Observations on the breeding and distribution of Lava Gull *Leucophaeus fuliginosus*

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La Gaviota de Lava *Leucophaeus fuliginosus*, endémica del archipiélago de Galápagos, es la gaviota más rara del mundo, cuyos hábitos de reproducción son poco conocidos. En los años 2011 y 2012 se observó anidación en la isla Genovesa en densidades mayores a las reportadas previamente en Galápagos. Las parejas reproductoras fueron muy territoriales, defendiendo áreas de hasta 70 m de diámetro contra coespecíficos. Las hembras fueron más agresivas que los machos frente a los intrusos de otras especias percibidos como una amenaza. La nidada de 1–2 huevos fue incubada por ambos miembros de la pareja en turnos de dos horas. Los polluelos salieron del nido 4–5 días después de la eclosión, seleccionando en el territorio lugares más protegidos a los cuales retornaron regularmente para descansar. Los adultos reproductores fueron depredadores oportunistas, alimentando a sus crías principalmente con huevos y polluelos de aves marinas y peces robados de las mismas aves. Reconocemos una relación parasítica entre la cleptoparásita Fragata Real *Fregata magnificens* y la Gaviota de Lava, y sospechamos que este es el medio principal por el cual en esta isla las gaviotas adquieren los peces que comen. Presentamos datos sobre las comunicaciones entre los padres y la cría, proporcionamos la primera serie de fotografías del desarrollo del polluelo de Gaviota de Lava y describimos una característica en el plumaje de los adultos que no ha sido descrita previamente. Clarificamos la distribución del área de reproducción de la Gaviota de Lava en todo el archipiélago mediante la recopilación de registros de anidación obtenidos de observadores independientes e informes históricos. Se determinó un total poblacional de 20–29 individuos en Genovesa. Proponemos una estimación revisada de 300–600 individuos para su población global.

Lava Gull *Leucophaeus fuliginosus* is endemic to Galápagos, and the rarest gull in the world. Exact population size is unknown, but is often estimated at 300–400 pairs, extrapolated from counts made on Santa Cruz Island in 1963, but generally considered to be too high[31]. It faces a variety of anthropogenic threats[15,34] and is considered Vulnerable[7].

Unsurprisingly for a rare bird, little is known concerning its breeding habits. Since the first nest was found in 1960[3] (120 years after the species' description[16]), breeding data have been sparse. In 1963–64 a banding study was conducted around Academy Bay, Santa Cruz, and the resulting paper included a history of nest sightings to date[31], namely 12 egg-laying records from four territories (one on Isabela Island, two on Santa Cruz and one on the islet of Caamaño, off Santa Cruz). A second study conducted four decades later, also on Santa Cruz, produced three more egg-laying records[1]. Based on these studies, we know that Lava Gull is a solitary breeder, laying 1–2 mottled, olive-green eggs close to water, often near lagoons or on offshore islets, either on rocky outcrops or directly on sand. Incubation in one case occupied 32–33 days and fledging occurred c.60 days later. Eggs have been found in various months, indicating an opportunistic breeding system typical of many Galápagos seabirds, with individual cycles of 9–12 months[1,30,31]. While some observations on moult, adult vocalisations, feeding and the influence of human activity on local distributions were also reported, data are still lacking on many aspects of the species' breeding biology. As few nests have been monitored (only intermittently), and several failed, nothing has been published on nest construction, behaviour at the nest, parent-chick communication and chick provisioning. Other than an allusion to 'an animated chop bone'[24] and reference to its speckled down[21], the chick has never been fully described, and just one known photograph has been published[21]. Both previous studies were conducted in areas heavily impacted by humans and introduced taxa, and almost nothing is known concerning breeding on uninhabited islands[24,32]. Its breeding range throughout the archipelago is poorly defined.

In 2011–12 we found Lava Gulls nesting on Genovesa Island at unusually high densities. Elsewhere in the archipelago no more than three active nests have ever been found simultaneously, all of them >3 km apart[1,31]. On Genovesa up to five nests were concurrently active along a 1.5 km-stretch of coast and all were 100–500 m apart. Here we record our observations on these nests, provide photographs of the chicks at various stages of development and describe a plumage characteristic missing from previous descriptions of Lava Gull. We also make comparisons with

other gull species, principally its closest relatives: Franklin's *L. pipixcan*, Laughing *L. atricilla*, Dolphin *L. scoresbii* and Grey Gulls *L. modestus*[25]. Finally, we provide a multi-island list of Lava Gull nest sites, based on observations over the last 50 years, discuss the species' geographical range, and propose a revised population estimate for the archipelago.

Study site and Methods

Genovesa is a small (14 km^2), low (64 m), uninhabited island in the north-east corner of the Galápagos archipelago[20]. It contains two collapsed calderas; one forms a large bay (Darwin Bay) and the other a hyper-saline inland lake (Lake Arcturus). While much of the coastline is characterised by high cliffs, c.1.5 km of patchy beach habitat is found in the bay, and on the outer eastern and western sides of the island. Genovesa has no introduced mammals and supports large colonies of native seabirds. Red-footed Booby *Sula sula websteri* and Magnificent Frigatebird *Fregata magnificens* nest within *Bursera graveolens* forests covering much of the island. Nazca Booby *Sula granti*, Great Frigatebird *Fregata minor ridgwayi*, Red-billed Tropicbird *Phaethon aethereus mesonauta*, Swallow-tailed Gull *Creagrus furcatus*, Wedge-rumped Storm Petrel *Oceanodroma t. tethys*, Band-rumped Storm Petrel *O. castro* and Galápagos Shearwater *Puffinus subalaris* nest primarily around the coast. The main predator is Short-eared Owl *Asio flammeus galapagoensis*.

We made observations on Genovesa primarily from 26 July to 15 August 2011, and 20 July to 15 August 2012 while camped on the island for other studies (SPNG Projects #PC-36-11, #PC-13-06). Additional observations were made on Genovesa during visits of 1–90 days' duration in 1978–82 (KTG) and 1982–2014 (KTG, GBE), and on Santa Cruz in 2012–14 (KTG, OHE, GBE).

