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Master Thesis

Male age is related to the heterospecific soundscape of the breeding territory in two Darwin's finch species


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Competing interests

I the author declare no conflict of interest.

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Zusammenfassung (Abstract in German)

Die Umgebung, in der wir aufwachsen, hat einen starken Einfluss auf unsere Entwicklung und Zukunft und kann durch das Alter und die Erfahrung der Eltern beeinflusst werden. Ältere und erfahrene Individuen sind möglicherweise von höherer Qualität als jüngere Individuen, die noch nicht den Härten der natürlichen Auslese ausgesetzt wurden. Aus diesem Grund könnten ältere Individuen Zugang zu besseren Ressourcen haben und ihre Nachkommen besser unterstützen. Im Allgemeinen ist die Rolle des Alters der Eltern für die Umwelterfahrung ihrer Nachkommen bei nicht-menschlichen Tieren noch wenig erforscht - eine Wissenslücke, die mit dieser Masterarbeit verringert werden soll. Wie Menschen lernen auch Singvögel ihre Vokalisationen von einem Tutor. Jüngste Studien haben gezeigt, dass das Gesangsrepertoire der lernenden Vögel auch vom Gesang der Nachbarn beeinflusst werden kann. Hier gehe ich der Frage nach, ob das Alter des Vaters vorhersagt, wo er sein Nest baut und in was für einer akustischen Umgebung sein Nachwuchs aufwächst. Ich untersuche diese Frage an zwei Darwinfink Arten auf den Galápagos-Inseln, der Kleine Baumfink (*Camarhynchus parvulus*) und Kleiner Grundfink (*Geospiza fuliginosa*). Darwinfinken gehören zu den Singvögeln und lernen ihren Gesang von einem Tutor. In der Regel ist dies der Vater, aber Jungvögel können auch von Gesängen benachbarter Artgenossen lernen. Ich wählte dieses System, weil die Männchen das Nest bauen, das Territorium wählen und bei diesen Darwinfinken das Gefieder der Männchen bis sie 5+ Jahre alt sind mit jedem Jahr der Mauser zunehmend schwarz wird. Dies bietet die seltene Gelegenheit, den Einfluss des Alters der Männchen auf den Standort des Nests und die Gesangszusammensetzung im Territorium zu untersuchen. Dafür habe ich GoPro-Kameras an 55 Nestern mit Eiern und Küken angebracht, um die Gesangsaktivitäten im Umkreis von 25 m um das Nest aufzuzeichnen. Ich habe das Alter der Männchen, die Charakteristiken des Nistplatzes und die Anzahl der con- und heterospezifischen Gesänge aufgezeichnet. Ich habe die folgenden Vorhersagen getestet: Ältere Männchen werden in Hot-Spot-Gebieten mit mehr heterospezifisch singenden Nachbarn nisten. Im Umkehrschluss werden jüngere Männchen weniger artfremde und mehr artgleiche singende Nachbarn haben. Ältere Männchen platzieren ihre Nester höher und mit dichterer Pflanzendecke, was ihnen Sicherheit vor Raubtieren bietet. Wenn es einen Preis hat viele singende Nachbarn zu haben, werden Nester mit höherer Gesangsaktivität häufiger geraubt. Die Ergebnisse geben folgende Einsichten: Ältere Männchen bauten Nester in Gebieten mit mehr heterospezifisch singenden Nachbarn als jüngere Männchen. Daher waren die Eier und Küken in den Nestern älterer Männchen einem artenreicheren Gesang ausgesetzt. Des weiteren bauten ältere Männchen ihre Nester in Gebieten mit mehr Vegetationsdecke, jedoch war dies nicht mit dem Raubtierrisiko verbunden. Zudem gab es keinen Einfluss der Gesangsaktivitäten auf das Raubtierrisiko. Zusammenfassend lässt sich sagen, dass sich das frühe Lebensumfeld der Nachkommen von Kleinen Baumfinken und Kleinen Grundfinken je nach Alter des Vaters und dem Territorium, das diese wählen, unterscheidet. Wie sich dies auf die zukünftigen Präferenzen und das Verhalten der Nachkommen im späteren Leben auswirken könnte, sollte in zukünftigen Studien untersucht werden.

Schlagwörter: Aufzuchtbedingungen, alter des Männchens, Darwinfinken

Abstract

The environment we grow up in has a strong influence on our developmental trajectory and future success, and can be mediated by parental age and experience. Older individuals have experience, and may be of better quality than younger individuals not yet exposed to the rigours of natural selection. Therefore, older individuals may have access to better quality resources to support their offspring. In general, the role of parents' age for offspring environmental experience has not been much studied in non-human animals, which is a knowledge gap this thesis hopes to fill. Like humans, songbirds learn their vocalisations from a vocal tutor. Recent studies have shown that neighbourhood song influences the song repertoire of vocal learning birds. Here I ask if a father's age predicts where he will build his nest, and what acoustic neighbourhood his offspring will grow up in. I test this question in two Darwin's finch species on the Galápagos Islands, the Small Tree Finch (*Camarhynchus parvulus*) and Small Ground Finch (*Geospiza fuliginosa*). Darwin's finches belong to the songbirds and are therefore vocal production learners that acquire their song from a tutor. Usually, the father is the vocal tutor, but young birds can also attend to the songs of neighbouring conspecifics. I focus on males in this system because they build the nest and choose the nest site, and in these Darwin's finches, males become increasingly black with each year of moult until 5+ years old. This creates the rare opportunity to test effects of male age on nest site location and singing behaviour near the nest. To answer that, I used GoPro cameras placed at 55 nests with eggs and chicks to record singing activity within 25 m of the nest. I recorded male age, nest site characteristics, and number of con- and heterospecific songs. I tested the following predictions. Older males will nest in hot-spot areas with more heterospecific singing neighbours. Conversely, younger males will have fewer heterospecific neighbours and more conspecific singing neighbours. Older males will build nests with more vegetation cover, in taller trees, and with higher nesting height, and this will confer safety against predation. If there is a cost to having many singing neighbours, I predict increased nest predation at nests with higher singing activity. The results lead to the following insights. Older males built nests in areas with more heterospecific singing neighbours than younger males. Therefore, the eggs and chicks in nests of older males were exposed to more species-rich song. While older males built nests in areas with more vegetation cover, this was not associated with predation risk. Also, I found no effect of neighbourhood singing activity on predation risk. In conclusion the early life environment of the offspring of Small Tree Finches and Small Ground Finches differs depending on the age of the father and the environment in which older males establish their territories. How that might affect future preferences and behaviour of the offspring in later life should be investigated in future studies.

