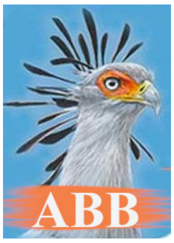

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Breeding biology of two sympatric *Nesospiza* finches at Nightingale Island, Tristan da Cunha

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Abstract

Nesospiza finches are a classic example of a simple adaptive radiation, with two ecologically distinct forms confined to the Tristan da Cunha Archipelago, South Atlantic Ocean: an abundant, small-billed dietary generalist, and a scarce, large-billed specialist. These have segregated into two species at Nightingale Island, but there is still local introgression between the two forms at Inaccessible Island. We describe the phenology and breeding behaviour of the two sympatric species at Nightingale Island (2.6 km^2): Wilkins's Finch *Nesospiza wilkinsi* (Endangered) and Nightingale Island Finch *N. questi* (Vulnerable). The finch breeding season starts in late October-November but the onset of breeding varies by 4–5 weeks among years. The small-billed Nightingale Island Finch typically (two of three study seasons) starts breeding 1–3 weeks earlier than the large-billed Wilkins's Finch, unlike at Inaccessible Island where the Wilkins's Finches start breeding first. Laying of initial clutches was quite well synchronised, peaking 1–2 weeks after the first nests were found. Females constructed the nests, which were mostly (>90%) in dense *Spartina arundinacea* tussock grass stands and occasionally in ferns or sedge grasses. Clutches comprised one or two eggs, with no difference between Wilkins's (1.66 ± 0.48) or Nightingale Island finch clutches (1.71 ± 0.46). Incubation periods averaged longer for Wilkins's Finch (18.3 ± 0.5 d) than Nightingale Island Finch (17.7 ± 0.5 d), but this difference was not statistically significant. Females incubated the eggs, and were fed by the males. The difference in egg volume within two-egg clutches was 2–13% for Wilkins's Finches (mean 5.9 ± 3.3%) and 1–19% for Nightingale Island Finches (mean 8.4 ± 5.3%). At least 31% of pairs re-laid after their first breeding attempt failed but there was no evidence of double brooding. Repeat nests were 0–20 m (mean 5.6 ± 4.9 m) from the initial nest site and inter-seasonal nest sites for 38 known pairs were 0–33 m apart (mean 12 ± 9 m). No inter-species pairs or hybrid birds were seen, but two instances of inter-species fledgling provisioning were observed.

Keywords: *Nesospiza wilkinsi*, *Nesospiza questi*, breeding phenology, speciation, adaptive radiation, clutch size
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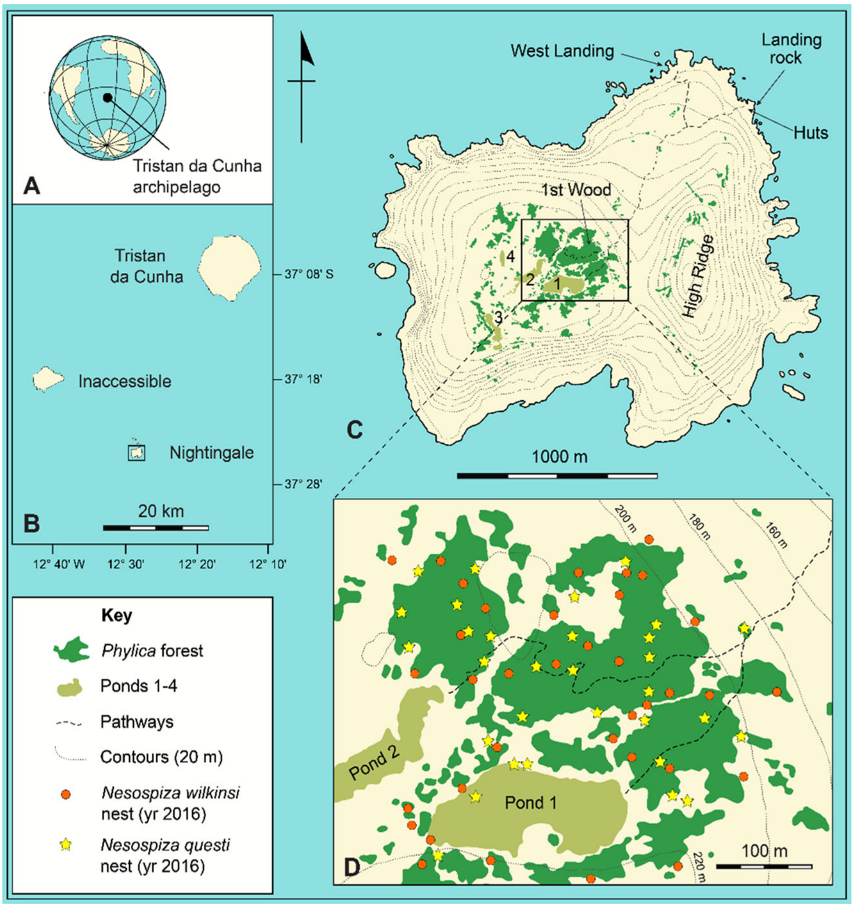
Introduction

The *Nesospiza* finches are endemic to the Tristan da Cunha Archipelago, a group of three mountainous islands in the central South Atlantic Ocean (37.25° S, 12.45° W, Figure 1). They evolved from vagrant tanager-finches (Thraupidae) that dispersed over 3000 km of ocean from South America (Rand 1955; Ryan et al. 2013). The finches on the main island of Tristan (96 km^2) died out in the 1800s, within 70 years of the island's colonisation by people (Stresemann 1953; Bond et al. 2019), but they persist on the two smaller, uninhabited islands in the archipelago. There, the finches underwent an adaptive radiation into two ecologically distinct forms (Ryan et al. 2007): an abundant, small-billed dietary generalist, and a scarce, large-billed specialist that feeds on the woody fruits of the Island Tree *Phylica arborea* (Hagen 1952). Lack (1947) contrasted this simple adaptive radiation with the more extensive radiations among Darwin's finches (Thraupidae) and the Hawaiian honeycreepers (Drepanididae).

