OVERLAND FLIGHT BY SEABIRDS AT ISLA ISABELA, GALÁPAGOS

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ABSTRACT

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Oceanic seabirds are generally thought to avoid overland flight, perhaps limiting larger-scale distribution, but examples exist to the contrary. We asked whether Blue-Footed Boobies *Sula nebouxii*, Brown Pelicans *Pelecanus occidentalis*, or frigatebirds *Fregata* spp. crossed the Perry Isthmus (width 12.25 km, minimum height 23 m), a low point in the wasp-waist shape of Isla Isabela, Galápagos. Except for the Perry Isthmus, Isla Isabela presents an elongated, high-elevation challenge to movement between the central and western waters of Galápagos. Daytime observations over 3.5 d in June 2012 revealed ≥48 crossings by boobies and more than two crossings by frigatebirds. Overland crossing of a terrestrial barrier of this size may be facilitated by the seabirds' ability to see water across the Perry Isthmus from an altitude of 42 m looking west and 43 m looking east, altitudes that both the boobies and frigatebirds attain during foraging.

Key words: Sulidae, Fregatidae, Suliformes, seabird biogeography, seabird distribution

INTRODUCTION

Volant seabirds are highly mobile, and many can fly hundreds of kilometers on most days of their lives (Prince *et al*. 1992). Despite this extreme vagility, some oceanic species are thought to avoid overland flight, except to reach their nesting sites (Friesen *et al*. 2007, Friesen 2015). Nonetheless, Arctic Terns *Sterna paradisea* migrate across the Andes and southern Argentina (Duffy *et al.* 2013), and boobies and albatrosses have appeared hundreds of kilometers inland in the absence of forcing by severe weather (Dunn & Unitt 1977, Patten & Minnich 1997, Sullivan *et al*. 2009), suggesting that some oceanic birds fly deliberately (although maladaptively in some cases) over land. Understanding whether pelagic seabirds cross land voluntarily or involuntarily is relevant to seabird biology in several ways. It can help us evaluate apparent terrestrial barriers to gene flow (Friesen 2015), whether movements inland of hundreds of kilometers (Sullivan *et al.* 2009) result from voluntary dispersal or environmental forcing, and degree of terrestrial isolation that impedes artificial social attraction to new colony sites (Sawyer & Fogle 2013).

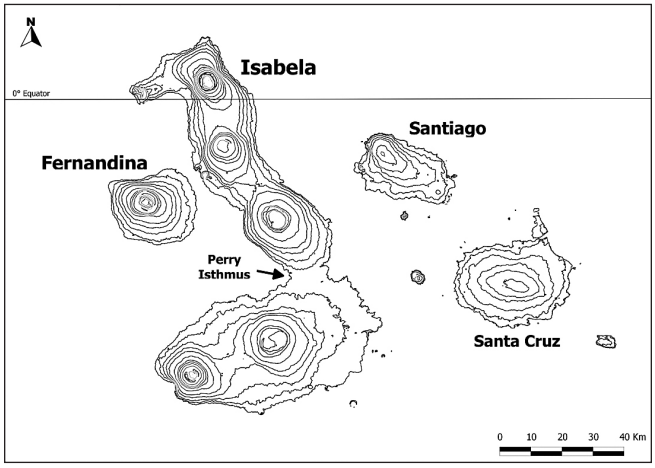

Fig 1. Isla Isabela, Galápagos, and location of the Perry Isthmus. Topographic contour lines indicate 150 m increments in altitude above sea level.

Isla Isabela, the largest of the Galápagos Islands, presents a significant north–south barrier to seabirds unable or unwilling to cross land along its 135 km length. The north and south lobes of the island join at the Perry Isthmus (Fig. 1), a land bridge 12.25 km wide and 23 m high at the lowest crest. We exploited these circumstances to ask whether this isthmus poses a barrier to movement between western and central waters of Galápagos. Significant numbers of Blue-Footed Boobies *Sula nebouxii* (>400 on the east side and >1 300 on the west side; Anchundia *et al*. 2014) foraged near the Perry Isthmus around the time of our observations, and frigatebirds *Fregata minor* and/or *F. magnificens* and Brown Pelicans *Pelecanus occidentalis* also foraged in this area (unpub. data). Movement between these foraging sites across the Perry Isthmus would cover much less distance than would the alternative around Isabela by water, allowing easier connections between nesting sites (some which are east of Isabela) and ecologically productive waters to the west (which have supported faster nestling growth of Blue-Footed Boobies; Ricklefs *et al.* 1984). We used an elevated vantage point on the Perry Isthmus to measure the frequency of overland crossings by seabirds, and we evaluated the shape of the isthmus as a visual barrier to crossing.

