorded during all daylight hours, and at all study sites, including those at which no nesting occurred (Espumilla, Quinta Playa).

Flamingos nested at five lagoons on four islands during 1976–9 (Table 5). Nesting occurred in all three years at Sartén and Mina de Sal, in two of the three years at Cementerio, and once each at Punta Cormorant and Bainbridge. Most laying (77.4 %) occurred Oct–Dec, although laying was recorded in all months except Apr–Jun (Table 5). Breeding sometimes occurred simultaneously at more than one lagoon: e.g. during Aug–Sep 1976, laying occurred at four sites on three different islands (Table 5). At individual lagoons, eggs were laid in batches; for example, of the 20 eggs laid at Mina de Sal during 1977–8, seven were laid during the first week of

Table 4. Percentage of flamingos in the flock engaged in feeding at Sartén and Mina de Sal lagoons during 6-h blocks over the 24-h cycle. Data are mean ± SD (n periods).

Period	Sartén	Mina de Sal
17h30–23h30	82.8 ± 14.5 (4)	56.0 ± 6.3 (4)
23h30–5h30	91.3 ± 4.2 (4)	78.6 ± 23.4 (4)
5h30–11h30	49.5 ± 27.0 (16)	49.6 ± 15.7 (16)
11h30–17h30	15.5 ± 9.4 (16)	37.9 ± 10.2 (16)
Overall	60.9 ± 33.5 (40)	62.5 ± 22.5 (40)

Table 5. Season totals of clutches laid and fledglings (= offspring that reached age 70 days) produced per breeding lagoon during 1976–9.

Lagoon	Season	Number of clutches laid (% of clutches at all sites that season)	Number of chicks hatched	Number of fledglings (fledglings per clutch)	Laying period
Cementerio ¹	1976–7	16 (22.2)	7	4 (0.25)	Sep 1976
	1977–8	0 (0)	0	0 (0)	
	1978–9	64 (51.6)	35	30 (0.47)	Aug, Nov 1978
	Total	80 (33.4)	42	34 (0.43)	
Sartén	1976–7	24 (33.4)	14	11 (0.46)	Sep 1976
	1977–8	23 (53.4)	15	12 (0.52)	Nov–Dec 1977
	1978–9	17 (13.7)	12	11 (0.65)	Sep–Dec 1978
	Total	64 (26.7)	41	34 (0.53)	
Mina de Sal	1976–7	16 (22.2)	6	1 (0.06)	Aug, Dec 1976
	1977–8	20 (46.5)	5	2 (0.10)	Nov 1977 to Feb 1978
	1978–9	12 (9.7)	?2	1 (0.08)	Nov 1978
	Total	48 (20.0)	?13	4 (0.08)	
Bainbridge	1976–7	16 (22.2)	9	?5 (?0.31)	Aug, Nov 1976
	1977–8	0 (0)	0	0 (0)	
	1978–9	0 (0)	0	0 (0)	
	Total	16 (6.7)	9	?5 (?0.31)	
Punta Cormorant	1976–7	0 (0)	0	0 (0)	
	1977–8	0 (0)	0	0 (0)	
	1978–9	31 (25.3)	?	-	Feb–Mar 1979
	Total	31 (12.9)	?	-	
All sites	1976–7	72	36	?21 (?0.29)	
	1977–8	43	20	14 (0.32)	
	1978–9	124	?49 ²	42 (0.45) ²	
	Total	239		77 (0.37) ²	

¹23.6 ± 28.5 clutches per annum were laid in a total of eight breeding attempts at Cementerio lagoon during 1968–81 (including the three years for this lagoon in this table), producing 0.32 fledglings per clutch in the seven attempts for which outcomes were known. ²Punta Cormorant not included.

Nov, seven during the second half of Dec, and six from the last week in Jan to first week in Feb. Two, more-clearly distinct, periods of laying occurred at some lagoons in some years (Mina de Sal 1976, Bainbridge 1976, Cementerio 1978, Table 5), though this pattern was not consistent throughout the islands.

The colonies (one lagoon = one colony) comprised 1–5 groups of nests of mud, sand or gravel, containing 3–16 nests per group (n = 5 lagoons) at a within-group, nearest-neighbour inter-nest distance of 88.3 ± 18.4 cm and a mean within-group density of 1.16 nests per m² (n = 108 nests). The separation of groups of nests was associated with local physical features (rocky outcrops, protruding mangrove roots). Where measured, distances between nearest-neighbour groups was 178 ± 66 cm (n = 7 groups). The frequency of nest-building bouts did not differ significantly between male and female partners of individual pairs ($t_{13} = -1.098$, $P = 0.292$) (15 pairs: male 0.068 ± 0.034 bouts.nest⁻¹.h⁻¹, n = 136 bouts; female 0.094 ± 0.054 bouts.nest⁻¹.h⁻¹, n = 188 bouts). Nest building occurred primarily between 5h00 and 10h00 (mean = 0.28 bouts.nest⁻¹.h⁻¹, n = 324 bouts).

The single egg (mean size 88.1 × 51.5 mm, n = 58) was attended constantly by alternating parents. The durations of attentive periods at the nest, measured as maximum and minimum values, did not differ significantly between

male and female partners of individual pairs ($LogLik_3 = -234.19$, $Dev = 5.178$, $P = 0.159$). Most derived attentive periods lasted 21–60 h (Table 6). In 15 cases (out of 147, = 10.2%) where the exact durations of attentive periods were known there was also no significant difference between males and females (male 57.7 ± 10.3 h, n = 9; female 62.6 ± 6.06 h, n = 6; Mann-Whitney $U = 18.50$, $P = 0.345$).

Comparison of attentive periods between a colony where parents fed in the same lagoon (Sartén) (n = 103 attentive periods) and a colony where parents travelled to other lagoons to feed (Cementerio) (n = 44 attentive periods) indicated some evidence for a longer attentive period for females (Pearson’s $\chi^2_1 = 8.47$, $P = 0.033$) but not males (Pearson’s $\chi^2_1 = 6.18$, $P = 0.099$) at the latter.

Table 6. Number (%) of nest-attendance periods of different durations (derived maximum/minimum values) during incubation and brooding, until chick left nest at age 7–11 days.

Duration of attentive periods (h)	Incubation		Brooding	
	Male (n = 70)	Female (n = 77)	Male (n = 32)	Female (n = 27)
≤ 20	13 (19)	9 (12)	4 (12)	5 (18)
21–60	48 (69)	50 (65)	27 (84)	21 (78)
61–90	6 (9)	8 (10)	0 (0)	1 (4)
> 90	3 (4)	10 (13)	1 (3)	0 (0)

Chicks on the nest were attended constantly by one or other parent, up to 7–11 days of age. The duration of attentive periods measured as maximum and minimum values did not differ significantly between male and female partners of individual pairs ($\text{LogLik}_3 = -57.54$, $\text{Dev} = 6.259$, $P = 0.398$) (Table 6). In the 12 cases (of 59, = 20.3%) where the exact durations of attentive periods were known there was also no significant difference between males and females (male 28.7 ± 6.1 h, $n = 6$; female 21.7 ± 2.2 h, $n = 6$; Mann-Whitney $U = 10.50$, $P = 0.262$). The duration of attentive periods measured as maximum and minimum values did not differ between a colony where parents fed in the lagoon (Sartén, $n = 35$ attentive periods) and a colony where parents travelled to other lagoons to feed (Cementerio, $n = 24$ attentive periods) ($\text{LogLik}_3 = -57.54$, $\text{Dev} = 6.124$, $P = 0.101$).

During incubation, nest relief took place predominantly in late afternoon at colonies where parents fed in the lagoon (Sartén and Mina de Sal) and predominantly in early morning at the colony (Cementerio) where parents travelled to other lagoons to feed (Table 7, $\chi^2_2 = 35.5$, $P < 0.0001$; nocturnal (18h30–5h30) period excluded from the analysis because expected values too low). During brooding of chicks aged 7–11 days, nest relief was spread throughout the day at the colonies where parents fed in the lagoon and was predominantly nocturnal at the colony where parents travelled to other lagoons to feed (Table 7, $\chi^2_3 = 17.93$, $P < 0.0005$).

The frequency with which chicks received feeds from their parents fell dramatically between day 3 and leaving the nest to form crèches, and progressively reduced to near zero at age *c.* 105 days ($n = 701$ feeds) (Fig. 5). The duration of individual feeds received by chicks increased until they reached age *c.* 45 days, and then remained more or less constant (Fig. 5). Overall, the amount of time spent receiving food from parents decreased from hatching to *c.* 105 days, and the decrease was greatest after the chick left the nest at 7–11 days (Fig. 5). By 105 days of age, individual chicks had received 265 ± 82 feeds from parents, lasting a total of 1921 ± 551 minutes. Beyond three weeks of age, chicks also foraged for themselves.

In 197 (out of 701, = 28.1%) feeds where the sex of the parent and the identity of the chick were known, the frequency of feeds by male and female partners ($n = 12$ pairs) did not differ significantly ($\chi^2_1 = 0.081$, $P = 0.775$)

Table 7. Number (%) of nest reliefs at different times of the day during incubation and brooding of chicks aged 7–11 days. (A) colonies where adults fed in their nesting lagoon and (B) colony where they fed in other lagoons.

Time of day	Incubation		Brooding	
	A (n = 41)	B (n = 59)	A (n = 25)	B (n = 33)
5h30–9h30	7 (17)	45 (76)	7 (28)	5 (15)
9h30–14h00	5 (12)	4 (7)	6 (24)	2 (6)
14h00–18h30	28 (68)	9 (15)	9 (36)	4 (12)
18h30–5h30	1 (2)	1 (2)	3 (12)	22 (67)

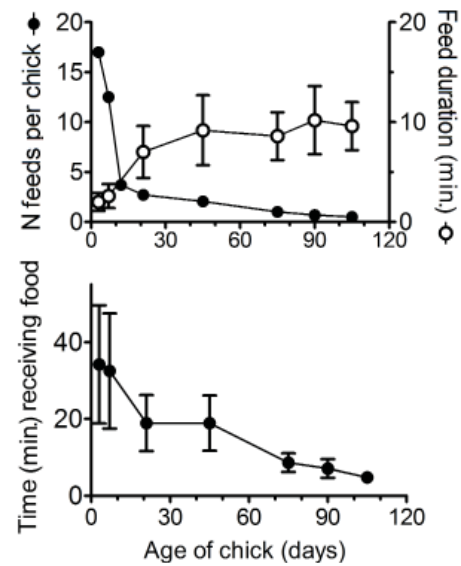


Figure 5. Chick feeding by Galapagos flamingos: mean number of feeds received per chick per 24 h, mean duration of feeds and mean amount of time spent receiving food per chick per 24 h ($n = 701$ feeds).

(males, $n = 93$ feeds; females, $n = 104$ feeds), nor did the duration of these feeds ($\chi^2_9 = 0.159$, $P = 1.000$). There was no significant difference in the frequency with which chicks in the various age groups were fed at a colony where parents were resident in the lagoon (Sartén, $n = 254$ feeds) and a colony where parents travelled to other lagoons to feed (Cementerio, $n = 243$ feeds) ($\chi^2_7 = 1.01$, $P = 0.995$). Before chicks left the nests, feeds were spread over 24 hours, but thereafter feeds were predominantly nocturnal, peaking toward dawn (Fig. 6). Parents who foraged in other lagoons returned to the colony lagoon predominantly in the evening (17h00–20h30; 57.1 % of arrivals) or at dawn (5h00–6h30; 28.6 % of arrivals). Chicks were fed more than once by an individual parent at each visit to the nest.

Breeding outcome averaged 0.37 young fledged per clutch, being highest at Sartén (0.53) and lowest at Mina de Sal (0.08) (Table 5). Breeding outcome barely differed between a colony where parents were resident in the lagoon (Sartén) and a colony where parents travelled to other lagoons to feed (Cementerio) ($\chi^2_1 = 3.94$, $P = 0.047$).

Several nests and eggs were abandoned after tidal floods at Cementerio and Punta Cormorant lagoons. Eggs which rolled from nests were usually abandoned. In crèches, older chicks harassed later-hatching chicks, which in some cases showed signs of emaciation. Chicks that became separated from the crèche usually died. Some died following accident to legs or wings entangled among roots and tree debris in some lagoons or (rare) predation by Galapagos Hawks *Buteo galapagoensis*. Some starved at the Cementerio colony, when parents failed to return from feeding lagoons to feed them. At Mina de Sal most eggs and nests were submerged by rainwater accumulating in the crater in all three years of the study; of the few hatchlings, most perished (Table 5).