Because few people visited these remote islands, the large-billed form of finch was only discovered in May 1922 (Wilkins 1923; Lowe 1923). The two bill forms have segregated into separate species on tiny Nightingale Island (2.6 km^2), where large-billed Wilkins's Finches *N. wilkinsi* (Figure 2B) and small-billed Nightingale Island Finches *N. questi* (Figure 2E) coexist with no records of hybridisation (Ryan et al. 2007). On larger Inaccessible Island (14 km^2), the two bill forms hybridize in some parts of the island (Ryan et al. 2007) and one polytypic species *N. acunhae* is recognised, comprising large-billed Dunn's Finches *N. a. dunnei*, and small-billed Lowland Inaccessible Finches *N. a. acunhae* and Upland Inaccessible Finches *N. a. fraseri* (Ryan 2008). The earliest records on *Nesospiza* finches from the outer Tristan islands were based on infrequent, short visits to Nightingale and Inaccessible islands (Moseley 1892; Wilkins 1923; Hagen 1952; Elliott 1957; Richardson 1984). More recently, the evolution, biology and species complexities of the finches at Inaccessible Island have been extensively studied, most notably during the summers of 1982/83, 1989/90 and 1999/2000 (Fraser and Briggs 1992; Ryan 1992; Ryan et al. 1994; Ryan 2001, Ryan and Moloney 2002; Ryan et al. 2007; Ryan 2008). By comparison, the *Nesospiza* finches on Nightingale Island have been relatively little studied, with a few early records of nests and clutch sizes by Hagen (1952) for Nightingale Island Finches (n = 3)



(A) The location of Tristan da Cunha Archipelago; (B) the outer islands to the southwest; (C) Nightingale Island, showing the distribution of *Phylica* forests; and (D) the core study area of 1st Wood where we studied *Nesospiza* finches (nests from the 2016 breeding season shown here).

and by Elliott (1957) for Nightingale Island (n = 3) and Wilkins's finches (n = 5). Richardson (1984) observed recently-fledged juvenile Nightingale Finches in late November 1973, but made no breeding observations of Wilkins's Finches.

All *Nesospiza* finches are listed as threatened due to their extremely small range and the potential arrival of invasive mammals from neighbouring Tristan da Cunha (where the finch population is extinct; BirdLife International 2016). Wilkins's Finch is listed as Endangered as it is one of the naturally rarest birds in the world. Its total population is only a few hundred individuals, despite minimal human impact on its environment (Elliott 1957; Richardson 1984; Ryan 2008). Knowledge of these species' breeding biology not only broadens our understanding of their life history evolution (Lack 1947), but may also help to identify mechanisms that support their population stability (Van Allen et al. 2012). We studied *Nesospiza* finches at Nightingale Island in the austral summers of 2012, 2016/17 and 2017/18. Here we describe their breeding biology, with a focus on breeding phenology, nest site and structure, clutch sizes and breeding behaviour of the two sympatric species. Breeding success and causes of nest failures will be reported elsewhere.

Methods and Study Area

Nightingale Island has a moist temperate climate (Höflich 1984). With no land-buffer to the South Atlantic weather fronts, it frequently has strong winds and heavy rainfall. Because it is smaller and appreciably lower (max elevation ≈300 m) than the main island of Tristan (max elevation = 2062 m), Nightingale receives less rainfall than Tristan (where the mean annual rainfall has been recorded as 1670 mm at the coast; Holmgren et al. 2013). It is also slightly warmer than Tristan (Richardson 1984). The island rises steeply from the sea, with the elongated 'High Ridge' in the east dominating Nightingale's landscape. The western plateau (≈200 m) is broken up into small hills and valleys with four boggy 'Ponds' in shallow depressions (total area 2.7 ha), covered mainly with the sedge *Scirpus sulcatus* and scattered Bogferns *Blechnum palmiforme* (confined to Ponds 1 and 2).

Most of the island (82%) is covered with tussocks of *Spartina arundinacea* grass (total area 213 ha), which form dense almost uniform stands 2–3 m high. The abundant tussock is broken only by small meadows of hummock-forming sedges *Scirpus bicolor* ('Scirpus patches' or 'Lamb Houses', 0.4 ha) and copses of Island Trees (12.2 ha) of which '1st Wood' is the largest (≈3 ha, Figure 1, Figure 2D). The forest understory is a lush complex of ferns (dominated by dense bracken *Histiopteris incisa* with patches of *Asplenium obtusatum* and *A. platybasis* and isolated *Elaphoglossum* spp.), sedges (*Carex*, *Scirpus* and *Uncinia* spp.) and various grasses (Roux et al. 1992; Ryan 2007).

Fieldwork

Breeding among *Nesospiza* is seasonal, occurring from November–February (Fraser and Briggs 1992; Ryan and Moloney 2002). HO stayed on Nightingale Island from 14 September to 26 November 2012; BD and DD stayed on Nightingale Island for two successive austral summers: 7 October 2016 to 25 January 2017 and 15 September 2017 to 22 January 2018. Our main study area was the forests and immediate tussock habitat surrounding Ponds 1 and 2 (Figure 1, Figure 2D, 2G). Once signs of breeding were seen, we systematically searched these areas for nests every two days. Some nests, where females had finished nest building and were sitting tight on the nest, were checked daily (or in some cases twice daily) to record laying intervals and dates. Since males provision females during incubation, their frequent provisioning trips to and from the nest helped us locate nests. The *Phylica* woodlands surrounding the core study area (Figure 1, Figure 2D) were searched less frequently (2–4 days). Finches were caught using hand-nets and mist-nets. Birds were aged (juvenile or adult), sexed (using plumage characters described in Ryan et al. 1994), measured (mass to the nearest 0.1 g; wing, tarsus, head and culmen lengths and bill depth to the nearest 0.01 mm using digital Vernier callipers) and individually colour-banded (as part of a separate population demography study). When assessing the proportion of pairs that relayed, we only included known (colour-banded) pairs where the initial breeding attempt was known to have failed.