In 2011–12 we undertook a Lava Gull census by counting all individuals observed on coastal walks around Genovesa. Double-counting was avoided by positioning observers on different beaches, and maintaining radio contact. Progeny in nests were excluded. Counts were made on 7 and 9 August 2011, and on 5 and 8 August 2012.

All Lava Gull nests were located by the second day after arrival on the island, and their positions were recorded using a Garmin GPS. As gull chicks tend to wander from their natal area, 'nest' is loosely defined here to include parent-attended chicks away from the original egg-laying site. Nests were checked every 1–3 days. In 2011–12, 68 person-hours were spent observing nests during 44 nest watches. Nest watches involved 1–2 observers and lasted 1–3 hours (mean = 1.6 hours), between 05h45 and 17h30. Disturbance was avoided by sitting or lying on the ground, as adoption of a more elevated position provoked alarm calls by the attendant adults. Observations were made at a distance of 3–10 m, using binoculars.

As Lava Gull exploits other breeding seabirds for food, seabird densities in the Genovesa study area were also assessed. Nazca Booby and Great Frigatebird nests were counted in four 50 × 50 m quadrats in the vicinity of Lava Gull nests, and Swallow-tailed Gull nests in three 100 × 25 m quadrats along the shoreline, where densities were highest. Red-billed Tropicbird was not counted but densities were broadly similar to Great Frigatebird. Red-footed Booby nests were counted along a 2,000 × 20 m transect inland of Lava Gull nests. Counts were made during the first week of August 2011 and 2012. In 2011, seabird nesting was synchronous, with many eggs and young chicks. In 2012, Nazca Booby was mostly in courtship, Great Frigatebird had young chicks and Swallow-tailed Gull was completing its breeding cycle, with only older chicks and juveniles present. Red-footed Booby was in all stages of breeding in both years.

No birds were handled or marked. One gull with a metal band on its left leg (AVISE band 865-38457) had been ringed as an immature in March 2006 on Santa Cruz[1]. This individual was identified as a female when found nesting on Genovesa in July 2011.

Males were distinguished from females by size, with males always being larger, both from observed copulations and published measurements of specimens[13]. Additional sexually dimorphic features were sought and evaluated for their usefulness in distinguishing the sexes in the field.

Chicks were photographed daily. Chicks that had hatched prior to the study were aged by comparing their plumage to photographs of chicks of known age. Plumage changes in a fledged juvenile were also recorded. The following terminology is used: a 'chick' is a young, dependent gull unable to fly; a 'juvenile' is a dependent fledgling with juvenile plumage, able to fly; an 'immature' is an independent brownish-grey bird that has lost its juvenile plumage; a 'subadult' has basic adult plumage that is still poorly defined.

Information on Lava Gull distribution and nesting elsewhere in the archipelago was obtained using a targeted citizen science approach. We selected and interviewed (in person or by e-mail) 154 people considered likely to have encountered a Lava Gull nest due either to the nature of their work and / or them having spent long periods living in different areas of the archipelago. The interviewees (research scientists, naturalist guides, Galápagos National Park employees, and long-term residents with an interest in natural history) were questioned about Lava Gull sightings and nesting observations. As Lava Gulls sitting in proximity

to beach vegetation can give a false impression of nesting, reports of incubating gulls had to be supported by evidence. Direct visualisation of eggs or chicks, intense alarm calls from a sitting gull upon approach, and 'dive-bombing' defence behaviour were regarded as verification. Juveniles begging from an attending adult were also recorded as a 'nest', but immature gulls, which fly longer distances from their natal territory were excluded.

Approximately one-third (50) of the interviewees had observed plausible evidence of nesting, with 19 having recorded nesting more than once. Whilst none of the reports could be confirmed, multiple reports from the same site were considered a reliable indication of nesting. Information obtained from this survey is indicated SURV. Observations made solely by one of the authors is distinguished with his or her initials (KTG, OHE, GBE).

Results

Physical characteristics.—The plumage of adult Lava Gull is almost entirely grey and black, with white eye-crescents and upper- and undertail-coverts, and whitish feather tips forming a narrow secondary bar, scapular crescent and tertial crescent[11,13,19,23,26,31]. A line of white marginal-coverts also defines the leading edge of the wing. This feature has not previously been included in descriptions of Lava Gull, presumably because it is usually hidden by the breast and flank feathers. Nonetheless, it is highly visible during territorial displays (Fig. 1) and when birds are incubating or standing over young chicks (Fig. 2), as well as in flight.

The following sexually dimorphic features were observed. Compared to the female, the male has browner cast to upperparts, possibly attributable to age and moult. Males stand taller, are more robust, with a stouter bill base, and a more gently sloping forehead and occiput (Fig. 3). Although subtle, these differences are sufficient to distinguish the sexes when a pair is seen together. While morphometric measurements of live gulls will be needed to quantify size differences, initial observations suggest that tarsus length, chest circumference, bill depth and head length may be the most reliable characters for distinguishing the sexes in the field. Bill length appears to be more variable, and is not considered useful for sexing Lava Gulls.

Chick development.—Fig. 4 illustrates plumage development from hatching to fledging. Newly hatched chicks are mottled with grey, beige and black down. Tip of culmen salmon-pink, but barely extends to mandible. By the middle of the third week this colour is no longer evident. Egg tooth disappears by day five. Feather pins are visible in the wings by the second week. Unsheathed scapulars and median coverts are visible in the third week. In weeks 4–5, feathers appear on the head, and by week six the chick has lost almost all of its down. One chick observed on Santa Cruz flew short (<5 m) distances by the end of week seven. It fledged (flew c.200 m from its natal territory and did not return) on day 55 (7.5 weeks), but continued to be attended by parents. Wing and tail feathers were close to full length by day 69, when it was last observed.