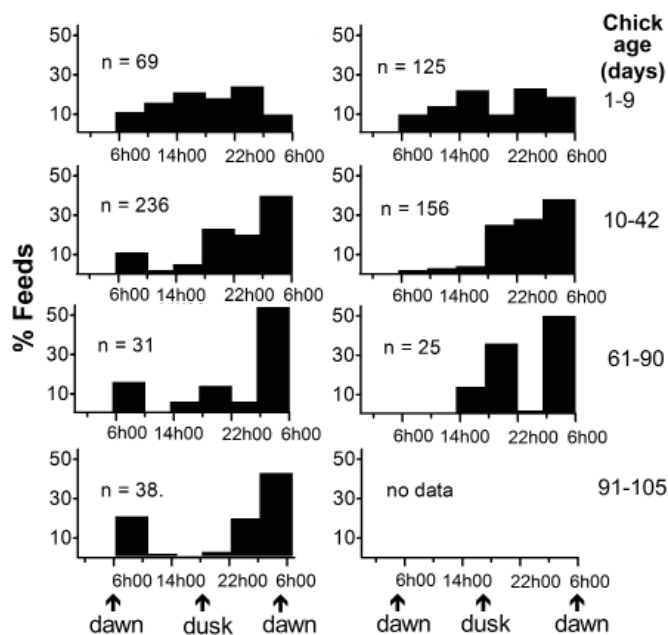


Figure 6. Timing of feeding of Galapagos flamingo chicks. Left: colonies where adults fed in the nesting lagoon. Right: Cementerio colony, from which adults travelled to other lagoons to feed.

Moult

Synchronous moulting of flight feathers occurred in at least some adult birds. Between 18 and 37 flightless flamingos were recorded at Sartén during Jan–Feb in all three years of the study, 200–250 at Quinta Playa in Dec 1978, and two at Bainbridge in Feb 1979. Birds at various stages of moult (from complete absence of primaries and secondaries to advanced regrowth) were recorded.

DISCUSSION

Distribution

Fluctuating physical conditions resulting from the interplay of tidal seepage and overspill, irregular precipitation, and varying topography determining the extent of rainwater drainage into Galapagos lagoons predispose them to highly variable water level and productivity. These conditions do not affect all lagoons to the same extent, leading to spatially and temporally fluctuating availability of suitable feeding and nest locations within the archipelago. The distribution of Galapagos flamingos was associated with lagoon water chlorosity which determines the occurrence of putative food items, and with low lagoon water level exposing breeding sites. Galapagos flamingos take opportunistic advantage of any abundant population of aquatic invertebrates. Flamingos elsewhere have evolved to exploit such locally unpredictable feeding conditions: while primarily philopatric, they quickly become nomadic, moving to sample food and water level if local conditions deteriorate (Rooth 1965, Arengo & Baldassarre 1995, Bildstein *et al.* 2000, Bruderer & Boldt 2001, Johnson & Cézilly 2007, Béchet *et al.* 2009).

Radio-tagged American Flamingos in the Yucatán changed sites up to seven times a year (Baldassarre & Arengo 2000).

Census results since 1981 have demonstrated that Quinta Playa and Cementerio lagoons together account for as much of the total Galapagos flamingo population as all other lagoons combined. Vargas *et al.* (2008) demonstrated significant correlations between flamingo abundance and rainfall, lagoon water level and temperature at these lagoons: flamingo numbers fell at some lagoons during rainy seasons and particularly during the severe El Niño Southern Oscillation (ENSO) event in 1982–3. However, the total population did not fall: when numbers at Cementerio and Quinta Playa decreased, the combined population at other lagoons increased, presumably as birds sought feeding lagoons less affected by heavy rainfall (Vargas *et al.* 2008). Similarly, the total flamingo population in Galapagos was not reduced following a severe ENSO event in 1997–8 (unpublished census reports of CDRS). Our observations of flamingos moving between lagoons and islands also indicate that the flamingo population is mobile and opportunistic. Our visits to some lagoons were infrequent, so our re-sightings after banding are probably underestimates. All Galapagos lagoons containing putative food items are visited by flamingos. The population is probably a single dispersive panmictic unit which tracks patchy resources, resembling an “ideal free distribution” model (Fretwell & Lucas 1970). However we cannot discount an “ideal despotic distribution” model in which some dominant individuals prevent others from occupying high-quality habitat, as described for the Greater Flamingo in southern Spain (Rendón *et al.* 2001).

The lagoons frequented by c. 90 % of the current flamingo population have existed since observations began, and the pattern of flamingo distribution among them has remained relatively constant. However, in earlier times, suitable lagoons may have differed in number and location from those seen today, given the topographic volatility of the archipelago’s volcanic landscape. This may have affected the size of the total flamingo population.

Feeding

The classes of potential food item available in Galapagos are broadly similar to those elsewhere in the range of the American Flamingo, including organic mud, crustaceans, annelids, insect larvae, molluscs and plant seeds (Arengo & Baldassarre 1995). While *A. salina* and *T. reticulata* are major potential food items, it is unlikely that food was restricted to these two organisms since in a given lagoon flamingos displayed other feeding techniques in addition to “skimming”, e.g. “stamping” and “walking, leaving tracks of bill” (Jenkin 1957, Rooth 1965, Mascitti & Kravetz 2002), known to be associated with different classes of food. Furthermore, additional food items may be swallowed simultaneously with major food items (Jenkin 1957, Tuite 2000).

The contribution of foraging to the activity budget of Galapagos flamingos (Table 4) is similar to that at a

major feeding lagoon in the Yucatán where 5000–8000 American Flamingos accumulate to breed (Espino-Barros & Baldassarre 1989). The percent time spent foraging may be inversely related to food abundance (Arengo & Baldassarre 1999). However since the activity budget also reflects competition with behavioural patterns other than foraging, one cannot infer that food availability at the Galapagos lagoons is similar to the Yucatán feeding site, without further investigation.

The contribution of feeding to the daily activity budget was similar in a lagoon where *A. salina* was the most abundant potential food item (Mina de Sal) and a lagoon where *T. reticulata* was the most abundant (Sartén) (Table 4). However, whether *A. salina* and *T. reticulata* provide comparable nutritional benefits requires additional investigation. Other factors, not so far studied, which might affect food availability include large flocks accumulating at sites of high food density and causing food depletion, and competition for food. An interplay of these factors could contribute to an equilibrium between abundance and quality of food and flamingo distribution among Galapagos lagoons.

The reasons for the observed extensive nocturnal feeding by Galapagos flamingos are unclear. Diurnally fluctuating food availability (Johnson & Cézilly 2007), predator avoidance (Beauchamp & McNeil 2003) and thermoregulation (Jutglar 1992) have all been suggested to predispose to nocturnal feeding. If nocturnal foraging allows individuals to supplement inadequate diurnal food intake (McNeil *et al.* 1992), then only less successful foragers should forage at night. At Sartén lagoon nearly all the flock foraged during the night, suggesting that the flock was unable to obtain enough food by day (Table 4). There are no regular predators of adult flamingos in Galapagos, and daytime temperature rarely exceeded 30°C at either of the study lagoons, so these two factors are unlikely to preclude daytime feeding.

When food was abundant, nesting flamingos fed in the lagoon along with a non-breeding flock. When a lagoon was poor in food items, one parent attended the nest while the other left the colony to feed elsewhere, so enabling them to breed at locations that were sub-optimal for feeding, as has been reported elsewhere (Rooth 1965, Rendón-Martos *et al.* 2000, Amat *et al.* 2005, Johnson & Cézilly 2007, Béchet *et al.* 2009).

Breeding

Our data (*e.g.* Fig. 4) suggest that flamingos accumulate and breed when falling lagoon water level exposes suitable nest sites. The pattern we report of intermittent breeding, shifting of nesting location, rapid onset of breeding when conditions become favourable, and use of both food-rich and food-poor lagoons for breeding is typical of flamingos elsewhere. The clutches we recorded at Punta Cormorant in 1978 were the first at that site for 13 years. Breeding has been sporadic at Quinta Playa, Mina de Sal and Cementerio over the last 45 years.

In contrast to other populations of American Flamingo (<<http://aviansag.org/Husbandry/>> consulted 28 Aug 2014), Galapagos birds undertake group display involving *c.* 20 birds or less and colonies may contain as few as three concurrently active nests. Flamingos have populated at least 11 islands or groups of islands worldwide. Founder populations on distant islands would presumably have been small and infrequent (Johnson & Cézilly 2007) and breeding may have been limited by the habit of group display involving large numbers of birds. The size of the original (and any subsequent) flamingo colonization of Galapagos is unknown, but as well as facilitating establishment, the capacity to breed in low numbers is vital to the present small population.

The group display of Galapagos flamingos was not restricted to either onset of breeding or locations of nesting sites, and presumably maintained the birds in a state of near-readiness for breeding. By reacting quickly to improving local conditions the flamingos were able to breed somewhere in the archipelago for nine months of the year. Breeding started with onset of the coastal drier season, which provided suitable areas for nesting. Elsewhere, flamingo breeding is strongly associated with high water level and consequent high food availability, determined by local precipitation, managed sea-water flooding of salt pans, and fresh water from irrigated rice fields (Gerharts & Voous 1968, Cézilly *et al.* 1995, Béchet & Johnson 2008, Béchet *et al.* 2009). In contrast, in Galapagos most egg-laying occurred in the season when low precipitation occurs at low altitudes (Trueman & d'Ozouville 2010).

Of the estimated total population of *c.* 500 adult birds, *c.* 30 % incubated clutches per year (Table 5) (= 45 % of adults capable of breeding; see "Population" below). The laying period of a colony varied from a week to *c.* 3 months, the longer spreads probably reflecting the persistence of available nesting areas, as illustrated by Cementerio (Fig. 4) and Mina de Sal. The period from laying to chick independence per individual breeding pair lasted *c.* 4 months. Breeding success varied considerably between nesting locations (Table 5), characteristic of opportunistic breeding (Johnson & Cézilly 2007). The overall average nesting success of 0.37 juveniles per clutch (Table 5) in Galapagos is similar to that of large flamingo colonies elsewhere, *e.g.* the Greater Flamingo colony at Elmenteita, east Africa (historically 0.32: Brown 1975) or the American Flamingo in the Caribbean (0.41–0.44: Sprunt 1975). The nesting success we report for Galapagos may have been lower than usual over a longer term because of flooding at the Mina de Sal colony in all three years of the study, where most eggs and chicks perished (Table 5).

There was little evidence that absences from the nest site by off-duty parents during incubation and brooding were longer at a colony where parents travelled to other lagoons to feed, compared with a colony in a lagoon where parents fed. The time an off-duty parent spends away from the nest during brooding depends on food availability

(Johnson & Cézilly 2007) and the periods of absence we report are similar to those for Greater Flamingos which successfully raised offspring in the Carmargue (Johnson 2000). The frequency, timing, and duration of feeds to offspring that we report are similar to those observed for other populations of American Flamingo (Rooth 1965, Studer-Thiersch 1975).

Population

The estimated total population of *c.* 250 pairs produced 25.7 fledglings per annum (data from Table 5), *i.e.* 0.103 fledglings per pair per annum. Allowing for survival from fledgling to breeding (at five years old: Johnson & Cézilly 2007) of 46.06 % (Johnson et al. 1993), the likely recruitment rate of replacement breeders into the population is 0.047 breeders per adult per annum. An adult flamingo in Galapagos would thus probably replace itself with a five year-old offspring breeding for the first time, in *c.* 21 years.

Approximately 370 of *c.* 500 adult birds (74 %) will be old enough to breed (≥ 5 years) at a given time. During the study, on average 168 birds bred per annum, which is 45.3 % of 370. Assuming a conservatively estimated longevity of 20–30 years (as reported for Greater Flamingo) and little decline in reproduction in older birds (Johnson & Cézilly 2007), the growth rate of the population would approximate to zero, which accords with the census results of the past 45 years. Growth of the population is probably restricted by the low recruitment by reproduction, which is typical of *Phoenicopterus* spp. (Simmons 1996). However, inter-island movements within the archipelago and the likely annual mate changing (observed for Greater Flamingo: Cézilly & Johnson 1995) will enhance genetic mixing in this small isolated population.