When practical, eggs in the 2016 season were weighed using a 5-g Pesola spring balance (± 0.01 g) and measured (length, L, and maximum width, W, to the nearest 0.01 mm). Where laying sequence was known, the first egg was marked with a small black dot using a permanent marker pen. Egg masses measured within the first two days of laying were taken as the approximate fresh egg mass. An egg elongation index was calculated as L/W (Preston 1969) and an index of egg volume was calculated as $L \times W^2$ (Grant 1982). Where nests were found at early incubation stage, laying dates were calculated by extrapolation (mean incubation period of 18 d - see Results) for those eggs that hatched. Details of nest sites and nest structure were recorded for a sub-sample of nests found; nest locations were recorded with a handheld GPS, and these locations were used to estimate the distances between nests. The perimeters and planar surface areas of the *Phylica* copses were captured remotely using Google Earth imagery and QGIS (version 3.4 LTR). This method does not account for slope, but apart from the steep slopes of High Ridge (≈5% of the island's *Phylica*), the remaining *Phylica* areas are relatively flat and we therefore did not adjust any of the remotely captured area estimates.

Statistical analyses were run using R 3.6.0 (R Core Team 2019). We used a binomial exact test to assess if the proportion of 'large first-laid eggs' in two-egg clutches differed from the expected 0.5. To assess if relay clutch size among individual females differed from a random expectation, we used a 2 × 2 contingency table with Yates' correction for continuity (0.05 significance level). Means are presented ± SD. Breeding years refer to austral seasons (i.e. 2016 for the 2016/17 summer breeding season).

Results

Over the 2012, 2016 and 2017 summer breeding seasons, 186 *Nesospiza* nests were located, of which 150 were monitored from the nest building or early incubation stage through to termination (fail/fledge). In the latter seasons, we dedicated more search effort to finding Wilkins's Finch nests (41 in 2016 and 46 in 2017), but also monitored a similar number of Nightingale Island Finch nests (n = 31 in 2016 and n = 32 in 2017).

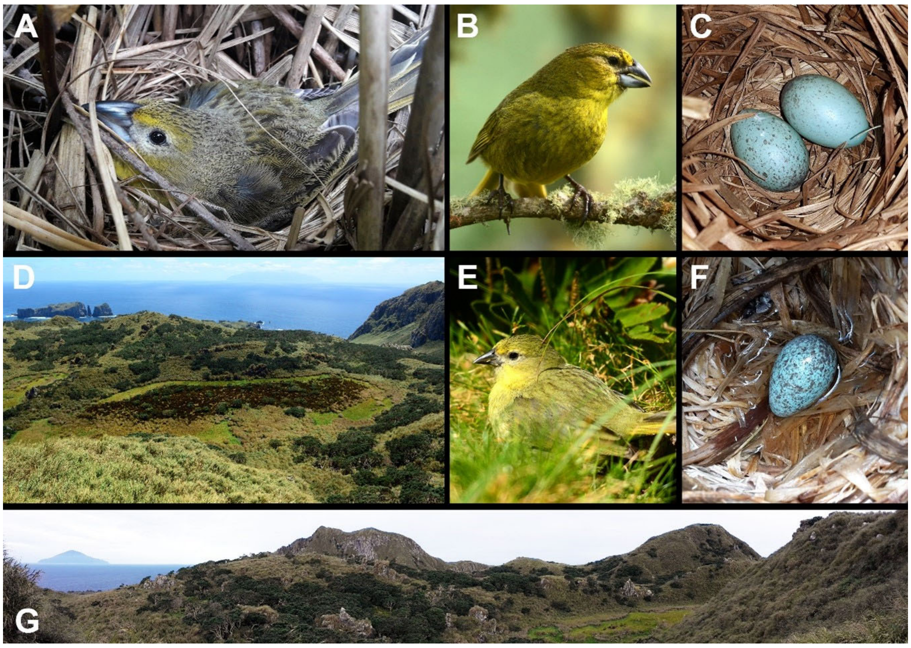


Figure 2: (A) Female Wilkins's Finch *Nesospiza wilkinsi* on her nest in tussock grass *Spartina arundinacea*; (B) Male Wilkins's Finch in *Phylica arborea* forest; (C) Wilkins's Finch eggs in a tussock nest; (D) Nightingale Island viewed from High Hill looking north, with Pond 1 (lime green oval shape) in the centre and the main study area of '1st Wood' beyond (dark green forest); (E) Male Nightingale Island Finch *N. questi* among sedge grasses *Scirpus* spp.; (F) Nightingale Island Finch egg in a sedge grass *Scirpus sulcatus* nest waterlogged after heavy rains; (G) Panoramic view of Nightingale Island from a vantage point northwest of Pond 2 (bottom right) with Tristan da Cunha Island visible in the distance (top left).

Laying periods

In 2012, Wilkins's Finch females were the first seen to carry nesting material (on 26 October), however Nightingale Island Finch females were first to do so in the latter two study seasons (on 10 November 2016 and 24 October 2017). Nest construction took 4–11 days. Once construction was complete, laying usually followed 1–12 days later. In 2012, the first Wilkins's Finch eggs were found on 14 November, however no Nightingale Island Finch nests were found by 26 November when HO left the island. In 2016, breeding also started in mid-November, with the first eggs found on 21 November (Nightingale Island Finch) and 30 November (Wilkins's Finch). In 2017, the onset of breeding was 2–3 weeks earlier, with nest building starting in late October and nests with eggs by 3 November (Nightingale Island Finch) and 7 November (Wilkins's Finch; Figure 3). We are confident these dates represent the timing of first breeding for these years because we did not observe fledglings from elsewhere before the first chicks fledged from the monitored nests (fledglings are easily detected by their persistent begging calls, Ryan and Moloney 2002). Laying was quite well synchronised in 2016 and 2017 with a peak 1–2 weeks after laying first started (Figure 3); nests with eggs were found up to mid-January (eight weeks after laying began), but these nests were relays which, if successful, would have fledged chicks in mid-late February.

