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Nesting success in Darwin's small tree finch, *Camarhynchus parvulus*: evidence of female preference for older males and more concealed nests

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Age-assortative mating has been documented among birds, but there is little evidence of direct benefits to females that pair with older males. In this study, I examined nest concealment in Darwin's small tree finch and tested the following predictions: (1) nest concealment increases with male age, (2) females prefer males that build well-concealed nests, and (3) females receive direct benefits through reduced predation at concealed nests. Darwin's small tree finch has a pattern of annual moult that makes it easy to observe age-related variation in reproductive success. In this species, males build a display nest that is sometimes used by the female for nesting. Controlling for male age, females preferred display nests for nesting that were well concealed by surrounding vegetation, whereas exposed display nests were rarely used for nesting (although occasionally a female paired with the male that built the unused display nest). Using cross-sectional and longitudinal data, this study found evidence of a female pairing preference for older males, as well as increased nest concealment among older males. Females that paired with older males had higher fledging success (using the longitudinal data), mostly due to reduced predation.

Keywords: age; assortative mating; *Camarhynchus parvulus*; Darwin's small tree finch; nest concealment; predation outcome; display nest

Age-assortative mating has been documented among birds (e.g. Komdeur et al. 2005), but there is little evidence of direct benefits to females that pair with older males. Females may choose males on the basis of visual traits that honestly reflect male age, such as male plumage coloration (Grant & Grant 1983, 1987; Price 1984; Komdeur et al. 2005), or they may choose nonvisual traits that covary with male age, such as song (Eens et al. 1991; Gil et al. 2001). There is a paucity of information on traits that covary with male age that reliably signal direct benefits for females.

Nest concealment is increasingly recognized as an important determinant of avian reproductive success, as predation is often higher at visually conspicuous nests (Martin 1993; Kleindorfer et al. 2003; Lambert & Kleindorfer 2006). Uniparental incubators at exposed nests experience greater predation risk during the incubation phase (Martin et al. 2000; Lambert & Kleindorfer 2006), a finding that leads to the prediction that uniparental female incubators should be more selective about nest concealment to reduce predation risk to themselves and the brood. Evidence that older males occupy safer nest sites comes from Pärt (2001) in an experimental study of northern wheatears, *Oenanthe oenanthe*, however, female preference was not examined for male nest site.

In bowerbirds, males build a bower solely to attract females for mating (Borgia 1995; Madden 2003), while in other bird species, a nest may be used for both mate attraction and subsequent nesting (Soler et al. 1998; Hansell 2000). Darwin's tree finches build domed nests that serve both for mate attraction and nesting (Lack 1947). During nest construction, and once the display nest is built, a male small tree finch will sing in the vicinity of the nest to attract a female. Small tree finch females arrive and inspect the display nest by entering it, and a selection by the female is made with three possible outcomes: (1) the female rejects both the male and the display nest,

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(2) the female accepts the male but rejects the display nest in which case the pair will build a new nest together, or (3) the female accepts both the male and the display nest for nesting.

Darwin's ground finches increase the proportion of black in their body plumage with each annual moult. Males require, on average, about 5–6 years to acquire fully black body plumage (Orr 1945; Grant & Grant 1983), but are reproductively active within their first year of life. Females remain grey/brown throughout their lives. A similar pattern of annual moult and sex differences in plumage coloration has been observed in Darwin's tree finches. In tree finches, only the males' crown and chin attain black plumage (and not their entire body), but this pattern has not been quantified (Lack 1947; Bowman 1961; Grant 1999). This age difference in plumage coloration provides a good opportunity to monitor age-related variation in male nest site attributes and fledging success.