Keywords: rearing environment, male age, Darwin’s finches

1. Introduction

Darwin's finches (Passeriformes: Thraupidae) have become a classic model species for evolutionary research in wild vertebrates. The attention to Darwin's finches was sparked by Charles Darwin and fellow members of the Beagle expedition who collected these birds on the Galápagos Islands in 1835 (Abzhanov 2010), and the myriad forms and assemblages on different islands helped inspire the theory of evolution by means of natural selection. To this day, Darwin's finches continue to be a valuable source of biological discoveries. The benefits of birds that do not show altered behaviour in the presence of humans, perhaps because of the absence of native mammalian predators, yet confronted with a suite of introduced species and natural laboratory conditions on many islands has created advantages for studying this group. Many contemporary insights have been gained in our understanding of mechanisms of speciation and hybridization (Podos, 2007, 2010; Kleindorfer *et al.*, 2014; Grant and Rosemary Grant, 2018; Peters and Kleindorfer, 2018; Kleindorfer and Dudaniec, 2020; Colombelli-Négrel and Kleindorfer, 2021), foraging behaviour and selection on beak size (B Rosemary Grant and Grant, 1996; Podos, Southall and Rossi-Santos, 2004; Herrel *et al.*, 2005; Huber and Podos, 2006; Tattersall, Chaves and Danner, 2018; Kleindorfer, Custance, *et al.*, 2019; Reaney *et al.*, 2020), parasite and host interactions (O'Connor, Dudaniec and Kleindorfer, 2010; Lincango *et al.*, 2015; Kleindorfer and Dudaniec, 2016; Kleindorfer, Custance, *et al.*, 2019; Heyer *et al.*, 2021; Kleindorfer, Common and Sumasgutner, 2021), and, during the Anthropocene, increasing research in the field of urban ecology (Villa and Segarra, 2010; de León *et al.*, 2011; Dvorak *et al.*, 2012; Gabela, 2014; De León *et al.*, 2018; Gotanda, 2020; Harvey *et al.*, 2021), just to name a few examples. Despite the significant research that has been carried out in the Darwin's finch model system, we still can gain much insight into details of nesting behaviour and neighbourhood species composition that may affect the ontogeny of behavioural and vocal development, which this study aims to do.

Oscines (i.e., songbirds) are vocal production learners that acquire their song from a tutor (Plamondon, Goller and Rose, 2008; Konishi, 2010). They first memorize the tutor's song (i.e., song template) and later learn to imitate and produce this song (Nottebohm, 1972; Rosemary Grant and Grant 1996). New research shows that sound learning can begin already during the egg phase in some songbird embryos. For example, Superb Fairy-wrens

(*Malurus cyaneus*) produce a vocally acquired call after hatch copied from their (foster) mother's in-nest calls during incubation (Colombelli-Négrel *et al.*, 2012), and embryos across avian taxa learn sound in ovo (Colombelli-Négrel and Kleindorfer, 2017; Rivera *et al.*, 2018; Colombelli-Négrel *et al.*, 2021). Mennill et al (2018) showed that wild Savannah Sparrows (*Passerculus sandwichensis*) learned their songs from experimentally broadcast tutors placed near the nest in the wild. Specifically, birds preferentially learned songs heard in both their natal summer and first spring, and passed that learned song on to the next generations (Mennill et al., 2018). In a recent study, Thomas et al. (2021) showed that in Savannah Sparrows, at first, young birds produce song types from many neighbours but then they prune the vocal repertoire to only produce one song type as an adult, producing the song type of their closer rather than more distant neighbour. In conclusion, the role of the acoustic neighbourhood is expected to play a significant role in vocal learning when embryos and nestlings are exposed to song in general, though to date there are few studies that measure the acoustic neighbourhood at the time of nesting across species.

In many avian systems, the males establish a territory and females select the preferred male and territory (O'Donald, 1980). Therefore, occupying the best territory can represent a great fitness benefit for males. For example, Alatalo and colleagues (1986) found that in Pied Flycatchers (*Ficedula hypoleuca*, Muscicapinae), territory quality is the most influential factor for earlier selection of a mate by the females. In the Pied Flycatcher system, females preferred nests positioned higher up a tree with a thick trunk and fewer birches in the surroundings. The authors conclude that female preference for nest position can be favoured by selection because higher and less accessible nests experienced less depredation by ground predators, and nest sites with fewer birches in the area can increase foraging efficiency as birches do not provide good foraging substrate. Other studies in songbirds have found that lower nests tend to be depredated by rodents and higher nests by avian predators (e.g., Colombelli-Négrel and Kleindorfer, 2009). This pattern has also been found in Darwin's Medium Tree Finch (*Camarhynchus pauper*) (Kleindorfer, Common and Sumasgutner, 2021), showing that the position of the nest can be an important influence on nesting success.