Nest site and construction

Nests were constructed by the female, typically using *Spartina* leaves that were woven into a deep open cup. Sedge *Carex insularis* leaves were occasionally mixed with *Spartina* leaves, and were used exclusively at four nests. Nest linings were usually absent, but some birds sparsely used Old Man's Beard lichen *Usnea* spp., *Scirpus* or *Spartina* inflorescences to line the base of the nest cup. Females gathered all nesting material. Most Nightingale Island Finch nests were in dense *Spartina* tussock stands (>90%), 0–110 cm off the ground (mean height 35 ± 40 cm, 43% of nests were on the ground, n = 32); nests were often situated near the central core of the *Spartina* tussock where the near vertical grass stems provided a good barrier against thrushes. Females occasionally favoured dense stands of *Scirpus* sedges, such as the large expanses in the Ponds, or *Carex* spp. hummocks, where females would line a natural hollow created between hummocks. These nests were on the ground and well concealed, but were prone to flooding after heavy rains (Figure 2F) and once discovered they were easy for thrushes to access. Two Nightingale Island Finch nests were found in the introduced grass *Holcus lanatus* along the main pathway and one on a small rock ledge, well concealed by a large *Elaphoglossum* fern.

Despite the dense understory in the *Phylica* copses, which provided seemingly good nesting sites, Wilkins's Finch females mostly nested in *Spartina* (>95%), often on the fringe of their *Phylica* forest territory, or sometimes in a small *Spartina* stand or single *Spartina* tussock within the forest. Nests in *Spartina* were 0–110 cm off the ground (mean height 36 ± 30 cm, 24% of nests were on the ground, n = 43). Unlike Nightingale Island Finches, nests were usually built away from the central core of the *Spartina* plant where the tussock stems are less dense (Figure 2A), which provided less of a barrier against intruders and wind. Four Wilkins's Finch nests were found on small rock ledges with overhanging *Scirpus* sedges, where the entrance was well concealed and a small passage led to the nest. These cryptic nests were not woven cups, but rather loose grass bowls supported by the rock ledge, and were prone to being waterlogged in heavy rains. Five nests (four built by the same female) were constructed in large patches of *Asplenium obtusatum* ferns; these nests were built from *Carex insularis* leaves at the inner core of a fern with little protection from

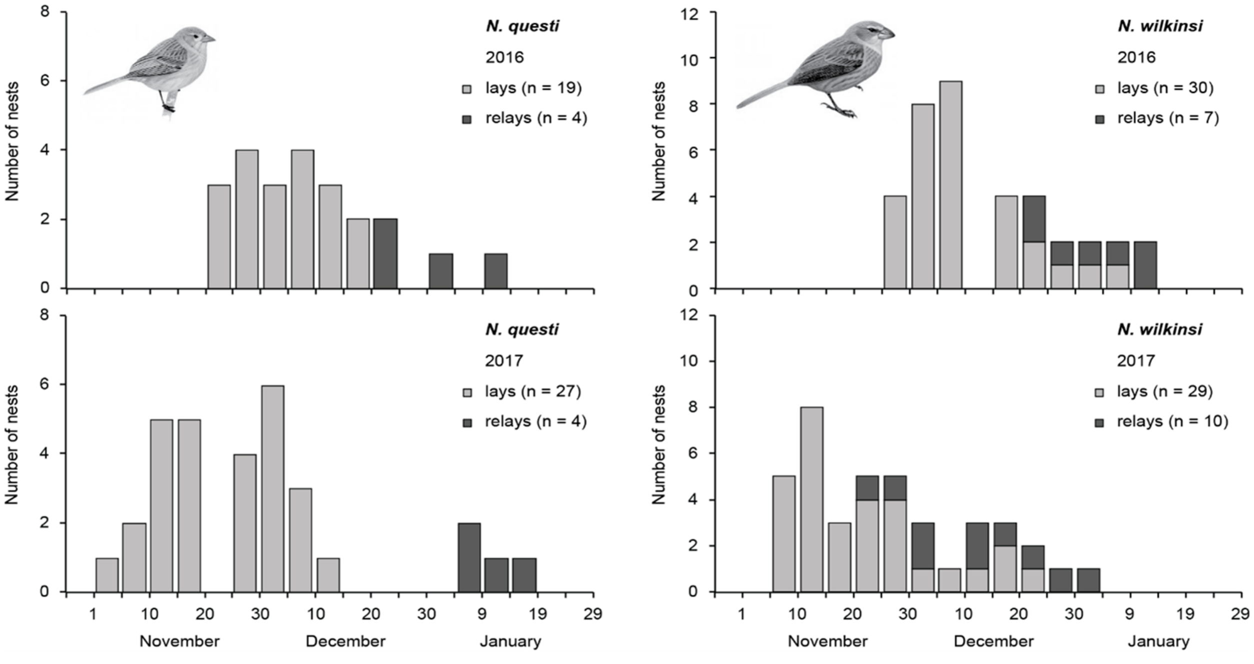


Figure 3: Laying dates of *Nesospiza* finch eggs at Nightingale Island during the summers 2016 and 2017.

thrushes or rain. Three nests were made of only *C. insularis* leaves, tightly woven into deep cups between *C. insularis* hummocks in the forest understory.