Moult

It has been debated to what extent flamingos moult to flightlessness in the wild (Ogilvie & Ogilvie 1986). Allen (1956) reported a flock of *c.* 2000 flightless American Flamingos away from breeding sites in Cuba. We encountered flightless birds in Galapagos both at a breeding lagoon (Sartén), and at a lagoon where breeding did not occur that year (Quinta Playa). In the former, the flightless birds were encountered while young chicks were being reared there, although flightless birds were not engaged in parenting. We were unable to determine whether the flightless birds had been breeding earlier that year. In flamingos elsewhere, simultaneous flight feather moult has been recorded before, during, or after breeding (Shannon 2000). That we did not record synchronous moult outside of the breeding season may reflect fewer observations during those months. At least two of the three lagoons where flightless birds were recorded contained relatively high and stable levels of food organisms (Fig 3; no data for Bainbridge); it seems unlikely that birds apparently needing to spend *c.* 60 % of

their time feeding could afford a period of flightlessness in a food-impooverished lagoon.

The Future

The population is considered at risk because of its small size and therefore management is important, particularly in view of the population's genetic uniqueness. The current census programme should be maintained. Based on early censuses, which showed that most of the flamingo population was found at the same ten lagoons, a standard procedure for the census has been followed since 1995, in which lagoons are simultaneously surveyed once a year (Jiménez-Uzcátegui & Naranjo 2010). However, regular monitoring of breeding effort and success is also required, which would require more than one visit to each breeding lagoon per season, particularly since a wide spread of laying may occur (Table 5).

El Niño Southern Oscillation climatic events have occurred in the Galapagos Islands for at least the last 6000 years (Riedinger *et al.* 2002) and are predicted to continue (Sachs & Ladd 2010). The events of 1982–3 and 1997–8, in which many Galapagos seabirds suffered reduced populations (Valle & Coulter 1987, unpublished reports at CDRS), did not grossly affect the size of the flamingo population. The distribution of flamingos changed temporarily as they sought feeding lagoons less heavily affected by extreme heavy rainfall. Their nomadic opportunistic behaviour probably facilitates their survival in such climatic conditions. However, possible rising of sea-level and increased precipitation associated with global climate change (Sachs & Ladd 2010) pose a threat of flooding at important lagoons, and concomitant reduction in breeding success. Natural changes to physical characteristics of lagoons may have impacts on the flamingo population; Espumilla lagoon has been dry for most of the last 20 years probably due to some local hydrological change.

The distribution, opportunistic breeding, and pattern of nest attendance and chick provisioning of the Galapagos flamingo population are similar to those of its conspecifics in the Caribbean. However, this unique population is extremely vulnerable to local habitat disturbance whereas in the Caribbean flamingos can readily move greater distances in response to decrease in habitat quality. Periods of reduced food abundance in Galapagos would probably lead to reduced reproduction and productivity, with severe effects, since flamingos reproduce slowly and show deferred maturity (Cézilly *et al.* 1995). Conservation of the Galapagos flamingo requires that the protection of habitat by the Galapagos National Park Directorate (GNPD) be maintained over the whole range of the population, to accommodate fluctuations in food availability and nesting conditions. This is necessary even though particular sites might not be in use at a given time. Enough habitat needs to be available to provide *c.* 50 t food per year (assuming an estimated consumption per flamingo per day of 270 g; Rooth 1976). Long term trends in food availability at major feeding lagoons need to be estimated.

The threat from introduced land mammals is small at two of the most successful and regularly used breeding sites (Sartén and Cementerio), because flamingos nest on islets within the lagoons. Only sporadic breeding occurred at Quinta Playa and Espumilla lagoons, which were devoid of islets, and where nests located along the shores have been susceptible to trampling and predation by introduced pigs, donkeys, goats, cats or rats (Lévêque 1964, Jiménez-Uzcátegui *et al.* 2007). Mammalian incursion could be counteracted by construction of artificial islets and/or mud nests within some lagoons, as in the Carmargue (Johnson 1982).

Disturbance of flamingo habitat by humans in Galapagos has hitherto been local, such as at lagoons where fish were salted or salt collected by local inhabitants. They were disturbed by clearing of vegetation for a chicken farm at Cementerio in the 1960s (Tupiza 1965). These activities have now ceased. Tourist groups visit several lagoons which support c. 10 % of the total flamingo population. Tourists are restricted to trails located so as not to disturb the fauna, and access to most such sites must be in the company of licensed guides. Tourism has so far posed little or no threat to the flamingo population (Tindle 1978). However, flamingos are stress-prone (*e.g.* Galicia & Baldassarre 1997), and would be vulnerable were current high standards of tourist management to lapse.

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SOME OFF-SHORE MARINE SPECIES COMING TO LIGHT IN GALAPAGOS, ECUADOR

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SUMMARY

With the recent deployment of a Phantom XTL remotely operated submarine vehicle (ROV) with video camera it has been possible to investigate the Galapagos inshore marine environment below SCUBA-diving limits, between 40 and 150 m depth. Video recordings are rare of species at these depths and are shedding light on the presence, abundance and behavior of various species. The side-gilled opisthobranch mollusk *Berthella californica* and a nudibranch *Flabellina* sp. were recorded at depths where they had not previously been seen in Galapagos. Other species filmed by the ROV may be new records for the archipelago such as a squat lobster *Munida* sp. and an octocorallian of the family Aquaumbridae. Several other octocorallians, including *Virgularia* cf. *galapagensis*, *Cavernulina* cf. *darwini* and *Ptilosarcus* cf. *undulatus*, rarely seen since 1984, were recorded. The Sideblotch Bass *Serranus stilbostigma* has now been identified in seven new sites throughout the archipelago.

RESUMEN

Algunas especies marinas de profundidad media se revelan en Galápagos, Ecuador. Con la reciente utilización de un vehículo submarino de control remoto Phantom XTL con cámara de video ha sido posible investigar el medio ambiente de la costa submarina de Galápagos más allá de los límites de buceo, entre los 40 y 150 m de profundidad. Grabaciones de video de especies a estas profundidades son raras, y están revelando la presencia, abundancia y el comportamiento de varias especies. El opistobranquio *Berthella californica* y un nudibranquio *Flabellina* sp. fueron grabados a profundidades a las que no habían sido observados antes en Galápagos. Otras especies grabadas por el minisub podrían ser nuevos récords para el archipiélago, tales como un saстре *Munida* sp. y un octocoralio de la familia Aquaumbridae. Varios otros octocoralios, incluidos *Virgularia* cf. *galapagensis*, *Cavernulina* cf. *darwini* y *Ptilosarcus* cf. *undulatus*, raramente vistos desde 1984, fueron grabados. El serránido *Serranus stilbostigma* ha sido identificado ahora en siete nuevos sitios a lo largo del archipiélago.

INTRODUCTION

The Phantom XTL remotely operated submarine vehicle (ROV), carried aboard the ship *National Geographic Endeavour* (hereafter *Endeavour*), has recently captured video footage of several marine species that had been recorded only a few times over the past few decades, and which were found in previously unknown sites or at previously unexplored depths. These included a number of gastropods, octocorals and fish, reported here.

METHODS

The Phantom XTL ROV has a cable connection allowing a maximum depth of 150 m and incorporates a Sony EVI-330/331/T standard-definition video camera. The cable connects to a distribution box that is in turn connected to the console for controlling the ROV. The pilot watches the camera output on a connected computer screen. Power comes from a 110 V generator connected via a small transformer to the distribution box, which passes power on to all components. Deployment of the ROV requires the assembly of the components inside a pilothouse that is subsequently lowered, along with the ROV itself, into

an inflatable outboard-propelled dinghy. The dinghy then proceeds as an autonomous unit to the selected area of investigation.

Sites were selected for their ease of access within the constraints of the schedule of the *Endeavour*. Following an itinerary approved by the Galapagos National Park, the *Endeavour* regularly travels a 15-day circuit within the Galapagos Islands, allowing for repeated visits to the selected sites. Before operating the ROV at each site, consideration is given to the depth, current and other sea conditions at the time. The ten sites chosen for routine exploration were: Punta Espinoza, Fernandina Island; Tagus Cove, Isabela Island; James Bay, Santiago Island and Bartholomew, off Santiago; Guy Fawkes Islets and the northeastern corner of Baltra, off Santa Cruz Island; Punta Cormorant and Post Office Bay, Floreana Island; León Dormido, off San Cristobal Island; Punta Suarez, Española Island. All video recordings were saved and later stored on an external hard-drive. The recordings were subsequently provided to both the Galapagos National Park and the Charles Darwin Research Station (CDRS).

The observations reported here were made during the period between April 2012 and May 2013.

RESULTS

Anthozoa: Octocorallia, Pennatulacea

Observations from the ROV have confirmed the presence of dozens of octocoral sea pens at several locations around the archipelago.

Cavernulina cf. darwini (Veretillidae). This Galapagos endemic was found at Punta Espinoza (Fernandina Island) at 43.2 m (Fig. 1, lower left), at James Bay (Santiago Island) at 39.9 m where over a dozen “individuals” (an “individual” coral meaning hereafter a colony of polyps) were repeatedly recorded over the year, and in Tagus Cove at 63.3 m, where there appear to be several dozen individuals spread over the floor of the cove.

Virgularia cf. galapagensis (Virgulariidae). Specimens very similar to this species were seen and filmed repeatedly over the year at NE Baltra Island at 75.2 m (Fig. 1, top), Guy Fawkes at 70.4 m and 80.1 m, Punta Cormorant (Floreana Island) at 42.6 m, James Bay at 39 m (Fig. 1, centre) and Tagus Cove at 55.7 m (Fig. 1, lower right) and 64.3 m. These individuals differed in coloration, from pale yellow or pink to deep red, and in the length of the polyp “leaves” off the central rachis, making the specimen appear either tall and slender or shorter and “bushy”.

Ptilosarcus cf. undulatus (Pennatulidae). Colonies resembling this rare species were found twice, in James Bay at 39.9 m on 27 February (Fig. 2) and at Bartholomew Island at 39.6 m on 21 March. The photographed specimens appeared to have peduncles of more slender dimensions than *Ptilosarcus undulatus* (Hickman 2008). The only sightings of this species since the 1982–3 El Niño were made off Wolf Island in 2006 (Hickman 2008b) and at Tagus Cove (Breedy et al. 2009).

Anthozoa: Octocorallia, Alcyonacea

Aquaumbra cf. klapferi (Aquaumbridae). The shallow sea floors off Bartholomew Island (86.8 m, 7 March; Fig. 3) and Punta Espinoza (99.6 m, 27 March) were found to have extensive colonies of an octocorallian of the order Alcyonacea resembling this species (G. Williams pers. comm.). The only previous specimens were recently collected from seamounts and canyons off Isla del Coco (Costa Rica) down to 400 m (Breedy et al. 2012). Our recordings come from a considerably shallower depth and further exploration will be required to determine whether they indeed represent *Aquaumbra klapferi*, or a new member of the Aquaumbridae.

Crustacea: Decapoda

Munida sp. (Munididae). Populations of *Munida* “squat lobsters” were found in abundance over a large area of the sea floor off Guy Fawkes at 74 m and 72.5 m on 6 and



Figure 1. *Cavernulina cf. darwini*, Pta. Espinoza, Fernandina Island (lower left) and three forms of *Virgularia cf. galapagensis*: NE Baltra Island (top), James Bay, Santiago Island (centre) and Tagus Cove, Isabela Island (lower right).



Figure 2. Sea pen (Pennatulacea) resembling *Ptilosarcus undulatus*, James Bay, Santiago Island.



Figure 3. *Aquaumbra* cf. *klapferi*. Bartholomew Island.

20 March respectively, and off Bartholomew Island at 86.8 m on 21 March (Fig. 4). Its abundance at such shallow depths is of particular note. These small animals (1–2 cm) had strikingly long, slender chelipeds that were banded orange and white. Three species of *Munida* were collected early on in the Galapagos: *M. hispida*, *M. mexicana* and *M. perlata* (Benedict 1902). Since then, *M. hispida* and *M. mexicana* have been found in the islands several times (Schmitt 1921, CAS 1995, Hendrickx 1999) at 165–500 m and 16.5–145 m depth respectively, with *M. mexicana* known as the most shallow-water species to date (Hendrickx 2000). Much deeper and rarer is *M. perlata*, of which only two specimens exist, one found in the Galapagos Islands (type specimen) and the other in the southern Gulf of California (Hendrickx 2000). Recently, more specimens of the Munididae have been collected by the CDRS in the islands and are currently under study (R. Calderón pers. comm.). Only the collection of specimens at the locations

where they were filmed by the ROV will clarify whether they belong to one of the three species already known in the islands (Hendrickx & Harvey 1999).