In addition to nest site position, females may show a preference for older males (Hansen and Price 1995) and hence age signalling by males can lead to a fitness advantage. In some systems, birds signal their age with plumage (Grant and Grant, 1987; Siefferman, Hill and Dobson, 2005; Probst *et al.*, 2007). For example, in Kirtland's Warblers (*Dendroica kirtlandii*) the plumage of males becomes more distinctive and brighter with age (Probst *et al.*, 2007). Kleindorfer (2007) showed that Small Tree Finch (*C. parvulus*) males gain increasing black plumage in the head and chin with each annual mould until they attain a completely black head in their fifth year. In line with predictions about the benefits of older age in male partners for females, female Darwin's finches more quickly paired with older males (Kleindorfer, Custance, *et al.*, 2019). Additionally, those pairs experienced higher breeding success because of lower nest predation (Kleindorfer 2007). The causal mechanism for lower nest predation is thought to be nest placement, and nests of older males were more concealed and positioned higher up in the canopy (Wappl *et al.*, 2020; Heyer *et al.*, 2021). Males may use their own local breeding success as a patch quality cue that integrates the effect of the various patch attributes on breeding performance (referred to as the "private" and "public information" hypotheses), and perhaps older and more experienced males have a benefit over younger males in terms of nest site selection (Danchin, Boulinier and Massot, 1998; Doligez, Danchin and Clobert, 2002; Mariette and Griffith, 2012). For example, Møller (1989) showed that older males adjusted nesting height in relation to previous nesting outcome and that experienced birds in ground nesting passerine guilds adjust their nesting site and nest concealment according to predation risk.

The age of nesting birds may also be associated with tenure in a territory (Beletsky and Orians, 1987). The quality of the nest site may be associated with the local neighbourhood given benefits of nesting in groups, described for example by a dilution effect (Hamilton, 1971; Rubenstein, 1978). Nesting in proximity to heterospecifics can provide a benefit of dilution against predator detection without increasing risk of cuckoldry, which would be higher when surrounded by conspecifics. Close proximity to conspecifics also increases food competition, and therefore the abundance of food resources in the territory might also affect the amount and composition of individuals that can be maintained in one area (Forero *et al.*, 2002; Booth, 2004). There is empirical support for lower predation risk in Darwin's finches on Santa Cruz Island, where focal Darwin's finches nesting in 'mixed species associations' with heterospecific neighbours experienced less nest predation (Kleindorfer, Sulloway and O'Connor, 2009). Therefore, the neighbourhood composition may influence not only the acoustic development of fledglings but also the general survival expectancy.

There is evidence that a diverse vegetation community could sustain a more diverse avian community. The vegetation structure associated with avian nesting can provide different types of benefits that may also result in survival increase. Vegetation structure provides foraging substrates and may therefore influence the local species abundance (Lantz, Gawlik and Cook, 2011; Weisshaupt *et al.*, 2011; Geladi *et al.*, 2021). For example, Hobson and colleagues (2001) showed that canopy cover and tree hight were associated with avian forest species abundance. And avian species richness in urban areas has been shown to be related to urban green space and was higher in parks with more vegetation coverage (La Sorte *et al.*, 2020).

In summary, local nest site attributes may be associated with multi-level species richness and different levels of breeding success or survival risk. If a nest site with many heterospecific neighbours is beneficial, for example given increased interspecific defence against predators and reduced intraspecific foraging competition, then we may expect older male songbirds to nest in areas with more heterospecific neighbours. Both parents, often especially the males in temperate systems, defend the nest site against conspecific intruders (Pearson, Nisbet and Ottinger, 2005; Clark, Kleindorfer and Dudaniec, 2018) to maintain the territory, reduce the risk of cuckoldry (Griffith, Owens and Thuman, 2002; Brouwer and Griffith, 2019), and reduce food competition (Fedy and Stutchbury, 2005; Murray, Ecology and May, 2016; Mentesana *et al.*, 2020; Zimmermann *et al.*, 2021), indicating that nesting areas with fewer conspecifics in close proximity could be preferred. Thus, in general, older males are expected to inhabit higher quality territories with more abundant resources (Sherry and Holmes, 1989; Pärt, 2001), and safer nesting areas and with more heterospecific species and lower predation risk (Hill, 1988).

The aim of this study is to test if the nest sites of older male Small Ground Finches (*Geospiza fuliginosa*) and Small Tree Finches (*Camarhynchus parvulus*) differ in predictable ways from the nest sites of younger males, with specific attention to singing activity of heterospecific and conspecific neighbours, as well as vegetation characteristics. We test the well supported prediction that older males occupy areas with more vegetation cover, in taller trees, and with higher nesting height. Also, we test a new prediction that the acoustic environment experienced by the offspring of older males will be more species rich with high singing activity. Specifically, we predict that if older males nest in areas with more heterospecific neighbours, then we see and record more singing of different species and conversely, more conspecific singing neighbours near nests of younger males. We also predict that the nest sites of older males will have more canopy cover and nests will be located higher up in taller trees. If nest predation is associated with singing activity (because sound alerts predators to an active area to search for nests), then we predict increased nest predation at nests with higher singing activity.

2. Methods

Study Species and age classification

Darwin's finches are socially monogamous per brood (Grant and Weiner, 1999; Kleindorfer, 2007; Kleindorfer *et al.*, 2021) with peak breeding time and the onset of breeding during the rainy season from January to March. The males occupy small nesting territories (ca. 20 m2) and defend the nesting area against intruders. They build several nests while singing to attract females (Kleindorfer, 2007b). The females visit several territories before choosing one of the newly built nests, or the pair build a new nest together (Grant and Grant, 2018). After egg laying, the female incubates the eggs for 12-14 days (Kleindorfer, 2007). Both parents provide food to nestlings until they fledge after approximately 12–14 days (Kleindorfer *et al.*, 2021). Between 17% to 60% of highland Darwin's finch nests are depredated across species and years (Kleindorfer, 2007; Kleindorfer and Dudaniec, 2009; O'Connor, Dudaniec and Kleindorfer, 2010; Cimadom *et al.*, 2014; Kleindorfer, Common and Sumasgutner, 2021).