The nest shape and design were similar for both species, but more variable among Nightingale Island Finch nests. Wilkins's Finch nests averaged 10.8 ± 2.0 cm wide (range 7–14 cm), with cups 8.0 ± 0.6 cm wide (7–9 cm) and 6.9 ± 1.4 cm deep (5–10 cm, n = 24). Comparative values for Nightingale Island Finch nests were 9.5 ± 2.7 cm wide (7–17 cm), and cups 6.5 ± 0.6 cm wide (5–7 cm) and 5.9 ± 2.7 cm deep (3–12 cm, n = 15).

Egg and clutch size

All finch eggs were pale blue with rust-coloured speckles, with some variation in the density of speckles and the shade of blue (Figure 2C, 2F). *Nesospiza* finches laid one or two eggs (n = 150 clutches), with no difference in clutch sizes between taxa: Wilkins's Finch mean clutch size 1.66 ± 0.48 (n = 87); Nightingale Island Finch 1.71 ± 0.46 (n = 63; t = -0.601, df = 148, p = 0.548). There was no difference in clutch size between the first and second (relay) clutches for Wilkins's (t = 1.426, df = 32, p = 0.082) or Nightingale Island finches (t = 0.509, df = 16, p = 0.309). Including relay clutches, the proportion of one to two-egg clutches in Wilkins's Finch nests (30:57) was similar to Nightingale Island Finch nests (19:44, χ2 = 0.145, df = 1, p = 0.703). Of the females monitored in both seasons, 64% (14/23 Wilkins's Finch and 11/16 Nightingale Island Finch) laid the same size first clutch in both seasons. However, the size of relay clutches among individual females was independent of the size of their first clutch for both Wilkins's (χ2 = 0.36, df = 1, n = 17 relays) and Nightingale Island finches (χ2 = 1.60, df = 1, n = 8 relays).

In accord with their larger body size, Wilkins's Finches laid larger eggs than Nightingale Island Finches (Table 1 and 2). Laying order was known for 12 two-egg clutches (both taxa combined) and in all but one nest (the first Wilkins's Finch eggs found in the 2016 season) the first-laid egg was larger than the second-laid egg (based on egg volume index; binomial exact test, p = 0.003). We thus considered the larger egg α and the smaller egg ß for all two-egg clutches, including those where we did not observe the laying order. Wilkins's Finch eggs showed a smaller difference in volume within two-egg clutches (mean difference of 5.9 ± 3.3%, 1.9–13.4%, n = 14 clutches) compared to Nightingale Island Finch eggs (8.4 ± 5.3%, 0.3–18.7%, n = 13, Table 1). Nightingale Island Finch eggs tended to be more elongated than Wilkins's Finch eggs (Table 2), often with a pronounced point (t = -4.134, df = 60, p < 0.001; Figure 2F). Wilkins's Finch eggs weighed 5.44 ± 0.28 g (range 4.90–6.05 g, n = 16) and Nightingale Island Finch eggs 3.61 ± 0.98 g (range 3.00–4.10, n = 15). In relation to female body masses, Wilkins's Finches laid relatively smaller eggs (10.7% of mean female mass of 50.6 ± 1.7 g, range 45.5–54.5 g, n = 142) than Nightingale Island Finches (13.7% of female mass of 26.2 ± 1.9 g, range 23.0–30.2 g, n = 70).

Incubation and nestling periods

Among two-egg clutches, Wilkins's Finch females laid their eggs 0.5–4 d apart (mean 1.5 ± 0.7 d, n = 34 nests), whereas Nightingale Island Finch females had slightly shorter intervals between laying (0.5–2 d, mean 1.2 ± 0.5 d, n = 26). Where incubation was known to the nearest day, eggs hatched after 18.3 ± 0.5 d in Wilkins's Finches (range 18-19 d, n = 4) and 17.7 ± 0.5 d in Nightingale Island Finches (range 17–18 d, n = 6). Few hatching intervals for two-egg clutches were recorded; they averaged 1.3 ± 0.5 d (range 1–2 d, n = 6) for Nightingale Island Finches and 1.4 ± 0.6 d (range 1–2 d, n = 5) for Wilkins's Finches, but neither Wilkins's Finch nest where the laying interval was >2 d hatched both eggs so this might underestimate the hatching interval for this species. In all cases where laying and hatching sequence was known, the first laid egg hatched first (n = 10). Infertile Wilkins's Finch eggs were incubated for 19–29 d (mean 24 d, n = 16) and Nightingale Island Finch eggs for 20–24 d (mean 22 d, n = 5). The nestling periods for both species were 18–20 d (Wilkins's Finch mean 19.5 ± 0.6 d, n = 29 fledglings; Nightingale Island Finch mean 18.9 ± 0.7 d, n = 35 fledglings; t = 0.625, df = 62, p = 0.534); by 21 d chicks were mobile and able to sit next to the nest or in the dense cover nearby. Fledglings stayed quietly within a few metres of the nest for up to 10 d, then ventured farther from the nest, often begging noisily from their parents.

Repeat breeding attempts

At least 31% of pairs laid a second clutch after their first breeding attempt failed (n = 25/81 pairs which failed, pooled

Table 1. The mean (± SD) egg volumes (calculated as $L \times W^2$) and female bird mass (excluding gravid birds) among *Nesospiza* finches at Nightingale and Inaccessible islands. Sample sizes shown in parentheses. The percentages indicate differences in values between species.