***Stenorhynchus debilis* (Inachidae).** A recording in Tagus Cove at 56.9 m showed what might indicate a commensal relationship of this species, the Panamic Arrow Crab, with a Blackfin Conger *Paraconger californiensis* (Fig. 5). For several minutes the crabs were filmed moving about, around and over the head and face of the eel, at times in direct contact with its eyes, eliciting no discernible reaction from the eel.

Gastropoda: Opisthobranchia

***Berthella californica* (Pleurobranchidae).** The uncommon Sidegill Slug was recorded twice: at 87.8 m off the coast of Bartholomew Island on 3 March 2013 (Fig. 6), and at Guy Fawkes Islets travelling across a sandy bottom at 72.5 m on 30 March 2013. With a Pacific Ocean distribution, *B.*

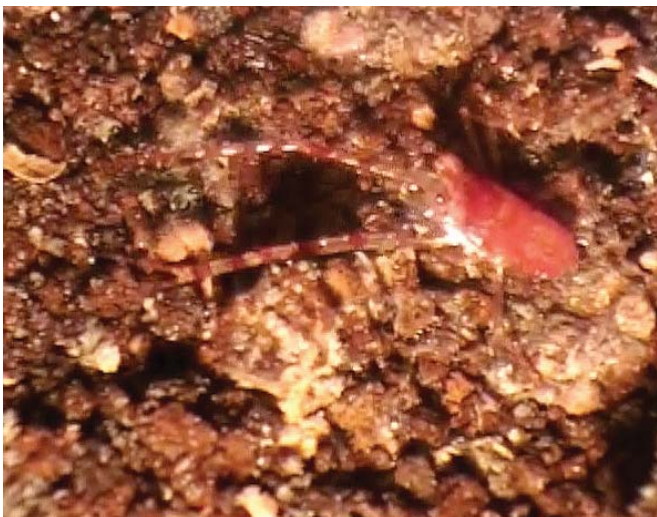


Figure 4. *Munida* sp., Bartholomew Island.



Figure 5. *Stenorhynchus debilis* on *Paraconger californiensis*, Tagus Cove, Isabela Island.



Figure 6. *Berthella californica*, Bartholomew Island.

californica has been recorded from Alaska to Galapagos, Russia and Korea, but almost exclusively in shallow waters (<<http://www.itis.gov>>, consulted 18 Apr 2014). Behrens (2004) considered its presence in Galapagos as tentative and only recently was it accepted for the islands (Hickman 2008a). It has not been recorded in recent marine surveys (S. Banks pers. comm.).

Flabellina sp. (Flabellinidae). A single recording was made of what appears to be a species of *Flabellina*, at 71.9 m off the Guy Fawkes Islets on 6 March 2013 (Fig. 7). Three species in the family (*F. telja*, *F. marcusorum* and an as yet undescribed species) are currently recognized as occurring in Galapagos (Hickman & Finet 1999), and *Flabellina* spp. are regularly recorded by CDRS annual marine biodiversity surveys (S. Banks, pers. comm.). The image captured by the ROV shows an individual with a pale rosy ground color and long cerata with pale cream-colored tips, rather than the more vibrant colors of the better-known *F. telja* and *F. marcusorum*, so it remains unidentified until further information or specimens are collected (T. Gosliner pers. comm.). The depth of this record might suggest a species other than *F. telja*, which is



Figure 7. *Flabellina* sp. Guy Fawkes Islet.

reported as having a rocky intertidal and shallow subtidal range (Hickman & Finet 1999).

Unidentified nudibranch. A large, bright red-orange nudibranch, possibly a *Dendrodoris* sp. (Dendrodorididae) (T. Gosliner pers. comm.) was recorded travelling across a sandy substrate at 65.2 m in Tagus Cove (Isabela Island), 26 February (Fig. 8). Three species of this family, in two genera, are provisionally registered in Galapagos (<<http://checklists.datazone.darwinfoundation.org/marine/>>, consulted 23 Jan 2014).



Figure 8. Unidentified nudibranch resembling *Dendrodoris* sp., Tagus Cove, Isabela Island

Chordata: Osteichthyes

Serranus stilbostigma (Serranidae). Over a period of one year starting in April 2012, the Sideblotch Bass was recorded seven times at four separate locations, with three islands providing repeated recordings. The first sighting was off the westernmost Guy Fawkes Islet at 74 m on 27 June (Fig. 9). Subsequently it was recorded off Bartholomew at 95.4 m on 28 June, in Tagus Cove at 64.3m on 26 February, off Pta Cormorant at 96 m on 4 March, again off the Guy Fawkes Islet at 71 m on 6 March, off Bartholomew at 100.5 m on 7 March, and once more in Tagus Cove at 73.1 m on 12 March. In the original description, Jordon & Bollman (1890: p. 159) wrote "color reddish brown (probably crimson in life), becoming paler beneath, breast somewhat orange". McCosker & Rosenblatt (2010) commented that they did not observe any of the red or orange coloration, and our video records mostly support this observation, although showing a slight pink tinge along the nape and on the ventral surface of the caudal peduncle. The ROV video also caught the "large creamy blotch" mentioned by McCosker & Rosenblatt (2010). This patch reflected the light from the ROV so brightly (Fig. 9, patch at mid-body; the anterior reflective area on the photo is the base of the pectoral fin) that it could be detected from a considerable distance, before



Figure 9. *Serranus stilbostigma*, Guy Fawkes Islet.

the rest of the body could be distinguished. The first specimen of *S. stilbostigma* (which was originally placed in *Prionodes*) was collected during explorations by the U.S. Fish Commission steamer *Albatross* in 1888 (Jordan & Bollman 1890). It was not seen again in Galapagos until 1995 when it was filmed by the untethered submersible Johnson-Sea-Link of the Harbor Branch Oceanography Institution. Over one seamount at 195–203 m depth, southeast of San Cristobal Island, several of these fish were photographed and filmed, and one collected (McCosker & Rosenblatt 2010). Since then, no further sightings had been made until those reported from the Endeavour ROV. *Serranus stilbostigma* is considered endemic to the Galapagos Islands. Although it was included in a list of Ecuadorian mainland marine fishes (Béarez 1996), this has since been considered to be based on a dubious record (Jiménez-Prado & Béarez 2004, P. Béarez pers. comm.).

DISCUSSION

With the regular deployment of the ROV, we have now been able to demonstrate that several species, previously thought rare, are present in several new locations and are possibly more numerous than previously thought.

The four species of Pennatulacea sea pens known in Galapagos (*Scytalium* sp., *Virgularia galapagensis*, *Ptilosarcus undulatus* and *Cavernulina darwini*) were not considered endangered prior to the 1982–3 El Niño event, yet in subsequent years only a few specimens have been found, in few locations (Breedy et al. 2009). The ROV has allowed us to record the benthic environment, population densities and distribution of *Virgularia* cf. *galapagensis*, *Cavernulina* cf. *darwini* and a species resembling *Ptilosarcus undulatus*, in several locations. The discovery of color and shape variations in what is provisionally identified as *Virgularia galapagensis* perhaps indicates the presence of other Pennatulacea in the waters of Galapagos. The genus *Cavernulina* has an Indo-Pacific distribution with

four recognized species. *C. darwini* is poorly known and its range within the archipelago just beginning to come to light. The recent ROV images suggest that its distribution is more extensive than previously known.

Berthella californica is not easily found in the archipelago and little is known of its range and ecology there. The new recordings by the ROV have added information not only about the geographical and depth range of *B. californica* within the archipelago but also of its habitat and behaviour. Similarly, despite the scarcity of previous records of *Serranus stilbostigma*, recordings by the ROV indicate that it can be found in many locations around the archipelago, with a range that extends from 64 m (this study) to at least 203 m (McCosker & Rosenblatt 2010), with preferences for sandy substrates around small rock outcrops.

One of the biggest benefits of capturing marine life on film is the discovery that the living organism is sometimes of a different coloration or pattern than was supposed from a preserved specimen, as with *Serranus stilbostigma* (McCosker & Rosenblatt 2010). Given the apparent differences of some of the organisms filmed by the ROV from the descriptions of the species with which they are provisionally identified here, future collection of Galapagos specimens of these organisms may reveal more cases of this phenomenon.

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ALF WOLLEBÆK AND THE GALAPAGOS ARCHIPELAGO'S FIRST BIOLOGICAL STATION

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SUMMARY

Much has been written on the human history of Floreana Island, but the story of its oldest standing building, a lava house in Post Office Bay, has remained untold. We determined, and demonstrate with photographs, that the structure, now 90 years old, was once a biological station: the archipelago's first. It was built by the 1925 Norwegian Zoological Expedition to the Galapagos Islands, led by Alf Wollebæk, then director of the Natural History Museum of the University of Oslo. The Galapagos portion of the expedition, which was preceded by short explorations of the West Indies and Colombia, spanned five months and five islands, and resulted in the collection of more than 500 biological specimens, the publication of over 20 articles and books, and the discovery or reclassification of several species, most notably the Galapagos Sealion *Zalophus wollebæki*. Wollebæk's accounts of the expedition were written in Norwegian, and are not well known outside Scandinavia. We provide a brief account of the expedition, a summary of Wollebæk's observations in the Galapagos, and a history of the biological station that Wollebæk and his assistant, Erling Hansen, built.

RESUMEN

Alf Wollebæk y la primera estación biológica en las Islas Galápagos. Mucho se ha escrito sobre la historia humana de la Isla Floreana pero la crónica de su edificio más antiguo aun en pie, una construcción de lava en la Bahía Post Office, permaneció en la oscuridad. Hemos determinado y demostramos con fotografías que esta estructura, que cumple ahora 90 años, fue alguna vez una estación biológica: la primera en el archipiélago. Fue construida por la Expedición Zoológica Noruega a las Islas Galápagos de 1925, bajo la dirección del entonces Director del Museo de Historia Natural de Oslo, Alf Wollebæk. El segmento de la expedición dedicado a Galápagos, que fue precedido por cortas exploraciones del Caribe y Colombia, abarcó cinco meses y cinco islas, resultando en la colección de más de 500 especímenes biológicos, la publicación de más de 20 artículos y libros, y el descubrimiento o reclasificación de varias especies, entre las cuales se destaca la del Lobo marino de Galápagos *Zalophus wollebæki*. Los relatos de Wollebæk acerca de la expedición fueron escritos en noruego y son poco conocidos fuera de Escandinavia. Proporcionamos un breve recuento de la expedición, un resumen de las observaciones de Wollebæk en Galápagos, y una crónica sobre la estación biológica que él y su asistente Erling Hansen construyeron.

INTRODUCTION

Roughly 1 km northeast of the post office barrel in Post Office Bay, Floreana Island, stand the remains of an old lava building. Tucked amongst Palo Santo trees *Bursera graveolens*, about 50 m inland from the shore, the structure is partially visible from the water, at least during the leafless dry season. Although the existence of this lava house is known to many Galapagos residents, its history has remained a mystery. It stands in the dry lowlands on the most arid side of the island, 7 km from the nearest permanent freshwater source: an impractical location for any building. What on earth was its purpose? Who built it, and when?

We photographed the structure in 1996 during a field trip to retrace Charles Darwin's movements on the island (Grant & Estes 2009), and again more recently, when we decided to investigate its origin.

We began with the only other historical building in Post Office Bay, Casa Matriz, the story of which has been elucidated in Hoff's (1985) history of Norwegians in Galapagos, which has recently been translated into English (Hoff *et al.* 2014). Casa Matriz was a large, elaborate, wooden house (complete with generator and electrical lighting) built in 1925 by Norwegian settlers attempting to establish a lucrative fishing, whaling and cattle-ranching enterprise on the island. The building is long gone but eroded remnants of its concrete pilings lie where it once stood, behind the post office barrel.

The lava house is clearly not the remains of Casa Matriz, as neither the building materials nor the location

is correct, but their history is intricately linked. The same yacht (aptly named *Floreana*) that brought ten Norwegian settlers to Floreana (Santa María) Island in August 1925, also transported the Norwegian Zoological Expedition to the Galapagos Archipelago at the same time (Hoff 1985). The expedition members were Alf Wollebæk (1879–1960), Director of the Natural History Museum of the University of Oslo (NHMO), and Erling R. Hansen (1901–53), museum preparator and taxidermist. While the colonists set up camp behind the landing beach at Post Office Bay, Wollebæk and Hansen pitched their tents on a projection of land to the east of the bay, which was dubbed "Peninsula Oslo Museum". They were later joined by John W. Nylander (1869–1949), who moved from the colonists' camp and became their cook. The scientists spent the next five months exploring the island, making biological observations and compiling an extensive collection of specimens for their museum back home. They also built a biological station.