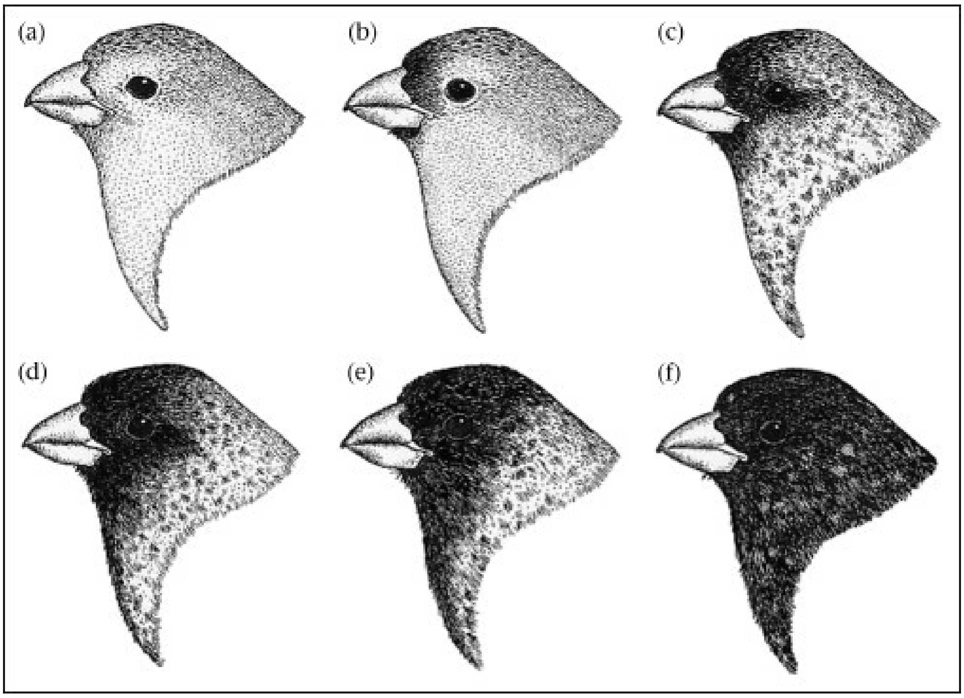

Figure 1. **Changes in plumage coloration in male Small Tree Finches with each annual moult**. Males require, on average, 5 years to attain a fully black head. (a)–(f) correspond to the colour and age categories 0–5 used, with 0 being yearling males and 5 including 5 year- and older males. (Figure used with permission, Source: Kleindorfer et al. 2007)

Darwin’s finch males can be aged non-invasively based on the proportion of black plumage. In Darwin’s Tree finches (Figure 1), the proportion of black plumage on the chin and crown increases with each year of moult until they obtain a fully black head after five years (Lack, 1947; Kleindorfer, 2007). In Darwin’s Ground Finches, the proportion of black plumage increases with each year of moult also for five years (Supplement Figure 4), but extends across the whole body (Grant and Grant, 1987). Female Tree Finches remain olive green and female Ground Finches remain greyish across their lives and cannot be aged from plumage. The age classification of males is in accordance with the six classes defined by Grant and Grant (1987) for Small Ground Finches and (Kleindorfer, 2007) for Small Tree Finches (Figure 1). This gives us the rare opportunity to study the effects of age on nest site attributes, and how these are associated with the acoustic soundscape near the nest, nest site vegetation, and predation outcome without using invasive methods.

Study Site

This study was conducted on Floreana Island (-1.299829, -90.455674) during the onset of nesting and the Darwin’s finch breeding season that peaks during February and March together with the onset of the heavy rains usually during January and February. Video and audio data were collected from 02.02.- 04.03.2020 and 07.02.- 26.02.2022 at 55 Darwin’s finch nests (Table 2), including Small Ground Finches (*G. fuliginosa*) (N = 33) and Small Tree Finches (*C. parvulus*) (N =22). The nests were located across eight 100 x 200 m^2 study plots in the highland *Scalesia* forest near Cerro Pajas or in two 100 x 200 m2 study plots at Asilo de la Paz *Scalesia* forest.

There are a total of 6 songbird species in the highlands of Floreana Island, and birds from 6 other avian Taxa (Kleindorfer, Fessl, *et al.*, 2019) (see Table 1).

Table 1: **Landbirds in the Floreana highlands**, separated into Passeriformes and other avian taxa

Songbirds (Passeriformes)	Other avian Taxa
Small Ground Finch (*Geospiza fuliginosa)*	Whimbrel *(Numenius phaeopus*),
Medium Ground Finch (*Geospiza fortis*)	Galapagos Dove (*Zenaida galapagoensis*)
Small Tree Finch (*Camarhynchus parvulus*)	Short-eared Owl (*Asio flammeus galapagoensis*)
Medium Tree Finch (*Camarhynchus pauper)*	Dark-billed Cuckoo (*Coccyzus melacoryphus)*
Yellow Warbler (*Setophaga petechia aureola*)	Paint-billed Crake *(Mustelirallus erythrops)*
Galapagos Flycatcher (*Myiarchus magnirostris)*	Smooth-Billed Ani (*Crotophaga ani*)

Video and audio recordings

Video and audio data were collected using GoPro cameras placed within 10 m of the nest. The nests were monitored using standard protocols developed since 2000 (Common *et al.*, 2020) also including taking nest site attributes (see below). For this study, we analysed song activity at active nests during building, incubation and feeding. GoPro cameras were attached to metal hooks and hung on branches with an extendable 6m pole 1-10m from the nest. Each nest was recorded during either building, incubation and/or feeding once (sample size in Table 2). The average GoPro recording duration per nest was 33.22 ± 2.7 (mean ±StDev) minutes.

Solomon coder (Péter, 2019) was used to systematically extract information from video recordings to calculate number of singing events in the neighbourhood of the nest. All songs heard were recorded and sampled at a radius of 25 m per nest, as this was the detectability of sound recordings on the GoPro.