METHODS

We observed seabird movements from Cerro Iguana (0.625178° S, 90.975286° W, elevation 68 m above sea level), a hill within the saddle forming the Perry Isthmus, on 12–15 June 2012. From this hill, the entire width of the isthmus was clearly visible and birds passing through the low point of the valley at 23 m elevation above sea level were seen easily. Atmospheric conditions were clear on

all days of observation. An 8×42 binocular and 60× spotting scope were used to identify and count all seabirds observed crossing the isthmus as they passed Cerro Iguana. We used a handheld global positioning system (GPS) unit, compass, and direct observations to determine the heading of each individual visually. Flight altitudes were determined by eye with no estimate of error. Two observers scanned for seabirds continuously and recorded counts and identifications independently, and their data were identical except in one case. Frigatebirds were identified to genus only due to the difficulty of identifying males to species. In all cases, birds that we sighted over the isthmus passed from one coast to the other in a direct, continuous path. The altitude of passing birds was estimated visually by comparing the vertical position of the bird with the elevation of the observer (68 m) and with the elevation of land under the bird.

We calculated the altitude required for a bird to see from the coast on one side of the isthmus to the ocean's horizon on the other side as follows. First, we calculated the linear distance D_1 from the top of the obstacle to the horizon, accounting for the curvature of Earth, as

$$D_1 = \theta_1 \times r \quad \text{(in kilometers; see Fig. 2),} \quad \text{Eq. 1}$$

where

$$\theta_1 = \arccos(r/(r + E)) \quad \text{(in radians),} \quad \text{Eq. 2}$$

r = 6 378 km (the radius of the Earth at the Equator), and E is the elevation of the obstacle in kilometers. We then calculated the altitude (A) required of the bird, flying directly over the coastline on its own side of the obstacle, to see over the obstacle to the horizon beyond as

$$A = r \times (1/\cos(\theta_1 + \theta_2) - 1) \quad \text{(in kilometers),} \quad \text{Eq. 3}$$

where

$$\theta_2 = D_2/r \quad \text{(in radians)} \quad \text{Eq. 4}$$

and D_2 is the distance in kilometers from the obstacle to the observer. This method may overestimate A slightly because it does not adjust A for the effect of the atmospheric refractive index on the appearance of the horizon. We have ignored this effect because it is minor and because its estimation requires time-dependent information on air density and temperature along the line of sight (French 1982). Anomalies in these variables produce the optical illusion of mirages; their measurement is not practical in most field situations.

RESULTS

We counted 48–50 Blue-footed Boobies and two frigatebirds crossing the Perry Isthmus (Table 1). Most of the birds were seen crossing during late morning and early afternoon, and many were observed flying over land during the hottest time of the day. Brown Pelicans were known to be present on both sides of the isthmus but did not cross during our observations.