Local distribution and population numbers.—In order of decreasing densities, Lava Gull was found on beaches on the west coast, east coast, within

Figure 1. A pair of Lava Gulls *Leucophaeus fuliginosus* defending their territory (K. Thalia Grant)

Figure 2. The white line along the curve of the wing contrasts against the dark plumage of the adult gull. It is visible when gulls are incubating, and can help distinguish nesting gulls (above) from resting gulls (bottom) (K. Thalia Grant)

Table 1. Nest records from territories 1–9. Dates are based on a 32-day incubation period[31] and 55-day fledging date. Juveniles were aged based on the appearance of grey scapulars, which replace the juvenile feathers at a crudely estimated 115 days[31]. Natal territories for fledged juveniles could not be confirmed and are indicated with a question mark following the territory in which the juveniles were most frequently observed. Observed dates in bold type. Extrapolated dates in italics.

Territory	Distance from sea (m)	Clutch size	Found as	Date of egg laying	Date of hatching	Date of fledging	Comments
1979							
8	10	1	Egg	**31 May<7 June**	2<10 July		Died 10<20 July
9	35	2	Eggs	*3<20 July*	*3<21 Aug*	*26 Sept<14 Oct*	Found with eggs 20 July and 4 Aug
2010							
3	10	1	Chick	*31 May*	*1 July*	*25 Aug*	Found when ten days old
6	35	2	Eggs	*8 June<11 July*	10 July <12 Aug	3 Sept <1 Oct	
2011							
1	5	2	Eggs	*1 July; 3 July*	**1 Aug; 3 Aug**	*24<26 Sept*	
2	10	2	Eggs	*7 July*	**7 Aug**	*1 Oct*	
3	10	1	Chick	*23 May*	*24 June*		Died 8 Aug
5	25	1	Egg	*1 July*	**1 Aug**	*25 Sept*	
6	30	2	Eggs	**31 July; 2 Aug**	*2 Sept*	*26 Oct*	First egg hatched 1 Aug
2012							
1	5	1	Chick	*28 May*	*29 June*		Died 30 July
2	10	2	Eggs	*6 July; 7 July*	**7 Aug; 8 Aug**	*2 Oct; 3 Oct*	
4?	*25–50*	1	Juvenile	*15 March*	*15 April*	*9 June*	Found c.100 days old.
7	*40–50*	2	Chicks	*1 June*	*2 July*	*26 Aug*	
2013							
1	*5*	2	Chicks	*Dec 2012*	*Jan 2013*		Found dead c.30 and c.40 days old.
2	5	2	Eggs	*29 June<31 July*	*1<31 Aug*	*24 Sept <25 Oct*	
2014							
2	15	2	Eggs	*2 June<1 July*	*3 July<3 Aug*		
6	30	1	Chick	*17 March*	*18 April*	*12 June*	
4?	?	1	Juvenile	*23 Jan*	*23 Feb*	*18 May*	Found c.130 days old

Figure 3. A pair of breeding Lava Gulls *Leucophaeus fuliginosus*; the female is closest to the camera (K. Thalia Grant)

