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Author for correspondence:

*Marc-Olivier Beausoleil, Email: marc-olivier. beausoleil@mail.mcgill.ca

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Nest building by Darwin's finches as an overlooked seed dispersal mechanism

Carlos Camacho¹, Marc-Olivier Beausoleil^{2,*}, Julio Rabadán-González³ and Roxanne Richard²

¹Department of Evolutionary Ecology, Estación Biológica de Doñana – CSIC, Av. Américo Vespucio 26, 41092 Seville, Spain; ²Department of Biology and Redpath Museum, McGill University, 859 Sherbrooke Street West, Montreal, Quebec, Canada H3A 2K6 and ³Observado.es, Gordal 8, 41940 Tomares, Seville, Spain

Abstract

Caliochory, or seed dispersal by birds as nest material, has been reported for several species, but its effectiveness remains unclear in most cases. Darwin's finches are traditionally regarded as seed predators, but the observation of two nests challenges this assumption by demonstrating that they can act as seed dispersers via caliochory. Darwin's finches incorporate cotton-like materials into their nests, including seeds of Darwin's cotton (*Gossypium darwinii*), a shrub endemic to the Galápagos (Ecuador). Bird nests typically break down after intense rainfall, so the seeds incorporated into nests might benefit from suitable conditions for germination. By simulating the germination conditions experienced over a 72-h period by cotton seeds in a naturally fallen nest, this study qualitatively confirms the long-term viability of at least a small fraction of the seeds at the surface of the nest. Darwin's finches might therefore provide seed-dispersal services to Darwin's cotton and possibly, other native and exotic plants of the Galápagos commonly incorporated into nests. However, larger confirmatory studies are needed.

Dispersal is a fundamental aspect of the life history of plants and understanding seed dissemination mechanisms is critical to understanding plant community structure and distribution. Despite being difficult to observe, some peculiar dispersal mechanisms, such as seed adherence to the beaks of birds, pellets containing undigested seeds, and even muddy feet of birds, have long been noted by naturalists (Darwin 1859), while others have almost completely eluded their attention. Caliochory (sensu Warren *et al.* 2017), or seed dispersal by birds as nest material, is one of those non-canonical mechanisms, first described by the eminent botanist Henry Ridley (Ridley 1930) nearly a century ago. Nest-mediated seed dispersal has been reported for several bird species, but its effectiveness and importance remain unclear. Here we describe for the first time a form of caliochory that raises new questions about the role of Darwin's finches in structuring plant communities in the Galápagos Islands.

Darwin's finches in the genus *Geospiza* obtain much of their food by crushing fruits and have therefore traditionally been regarded as seed predators. However, recent studies challenge this assumption, suggesting that effective seed dispersal by these iconic species is more common than previously thought (Guerrero & Tye 2009). Mechanisms of seed dispersal by Darwin's finches reported in the literature fall into two categories: seed discarding prior to fruit consumption, and defecation of undigested viable seeds, sometimes far away from the feeding site (Guerrero & Tye 2009). Based on the observations in this study, we propose nest building as a third, previously overlooked, seed dispersal mechanism by Darwin's finches.

On 23 February 2018, after 3 d of intense rainfall, an old small ground finch (*Geospiza fuliginosa*) nest fell from an ornamental flame tree (*Delonix regia*) located in an urban area on Santa Cruz Island (Galápagos, Ecuador). Later, on 13 March 2018, another finch nest fell from a papaya tree (*Carica papaya*) in the small town of Floreana Island during a severe storm but, unlike the previous one, this nest was still under construction by a pair of medium ground finches (*Geospiza fortis*; Figure S1). Darwin's finches use a range of natural and anthropogenic material to build their nests (e.g. grass, plastic strands and ribbons) and typically use cotton-like materials to line them (Orr 1945; a video can be seen at: https://youtu.be/I29JZaAeNBA). Finches in urban areas usually incorporate synthetic cotton into their nests (85% of nests analysed by Knutie *et al.* 2014). However, the two nests we found lacked synthetic cotton, but contained numerous (\leq 250 counting only the seeds at the top and bottom surface of the nest) seeds of Darwin's cotton (*Gossypium darwinii*), a shrub endemic to the Galápagos Islands (Figure 1a, b).