	Egg Volume Index		Body mass (g)	
Large-billed finches				
N. wilkinsi	9752 ± 822 (33)	12.1%	50.6 ± 1.8 (90)	23.9%
N. a. dunnei	8700 ± 645 (21)		40.9 ± 1.9 (58)	
Small-billed finches				
N. a. fraseri	7381 ± 484 (54)	5.9%	27.1 ± 1.2 (108)	3.3%
N. a. acunhae	7074 ± 567 (68)	1.5%	26.3 ± 1.3 (143)	0.1%
N. questi	6972 ± 560 (32)		26.2 ± 1.9 (70)	

Table 2. Size and shape of the eggs of *Nesospiza* finches breeding at Nightingale Island in 2016. Elongation index is length/width and egg volume index is L × W^2 (see Methods). Data from 19 Wilkins's Finch nests (5 one-egg and 14 two-egg clutches) and 19 Nightingale Island Finch nests (6 one-egg and 13 two-egg clutches).

	All eggs		**One-egg clutches**		**Two-egg clutches**			
Size and shape of eggs	**Mean ± SD**	**Range**	**Egg ± SD**	**Range**	**α egg ± SD**	**Range**	**ß egg ± SD**	**Range**
Egg length (mm)								
Wilkins's Finch	26.55 ± 1.49	22.87-28.60	27.03 ± 1.25	25.11-28.56	26.86 ± 1.48	23.89-28.60	26.86 ± 1.48	23.89-28.60
Nightingale Island Finch	24.44 ± 0.79	22.81-26.80	24.96 ± 0.95	24.29-26.80	24.78 ± 0.48	24.11-25.50	23.84 ± 0.61	22.81-24.73
Egg width (mm)								
Wilkins's Finch	19.15 ± 0.40	18.20-19.92	19.09 ± 0.25	18.67-19.31	19.20 ± 0.39	18.31-19.82	19.12 ± 0.48	18.20-19.92
Nightingale Island Finch	16.88 ± 0.53	15.25-17.80	17.41 ± 0.39	16.78-17.80	16.87 ± 0.48	15.25-17.49	16.63 ± 0.38	16.01-17.42
Elongation index (%)								
Wilkins's Finch	1.387 ± 0.068	1.210-1.498	1.417 ± 0.069	1.306-1.498	1.399 ± 0.064	1.242-1.477	1.363 ± 0.069	1.210-1.484
Nightingale Island Finch	1.449 ± 0.052	1.379-1.591	1.434 ± 0.065	1.394-1.561	1.470 ± 0.056	1.379-1.591	1.434 ± 0.037	1.387-1.500
Egg volume index								
Wilkins's Finch	9725 ± 822	8169-11235	9848 ± 506	9285-10386	10025 ± 749	8599-11235	9444 ± 915	8169-11023
Nightingale Island Finch	6972 ± 560	5644-7927	7571 ± 430	6839-7927	7133 ± 291	6557-7620	6534 ± 484	5644-7332

data for both seasons and taxa), of which 23 pairs failed during incubation and two at chick stage. This proportion is likely an underestimate, since some relays may have gone undetected (e.g. relay nests that failed quickly before being recorded and relays in February after we left the island), especially in the woodlands surrounding the core study area that were checked less frequently. Wilkins's Finch females laid second clutches 3–34 d after losing their first clutch (mean 12.8 ± 7.3 d, n = 17 clutches, pooled for both seasons) and Nightingale Island Finch females 6–13 d (mean 9.0 ± 2.8 d, n = 8).

Generally, females built another nest for their new clutch, but on five occasions (20% of relays), females used the same nest cup for their relay clutch. This strategy did not appear to reduce the relay interval since nests were enthusiastically refurbished, with four Wilkins's Finch females relaying after 14.2 ± 3.8 d and one Nightingale Island Finch after 6 d. In general, nests that failed early in the nesting cycle tended to have shorter intervals between failure and relaying than nests that failed at a much later stage in the nesting cycle. The distances between nests in the same season were 5.9 ± 5.6 m (range 0–20 m, n = 17) for Wilkins's Finches and 5.0 ± 3.4 m (0–11 m, n = 8) for Nightingale Island Finches. The distribution of inter-seasonal nest sites was similar between taxa: in 2017 Wilkins's Finch nests were an average of 12.9 ± 9.4 m away from their 2016 nest (range 0 –33 m, n = 23, representing only pairs that retained their partner and previous seasons' territory) and Nightingale Island Finch nests were an average of 11.1 ± 8.1 m away (range 0–23 m, n = 15).

Inter-year consistency

Three pairs of colour-banded Wilkins's Finches were monitored in all three seasons (2012, 2016 and 2017). The first pair was one of the first (observed) pairs to lay in all three seasons. This female nested in the same small patch (3-m radius) of *Asplenium* ferns (five nests including two relays). The second pair nested in the same *Spartina* tussock (<1 m radius) in 1st Wood in all three seasons (four nests). The third pair also nested in the same patch of *Spartina* tussock (4 m radius) where their 2012 and 2017 clutches were laid a day apart in November (of their respective years).

Inter-species observations

Despite overlapping territories (Figure 1), instances of inter-species aggression or other interactions were rare and no hybrid birds or inter-species pairs were found. On one occasion, a Wilkins's Finch male defended a Nightingale Island Finch fledgling from persistent attacks by thrushes. Inter-species feeding was observed on two occasions, both where a Nightingale Island Finch female fed a Wilkins's Finch fledgling. The first occasion appeared to be an isolated event in 1st Wood, where the known fledgling (25 d old, banded) was still within its natal territory. The other unknown fledgling, southwest of Pond 4, was older (≈30 d, caught and confirmed to be a Wilkins's Finch) and was fed three times within 40 minutes by the returning female.

Other behavioural observations

Nightingale Island has no rivers, and most finch territories had no water source, but there are coastal seepages and small pools in Ponds 1–3 and a muddy pool in 1st Wood. Two tiny wells were found in 1st Wood and another in the forest northwest of Pond 3. These were small depressions at the base of large trees, usually under exposed roots, where water was always available. Finches visited these cryptic wells to drink and bathe, but approached cautiously as they were vulnerable to thrushes, which would often mob and sometimes attack finches when leaving the well, often resulting in fierce tussles through the undergrowth. Finches also gleaned water droplets off *Usnea* spp. lichens and the edges of *Asplenium* spp. fern leaves after rains or in foggy weather. Only Nightingale Island Finches were seen drinking from the coastal seepages at the Landing Rock and West Landing (Figure 1).