THE BIOLOGICAL STATION

A crude property map of the island drawn by August F. Christensen (instigator of the colonization attempt) and Anton Stub (captain of the *Floreana*), and reproduced by Hoff (1985), places this "Biol. Station" in the same general area as the lava house (Fig. 1). It seemed highly likely that the buildings were one and the same, but given that Casa Matriz was built from timber, there remained the possibility that the biological station had also been a wooden structure, since disappeared. When no further clues could be extracted from Hoff *et al.* (2014), nor from Wollebæk's primary account of the expedition (Wollebæk 1934), we contacted Stein Hoff.

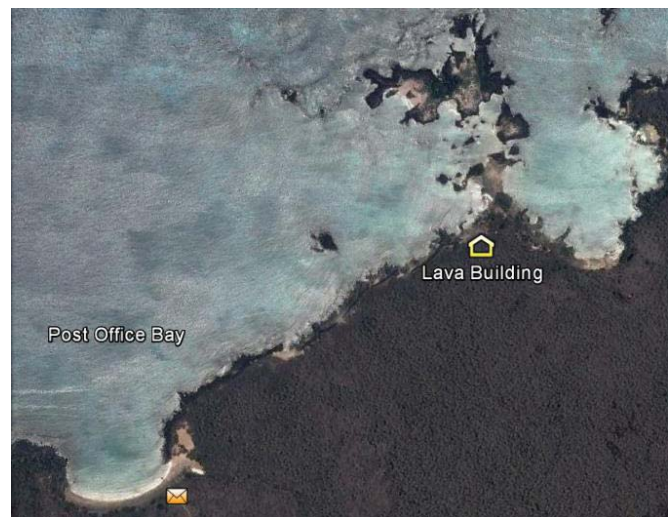


Figure 1. Left: Detail from Christensen and Stub's 1925 map of Floreana showing the location of the "Biol. Station" (approximately in the centre of the map). Numbers indicate property lots. Though not part of the colonization attempt, the scientists were also given land: number 10 was Wollebæk's land and number 4 (by Black Beach on the west of the island, not shown here) was claimed by Hansen. (Photograph courtesy of Stein Hoff). Right: Google image of the same area showing the location of the lava house ($1^{\circ}13'50.8''S$, $90^{\circ}26'34.4''W$), in relation to the post office barrel (indicated by the envelope symbol) and Casa Matriz (just inland from there).



Figure 2. The biological station, photographed by A. Wollebæk in 1925 (left, from copy of Wollebæk's photograph in collection of S. Hoff.) and G.B. Estes in 2015 (right). Note the "Mickey Mouse" configuration of three pale rocks (two large "ears" and one small "face") in the upper left corner of the main wall, in both photographs. The timbers have gone, most likely removed when Casa Matriz was dismantled by the Ecuadorian military and taken in part to Isabela, between late 1937 and early 1938 (Conway & Conway 1947)..

Hoff, it turned out, had looked for the remains of the biological station during a visit to Floreana in 1985, but had lacked the time for a thorough search (S. Hoff pers. comm.). Upon hearing of the lava house he enthusiastically produced copies of three old photographs (glass negative slides) of the building, all taken by Wollebæk, one of them unlabelled (Fig. 2) and the other two labelled "Biolog. Stasjon" (Fig. 3) or "Biolog. St." (abbreviations of Biologisk Stasjon) followed by "Floreana, Nov. 1925. AW." The photograph not reproduced here is similar to that in Fig. 3 but without Hansen. The two labelled photographs are part of a collection of memorabilia documenting Thorolf Østmoen's 1926 journey to Galapagos on board the *Ulva*, and his temporary residence on Santa Cruz Island. Wollebæk could have given Østmoen the photographs shortly after Wollebæk returned to Norway in early 1926, before Østmoen departed for Galapagos in May of the same year, but alternatively they may have changed hands years later, when Østmoen was back in Norway. Østmoen's collection was acquired by Hoff and is now housed in the archives of Drammen, Norway.

Independently, we uncovered a fourth photograph, published by Wollebæk (1926), with a caption reading "Den biologiske stasjon — i Post office Bay, Santa Maria. Stasjonen er bygget av lavablokker ifjor høst." (The biological station — in Post Office Bay, Santa María. The station was built from lava blocks last autumn.). There was our answer. All we needed now was to compare Wollebæk's photographs to our own. The size, shape and placement of individual lava blocks in the lava house and the biological station were a match (Fig. 2).

The building consists of a single room measuring roughly 3 × 4 m on the inside, and currently standing <1.8 m tall. There is a doorway in the middle of the inland-facing wall, and two window holes in the opposite wall, looking northwest towards the sea. A low outer wall runs parallel to this side of the house, and appears to surround

a 2 m wide garden or patio, but actually disguises an L-shaped lava ramp. This ramp begins at ground level on



Figure 3. The biological station, with Erling Hansen (identified by S. Hoff) seated to the left, in November 1925. (Photograph courtesy of Stein Hoff.)

the southwest side of the building and angles up along the northwestern wall, underneath the windows; it may have facilitated construction.

With walls two to three lava blocks thick, the biological station was clearly built to last. Though Wollebæk and Hansen were only on the island for a few months, they intended the biological station to be used after their departure: through Christensen, in a popular, multi-authored book on Galapagos, they extended an open invitation to future visiting scientists to use the building as they wished (Christensen 1926). However, the building may never have been completed. Wollebæk's four photographs (all showing the northwest side of the house) show a skeleton roof, made from wooden planks perhaps left over from Casa Matriz, with plenty of gaps. Rough-hewn timbers comprise the jambs for the windows, which are otherwise open to the air (Fig. 3). With the collapse of the colonization attempt in late 1926, due to economic woes (Hoff 1985), timber to finish the building apparently never came.

ALF WOLLEBÆK'S NORWEGIAN ZOOLOGICAL EXPEDITION

Wollebæk's writings have not been published in English, and as a result his exploits have been under-appreciated in the English-speaking world. He is, however, recognized in the scientific name of the Galapagos Sealion *Zalophus wollebæki*. His collection of two sealions (at the time lumped with Southern Sealion under the name *Otari jubata*) were examined by a specialist and described as a distinct species (Sivertsen 1953). Aside from his Galapagos work, Wollebæk's research on Norwegian fishes, oysters, whales, seals and reindeer, and on North European polychaete worms, made him one of Norway's most respected zoologists, and earned him the King's Medal of Merit in gold in 1959 (Nissen, H. 2009 <https://nbl.snl.no/Alf_Wolleb%C3%A6k>, consulted 5 Mar 2015). His expedition to the Galapagos Islands also took him to the West Indies and South American continent, and resulted in the description of over a dozen new or reclassified species (Bøckman 2009), 15 taxonomic papers (Banks 1931, Curran 1932, Soot-Ryen 1932, Stach 1932, Stitz 1932, Augner 1933, Meise 1933, Sivertsen 1933, 1953, Stejneger 1933, Barber 1934, Esben-Petersen 1934, Hebard 1934, Schulze 1936, Bergenhyn 1937), four geographically-themed articles (Wollebæk 1926, 1927, 1935, 1936) and two books (Wollebæk 1932, 1934).

The expedition's itinerary was as follows. In March 1925, after prearranging a rendezvous with the *Floreana* (and Hansen) in Guayaquil in the middle of that year (Anon 1925), Wollebæk headed from Oslo to Antwerp for passage to the Caribbean (Wollebæk 1932). April was spent exploring Martinique, Puerto Rico, the Dominican Republic and Haiti. In early May he continued south to Baranquilla, Colombia, and in late May detoured east to explore Curaçao (Wollebæk 1934, 1935). At the beginning of June he passed through the Panama Canal (Wollebæk

1935, 1936), and continued his exploration of Colombia in Buenaventura, Cali and the Cauca valley (Wollebæk 1932). He then headed to Ecuador, to take his voyage to Galapagos. The *Floreana* arrived at Guayaquil late, on 10 July, and paperwork delays kept it docked for another two weeks. Finally, on 24 July, Wollebæk, Hansen, Nylander (who intended to study and write about the colonization attempt), Christensen and the colonists departed for Galapagos (Wollebæk 1927, Hoff 1985).

Currents pulled the ship further north than intended, so the first "enchanted isle" Wollebæk laid eyes upon, on 2 August, was Genovesa (Wollebæk 1934). The men did not land, but while circumnavigating the island, a pair of Lava Gulls *Leucophaeus fuliginosus* flew out to the ship, and Wollebæk bagged his first Galapagos specimens. He would later collect nine more Lava Gulls on Floreana, where they were attracted to the fishing activities of the Norwegian colonists, but where they are almost never seen today. The next day was spent on San Cristóbal, as guests of Manuel A. Cobos Jr. On 4 August the *Floreana* proceeded to its island namesake, anchoring at Black Beach. While Wollebæk and Hansen spent the next day exploring the highlands of their new island home, the colonists decided the harbour was too choppy for their fish processing scheme. On 6 August they all continued on to Villamil, on Isabela Island, where, Wollebæk noted, every house contained a small pet tortoise *Chelonoidis* sp. but none could be found in the wild. Their next stop, on 7 August, was Academy Bay, Santa Cruz Island, where the colonists filled their large water tanks with drinking water (and more than a few *Macrobrachium* shrimp) from a brackish well in the area now known as Pelican Bay. There, to the delight of a small party of resident Ecuadorian fishermen, Wollebæk shot four Galapagos Hawks *Buteo galapagoensis* (now extinct as a breeding species on Santa Cruz) which were so infested with itchy "lice" that after preparing the skins, the scientists were forced to strip off their clothes and wash with alcohol. On 8 August they motored around the island to Conway Bay, where Wollebæk collected both Marine Iguanas *Amblyrhynchus cristatus* and Land Iguanas *Conolophus subcristatus*. By 10 August they were back at Floreana, this time at Post Office Bay. Not only was Post Office Bay calmer than Black Beach, but here the colonists could expect a stream of freshwater to flow during the rainy season; or so they hoped. There was certainly a promising river bed at the northeast end of the landing beach, which they christened *Wollebæken*, meaning "the hillside creek". Unfortunately, it would run just once, and then all too fleetingly, during their stay. The colonists claimed the beach for their enterprise and Wollebæk and Hansen moved to the peninsula, their home base until the end of the year. On 28 Dec 1925 the scientists returned to San Cristóbal, in the first downpour of the season, saw in the New Year, and headed home to Norway (Wollebæk 1934).

Wollebæk's account of his experiences on Floreana Island paints an idyllic, if somewhat frontier-flavoured,

time on the island (Wollebæk 1934). The scientists' camp, consisting of several large canvas tents and an open, low-walled lava kitchen partially shaded with saplings (Fig. 4), was situated in a picturesque area behind a beach adorned with "carpets of bright red beach plants" (*Sesuvium edmondstonii*) and overlooking a series of "glorious small islets with groups of tall-stemmed cactus trees, green

on coal black lava rock, surrounded by light, fine sandy beaches with ornate imprints of waves" (all quotes here and below translated from the Norwegian by K.T. Grant, checked by S. Hoff). It was also right next to a thriving sealion colony, which took some getting used to. The first, sleepless, nights were spent listening to thunderous surf accompanied by "the most awful roaring as well



Figure 4. Top left: The scientists' camp at "Peninsula Oslo Museum", with Hansen, Wollebæk and Nylander, most likely photographed by Christensen (photograph courtesy of Hvalfangstmuseet, Sandefjord, Norway). Top right: Nylander drying dishes in the kitchen. Bottom: Wollebæk smoking a pipe of "Garter Mixture" with the kitchen in the background. (Photographs top right and bottom from Wollebæk's collection, courtesy of Stein Hoff.)

as dogs barking and growling, goats bleating, people sighing and retching in terrible seasickness". They even imagined the distorted music of sealions on the reef as the "death rattle from people fighting their last battle against ocean waves". Later, a large male sealion regularly took "night quarters outside the tents and sent his loathsome roar through the tent door, a not exactly pleasant way to be woken". Otherwise Wollebæk found the pinnipeds fascinating, and dedicated many hours to observing their entertaining behaviour: tossing fish in the air, shooting through the water "at lightning speed" before suddenly stopping and spinning around, porpoising after the colonists' small fishing skiff, and rolling back and forth on the beach to cover themselves with wet sand: a trick for evading flies, which the scientists soon learned to mimic (Wollebæk 1934).