Table 2: **Sample size per nesting phase**
number of recordings and number of nests for each year

Nesting phase	Small Ground Finches				Small Tree Finches			
	recordings		nests		Recordings		nests	
	2020	2022	2020	2022	2020	2022	2020	2022
Nest building	0	7	0	7	4	12	1	12
Incubation	26	0	10	0	4	1	3	1
Feeding	40	0	18	0	13	0	7	0
Total number of nests			33				22	

Species identification from song

Songs and calls were compared against a long-term data base managed by Kleindorfer for two decades with 6900+ songs and calls from most species; if a sound could not be identified, the clip was posted on the Galapagos Land Bird WhatsApp group and long-term Galapagos ornithologists (e.g., Birgit Fessl, Thalia Grant, Tui de Roy) provided their expert opinion, which always achieved 100% consensus. The sound identification was also facilitated because only 12 avian land bird taxa (Table 1) are present in the highlands of Floreana Island. The calls of the species listed are identifiable species signals and hence, after training on available recordings and with expert advice, it is likely that all vocalizations were correctly classified to species level.

Nest site vegetation

We measured the following nest-site vegetation characteristics per nest within two weeks of nest building: 1) nesting height (m above the ground) (ocular estimation after training with a laser pointer device on-campus at Flinders University), 2) nesting tree height (ocular estimation after training with a laser pointer device on-campus at Flinders University), 3) percentage canopy cover 1 m around the nest (ocular estimation after training calibration with botanist Heinke Jaeger), and 4) percentage ground cover (ocular estimation calculated for 4 x 5 m quadrants at the base of the nest).

Variables

In this study, the following variables were analysed: 1) male age (assessed from plumage categories shown in Figure 1), 2) number of total singing events per minute (conspecific + heterospecific songs) in the vicinity of active nests, 3) subset: number of heterospecific singing events per minute, 4) subset: number of conspecific singing events per minute, 5) number of neighbouring nests in a 35 m radius of the focal nest (we selected this cut-off as it could have overlapped with the 25 m audible recording range of the GoPro recordings), 6) vegetation canopy cover (% cover), 7) ground cover (%), 8) tree height (m), 9) nesting height (m), and 10) breeding status (nest building, incubation, chick feeding). In terms of nesting outcome, we analysed variables in relation to whether the nest was depredated or not, but only for the nests recorded in 2020 as this information is not available for 2022 (the field work ended before nesting outcome was known).

The variables of vegetation canopy and ground cover as well as tree height and nesting height were tested with a spearman correlation (Supplement Figure 1) and show a negative correlation between canopy and ground cover (*rho* = -0.491, $p < 0.001$) and a strong positive correlation between tree height and nesting height (*rho* = 0.783, $p < 0.001$). Therefore, we used only one of each correlated variables per pair for the later analysis.

Data analysis

All data analyses were conducted using R v.4.1.0 (R Core Team, 2021). To test our predictions ,we used linear mixed models with the package 'lme4' (Bates *et al.*, 2015) and 'arm' (Gelman, 2011). The distribution of the residuals and the models' assumptions were tested and assessed visually using the package 'DHARMa'(Hartig, 2021). For every prediction, we first conducted a general model without the species distinction and a second model where species was considered separately. First, we explored the general pattern for a difference between younger and older males regardless of the species. Next, we tested if there is a difference in this effect between the species.

Using a pseudo-Bayesian framework with non-informative priors using the packages 'arm' (Hilbe, 2009; Gelman, 2011) and 'lme4' (Bates *et al.*, 2015). For every linear mixed model (package ‘lme4’), the restricted maximum-likelihood estimation method was applied. In each model, we applied the function ‘sim’ and carried out 10 000 simulations to obtain the posterior distribution of every estimate, the mean value and the 95% credible interval (CrI) (Korner-Nievergelt, 2015) CrIs provide information about uncertainty around the estimates. We considered an effect to be statistically meaningful when the 95% CrI did not overlap with zero. A threshold of 5% is equivalent to the significance level in a frequentist framework (i.e. p-value of 0.05) (Korner-Nievergelt, 2015). For depredation, the response variable was binary (0 = no predation event, 1 = nest depredated) and modelled with a binomial distribution using the logit-link function.

1a. Acoustic neighbourhood: male age and heterospecific singing activity

To analyse weather older males choose nesting sites with more heterospecific activity, we used two linear-mixed-effect models (REML fit). In both, the response variable was the number of heterospecific songs per minute. In the first model, the explanatory variables were the total number of nests within 35 m (proxy for nesting density) and male age. In the second model, the explanatory variables were the total number of nests within 35 m, the male age and the interaction between male age and species. In both models, Nest ID was included as a random factor to account for repeated measures of the same nest and breeding status to account for the variance across different breeding stages.

1b. Acoustic neighbourhood: male age and conspecific singing activity

To analyse the converse of our predicted association between male age and the number of heterospecific neighbours, we tested if younger males have nest sites with more conspecific neighbours and more conspecific singing activity (and hence, likely, more conspecific competition). We used the same approach as above. Namely, two linear-mixed-effect models (REML fit) with the response variable ‘number of conspecific singing events per minute’. In the first model, the explanatory variables were the male age the total number of nests within 35 m (proxy for nesting density) and their interaction. In the second model, the explanatory variables were the total number of nests within 35 m and the male age in interaction with species. In both models, Nest ID was included as a random factor to account for repeated measures of the same nest and breeding status to account for differences the breeding phase. Here, the residual diagnostics in both models showed slight (but still acceptable) deviation in one assumption (slight deviation in residual vs. predicted quantiles) that could probably be overcome with larger sample sizes. In 2022, singing activity was lower as rainfall was lower than 2020 and with a later onset (mean rainfall on Floreana in February 2022 = 2.312 mm; in comparison the mean average historic rainfall on Floreana in February = 104.107 mm, the link used for this data https://www.galapagosvitalsigns.org), and there were many zero values for conspecific song compared with 2020 (but heterospecific song activity occurred).

We performed an additional model (generalized mixed-effect model with binominal distribution and the natural link function) to determine if male age is related to the number of conspecific nests in a 35 m radius. The number of neighbours is expected to covary with the amount of singing activity.