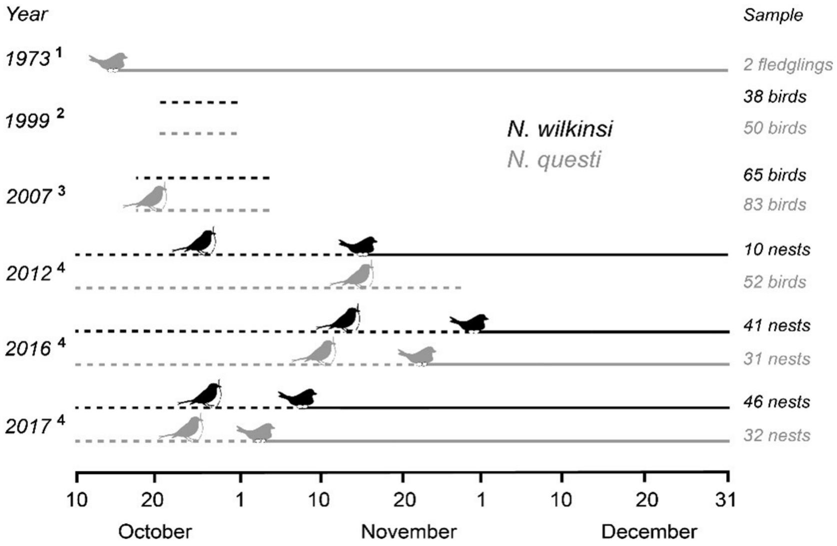


Figure 4: Breeding seasonality of *Nesospiza* finches at Nightingale Island. Dashed lines indicate the periods of field observations before breeding commenced (i.e. no females with brood patches or nests with eggs) with first sightings of females carrying nesting material indicated; solid lines show confirmed breeding periods. Sample sizes in years with no confirmed breeding are numbers of birds caught. Data sources: (1) Richardson 1984 (approximate laying date is inferred here based on record of "several very recently fledged young being fed on 25 November [1973]", p. 175); (2) Ryan (unpublished data from 20–29 October 1999); (3) Ryan (unpublished data from 18 October–4 November 2007); (4) This study.

Discussion

The breeding behaviour of Nightingale Island's finches was generally consistent with that already described for *Nesospiza* finches mainly at Inaccessible Island (Stoltenhoff 1952; Elliott 1957; Richardson 1984; Fraser and Briggs 1992; Ryan and Moloney 2002). However, there was a fair degree of inter-annual variation in the onset of breeding at Nightingale Island (Figure 4). In three of four seasons where breeding seasonality is reasonably well recorded for both species, Nightingale Island Finches started to breed 1–3 weeks earlier than Wilkins's Finch, which is opposite to the order exhibited by large- and small-billed finches at Inaccessible Island (Ryan and Moloney 2002). The exception was in 2012, when ten Wilkins's Finch nests (seven with eggs) were found by 26 November 2012 with no signs of breeding among Nightingale Island Finches. What caused the Nightingale Island Finches to start breeding more than two weeks later than Wilkins's Finch in 2012, when in 2016, 2017 and probably 2007, they started earlier? On Nightingale Island, bad weather appeared to restrict the birds' ability to build nests and some partly-built nests damaged by storms were abandoned. However, this affected both species, which perhaps partly explains the variability in the onset of breeding among years, but does not explain the variability among species.

The abundance of seeds available to sustain parents while breeding is perhaps a more plausible explanation, because the small-billed finches partly rely on seasonal grass and sedge seeds (Ryan 1992), whereas the large-billed finches rely on seeds from *Phylica* fruits, which are available year-round (Roux et al. 1992). This opposing flexibility could explain the very early start to breeding recorded by Richardson (1984), who reported fledged Nightingale Island Finch young on 25 November 1973, which means that laying took place before mid-October (Figure 4), more than two weeks earlier than any other record (3 November 2017). Interestingly, the onset of breeding at Inaccessible Island may also vary among years, with the first Lowland Inaccessible Finch eggs recorded on 25 October in 1982 (Fraser and Briggs 1992), 30 November in 1989 and 25 November in 1999 (Ryan and Moloney 2002). The nesting season for both species likely continues until late March, since some relay nests were still active when we left the island in late January 2017 (n = 3 active nests) and 2018 (n = 6 active nests). These clutches, if successful, would have fledged between February and mid-late March. Elliott (1957) also reported a nest 'had fresh eggs on 4 February 1950', which is likely a relay, and would have resulted in chicks fledging in mid-March.

Both species of finches displayed similar behavioural traits when breeding, but some Wilkins's Finch pairs were particularly quiet and cryptic. During incubation, males approaching the nest would usually call to the female, who responded with a sharp 'chirp' before emerging and noisily begging for food from the male. However, some male Wilkins's Finches arrived quietly and the female sneaked off the nest through the undergrowth. She remained silent while being fed, and returned to the nest via a different route. This behaviour was observed repeatedly in four Wilkins's Finch pairs, but never among Nightingale Island Finches. Tristan Thrushes *Turdus eremita* frequently and actively sought out finch nests and this silent approach presumably helped to deter these inquisitive predators. Females appeared to favour using plants