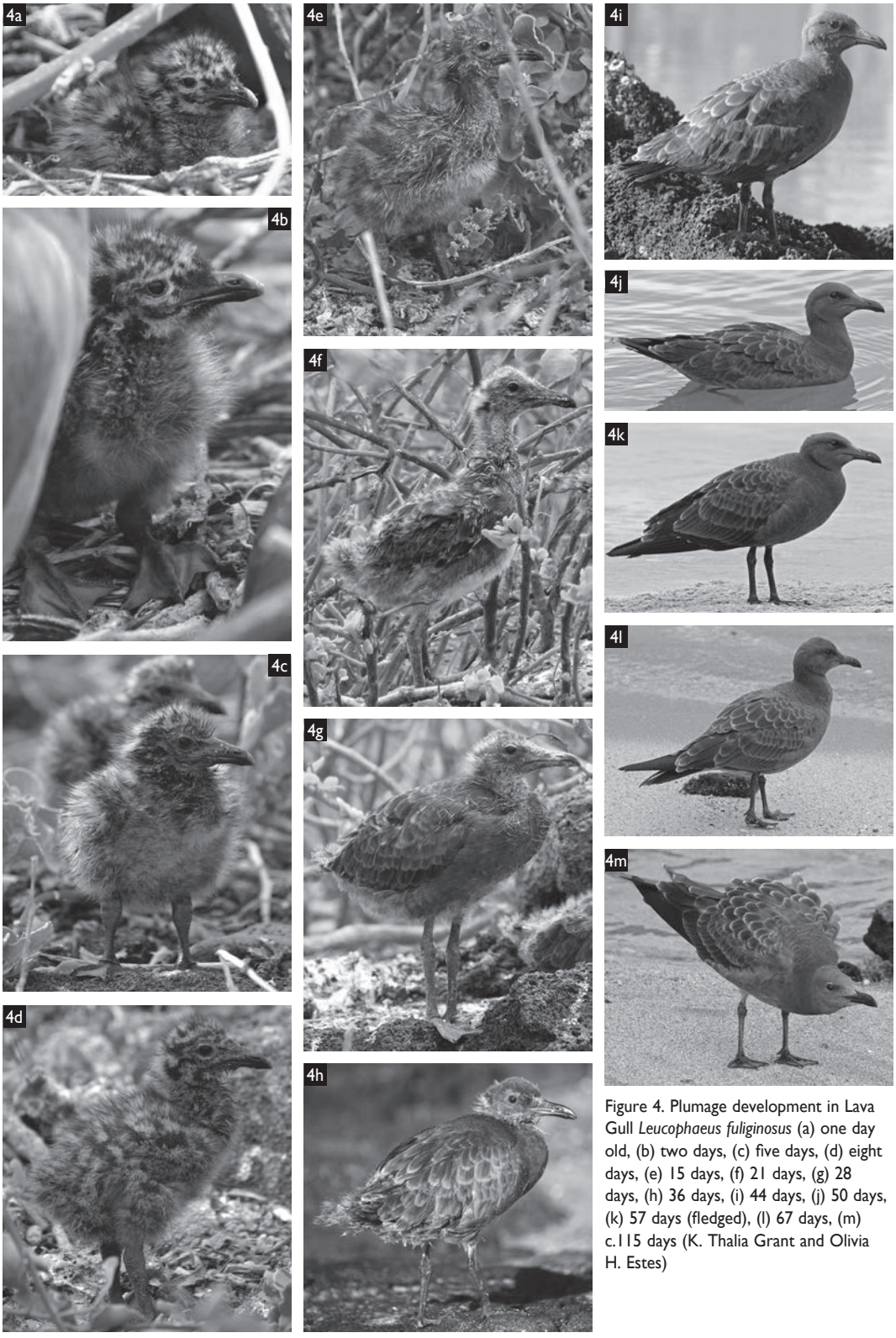


Figure 4. Plumage development in Lava Gull *Leucophaeus fuliginosus* (a) one day old, (b) two days, (c) five days, (d) eight days, (e) 15 days, (f) 21 days, (g) 28 days, (h) 36 days, (i) 44 days, (j) 50 days, (k) 57 days (fledged), (l) 67 days, (m) c.115 days (K. Thalia Grant and Olivia H. Estes)

Darwin Bay and the north-east shore of Lake Arcturus. Mostly immature and subadult gulls were at Lake Arcturus, following a demographic pattern also noted in previous years (KTG).

In 2011 we identified 23 individual gulls: 19 adults, two subadults and two immatures. An estimated six individuals may have been missed by excluding sections of tall coastal cliffs on the north-east and north-west sides of the island, and the inner eastern arm of Darwin Bay, due to access difficulties. These cliffs do not normally attract Lava Gulls, but individuals may have flown over them during our census walks.

In 2012 we identified 20 individuals: 17 adults, one subadult, one immature and one juvenile. Again it was estimated that no more than six individuals were missed.

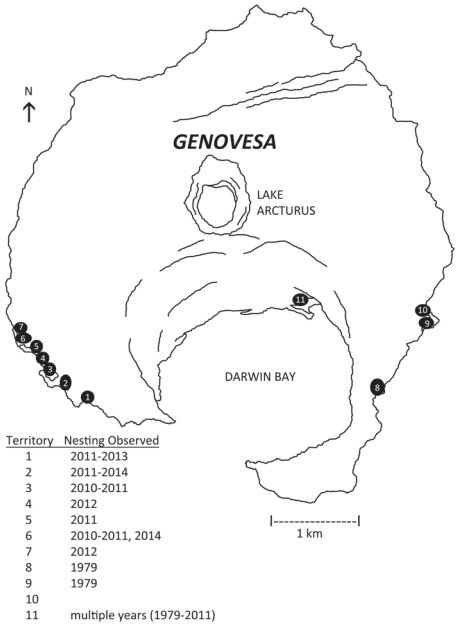
Territory location and breeding history.—We identified 11 Lava Gull territories on Genovesa (Fig. 5). Territories 1–7, on the west side of the island (the study area), contained active nests during 2011–12. Territories 8–10, on the east side of the island, and territory 11 in Darwin Bay, did not harbour active nests during the study period, but adult pairs defended territories 9–10 in both years.

A history of known nest activity in territories 1–9 between 1979 and 2014 is presented in Table 1. Single nests were observed within the study area 2–3 times during the 1990s, but are not included in the table due to missing details (SURV). Nests have never been recorded in territory 10. Nesting in territory 11 has been observed at least nine times (SURV): in 1964, in the 1970s (twice), 1984–1989 (twice), 1990–1994 (once) and 2001–11 (three times).

Territory description.—Lava Gull breeding territory, defined as the area defended by an adult pair against conspecific intruders, was c.2,000 m^2. Size was calculated after observing pairs consistently uttering territorial calls and initiating pursuits when conspecifics approached within 25–35 m of the nest.

Territories were characterised by white or grey beach sand with rocky outcrops and saltbush *Cryptocarpus pyriformis* in varying densities. The beaches in territories 1, 6 and 7 were berms, separated from the ocean by boulders, and isolated from the tide except during exceptionally rare storm surges. Territories 2 and 5 were located at the back of an exposed beach. Territories 3 and 4 were situated on the inland side of a protected lagoon.

Lava Gull nests were located 5–50 m from the high-water mark (Table 1). In territories 1, 2 and 6 we recorded nesting in multiple years, although nest sites were never reused, and new nests were located 4–30 m from previous nests.



Territory	Nesting Observed
1	2011-2013
2	2011-2014
3	2010-2011
4	2012
5	2011
6	2010-2011, 2014
7	2012
8	1979
9	1979
10	
11	multiple years (1979-2011)

Figure 5. Map of Genovesa showing the location of Lava Gull *Leucophaeus fuliginosus* territories 1–11, with nest records by year.

Foraging ranges encompassed but were not restricted to breeding territories, and it was estimated from observations that most food was obtained within 150 m of the nest. Gulls occasionally flew further inland but typically no more than 200 m from the coast. Foraging ranges encompassed colonies of Galápagos Sea Lion *Zalophus wollebaeki* (c.200 in the study area) and marine iguana *Amblyrhynchus cristatus nanus* (estimated >1,000) as well as overlapping several other seabird colonies. Mean nest densities of these seabirds (per 2,500 m^2) in 2011/2012 were: Nazca Booby 15/21, Great Frigatebird 2/5 and Swallow-tailed Gull 17/11. Red-footed Booby nested further inland in densities of c.6 pairs per 2,500 m^2.

Territory defence.—Breeding territories were defended against conspecifics by both pair members. The ringed female on Genovesa nested in territory 2 in July 2011, 2012, 2013 and 2014 confirming that the same bird can hold a territory over multiple years. This is supported by data from Santa Cruz where one pair (male #865-38411 and female #865-38427) constructed nests in consecutive years (2005 and 2006) that were just 30 m apart[1]. The male was observed defending the area with a different female (#865-38442) in July 2012 (KTG, OHE) and nesting (the eggs failed) in June 2013 (T. De Roy pers. comm.). It nested again (successfully) in June–August 2014 (KTG, OHE,

GBE), with a female that had lost part of its left leg through injury.