In exploring the island, the men frequently came across evidence of past visitors. In Post Office Bay, Wollebæk found a rusty German "mauser rifle", apparently of a type dating from World War I, along with a plethora of cartridges (mostly spent). At the lower spring ("Wolf's Source") above Black Beach, he and the colonists rediscovered a "magnificent fig tree" that Carl Skogman, officer aboard the Swedish frigate *Eugenie*, had found growing there in May 1852, and which now (in 1925) had numerous initials of subsequent visitors cut into its bark (Wollebæk 1934). In the highlands they came across a bamboo hut with a corrugated iron roof, built by the "Chilean" companion of two Norwegian journalists, Per Bang and Jens Aschehaug, who had lived in a nearby cave for four months. In a cliff above this cave Wollebæk found the year of their stay, 1922, carved alongside a much earlier date, "1689" (Wollebæk 1934). Wollebæk guessed this older engraving was the handiwork of pirate captain (Edward) Davis, but if so he misread the last digit, for 1687 was the last year Davis was in Galapagos (Beebe 1924). According to Hoff (1985), colonist Martin Skarass recorded the date of the engraving as 1648, so perhaps Wollebæk or Skarass misread the last two digits. We have been unable to find any such 17th or 20th century engravings near the cave, and suspect they may have been eroded away or covered with vegetation. There is, however, a legible 19th century date in the vicinity, reading 1868, and cut into the overhang above the fresh-water seep, about 50 m from the cave (Fig. 5). This date is preceded by the letters "TL" and was almost certainly engraved by long-term Galapagos resident Thomas Levick, whom Wollebæk knew by his adopted pseudonym "Mr. Johnson from London" (Wollebæk 1934). According to scientist Joseph Hunter (1906), 1868 was the year "Captain Levick" arrived in Galapagos. At the time he may have been captaining a small ship owned by orchilla-hunter José Valdizán (Bognoly & Espinosa 1918). Although Wollebæk did not record seeing Levick's carving, he did meet the legendary man. In August 1925, Levick, then 83 years old and living as retired lighthouse keeper on San Cristóbal, piloted the Norwegian colonists around some of the Galapagos

islands before they settled down on Floreana. During their stop at Academy Bay on 7 August, Wollebæk ventured into the highlands of Santa Cruz by following the remnants of an old "road" that Levick claimed he had built for Manuel Cobos Sr. in 1870, before Cobos established his colony on San Cristóbal. Levick lived with the Norwegians for a short time at Post Office Bay, then returned to San Cristóbal where he died soon after (Wollebæk 1934).

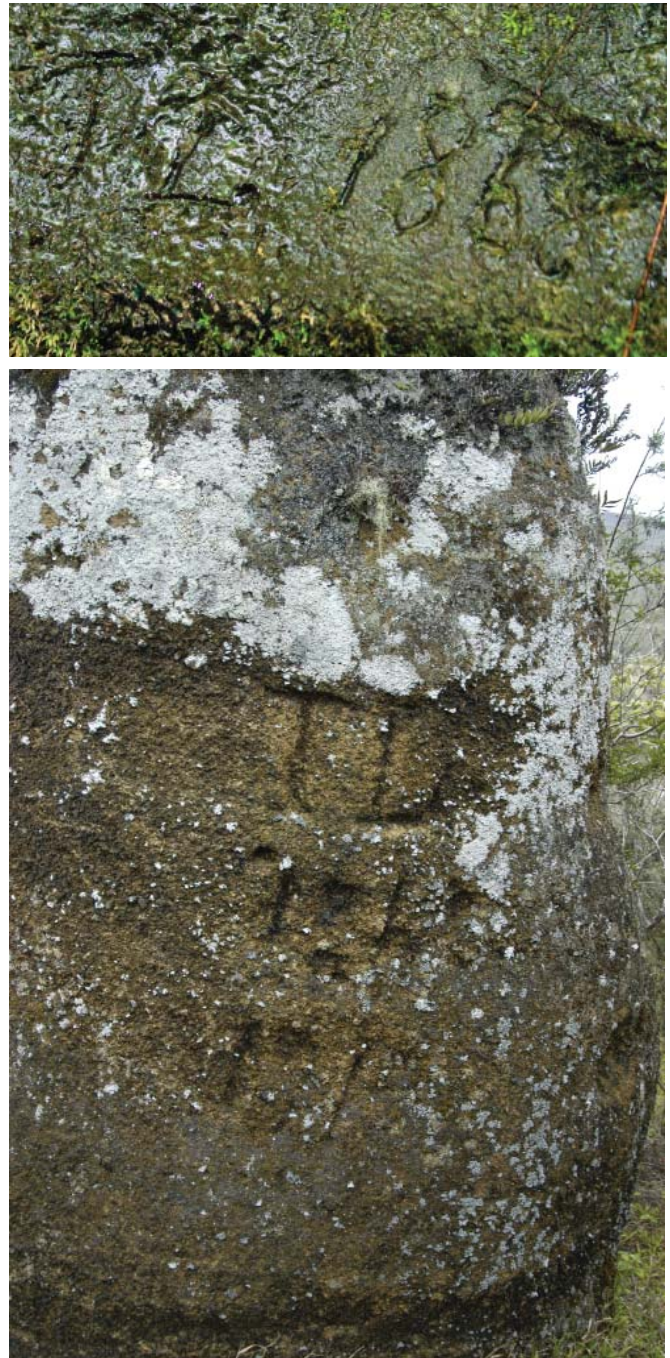


Figure 5. Top: "TL 1868" engraved at the upper spring on Floreana, probably by Thomas Levick (photograph: G.B. Estes). Bottom: the same initials, carved in similar style above some illegible marks, on a nearby cinder outcrop (photograph courtesy of John Woram).

By the time Wollebæk arrived, Floreana's long human history had already seen the endemic tortoise *Chelonoidis nigra* and Floreana Mockingbird *Mimus trifasciatus* become extinct on the island, replaced by a large array of introduced species, many edible. As a result the men were able to live largely off the island. Daily catches of (native) fish were supplemented with introduced oranges and lemons picked from the highlands, and frequent meals of feral beef, pork, goat and even donkey, shot with the same Mauser C96 pistol Wollebæk used to obtain specimens (Wollebæk 1934, Bøckman 2009).

Wollebæk certainly spun a number of "bloody" hunting yarns in his book, but his natural history observations were written in a style befitting both a zoologist and a poet (Wollebæk 1934). There were "radiantly beautiful sunsets" off Daylight Point (the western extremity of Post Office Bay), evenings spent admiring Whimbrels *Numenius phaeopus* descending from the highlands to settle on the flamingo lagoon at Punta Cormorant, dramatic scenes of Blue-footed Boobies *Sula nebouxii*, plunging like vertical harpoons from a height of "40–50 meters" into the water below. There were unusual occurrences, too: a Sperm Whale *Physeter microcephalus* entered the bay for an hour prompting Wollebæk to regret wryly that he had "no implement to take it, nor glass large enough to preserve it". While filling a drinking flask with water from a pool in the highlands, Wollebæk found it teemed with tiny crustaceans. "It is one of the few bitter reminiscences from my sojourn on these islands", he lamented, "that my hunting companion swallowed the whole flask's content in his thirst, forgetting the moment. When we some time later came back to the place, the puddles had disappeared away, dried and overgrown; I brought no *Daphnia* home with me." These crustaceans may have been *Eulimnadia*, as *Daphnia* is not known from Galapagos.

Despite the intriguing wildlife and stunning scenery, island life was not without its discomforts. In the highlands there were feral dogs, dangerous herds of cattle, and in one place where they camped a night, "tiny yellow ants" with burning stings, not collected but descriptive of the fire ant *Wasmannia auropunctata*, which was not otherwise reported from Floreana until 1972, although collected on Santa Cruz in 1905 (Herrera & Causton 2008). In the lowlands, there were relentless clouds of flies (eye, house and horse), and other pesky insects. "A horrid guest came tonight," he wrote in his diary for 16 December, "When I came out this morning, the whole tent roof and walls were covered with termites" (Wollebæk 1934). It was a complete surprise, for nowhere on the island had he found the kind of termite nests that had been so large and prominent in the trees of Curaçao. The enormous bloom of sexually mature adults (not identified but most likely the endemic *Cryptotermes darwini*: Light 1935) writhed about in a confetti of their own discarded wings and, while Wollebæk dusted off the tent in disgust, "tame" finches gorged on the feast. But all this was nothing compared to the mosquitoes. Bivouacking one night at the edge of the

flamingo lagoon, Wollebæk found the only way to survive the incessant onslaught of mosquitoes was to cocoon himself in his sleeping bag, and smoke a pipe of "Garther Mixture" (a Norwegian brand of tobacco), throughout the night. Finally there was the isolation. Despite having a dozen Norwegian neighbours, the men found themselves longing for news from home. They had almost no outside visitors. A letter Wollebæk dropped through the "teeth" of the post office barrel in early August remained there for the duration of his stay.

As for the biological station, not much is known. Despite publishing extensively on the expedition, Wollebæk only mentioned the building once, in the first article he wrote upon his return to Norway (Wollebæk 1926). His assistant Hansen fared worse, for he was never mentioned at all. While we can only speculate as to why Hansen was never acknowledged by Wollebæk, the biological station's omission is easier to understand, for with the collapse of the Norwegian colonization attempt on Floreana, and total abandonment of the island by January 1927 (Hoff *et al.* 2014), all hopes for the biological station's future and continued property rights simply disappeared.

Nevertheless, while the expedition was in progress, the biological station was surely used (or intended to be used) as a laboratory for preparing skins and as a storage facility for Wollebæk and Hansen's specimens. The collection included the hide of an American Crocodile *Crocodylus acutus* caught in Guayaquil and hung to dry on the decks of *Floreana* (Wollebæk 1927). It also included several shrunken human heads from a "Jivaroan" (Shuar) tribe, purchased in Ecuador (Wollebæk 1934), and frogs, snakes, snails, ants, spiders and birds from the West Indies and Colombia (Stitz 1932, Wollebæk 1932, 1935, Stejneger 1933), although these may have been sent home ahead of time. The Galapagos specimens numbered well over 500 by the end of the year, of which a large number were birds: 239 specimens representing 38 species are listed in the ornithological catalogue of the NHMO. There were also 84 reptile specimens: eight young tortoises from Isabela, two Land Iguanas from Santa Cruz, eight Marine Iguanas (six from Santa Cruz, where they were common and two from Floreana, where they were rare), 19 lava lizards (*Microlophus albemarlensis* from Isabela and Santa Cruz, and *M. bivittatus* from San Cristóbal), and 47 geckos *Phyllodactylus baurii* from Floreana (Stejneger 1933, Wollebæk 1934). Then there were Wollebæk's famous sealions: the skull of a male from Floreana (Fig. 6) and the skull and skin of a female from San Cristóbal (Sivertsen 1953). Among the remaining Galapagos specimens were a number of fish (Christensen 1926) and multiple jars of invertebrates: decapod crustaceans (34 species of shrimp, crabs, lobsters) (Sivertsen 1933), molluscs (19 bivalve species and a chiton) (Soot-Ryen 1932, Bergenhyn 1937), myriapods (at least one centipede and one millipede) (Wollebæk 1934), arachnids (21 spiders, one solpugid, and a scorpion *Centruroides exsul* new to science) (Banks 1931, Meise 1933), ants (six species) (Stitz 1932), flies



Figure 6. The holotypic skull of Galapagos Sealion *Zalophus wollebaeki*, collected by Wollebæk, is housed in the NHMO. This replica, crafted by Per K. Thorsland, was presented to the Charles Darwin Research Station on 7 Nov 2014 by Professor Øystein Wiig on behalf of the museum. (Photograph: G.B. Estes.)

(26 species) (Curran 1932), orthopterans (ten species of cockroaches, grasshoppers and crickets, and one praying mantis) (Hebard 1934), neuropterans (an antlion and a lacewing) (Esben-Petersen 1934), apterygotes (two silverfish and a collembolan) (Stach 1932), true bugs (seven species, including a bed bug) (Barber 1934), polychaete worms (eight species) (Augner 1933) and ticks (at least two species) (Schulze 1936).