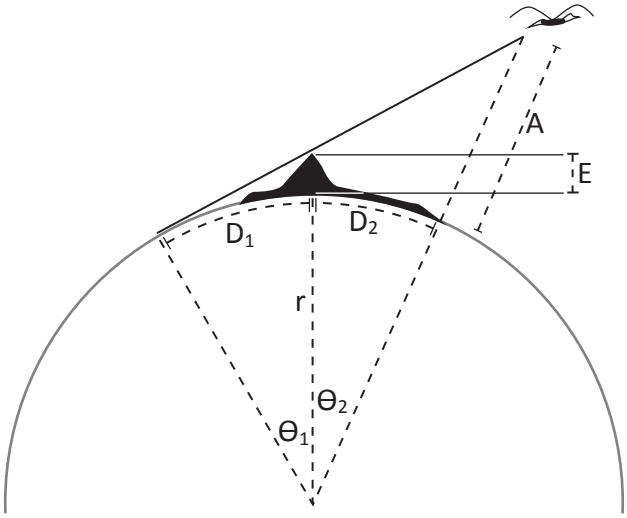

Fig. 2. Trigonometric values described in Methods (see Eq. 1–4), superimposed on a diagram of the curved surface of the Earth with water (gray) and a terrestrial mountain and adjoining lowland (black). The straight solid line from the bird to ocean is the line of sight from the minimum bird altitude to the ocean beyond the mountain, assuming that the bird remains over the ocean on its own side of the land.

TABLE 1
Birds observed crossing the Isthmus Perry, Isla Isabela, Galápagos Islands, in June 2012[a]

Date, time	Time of sighting	Species	Count	Direction of flight	Altitude above ground[b]
12 June, 12h15–16h45	14h52	Frigatebird	1	NE to SW	~90 m
	15h39	Blue-footed Booby	17	E to W	~25 m
13 June, 06h37–16h30		no sightings			
14 June, 06h35–16h45	08h58	Blue-footed Booby	11	E to W	~20 m
	09h06	Blue-footed Booby	5	E to W	~35 m
	09h38	Frigatebird	1	W to SE	~80 m
15 June, 06h38–16h45	14h24	Blue-footed Booby	6	E to W	~35 m
	15h22	Blue-footed Booby	10–12[c]	W to E	~40 m

[a] Flight paths of birds crossing were to the north of the hill (Cerro Iguana) from which our observations were made.
[b] The surface of the ground was approximately 23 m above sea level.
[c] The two observers had different counts. Civil twilight on 12–15 June 2012 in the Galápagos Islands was at 05h34 and 18h23.

Blue-footed Boobies flying over the sea alternate level flapping flight with gliding (Nelson 1978), but over the Perry Isthmus they flapped their wings constantly, and we judged them to be moving faster than when flying over water. In contrast, frigatebirds never flapped their wings during crossing. All crossing Blue-footed Boobies passed in groups below the observers' elevation (flying ~20–40 m above the ground), while frigatebirds were seen alone and flying above the observers' elevation (flying ~80–90 m above the ground). Two additional frigatebirds were observed flying behind our location, >100 m above land, moving from north to south, but they were not counted because they did not cross Isabela on the east–west axis.

To establish a line of sight from above the coastline over the crest of the Perry Isthmus to the ocean on the other side requires an altitude of at least 42 m from the east coast looking west, and at least 43 m from the west coast looking east.

DISCUSSION

Seabirds crossed the Perry Isthmus on three of the four days of our observations, indicating that this landform with a width of 12.25 km, but a minimum elevation of only 23 m, poses little barrier to movement of these species. Geometric considerations indicate that seabirds have a line of sight from the coast on one side across the Perry Isthmus to water on the other side from a height of 42 m or more above sea level under clear weather conditions; birds farther out to sea would require a higher altitude (Fig. 2). Delano reported (1817, in Murphy 1936, p. 838) that dives of Galápagos Blue-footed Boobies began at an altitude of 60–100 m, exceeding this altitude requirement. Our own observations are roughly consistent with Delano's, although we consider an altitude of 100 m to be unlikely for this species, and dives from lower altitudes are common (pers. obs.). Frigatebirds exceed the minimum altitude regularly, and probably on most days that they are at sea (Rattenborg *et al.* 2016, Weimerskirch *et al.* 2016). Brown Pelicans may not reach the required altitude during normal flight at sea, perhaps preventing them from having any reason to fly inland at the Perry Isthmus; however, our brief observations certainly do not rule out crossings by brown pelicans.

Attraction to water on the other side of the Perry Isthmus may lead to movement across the isthmus in species that reach the altitude required to see the water. Of course, after an individual's first crossing of a barrier like the Perry Isthmus, it may add this information to its spatial understanding of its foraging range and be more likely to cross again in the future. Even without personal knowledge of the geography, a naive individual may imitate informed individuals as they voluntarily cross terrestrial barriers like the Perry Isthmus.

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