Breeding birds frequently stationed themselves on a favoured rocky outcrop or other high point within 25 m of the nest. The appearance of a conspecific intruder provoked alarm calls, comprising repeated *kow* (*keow*[31]) notes, followed by a territorial 'long call'[31] (Fig. 1). Pairs made the territorial long call semi-synchronously, often with the male and female holding their body at angles to one another. Territorial calls were also uttered at the nest. If the intruder did not depart, it was charged and then pursued in flight.

Alarm calls were also uttered when large animals and birds such as Galápagos Sea Lion and Nazca Booby approached within 1–2 m of the nest. Immature Great Frigatebird and Red-footed Booby in nearby 'practice flights' also provoked frequent alarm calls, along with mobbing behaviour by the female of territory 1. In territory 3, intense and rapidly repeated alarm calls, and mobbing, were provoked by the appearance of Short-eared Owls. Although Short-eared Owl has never been observed to prey on chicks, three owls were observed killing an immature Lava Gull in 1978 (P. Grant pers. comm.), and the species is a known predator of Swallow-tailed Gull chicks[24], as well as of tropicbird and booby chicks on Daphne Island (KTG). At least three owls frequented the study area during the 2011–12 study period.

Humans were attacked by 'dive-bombing'. This involved the gull flying at eye level towards the person, at a distance of 25–70 m, then swooping upwards and skimming the top of the person's head at the final moment. Gulls were extremely skilful in their aerial manoeuvres and contact was rare. 'Dive-bombing' appeared most aggressive when eggs were at an advanced stage, or young chicks were present. It was also discriminatory; one individual consistently received the brunt of the attacks, whether alone or in the company of other observers. Similar targeted attacks of a single person within a group of people have been reported elsewhere in the archipelago (SURV). 'Dive-bombing' generally ceased within a minute of the observer dropping to ground level, and diminished rapidly during the study as the gulls became habituated to our presence.

Females were the main aggressors towards interspecific intruders, making repeated attacks against humans and other species. Males, in contrast, rarely made more than a single 'dive-bombing' attack against humans and were never observed mobbing other species. When both adults were present at a nest, the female alone left the nest to attack the intruder, even if this involved switching chick-attendance duties.

Chicks responded to alarm calls by crouching in the shadow of rocks or running into deeper vegetation.

Nest, incubation and hatching.—Nests were constructed on the ground, either next to or under saltbush, and lined with soft woody stems of the same plant (Fig. 6). On other islands, Lava Gull has been found nesting directly on patches of carpetweed *Sesuvium edmonstonei*[8,21], on bare lava[1,3] and on sand adjacent to unspecified vegetation (SURV). Most, if not all, of these nests were lined with plant material.

Nest material was added intermittently throughout the incubation period and when the chicks were newly hatched. The stems, 10–12 cm in length, were collected within 6 m of the nest and walked (never flown) to the nest by the parent taking over incubation or attendance duties. Adults were also observed on three occasions, after chicks had departed the nest, arranging fresh stems around the chicks in their new location. Nests were difficult to distinguish from the surrounding substrate within one week of being abandoned.

Clutch comprised 1–2 eggs varying from olive-green to pale brown, with grey and dark brown blotches of uneven size and distribution (Fig. 6). One bluish egg, with small blotches concentrated in a ring at the broader end, was found on Genovesa in 1979 (KTG). One freshly laid egg that broke (see below) measured 62 × 42.3 mm. In addition to two eggs measured in 1960[3] (58 × 41.5 and 60 × 44 mm) and one removed from the oviduct of a collected female in 1897 (61 × 43 mm)[13,27], this gives a mean egg size of 60.3 × 42.7 mm, similar to that of Dolphin Gull[35].

A laying interval of 25–66 hours between the first and second egg was determined at one nest (territory 6). The first egg was found breached within 17 hours of laying; a suspected case of conspecific egg predation. Two days later, the female was incubating a second egg, 1.5 m from the original nest.

Parents alternated incubation every c.2 hours during the day, with shortest turnover of 103 minutes and the longest on-bout of 135 minutes. The hatching interval between the first and second chick varied between nests. In one nest (territory 2) two chicks emerged 4–16 hours apart. At another nest (territory 1) the second chick hatched 30–70 hours after the first. One egg was pipped for >19 hours.

Parents were never observed removing eggshells from the nest. In two nests (one of which contained a single egg), the entire shell was trampled into the nest lining. At two other nests, part (<60%) of one eggshell was found 10–20 cm from the nest, after both chicks hatched. Due to the shallow depths of these nests, we suspect these were displaced by

Figure 6. A Lava Gull *Leucophaeus fuliginosus* nest with eggs, including pipping egg (6d) (K. Thalia Grant)

movements of the chicks rather than having been intentionally removed.

Lava Gulls consistently defecated away from the nest; adults walked 1–6 m away (or flew further) before defecating, and chicks consistently squirted away from the nest.

Movements away from the nest, vocalisations and parental care.—Newly hatched chicks remained in the immediate vicinity of the nest for the first 2–3 days, and left between days 4–5. Departure was accompanied by "chatter' calls[22], sounding like faint chirps—presumably the equivalent of the *chiz-ik* chatter call described for Laughing Gull chicks[6]. Parents responded with 'mew' calls that redirected the chick's attention towards the adult. Distance travelled from the nest varied at 1–6 m, depending on local topography. A new temporary resting place, reached by day eight, became the favoured spot to which the chicks regularly returned. This location (5–15 m from the natal nest) was always closer to cover (dense vegetation or large rocks) than the original nest.

Young chicks (<2 weeks old) were constantly attended by one adult and frequently by both. Older chicks (>3 weeks old) were left unattended for increasingly long periods, but with one adult almost always remaining inside the territory, often on a high lookout point.