In this study, I provide quantitative data on male plumage characteristics across sequential years in Darwin's small tree finch. I also examine nest concealment and male age (as inferred from plumage coloration) to test functional explanations of female preference for safe nests. I first test the hypothesis that females have a higher pairing level with older males. Next, I examine nest attributes in relation to male age and test the hypothesis that older males build more concealed nests. Current theory predicts high predation at nests with low vegetation concealment (Martin 2004). If females receive direct benefits from safe nests built by older (black) males compared with younger (brown) males, then I predict the following: (1) nest concealment is associated with lower predation; (2) older males build more concealed nests than younger males (using both cross-sectional and longitudinal data); (3) females discriminate between nests according to defined nest concealment parameters, with evidence of higher pairing success in males that build concealed than conspicuous nests; and (4) fledging success is higher at nests with older than younger males (indirect benefits).

METHODS

Study Site and Study Species

This study was conducted on Santa Cruz Island in the highland area surrounding Los Gemelos (0°37′S, 90°21′W) during the breeding season (January–March) of 2000, 2001, 2002, and 2004. Although Darwin's tree finches occur in both the lowlands and highlands of Santa Cruz Island, they attain their highest density in the highland *Scalesia* zone (300–750 m), an area that is dominated by the endemic composite tree *Scalesia pedunculata* (Asteraceae; Eliasson 1984).

Nest Monitoring

I monitored active nests from the first stage of nest building by the male. Nests were located by systematically searching three study plots (each 100 × 200 m) for singing males and/or evidence of nest building. I monitored a total of 176 nests across all years, and mist-netted 160 small tree finches. To ensure independence of the data, I only included the first nest encountered with known outcome per male in this study ($N = 132$), despite observations of repeated nesting within and across years for some colour banded males (44 nests were excluded from the analysis). Thus, the number of nests included in analyses across all years was as follows: 35 nests in 2000; 38 in 2001; 39 in 2002; and 20 in 2004. I explicitly test for a paired comparison of nest sites for 10 males that were observed in 2000 or 2001 and again in 2004.

Once a singing male and his display nest were detected, I monitored nests every 2 days for 20 min to establish whether the male and his nest were accepted by a female or were rejected. Nest monitoring was conducted for a minimum of 2 weeks per nest. After pair formation, I monitored incubation, feeding, and the nesting outcome. All nests were located at 6–10 m on horizontal branches of *S. pedunculata* and were positioned by interweaving surrounding smaller twigs and leaves.

The incubation and nestling phase were each approximately 12 days. The breeding system is considered socially monogamous (Lack 1947; Grant 1999), with no information on extrapair fertilizations (EPFs) in the focal species. In Darwin's cactus finch, *Geospiza scandens*, Petren et al. (1999) found a low level of EPFs, which did not exceed 8% in their study population.

Nesting success was determined from repeated observations of parental activity at the nest. If offspring were more than 8 days old and the nest was empty, I recorded 'possible fledging'. Nest predation was inferred if the following conditions were met: (1) the nest was empty and observations of the previous 3 days showed evidence of incubation or feeding; and (2) the missing nestlings were less than 8 days old. After suspected fledging, predation or abandonment (determined by 30-min observation without activity), the nest was collected and examined for evidence of abandoned eggs, eggshell, or nestling remains.

Nest Site Characteristics

Nest site characteristics were measured within 7 days of the completion of the nesting attempt. Using a compass, I created four quadrants that were aligned North–South and East–West, with a 5-m radius surrounding the nest. The following habitat variables were recorded for each nest: (1) nesting height from ground to base of the nest (m), (2) nesting tree height (m), (3) nesting tree perimeter (cm), (4) percentage canopy leaf cover for the nesting tree, (5) percentage leaf cover 1 m below the nest, (6) percentage leaf cover 1 m to the side of the nest (averaged for all four sides), (7) percentage leaf cover 1 m above the nest, (8) undergrowth plant height (mean of five point samples per quadrant) (cm), and (9) percentage ground cover within a 5-m nest radius using ocular estimation and averaged over four quadrants.

Male Colour and Age Determination

Birds were mist-netted and colour banded at the nest during incubation or early feeding. Standard morphological