The Galapagos collection, though from only five islands, was enough to make any museum proud. It was also sufficient to satisfy Wollebæk's curiosity regarding the origin of life on Galapagos. He had been keen to investigate first-hand the validity of George Baur's subsidence theory: that the Galapagos Islands once comprised a single large land mass that had been connected to the mainland (Baur 1891). Wollebæk (1934) concluded that the disharmonic fauna, particularly the absence of amphibians which he searched for on Floreana (and less thoroughly on Santa Cruz and San Cristóbal), negated the idea of a land bridge to the mainland: all ancestral organisms must have arrived by air or sea. He believed, however, (and would leave it to others to invalidate) Baur's claim that Galapagos had been but one island, whose peaks form the archipelago we see today.

FROM BIOLOGICAL STATION TO PIRATE'S LAIR

After Floreana was abandoned by the Norwegian colonists, Casa Matriz became the temporary living quarters or store for a series of famous visitors and settlers. Dore and Friedrich Ritter, arriving in September 1929, used Casa Matriz to store their gear while setting up house at the lower spring above Black Beach (Strauch & Brockman 1936). Captain Paul Edvard Bruun, Knud Arends and Arthur Worm-Müller used it as home base for a short-lived (1930–1) fishing enterprise (Strauch & Brockman 1936, Hoff 1985). Heinz and Margaret Wittmer, who arrived on the island in August 1932 and moved straight to the

highlands, used Casa Matriz as a depot for receiving supplies ordered occasionally from the mainland (Strauch & Brockman 1936, Wittmer & Wittmer 1936). The Baroness Wagner-Bousquet and her escort Robert Philippson lived in Casa Matriz for the first three months (Oct–Dec 1932) of their infamous stay on the island, while their ill-used companion Rudolph Lorenz brought them freshwater from the highlands on a gruelling daily trip (Wittmer & Wittmer 1936). They then joined Lorenz in the highlands to build their "Hacienda Paraiso".

In contrast, we have found no evidence to suggest the biological station was occupied during this same period, except once. In 1934, members of Allan Hancock's third scientific expedition to the Galapagos Islands aboard the *Velero III*, hatched a plan to make a pirate-themed film featuring Floreana's by then notorious colonists, the Baroness "Empress of Galápagos" and Philippson (Palmer 1934). The setting for the farce, which would further fuel the Baroness's reputation, would be a pirate's lair, and for this, they chose "the old stone house", as Heinz Wittmer later referred to it (Wittmer & Wittmer 1936). On 29 Jan 1934 Charles Swett and Emory Johnson headed over, with the protagonists, to what we now know was the biological station, and shot the film in one day (Palmer 1934). The short, silent movie, shown widely by Allan Hancock in the months that followed and reproduced recently in the documentary *The Galápagos Affair: Satan Came to Eden* (Geller & Goldfine 2014), is well known. Many viewers will have assumed that the pirate lair was the Baroness's actual abode on Floreana. This was not the case. Others may have guessed it was a movie set, constructed by Allan Hancock's men, specifically for the film. We now know this was not true either. By matching up the placement and shape of lava rocks in the pirate's lair to those in our photographs of the lava house (this time showing the front of the house), we are able to demonstrate that the building in the film was the biological station (Fig. 7). How the members of the Norwegian Zoological Expedition to Galapagos would have reacted to their edifice of science being used for such gimmickry, we can only imagine.

EPILOGUE

The Charles Darwin Research Station (CDRS) on Santa Cruz Island, established in 1964, is the oldest operating biological station in Galapagos, but it was not the first. Thirty-five years before ground was broken for construction of the CDRS (in 1960) a small biological station was built on Floreana. The year, 1925, was nine decades after Charles Darwin set foot on the same island, and this year, 2015, marks the 90th anniversary of the Norwegian biological station's existence. It may never have been completed, nor perhaps even used much, but the legacy of the scientific work conducted by its architects lives on. Indeed, the international spirit in which it was offered to scientists "of all nations" when Wollebæk and Hansen left the island (Christensen 1926) echoes in the very



Figure 7. The Baroness and Robert Philippon in pirate costume, at the entrance to the biological station, 29 Jan 1934 (top: photograph courtesy of University of Southern California, on behalf of the USC Libraries Special Collections). The same wall (note the pattern of rocks making up the doorway), photographed by K.T. Grant in 1996 (middle) and G.B. Estes in 2015 (bottom).

foundations of the CDRS. With the building's true identity rediscovered, let's hope it stands for another 90 years.

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GIZZARD CONTENTS OF THE SMOOTH-BILLED ANI *CROTOPHAGA ANI* IN SANTA CRUZ, GALAPAGOS ISLANDS, ECUADOR

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SUMMARY

The Smooth-billed Ani *Crotophaga ani* was introduced to the Galapagos archipelago in the 1960s, since when its population has grown significantly. We studied the dietary items in the gizzards of 56 anis sampled on the island of Santa Cruz. We confirmed that the diet of *C. ani* consists primarily of invertebrates and plant material, including native species and non-native invasives. The second most abundant seed in the anis' diet was that of the highly invasive plant, *Rubus niveus*. Our findings suggest that *C. ani* poses a threat to the Galapagos ecosystem by dispersing seeds of non-native plants and by competing with other insectivorous species on the islands. Furthermore, the discovery of a Darwin's Finch nestling in the gizzard of one *C. ani* establishes direct predation by this species on native birds.

RESUMEN

Contenido de la molleja del Garrapatero aní *Crotophaga ani* en Santa Cruz, Galápagos, Ecuador. El Garrapatero aní *Crotophaga ani* fue introducido en el archipiélago de Galápagos en los años 60 y desde entonces su población ha crecido significativamente. Estudiamos los elementos dietarios en las mollejas de 56 garrapateros colectados en la isla de Santa Cruz. Confirmamos que la dieta de *C. ani* consiste principalmente de invertebrados y materia vegetal, incluyendo especies nativas e invasoras no-nativas. La segunda semilla más abundante en la dieta de los garrapateros fue la de la planta altamente invasora, *Rubus niveus*. Nuestras observaciones sugieren que *C. ani* representa una amenaza al ecosistema de Galápagos ya que dispersa semillas de plantas no-nativas y compete con otras especies insectívoras en las islas. Además, el hallazgo de un pichón de pinzón de Darwin en el gizzard de un *C. ani* establece la directa predación de esta especie sobre aves nativas.

INTRODUCTION

Many Galapagos endemic birds are threatened by loss of habitat, introduced diseases, and competition and predation from introduced species (Grant 1999, Fessl & Tebbich 2002, Deem *et al.* 2008, Wiedenfeld & Jiménez-Uzcátegui 2008, Parker 2009). Ten bird species, including Cattle Egret *Bubulcus ibis* and Smooth-billed Ani *Crotophaga ani*, have been introduced to the Galapagos (Jiménez-Uzcátegui *et al.* 2007). The Smooth-billed Ani (from here on called ani) is considered one of the most detrimental to native birds and other wildlife in the Galapagos (Rosenberg *et al.* 1990).

The ani is native to the southern regions of North America and throughout Central and South America. It frequently feeds in groups, and prefers open habitat to dense forests (Ridgely & Greenfield 2001). On the South American mainland, anis are omnivores with a diet consisting mainly of insects (*e.g.* grasshoppers, caterpillars

and moths), and occasionally small vertebrates such as baby birds, frogs and lizards; additionally plants make up an important part of their diet, especially during the dry season (<http://bna.birds.cornell.edu/bna/species/539> consulted 2 Dec 2010). On the mainland, anis are commonly attracted by the insects that live on and around livestock (Ridgely & Greenfield 2001).

Anis were first recorded in the Galapagos in the 1960s, and there were an estimated 800 birds on the island of Santa Cruz in 1984 (Ballesteros 1984, Rosenberg *et al.* 1990). The last survey of ani populations, conducted between 1986 and 1987, provided an estimate of 4800 anis on Santa Cruz and 100 on Isabela Island (Rosenberg *et al.* 1990). Anis may have been initially introduced to the archipelago to control ticks on cattle (Rosenberg *et al.* 1990). However, anis have not been observed in strong association with cattle and appear to be dispersed throughout all vegetation zones. During the 1980s, anis were recorded on nine Galapagos islands: Santa Cruz, Isabela, Daphne, Genovesa, Santiago,

Floreana, Pinzon, Santa Fe and San Cristóbal (Rosenberg *et al.* 1990). Because of perceived threats associated with anis, including competition with endemic bird species, dispersal of introduced plants and spread of avian diseases, Rosenberg *et al.* (1990) recommended that anis be eradicated from the Galapagos.

Anis have increased since the surveys of the 1980s. In 2010, 80,000 anis were estimated on Santa Cruz, with a total of 250,000 across the archipelago (VC unpubl. data). Anis apparently lack competitors and have few predators in the Galapagos, which likely contributes to their success and continued spread. The growth of the ani population and presumed threat to native biota indicate the importance of understanding the ecology and impacts of this species. As a step towards this, the objective of this study was to examine the diet of anis on Santa Cruz by analyzing the contents of their gizzards.

MATERIALS AND METHODS

Ani gizzards were gathered between 5 Nov and 8 Dec 2009. Anis were collected at six locations in the Dry, Transition and Humid vegetation zones of Santa Cruz (Table 1). The Dry Zone, characterized by low rainfall and dry woodland and scrub, extends from sea level to c. 150 m above sea level, succeeded by the denser forests of the Transition Zone, up to c. 400 m. Above the Transition Zone is the Humid Zone. Santa Cruz also has an Agricultural Zone, which is located primarily within the Transition and Humid Zones, where it has displaced much of the native vegetation (Guerrero & Tye 2009). The gizzards were collected from birds hunted by Galapagos National Park (GNP) rangers as part of a pilot study for an attempt to eradicate anis from the archipelago, and in order to determine whether the anis harbour a recently discovered *Plasmodium* sp. which affects the Galapagos Penguin *Spheniscus mendiculus* (Levin *et al.* 2009). GNP rangers, using Ruger 22 Charger Rimfire Pistols and Ruger Mini-14 Ranch Rifles (Sturm, Ruger & Co., Inc., Newport, NH), opportunistically shot anis they located in the field.

The organs, including the gizzard, of each bird retrieved were collected for necropsy by SLD. For the first 27 samples, the intact gizzards were excised from the birds and placed in small plastic Nalgene bottles in the field. For the remaining 28 samples the contents of each gizzard were extracted in the field by opening the gizzard and

placing all contents into a cryotube. Samples were kept in a cooler in the field and placed in a -20°C freezer upon returning to the lab. In cases in which the gizzard was too damaged to analyze its contents completely, significant features were recorded (*e.g.* types and numbers of seeds).

Contents were analyzed within two months of collection. Samples were thawed for at least 15 min. prior to examination. The intact gizzards were cut open and the contents extracted. LC separated the contents of each sample, in a Petri dish, into three categories: insect, plant and seed, and indistinguishable (Fig. 1), using a Nikon Field microscope Mini. Each category was then further subdivided. Seeds were separated by their appearance, given descriptive names and counted. When possible, insects were separated by their appearance, given descriptive names (*e.g.* moth, beetle, caterpillar) and counted. There were many unidentifiable insect parts. The insects were further analyzed by HWH and the seeds by AG. Insects that could be identified were classified as endemic, non-endemic native, or introduced. Seeds that were identified were classified as native (none was endemic) or introduced.

RESULTS

Gizzards from four of the anis were destroyed by the gunshot wound and thus only a brief observation was made in the field. The contents of the other 52 gizzards were fully analyzed. The majority of the contents were categorized as either invertebrates or plant material. Most of the identifiable plant material was in the form of



Figure 1. Petri dish with the separated gizzard contents of one Smooth-billed Ani. Unidentifiable matter has been removed, seeds are in the upper right and insect parts fill the majority of the lower and left of the Petri dish. (Photo: Lillian Connett.)

Table 1. Sites of Smooth-billed Ani collection on Santa Cruz Island, Galapagos.