Adults always uttered a single sharp *kow* note when flying into or over their own territory, presumably to alert chicks and mates to their presence, and to distinguish themselves from intruders. Mates did not respond, but chicks answered with 3–4 note 'chatter' calls, similar to the *chiriah* calls of young Laughing Gulls[6]. Communication appeared important for the adult to locate the chick, which was often out of sight under vegetation. A harsher variation of the 'chatter' call was used by the juvenile when searching for its parent, as it continued to be fed by the male until c.15 weeks old.

Feedings were generally initiated within ten minutes of an adult's arrival at the nest, during which time the chick made constant *pee* begging sounds accompanied by head-tossing[22]. The adult responded with long-drawn *mew* calls before regurgitating a meal, which was held in front of the chick. Cycles of mewing, regurgitation and re-ingestion were repeated until the food was sufficiently digested for consumption. In one case, it took two hours and 11 regurgitations for a three-day old chick to pull apart and ingest part of a booby chick. Older chicks (>4 weeks) were able to swallow all food items whole.

In nests with young chicks (<2 weeks) adults also regurgitated just before leaving the nest. As chicks were never left unattended, this sometimes resulted in the outgoing and incoming parents feeding the chicks simultaneously.

Feedings were observed throughout the daylight hours, between 05h40 and 18h20. They were followed by the parent washing its head and bill at a nearby tide pool, the lagoon's edge or the swash zone of a beach. Washing sometimes included bill probing in wet sand, and elaborate splash bathing of the whole body.

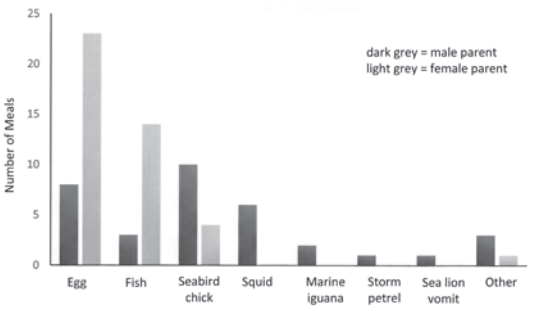


Figure 7. Meals provisioned to chicks in territories 1–7. *N* = 76 meals.

Diet.—The following dietary items were identified in 72 regurgitated meals: seabird eggs (n = 31), fish (n = 17), seabird chicks (n = 14), squid (n = 6), storm petrel (n = 2), marine iguana hatchling (n = 1) and sea lion vomit (n = 1). Four unidentified meals were also recorded, but appeared to consist of scavenged fish scraps and a soft-bodied marine invertebrate.

Most of the seabird prey were of Nazca Booby (identified by white eggshells and bill shape of the embryo or chick), with possibly some eggs (also white) of Great Frigatebird and Red-footed Booby. A Swallow-tailed Gull egg and chick were both identified by mottled pattern of the shell and down. Nazca Booby chicks were probably obtained during siblicides, where one booby chick ejects its smaller sibling from the nest[2]. One attempt by Lava Gull to steal an ejected booby chick, and three successful egg snatches from recently vacated nests (two Nazca Booby and one Great Frigatebird) were observed.

Fish identified were clupeids and exocetids, which are caught by boobies, tropicbirds and frigatebirds, and less frequently by Swallow-tailed Gull. Squid are the main prey of Swallow-tailed Gull. Fish and squid become accessible to Lava Gull when regurgitated by these birds, either to young at the nest, or in response to kleptoparasitic attacks by Magnificent Frigatebird (Great Frigatebird was never observed kleptoparasitising seabirds by us). The gulls snatch what is dropped in flight, making use of the confusion of a nest attack, in which the victim's attention is diverted towards the aerial frigatebirds and away from the gull on the ground. Several attempts by Lava Gull to profit from Magnificent Frigatebird attacks on boobies, Red-billed Tropicbird and Swallow-tailed Gull in flight, and from Nazca Booby, Great Frigatebird and Swallow-tailed Gull at their nests, were witnessed. In contrast, we never observed Lava Gull attempting to steal fish directly from nesting seabirds feeding their young.

The storm petrels were most probably the remains of kills by Short-eared Owls, which remove the head and guts of their prey, leaving the rest. Freshly decapitated petrels and owl pellets were commonly observed in the study area.

We never observed Lava Gull hunting marine iguanas, but saw an adult snatch a dead hatchling from the bill of a Yellow-crowned Night Heron *Nyctanassa violacea pauper*.

Unequal provisioning was recorded at nests with older (>4 weeks) chicks. In territory 3, the female provided 83% of 30 meals to the chick despite it begging more frequently from the male. The chick died aged 6.5 weeks, and we suspect the male's negligence was a contributory factor. In territory 7, seven of eight observed meals were provisioned by the male. The fledged juvenile in 2012 was observed being fed six times by the male. On Santa Cruz, five observed meals given to a chick aged between six and 9.5 weeks were also exclusively provided by the male.

Individuals showed some specialisation in their diets. In 2011, 75% of meals contributed by the female in territory 3 consisted of seabird eggs, with the female accounting for 62% of all egg meals recorded that year. In the other territories, two males contributed all of the squid meals. These differences are unlikely to be explained by variation in local food availability, as nesting seabird densities and egg availability did not vary significantly across the study area. Overall, females provided 82% of fish, and males contributed 71% of seabird chicks (Fig. 7).

Distribution and nesting elsewhere within the archipelago.—Table 2 presents an approximation of Lava Gull distribution throughout the archipelago, assessed from historical reports and specimens[4,5,12,13,16,26,29], more recent publications[1,32,33] and survey results. During the 19th and early 20th centuries, the largest concentrations were reported from Isabela (especially southern Isabela and Tagus Cove in the north), Santa Cruz, San Cristóbal, Genovesa, Santiago and Floreana. This distribution was probably influenced by the fishing and hunting activities of whalers, sealers and expedition vessels, with gulls attracted to regular anchorages (e.g. Tagus Cove). It might also have been determined by the distribution of seabird colonies. Currently, the highest densities of Lava Gull are located around port towns and other centres of human activity (e.g. the ferry terminus at Canal Itabaca) on Santa Cruz, San Cristóbal and Isabela, and on uninhabited Genovesa, with gulls being rarely seen on Santiago and Floreana.