2. Effect of male age on nest site vegetation characteristics

To assess if the vegetation characteristics of nest sites between older and younger males differed in terms of canopy cover, ground cover, tree height and nesting height, we first performed a spearman correlation test (see Supplement Figure 1). Because previous research identified an association between canopy cover and nesting height on nesting success in this system, we used those variables in the models to test the association between male age and nest site vegetation characteristics.

The association between male age and nest site canopy cover and nesting height was estimated using two linear regression models per variable. The first models had either canopy cover or nesting height as the response and male age as the explanatory variable. The second models had the same structure only including an interaction term between male age and species.

3. Effect of number of singing events (general song-activity) on predation outcome

To examine the effect of song activity on predation risk, we used predation outcome as a binominal variable in a generalized linear model with binominal distribution and the natural link function. The number of songs per minute was the numeric explanatory variable. The additional fixed effects ‘nesting height’ and ‘average canopy cover’ were included.

3. Results

3.1. Acoustic neighbourhood: soundscape composed of heterospecific and conspecific songs

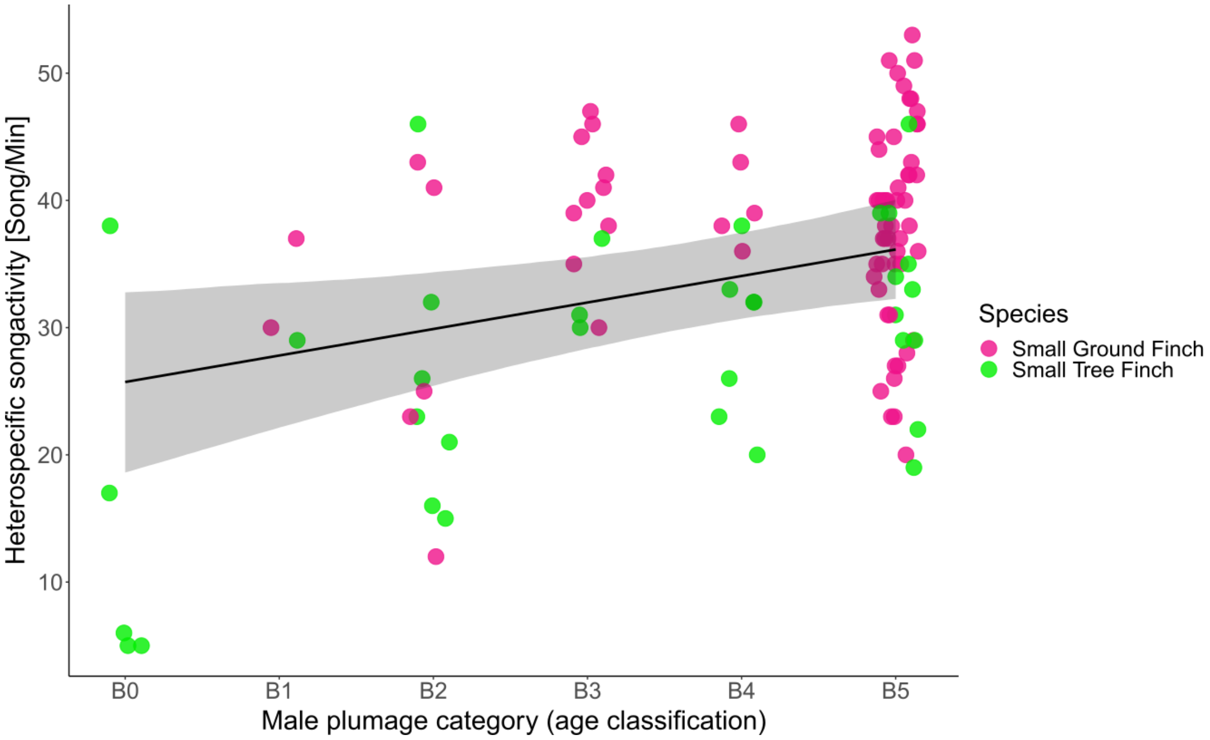

Figure 2*: **Heterospecific singing activity in relation to age***. X-axis: proportion of black in male plumage category is shown for B0 to B5, which corresponds with age in years from yearling to age 5+ In Darwin's finches; Y-axis: number of heterospecific singing events per minute. Increase in heterospecific singing activity with increase of age category (n=55, Mean estimate [95% CrI] = 2.088 [0.447, 3.714], Table S1a). Stronger relation in Small Ground Finches (pink) then in Small Tree Finches (green) (Table S1b). Black line represents the mean estimate, grey ribbon the 95% CrIs and dots the raw data.

With 55 observed nest sites, the results showed that nests of older males had significantly more heterospecific singing activity (n=55, Mean estimate [95% CrI] = 2.088 [0.447, 3.714], Table S1a) compared to younger males (Figure 2). This pattern was strongest in Small Ground Finches, and moderate in Small Tree Finches. The number of nesting neighbours did not have an effect on the heterospecific singing activity in the territory; neither did the breeding status during which the nesting territories were recorded.

There was no evidence that the level of conspecific singing activity within 25 m radius of a male's nest changed with male age (Figure 3). While younger males had more conspecific nesting neighbours (slope = -6.501, *p* < 0.001, Table S3), there was no statistical support for an effect of male age on the number conspecific songs (n=55, Mean estimate [95% CrI] = -0.394 [-2.049, 1.310], Table S2). Rather, the overall number of neighbours was associated with the number of conspecific singing events (n=55, Mean estimate [95% CrI] = 1.738 [0.024, 3.470], Table S2).