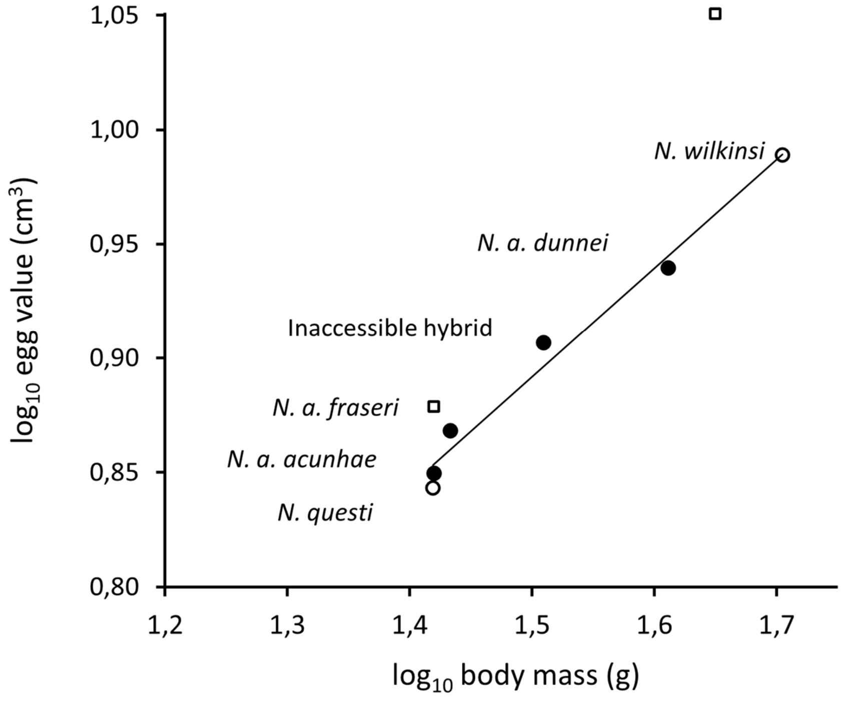


Figure 5: The relationship between female bird mass (excluding gravid birds) and egg volume (EV, calculated as L × W^2) among *Nesospiza* finches. The regression line is the best fit for all species (egg value = 0.477× + 0.176; R^2 = 0.981) from Nightingale Island (open circles) and Inaccessible Island (closed circles). Open squares are Elliott's (1957) anomalously large egg measurements (*N. wilkinsi* top right and *N. questi* at bottom left).

away from the nest site, possibly to deter predatory Tristan Thrushes from locating the nest. Nightingale Island Finches were less discreet than Wilkins's Finch females when nest building, usually flying directly to their chosen nest site with their nesting material, whereas Wilkins's Finch females were far more cautious. When returning to their nest site, Wilkins's Finch females would often pause on a nearby branch (5–10 m away), appearing to check the area for onlookers, before dropping to the ground and approaching their nest silently through the dense undergrowth.

Our observations of Nightingale Island Finch clutch sizes correspond with the first records of 1–2 eggs in 1950 (Elliott 1957, n = 3 nests) and are virtually identical to clutches at Inaccessible Island (Ryan and Moloney 2002; Ryan et al. 2007). Clearly the claim by Wyville Thomson (in Hagen 1952) of small-billed finches laying 4–5 eggs on Nightingale Island is in error. Our Wilkins's Finch nest observations also correspond with the only previous records by Elliott (1957, 5 nests) and are similar to large-billed birds on Inaccessible Island (Ryan and Moloney 2002).

Among *Nesopsiza* taxa on Inaccessible Island, egg size increases with increasing female mass less rapidly than expected compared to continental species of thraupid finches (Ryan and Moloney 2002). In this regard they are similar to Darwin's Finches (Grant 1983), possibly reflecting more rapid evolution in body size (linked to selection for bill size) than in egg size (Ryan and Moloney 2002). Elliott's (1957) small sample of egg measurements from Nightingale's finches were anomalously large when compared to finches from Inaccessible Island (Ryan and Moloney 2002). Our mean egg dimensions from Nightingale Island and Wilkins's finches are smaller than reported by Elliot (1957), giving a tight correlation between egg size and female body size among all *Nesospiza* taxa (Figure 5). Among the three small-billed taxa, the proportional difference between mean body masses and between mean egg masses are relatively small (0.1–3.3% among body masses and 1.5–5.9% among egg sizes; Table 1). However, between the two large-billed species, Wilkins's Finch females weighed an average of 24% more than Inaccessible Island Finch (*N. a. dunneii*) females and Wilkins's Finch eggs were 12% larger than Inaccessible Island Finch eggs (Table 1). Ryan and Moloney (2002) also showed a general tendency for thraupid eggs to become more elongate with increasing body size. However, at Nightingale Island, Wilkins's Finch eggs tended to be less elongate than those of Nightingale Island Finch.

Overall, the breeding biology and investment per breeding attempt of the two *Nesopsiza* finches endemic to Nightingale Island is similar to that recorded among the *N. acunhae* complex on Inaccessible Island (Fraser and Briggs 1992; Ryan and Moloney 2002), as might be expected given the close genetic similarity between the three species (Ryan et al. 2007). Their modest clutch size compared to other thraupid finches and single brood per season (contra Collar and Stuart 1985) could be interpreted as a further risk factor in terms of their susceptibility to external threats. However, these conservative life history traits probably reflect the high densities of finches on the islands (Ryan and Moloney 2002). It would be fascinating to know if clutch size and the number of broods per season might increase if more habitat were made available (cf. Seychelles Warbler *Acrocephalus sechellensis*, Komdeur 1994). If this were the case, the increase in reproductive potential might increase the speed at which *Nesospiza* populations can recover from short-lived catastrophic events (Komdeur and Pels 2005). One way to test this might be to translocate some small-billed finches from Inaccessible Island to Tristan da Cunha if House Mice *Mus musculus* and Ship Rats *Rattus rattus* are eradicated from Tristan da Cunha. However, the loss of large *Spartina* tussocks from Tristan da Cunha and extensive habitat modification for pasture on the lowlands, might hinder the successful restoration of finches to Tristan da Cunha even if introduced predators are removed from the island.

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