Darwin's cotton occurs on 13 of the islands of the archipelago in both urban and non-urban environments and, unlike its endemic congener *Gossypium klotzschianum*, produces numerous seeds covered by well-developed cotton balls that facilitate their dispersal on the wind (McMullen 1999, Sliwinska & Bewley 2014). Darwin's cotton is widely available as a source of nest material for the finches, so the plant could in turn receive seed-dispersal services,



Figure 1. Flower of *Gossypium darwinii* (a). Seeds of *G. darwinii* on Floreana Island (b). Top view of the old finch nest found on the ground on Santa Cruz Island (c). Same nest but view from below, showing the higher concentration of cotton seeds at the bottom of the nest (d). Seedling of Darwin's cotton after our germination experiment with the planted nest (e). Detail of the seedling collected from the nest after 10 days of germination (f).

provided that nest-building birds collect not only the cotton balls, but also the attached seeds (Rohwer *et al.* 2017). Darwin's finches generally occur in large numbers and, importantly, their need for building material is great. Finches are not only capable of breeding multiple times under good conditions, but also males often build one or more nests and tear it down before breeding (Orr 1945). Moreover, they occasionally move material from one nest to another, so it is likely that large numbers of cotton seeds are inadvertently transported by the finches every season.

Darwin's finches are opportunistic breeders that strongly depend on rainfall (Grant & Boag 1980) and, as suggested by this study, dispersal of cotton seeds as nest material might be directly facilitated by rainfall as well. Finches build domed - sometimes open - nests in cactus and trees, usually exposed to rain (Orr 1945). Bird nests often break down during rainy periods, so the seeds typically fall to the ground after intense rainfall (Dean et al. 1990). Nest collapse during the rainy season could improve the effectiveness of dispersal in dry and nutrient-poor environments for several reasons. First, cotton seeds would reach the soil surface under favourable conditions for germination. Second, the moisture retained in the nest material would further improve the germination conditions for a relatively long time. Caliochory might additionally increase the chance of germination, as fallen seeds not incorporated into nests may be at greater risk of predation by insects and rodents before the arrival of the rains (Dean & Milton 1991). Lastly, seeds incorporated into finch nests might benefit from the combination of decomposing organic material of the nest itself and nutrients in the form of either bird droppings or protein-rich feather sheaths that remain in the nest after the chicks have fledged (Dean & Milton 1991, Fedriani et al. 2015).

However, for effective dispersal to occur seeds should be able to remain viable in nests for relatively long periods of time (Dean & Milton 1991, Warren et al. 2017). To examine this possibility, we transferred the old nest we found on Santa Cruz Island - initially on tarmac - to a small area of top soil about 1.5 m away from the original location. Before collecting the nest, we noted that it had landed on the ground on the bottom surface, precisely where the majority of the cotton seeds concentrated (Figure 1c, d). Neither the soil composition nor the original structure or position of the nest were modified to simulate the germination conditions experienced by seeds in a naturally fallen nest. Examination of the nest after only 72 h revealed that three of the seeds closest to the soil surface had successfully germinated (i.e. the radicule was visible), thereby confirming the long-term viability of at least a small fraction of the seeds found in finch nests, as well as the convenience of the deposition conditions (Figure 1e, f). However, given the small sample size, additional analyses of seed number and germination rate in a larger number of nests are needed to determine the actual importance of caliochory in the dissemination of cotton seeds.

Lack (1947) already noted the use of cotton seeds as nest lining by finches, but the importance of nest building and subsequent collapse for seed dispersal has been largely underappreciated, as implicit in the statement of Stephens & Rick (1966) that 'a method of dispersal which would transport seeds rather widely but leave them suspended well above the soil surface for an indefinite period would not seem to be highly efficient'.

Caliochory is not unique to Darwin's finches (reviewed in Warren *et al.* 2017) and there is evidence to suggest that it is an important, albeit supplemental, dissemination mechanism in plants with cottony seed coverings adapted for wind dispersal (Dean *et al.* 1990, Sliwinska & Bewley 2014). Darwin's cotton is

one of those plants primarily dispersed by wind (Hutchinson et al. 1947, Stephens & Rick 1966), although nest-building birds might influence seed movement independently of the wind and thus influence its fine-scale distribution. Bird-dispersed seeds could reach different and/or more suitable microsites for germination and establishment than those on the wind, but a comparative study tracing the fate of seeds spread by birds and other means is required to confirm this hypothesis. Estimates of the foraging distances or the home-range size for small or medium ground finches would also be desirable to assess the magnitude of seed dispersal distances by this mechanism. Future research combining mechanistic dispersal models and empirical data on bird occurrence and distribution, and local wind dynamics should ideally be conducted to elucidate the relative role of biotic and abiotic vectors in the dispersal success of Darwin's cotton (Damschen et al. 2014).

In conclusion, nest collapse after rainfall could potentially increase the germination rates of viable seeds present in bird nests. Darwin's finches can thus act as additional dispersal agents for cotton seeds and, possibly also, other fluffy seeds incorporated into nests (see Orr 1945 for some examples). Further research to understand the actual implications of nest building for the dynamics of island plant populations is still needed, especially because of the potential role of birds in the spread of non-native species across the Galápagos Islands.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0266467418000378

Author ORCIDs. Carlos Camacho D https://orcid.org/0000-0002-9704-5816. Marc-Olivier Beausoleil D https://orcid.org/0000-0003-3717-3223

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