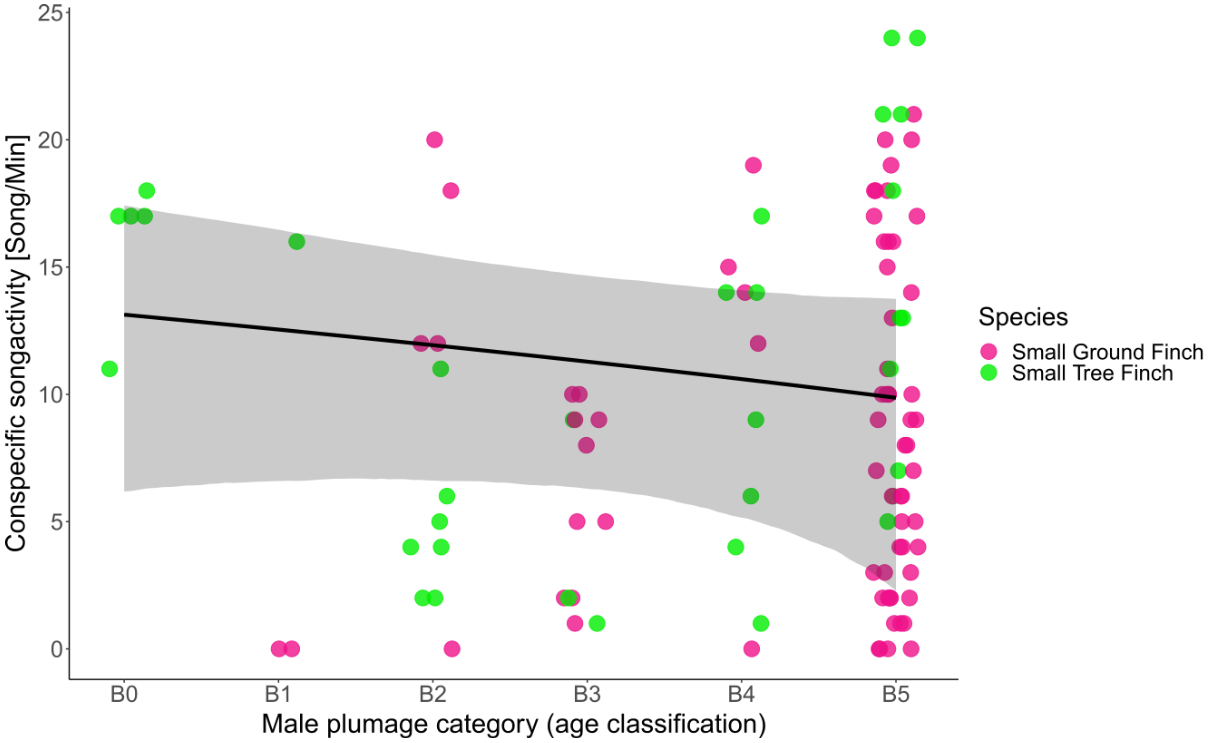

Figure 3***: Conspecific singing activity in relation to age***. X-axis: proportion of black in male plumage category is shown for B0 to B5, which corresponds with age in years from yearling to age 5+ in Darwin's finches; Y-axis: number of conspecific singing events per minute. No significant relation between male age and conspecific singing activity (n=55, Mean estimate [95% CrI] = -0.394 [-2.049, 1.310], Table S2), neither in Small Ground Finches (pink) nor for Small Tree Finches (green). Black line represents the mean estimate, grey ribbon the 95% CrIs and dots the raw data.

3.2. Effect of male age on nest site vegetation characteristics

We tested if the nest site characteristic in terms of nesting height, tree height, canopy and ground cover differed between the male age categories. As discussed above, we used only one variable per correlated pair. The nesting height did not vary in relation to male age, neither as a general pattern (n = 55, slope = -0.112, *p* = 0.399, Table S4), nor when taking species into account (n = 55, slope = 0.126, *p* = 0.642, Table S4). But we did find that older males nested in areas with significantly more vegetation cover (n = 55, slope = 3.927, *p* = 0.017, Table S4).

3.3. Effect of general song-activity on predation outcome

Song activity within a 25 m radius of the nest site was not associated with predation risk (n = 35, slope = 0.073, *p* = 0.449), nor was nest concealment associated with less predation (n = 35, slope = -0.020, *p* = 0.560). Increased nesting height seemed to be associated with more nest predation (n = 35, slope = 0.776, *p* = 0.049).

4. Discussion

The main aim of this study was to test if there are consistent differences in nest site characteristics such as acoustic environment and vegetation structure between younger and older males across species. We found support for the idea that the acoustic and nest-site vegetation environment experienced by the offspring of Darwin's Finches differs depending on the age of the nest-building male in two species, Small Ground Finch and Small Tree Finch. Nests of older males were exposed to more heterospecific song activity, a pattern found in both species. Though we found no significant effect of male age in relation to conspecific song activity. Nests of older males differed in relation to nest site concealment, and older males chose trees with more canopy cover for building their nests. Finally, we tested whether total song activity and nest site vegetation are associated with nest predation outcome, and found an effect of nesting height but not song rate. Higher placed nests experienced more depredation (see also Supplement Figure 3).

There are not many studies that have looked at male age in relation to nesting associations in a neighbourhood. In one study by Kleindorfer et. al. (2009) it was shown that Small Tree Finches on Santa Cruz Island may nest in mixed species associations and that males in such neighbourhoods are paired more quickly with females. But there was no measurable effect of male age on whether or not a male build his nest in an area with few or many neighbours (Kleindorfer, Sulloway and O'Connor, 2009). In that study, across 5 years, older males changed their nesting behaviour and in later years, older males tended to be building nests with fewer close neighbours. This could be explained by different causes. For example, perhaps different vegetation conditions due to "El Niño" events or general changing rainfall patterns over the years could have played a major role (Kleindorfer and Dudaniec, 2020). Another explanation could be that the finches are selected to use behaviour that reduces threat from the parasitic vampire fly *Philornis downsi* by not nesting in proximity to other possible hosts, as high host nesting density was associated with higher parasite intensity (Kleindorfer and Dudaniec, 2009). Multiple selection factors can shape nest placement, and experienced older birds may show behavioural adjustment of nesting height and placement within the community based on previous experience.