Lava Gull nests have been found on 12 islands: the six islands mentioned above, as well as on Lobos Islet off San Cristóbal, Marchena, and the following satellites of Santa Cruz: Caamaño, Mosquera,

Figure 8. Distribution of known Lava Gull *Leucophaeus fuliginosus* nesting sites in the Galápagos.

North Seymour and South Plaza (Fig. 8, Appendix 1). Populations on the latter islands probably mix with Santa Cruz populations.

Gulls seen elsewhere in the archipelago have presumably dispersed from these breeding locations. Lava Gull has been documented flying over lengthy coastal stretches of Santa Cruz, Santiago and northern Isabela (SURV, KTG), and occasionally riding on vessels between the neighbouring islands of Isabela and Fernandina (GBE), and between Santa Cruz and its satellite islets[1].

Discussion

In many respects Lava Gull is a typical 'hooded' gull, between Dolphin and Grey Gull in size, and similar to Laughing Gull in vocalisations, egg-robbing behaviour and nest structure. Key differences are Lava Gull's lava-coloured plumage and dark hood (which, atypically for gulls, shows no seasonal change), its solitary and opportunistic breeding habits, and its small population size. Other distinctions have been elucidated in the current study: (1) Lava Gull has a unique white wing line, created by white marginal-coverts contrasting against dark grey wing and breast feathers. Although white marginal-coverts are present in most gulls (including Franklin's and Laughing Gulls), they are largely invisible against the white, or otherwise pale, plumage of these species. Grey Gull's marginal-coverts are grey and therefore also non-contrasting. In this characteristic Lava Gull most closely resembles Heermann's Gull *Larus heermanni*. The function of the white wing line is unknown, but possibly serves as a visual cue during social interactions and for orienting young chicks, which were observed, on occasion, pecking at it. It may also help camouflage the incubating gull when nesting on twiggy vegetation or guano-streaked lava. (2) Lava Gull chicks most closely resemble Laughing Gull chicks, but are darker. Their departure from the nest is slightly earlier, but their fledging date of 55 days is two weeks later than Laughing Gull[9]. (3) Eggshells, removed by Laughing and Franklin's Gulls, purportedly to stop them interfering with the hatching of the second and third eggs[9,10], are by contrast left inside Lava Gull nests. (4) Lava Gull pairs nest much further apart than other gulls. Observed nests were all >100 m apart, and given the species' territory size as measured by us, are unlikely ever to be closer than 25 m. In contrast, other hooded gulls typically nest <10 m apart, and sometimes touching. (5) Initial observations suggest that Lava Gull exhibits sexually dimorphic parental care, with females investing more energy in nest defence against intraspecific intruders, and males possibly assuming a greater role in the provisioning of older chicks and fledglings. (6) On Genovesa, Lava Gull benefits from an association with Magnificent Frigatebird that differs from the recognised competitive relationship exhibited by these species on Santa Cruz (and other islands in the Galápagos) when searching for fish scraps washed up on shore or scavenged from humans or sea lions[1,17,31], and from the piratical behaviour of Magnificent Frigatebird on Laughing Gulls in Mexico[14]. On Genovesa, Magnificent Frigatebird, via its kleptoparasitism of other nesting seabirds, provides Lava Gull with food (seabird-disgorged fish and squid) that would be otherwise difficult to obtain. The extent to which frigatebird kleptoparasitism contributes to Lava Gull diet is unknown, but initial observations suggest that it may be significant; fish and squid comprised almost one-third (32%) of meals fed to chicks, yet no attempt to steal these items from their captors in the absence of a frigatebird attack was observed. Frigatebird attacks on seabird nests may also facilitate Lava Gull predation of eggs and chicks.

Population on Genovesa.—The large numbers of Lava Gull nests found on Genovesa in 2011–12 were probably the result of the large numbers of other nesting seabirds, with overlapping breeding cycles, producing an unusual abundance of food. Higher nest densities are unlikely to occur on

this island due to pressure from egg-robbing, distance between nests, limited nest sites and a heterogeneous food supply. The population of 20–29 Lava Gulls recorded is probably close to the maximum supported by this island. This conclusion is consistent with historical reports. Although island-wide census counts have not previously been conducted on Genovesa, and visitors to Darwin Bay rarely see more than 2–3 gulls, records of larger congregations associated with occasional fish-cleaning activities by humans (reflecting temporary intra-island movement to an unusual food source) give some indication of past numbers: in June 1929, 'two or three dozen' appeared on the main beach in Darwin Bay to feed on a Manta ray *Manta birostris* that was being dissected[12], ten were seen in April 1930[23], 14 in May 1980 (KTG) and 19 in February 1991 (KTG).

Distribution on other islands.—The 12 islands where Lava Gull nesting has been recorded are characterised by multiple sandy beaches, or are close (<1 km) to extensive beaches on neighbouring islands. In contrast, Lava Gull is rarely seen, and has never been recorded breeding, on isolated islands (>1 km from another island) with limited beach habitat, such as on Pinta, Rábida, Pinzón and Santa Fé, or those lacking beaches, e.g. Wolf and Darwin. Proximity to a reliable food source, such as occurs in seabird colonies and port towns, is undoubtedly of equal importance.

Habitat and food supply partially explain Lava Gull's distribution in Galápagos, but other variables must account for the species' virtual absence from Española. Like Genovesa, Española has multiple seabird colonies and no introduced mammalian predators. It is four times larger, has many more beaches, and might potentially support an even larger resident population of Lava Gulls. However, Lava Gull sightings on this island remain very rare[13,28]. A combination of factors could be responsible. (1) The extreme south-east position of Española in the archipelago means that birds have to fly against prevailing winds to reach it, which may limit regular movement to Española from other islands. (2) The absence of Magnificent Frigatebird on Española might diminish the ability of Lava Gulls to exploit the island's seabird colonies. (3) The presence of Galápagos Hawk *Buteo galapagoensis*, which preys on nesting seabirds, may inhibit Lava Gull breeding on Española, as is perhaps also the case on Fernandina. (However, Lava Gull has nested on Santiago and Marchena, where hawks also exist.) (4) Large numbers of endemic Española Mockingbird *Mimus macdonaldi* may prevent establishment of a resident Lava Gull population, through predation and competition. Española Mockingbird is larger and more aggressive than the other three mockingbird species in Galápagos, is the only one able to open and prey on seabird eggs[18], and has also been observed attacking booby chicks. It also feeds on many of the same food items (fish scraps, eggs, sea lion placenta, hatchling turtles and lizards) as Lava Gull[20,31].