Site Name	Coordinates (S, W)	Zone	n gizzards
Road to Garrapatero	0°40'7", 90°15'41"	Dry	13
El Mirador	0°43'57", 90°19'14"	Transition	8
Parque Artesanal	0°43'4", 90°19'49"	Transition	5
Finca de Carrión	0°41'17", 90°21'41"	Humid	17
Finca de Kastdalen	0°41'8", 90°18'53"	Humid	4
Reserva Pájaro Brujo	0°39'14", 90°24'32"	Humid	9

seeds. A few leaf and other plant pieces were detected, but they were unidentifiable. Seeds were identified in 37 birds (71 %), with a total of 5826 seeds classified. Twelve out of 13 birds (92 %) from the Dry Zone had consumed seeds, which accounted for 62 % (by number) of the total seeds found. Twelve out of 13 specimens (92 %) from the Transition Zone had consumed seeds, accounting for 19 % of all seeds found. Eleven out of 30 specimens (37 %) from the Humid Zone had consumed seeds, which accounted for 19 % of all seeds found.

Seeds from 11 plant species were recorded (Table 2), of which three were introduced species. Six species were native (Table 2). Among the introduced species, only 30 seeds from *Lantana camara* were found (from five gizzards), all in the Transition Zone. In contrast, seeds from *Rubus niveus* were numerous (1064 seeds from 11 gizzards) and primarily found in the Humid Zone, with the exception of eight seeds in one gizzard from the Transition Zone. The seeds of *Solanum pimpinellifolium* (405 seeds from eight gizzards) were all found in the Transition Zone.

Of the 3622 seeds found in the Dry Zone, 3507 were from four native species and 115 from two unidentified species. Of the 1083 seeds collected in the Transition Zone, 640 were from five native species and 443 from three introduced species. Of the 1121 seeds found in the Humid Zone, 63 were from two native species, 1056 from one introduced species and two from an unidentified *Desmodium* species. The average number of seeds per bird (of birds that had consumed seeds) was 301 in the Dry Zone, 90 in the Transition Zone and 101 in the Humid Zone.

Invertebrates were found in 51 of the 52 gizzards (98 %) (Table 3). Most fragments could not be identified, so the data in Table 3 are not representative of the scope of the

ani diet. However, 153 specimens were classified to order, including 19 specimens classified to genus level only and an additional 34 classified to species. Of the 53 specimens identified at least to genus level, 25 were classifiable as native, 17 endemic and 11 introduced. In addition to the species identified in the gizzards, HWH has seen anis eating the endemic grasshopper, *Schistocerca melanocera*.

One Darwin’s finch nestling (species undetermined) was recovered from the gizzard of an ani in the Dry Zone, on 5 Nov 2009. An ani was also recently photographed eating an introduced mouse, *Mus musculus* (Fig. 2), and B. Fessl (pers. comm.) has recorded anis eating lizards on Santa Cruz.

DISCUSSION

This study documents some effects of anis on the Galapagos flora and fauna, and confirms several earlier predictions (Rosenberg *et al.* 1990). While Rosenberg *et al.* (1990) conducted their study of gizzard contents at a similar time of year (Nov–Dec 1986), they did not find many seeds. They ranked items by weight and frequency, and seeds ranked eighth out of nine by weight and 5.5 out of nine for frequency (nine being the lowest rank for both weight and frequency). However, subsequent studies documented substantial seed consumption by anis and suggest that anis could be contributing to major ecosystem changes in the Galapagos. Guerrero & Tye (2011) found six species of seeds in the gizzards of anis, including four species found in our study (*Solanum americanum*, *Tournefortia psilotachya*, *L. camara*, and *R. niveus*). Soria Carvajal (2006), looking specifically at the dispersal of *R. niveus*, found anis to be the largest avian consumers

Table 2. Seeds identified from the gizzards of anis on Santa Cruz Island, Galapagos. Data are presented as: n seeds (n gizzards).

Seed species	Totals	Transition		Humid		
		Dry Road to Garrapatero	Parque Artesanal	El Mirador	Finca de Carrión	Finca de Kastdalen
Native species						
<i>Cordia lutea</i> Lam.	4 (2)			4 (2)		
<i>Chiococca alba</i> (L.) Hitchc.	17(2)		17 (2)			
<i>Solanum americanum</i> Mill.*	3173 (14)	2799 (7)	298 (4)	17 (1)	59 (2)	
<i>Tournefortia psilotachya</i> Kunth	992 (14)	703 (9)		289 (5)		
<i>Vallesia glabra</i> (Cav.) Link	4 (1)	4 (1)				
<i>Zanthoxylum fagara</i> (L.) Sarg.	20 (5)	1 (1)	15 (1)		4 (3)	
Total Natives	4210 (27)	3507 (12)	640 (11)	63 (4)		
Introduced species						
<i>Lantana camara</i> L.	30 (5)		12 (1)	18 (4)		
<i>Rubus niveus</i> Thunb.	1064 (11)		8 (1)		360 (4)	696 (6)
<i>Solanum pimpinellifolium</i> L.	405 (8)		260 (4)	145 (4)		
Total Introduced	1499 (19)	0	443 (9)	1056 (10)		
<i>Desmodium</i> sp.	100 (2)	98 (1)				2 (1)
Unknown species	17 (3)	17 (3)				
Total Unidentified	117 (4)	115 (3)	0	2 (1)		
Totals	5826 (35)	3622 (12)	610 (5)	473 (7)	423 (5)	698 (6)
		3622 (12)		1083 (12)		1121 (11)

*Until recently, often regarded as introduced to Galapagos, but shown to be native by Coffey *et al.* (2011).

Table 3. Invertebrates identified from the gizzards of anis on Santa Cruz Island, Galapagos. Data are n invertebrates identified (n gizzards containing given invertebrate species).

	Totals	Dry	Transition		Humid		
		Road to Garrapatero	El Mirador	Parque Artesanal	Finca de Carrión	Finca de Kastdalen	Reserva Pájaro Brujo
Native species							
<i>Xylocopa darwini</i> ¹	12 (12)	5 (5)	3 (3)	1	2 (2)		1
<i>Perepitragus fuscipes</i> ²	2 (2)		2 (2)				
<i>Neoconocephalus triops</i> ³	5 (5)	1			3 (2)		1
<i>Anaulocamera darwini</i> ³	1				1		
<i>Podisus</i> sp. ⁴	1				1		
<i>Podisus sordidus</i> ⁴	1	1					
<i>Acrosternum</i> sp. ⁴	1	1					
<i>Acrosternum viridans</i> ⁴	2 (2)	2 (2)					
Total natives	25 (19)	10 (8)	6 (5)	9 (6)			
Endemic species							
<i>Galapaganus</i> spp. ²	14 (13)	3 (3)			8 (7)		3 (3)
<i>Gryllus abditus</i> ³	1			1			
<i>Halmerus robustus</i> ³	1		1				
<i>Nesoecia cooksoni</i> ³	1	1					
Total endemics	17 (16)	4 (4)	2 (2)	11 (10)			
Introduced species							
<i>Copiphora brevicauda</i> ³	3 (3)				1		2 (2)
<i>Anasa</i> spp. ⁴	2 (2)	2 (2)					
<i>Anasa scorbutica</i> ⁴	3 (3)	3 (3)					
<i>Nezara</i> sp. ⁴	1			1			
<i>Nezara viridula</i> ⁴	2 (2)	1	1				
Total introduced	11 (10)	6 (5)	2 (2)	3 (3)			
Totals	53 (32)	20 (11)	7 (4)	3 (2)	16 (9)	0	7 (6)
		20 (11)		10 (6)		23 (15)	

Order: ¹Hymenoptera; ²Coleoptera; ³Orthoptera; ⁴Hemiptera.



Figure 2. An adult Smooth-Billed Ani with a mouse, *Mus musculus*, in its beak, on Santa Cruz Island. (Photo: Luis Die.).

of its fruit in the Galapagos, and that ani consumption of *R. niveus* remained fairly consistent in wet and dry seasons. Seeds were clearly a large part of the diet for anis in our study, with 71 % of ani gizzards having seeds, and seeds frequently making up the majority of the gizzard contents.

All three introduced plant species whose seeds we found in ani gizzards are invasive in Galapagos (Tye 2001). Most worrisome is the high number of *R. niveus* seeds identified, in three separate studies. This was the second most abundant seed found by us (> 1000 seeds), and we conclude that anis may contribute importantly to the dispersal of *R. niveus*. The plant species for which the most seeds were found (*R. niveus* and *S. americanum*) both have fruits that contain many seeds, whereas fruits of the five native species found typically have fewer seeds per fruit.

Birds contribute to the establishment of plants in new areas (Garcia *et al.* 2010, Herrera *et al.* 2010). *R. niveus* seeds collected from ani feces were viable (Soria Carvajal 2006). In contrast, very few of the *R. niveus* seeds gathered from the feces of native Galapagos birds were viable, suggesting that anis are superior dispersers of *R. niveus* (Soria Carvajal 2006). Guerrero & Tye (2011) found that most seeds recovered from the gizzards of anis were viable. These two studies also suggest that anis serve

as effective dispersers, but further data on viability of a range of seeds from ani feces would be useful.

Much of the ani's diet is composed of invertebrates, including many native and endemic species. As native and endemic invertebrate populations are stressed by competition (Causton *et al.* 2006), loss of habitat and the use of pesticides, these populations could suffer from additional pressure from an ever-growing population of anis. Furthermore, the ani's appetite for invertebrates puts it in direct competition with other birds that rely on these same invertebrates, especially during dry periods when food is short (Rosenberg *et al.* 1990).

While occasional ani predation on baby birds has been recorded before in locations in mainland South America and suspected to occur on the Galapagos Islands (Rosenberg *et al.* 1990), the Darwin's finch (Geospizinae) nestling found in this study is the first confirmation of ani predation on nestlings in the Galapagos Islands. The specimen is frozen and available for future genetic testing to determine the species, although it is probable that all Geospizinae species are predated. Our study was conducted during a dry period at the start of the nesting season for terrestrial Galapagos birds and thus few nestlings would have been available at the time. Further study of the ani's eating habits during the wet season (which is peak finch nesting season, but also the time of highest fruit and insect availability) is needed to determine if anis prefer nestlings or if they prey on them only when other food sources are limited. Either way, such predation by anis is troublesome at a time when nesting success of several native bird species is already low due largely to the introduced fly *Philornis downsi* (Fessl & Tebbich 2002, Dudaniec *et al.* 2006).

Ani predation on introduced rodents (Fig. 2) complicates the matter of eradicating the ani, as this might lead to rodent increase. Introduced rodents, such as *M. musculus*, adversely affect native Galapagos species and ecosystem functioning (Harper & Cabrera 2009). Thus, if anis are a significant predator of *M. musculus*, it may be necessary to pair efforts to eradicate the ani with similar efforts to eradicate invasive rodents.

Further information on the ani's eating habits may exist in Jara (1995) but we were unable to obtain this document.

Given the diet of the ani, their presence throughout the islands is most likely causing an impact on the Galapagos ecosystem. The spread of the seeds of invasive plants by anis may contribute to changing the landscape of the islands. Their high dietary preference for invertebrates adds stress on native birds and invertebrates in the form of competition and predation, respectively. And at a time when terrestrial bird populations are experiencing a number of threats in the Galapagos, predation by anis may be an added pressure (Fessl & Tebbich 2002, Deem *et al.* 2008, Wiedenfeld & Jiménez-Uzcátegui 2008, Parker 2009).

Although eradication of the ani will be difficult, given their numbers and wide distribution, our studies suggest it should be a priority, to ensure ecosystem health.

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GALAPAGOS COMMENTARY

THE HISTORY OF PROTHONOTARY WARBLER IN THE GALAPAGOS ISLANDS

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SUMMARY

The first and second records of Prothonotary Warbler *Protonotaria citrea* in Galapagos are clarified.

RESUMEN

La historia de Reinita protonotaria en las islas Galápagos. Esta nota aclara el primer y segundo registros de la Reinita protonotaria *Protonotaria citrea* en Galápagos.

Reck *et al.* (2010) recorded what was thought to be the first Prothonotary Warbler *Protonotaria citrea* in Galapagos, on Española Island in 2007. However, there is an earlier record from Daphne Major Island, in 1989 (Petit & Tarvin 1990), which has been overlooked in subsequent checklists (Castro & Phillips 1996, Swash & Still 2000, 2007, Wiedenfeld 2006).

Both articles describe well the distinguishing characteristics of the species, one with a photograph (Reck *et al.* 2010). Therefore, the first record of Prothonotary Warbler in the Galapagos Islands was that by Petit & Tarvin (1990), and the record of Reck *et al.* (2010) was the second. These two records were in October and January, during the northern winter when the Prothonotary Warbler migrates from North America to Central and South America (Venezuela, Colombia, Ecuador) (Meyer De Schauensee 1966, Ridgely & Greenfield 2001), and the species may best be considered a vagrant to Galapagos.

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