Table 2. Island distributions of Lava Gull *Leucophaeus fuliginosus* in Galápagos, based on qualitative data spanning 179 years (1835–2014). Double scores reflect apparent distribution shifts, from multiple numbers recorded historically to few individuals seen this century. Specimens located at the following museums: Academy of Natural Sciences (Philadelphia), Museum of Comparative Zoology (Cambridge, MA), Beatty Biodiversity Museum (Vancouver), United States National Museum (Washington DC), Royal Ontario Museum (Toronto), Los Angeles County Museum, Field Museum of Natural History (Chicago), Western Foundation of Vertebrate Zoology (Camarillo, CA), Denver Museum of Nature and Science, California Academy of Sciences (San Francisco), American Museum of Natural History (New York) and the Natural History Museum (Oslo).

Island	Resident/regular visitor	Possibly resident/regular in low numbers	Occasional visitor	Rare	Absent/Never recorded	No. of specimens
Isabela	x					78
Tortuga				x		1
Fernandina			x			4
Santiago		x	x			18
Bartolomé				x		1
Rábida				x		0
Pinzón				x		2
Santa Fé				x		3
Santa Cruz	x					40
Caamaño	x					0
S. Plaza	x					0
Baltra	x					4
Mosquera	x					0
N. Seymour	x					0
Daphne				x		0
Floreana		x	x			16
Española				x		1
San Cristóbal	x					10
Lobos	x					0
Genovesa	x					22
Marchena		x				3
Pinta				x		1
Darwin					x	0
Wolf					x	0

Concluding remarks.—The archipelago-wide Lava Gull population estimate of 300–400 pairs calculated in 1963 was based on counts made along 56 km of prime habitat on Santa Cruz, and multiplied for the entire coastline (1,336 km)[20] of Galápagos[31]. However, it was acknowledged that as parts of the coasts of many islands are unsuitable for the species, the actual population size was likely to be lower[31]. An improved understanding of the distribution and ecology of Lava Gull permits a revised estimate. Based on recent estimates of 78–81 individuals in southern Santa Cruz[1] and 20–29 individuals on Genovesa, and assuming that densities on San Cristóbal and Isabela are similar to (and no greater than double) those of southern Santa Cruz, the total population is probably 300–600 individuals. Future censuses, concentrating on islands where breeding has been reported, would undoubtedly yield a more accurate figure. A better understanding of populations on Isabela, Santa Cruz and San Cristóbal would be especially useful for assessing population trends, as apparent density increases around expanding towns on these islands, which might reflect relocation towards ever-growing food sources (i.e. fish and refuse provided by humans), rather than true population growth. As these areas are associated with significant threats from humans, introduced predators, pathogens and toxins, examining Lava Gull breeding success in, and movement patterns away from, these high-risk areas will help assess the species' vulnerability[15,34]. Given the absence of records outside Galápagos, the species is apparently more restricted in movements across open water than other gulls[16,28]. Nevertheless, at least one (ringed) individual undertook the 130 km crossing to Genovesa from its hatching location on Santa Cruz. Furthermore, boats may assist open ocean travel.

To date, population trends have been based primarily on observers' impressions, with few detailed data other than sporadic censuses. For conservation purposes, it is important to establish if the species experiences long-term population stability. Annual monitoring and scrutiny of breeding at sites both influenced by humans (e.g. Santa Cruz) and undisturbed (e.g. Genovesa), could shed light on the population dynamics of this rare endemic. The descriptive details of Lava Gull nesting on Genovesa and the summarised distribution data presented here will inform such a programme.

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Appendix 1. Summary of Lava Gull *Leucophaeus fuliginosus* nest records, from the authors' observations, survey results, and published reports[1,3,8,21,24,31,32]. * = No longer considered suitable nesting habitat due to urbanisation.

Island	Sites	Years	# nest sightings	# independent observers
Isabela	Puerto Villamil, several km west of Wall of Tears, Urvina Bay.	1960s, 1983–2014	10+	5
Santiago	Beach opposite Cousins Islet, beach opposite Rábida.	2001	2	1
Santa Cruz	Academy Bay (behind the Salina, behind Playa Aleman*, on an islet a few metres offshore from the Devine's property*), Tortuga Bay (west of Playa Mansa), Islote Fé (west of Tortuga Bay), El Garrapatero, Punta Rocafuerte, Las Bachas, between Las Bachas and Canal Itabaca.	1960–64, 1970s–2014	42	31
Caamaño		1962, 1963, 1964, 1970s	4	3
South Plaza	West and east coasts of islet, centre of islet, near cliff, near landing.	1977–2011	7+	8
Mosquera	North-east and south coasts of islet, middle of islet on east side.	1970s–2009	10+	7
North Seymour	South coast of island (near old landing site where beach trail veers inland at furthest point from landing).	1988–2009	7	7
Floreana	Playa de los Perros on east coast, facing Gardner and Caldwell Islets.	1983 or 1984	1	1
San Cristóbal	Playa Mann, Punta Carola, Puerto Grande, Manglecito, several locations between Cerro Brujo and Punta Pitt.	1981–82, 2005–2013	9+	5
Lobos		1996–2012	3+	3
Genovesa	Inside Darwin Bay, outside Darwin Bay (western beaches, eastern beaches).	1970s–2014	28+	14
Marchena	Playa Negra, Playa de los Muertos.	1979, 2000	3	2