From the perspective of nest predation, the intensity of introduced rats (*Rattus rattus*) and Smooth-billed Ani (*C. ani*) are increasing on the Galapagos islands, and this changing predation pressure may also be changing the optimal nest positioning to avoid predation (Kleindorfer, Common and Sumasgutner, 2021). In this study by Kleindorfer et al. (2021) on Floreana Island conducted in 9 breeding seasons spanning a 16-year sampling timeframe, the nesting success of the critically endangered Medium Tree Finch *(C. pauper*) was studied. It was found that even though older males had a higher pairing success they did not experience higher nesting success in terms of surviving fledglings, because, while older males had less predation, their offspring had high mortality from the vampire fly *P. downsi* Kleindorfer et al. (2021) found that there is no safe nesting height for the finches, and that the nesting height is associated with predator type. Nests higher up in the trees are easily detectable for avian predators (Kleindorfer, Fessl and Hoi, 2005; Latif, Heath and Rotenberry, 2012). Therefore, the highest nests can be depredated by avian predators, of which there are two Species left on Floreana Island, namely the endemic Galápagos Short-eared Owl (*A. flammeus galapagoensis*) and the introduced Smooth-billed Ani (*C. ani*). In the Floreana Island system, nests with intermediate height in the tree have the highest proportion of the vampire fly (Kleindorfer, Common and Sumasguter, 2021). As in other studies, lower nests are easy targets for rats (Colombelli-Négrel and Kleindorfer, 2009; Vanderwerf, 2012).

Floreana Island is besieged with introduced rats (*R. rattus*), and the detectability of rats is increasing across the decade (Sumasgutner et al. in prep), and because owls feed on rats, the owl population is increasing too. Therefore, Darwin's finches might place nests higher to avoid the increasing population and threat of the rats while the experienced older males also conceal their nests to avoid detection by avian predators. This is in alignment with what we found in this study. Namely nests placed higher up experienced more predation (probably from owls, possibly from ani) and older males built more concealed nests.

It has been shown that songbirds learn their song by forming a template (Rosemary Grant and Grant 1996) learned from a tutor (Plamondon, Goller and Rose, 2008; Konishi, 2010). The song templates do not have to come from the attending male but can also be learned from the surrounding neighbours (Thomas et al. 2021). In this way, the neighbourhood composition can be a determining factor in the acoustic development of chicks. The prenatal sound learning and sound familiarity can occur not only in hatchlings, but also in ovo (Colombelli-Négrel and Kleindorfer, 2017; Rivera *et al.*, 2018; Colombelli-Négrel *et al.*, 2021). Because sound learning may start during the incubation phase in songbirds, the soundscape experienced by the developing birds can play an important role for their phenotype. In addition to effects on learning their own song, the soundscape experienced during the first developmental stages can perhaps play a role in acoustic habitat imprinting, for example for the choice of nest sites and territories later in adulthood, similar to the idea of habitat imprinting (Davis, Davis and Stamps, 2004). In this study, the offspring of older males experienced more heterospecific songs. Nestlings surrounded by heterospecifics rather than conspecifics can have the advantage of group protection as described by the dilution effect (Hamilton, 1971; Rubenstein, 1978) while keeping food competition to a minimum. Additionally, it is more likely that the offspring may hear and learn syllable types from the attending male rather than from a neighbouring conspecific. Future research can aim to test if this heterospecific environment may shape offspring preference for a similar acoustic or heterospecific neighbourhood for its nesting attempts. And if there is a benefit in learning the nest-attending males song type over a different one.

In summary, the nest sites of Darwin Finches show variation in vegetation and soundscape depending on the age of the nest-building male. One implication of these findings is that the overall acoustic environment experienced by the males' offspring depends in part on the age of the attending male. Older males also nested in areas with more vegetation cover. Higher neighbourhood singing activity was not associated with predation risk in this study. These findings contribute to increasing our understanding of the breeding biology of Darwin's Finches, which was measured in 2020 and 2022 under contemporary conditions of extremely high predation risk. It will be interesting to see if and how these patterns in species composition might change after the planned eradication of the introduced black rats and house mice (*Mus musculus*) in 2023 by the Galapagos National Park Directorate with support of Island Conservation and other NGOs. Following the eradication of introduced rodents and feral cats, there are plans for future reintroductions of 12 endemic species that used to inhabit Floreana Island, in attempts to rewild and re-establish a functioning ecosystem. And with all these environmental changes, there is a wonderful opportunity to observe how Darwin's finches adapt their behaviour and keep evolving.

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6. Supplementary Material

Table S1a: Relation between male age (plumage coloration) to heterospecific singing activity

	Heterospecific songs per minute
	Fixed effects (ß) (95 % CrI)
Male age	**2.088 (0.447, 3.714)**
Number of neighbouring nests	-0.341 (-2.645, 1.954)
	Random effects (σ^2) (95 % CrI)
Nest ID	4.085 (0.184, 16.478)
Breeding status	29.447 (20.138, 42.170)

CrI: credible interval. Statistically meaningful effects are marked in bold. Model (linear mixed-effect model, Gaussian error distribution): Heterospecific songs ~ Age + #Nests + (1 | NestID) + (1 |BreedingStatus)

Table S1b: Relation between male age (plumage coloration) to heterospecific singing activity including species interaction

	Heterospecific songs per minute
	Fixed effects (ß) (95 % CrI)
Male age	1.011 (-0.978, 2.986)
Number of neighbouring nests	-0.308 (-2.395, 1.718)
Species (STF against SGF)	**-13.016 (-24.285, -2.050)**
Age * Species	1.404 (-1.297, 4.166)
	Random effects (σ^2) (95 % CrI)
Nest ID	0.663 (0.023, 3.271)
Breeding status	17.134 (11.289, 25.445)

CrI: credible interval. Statistically meaningful effects are marked in bold. Model (linear mixed-effect model, Gaussian error distribution): Heterospecific songs ~ Age * Species + #Nests + (1 | NestID) + (1 |BreedingStatus)

Table S2: Relation between male age (plumage coloration) to conspecific singing activity including species interaction

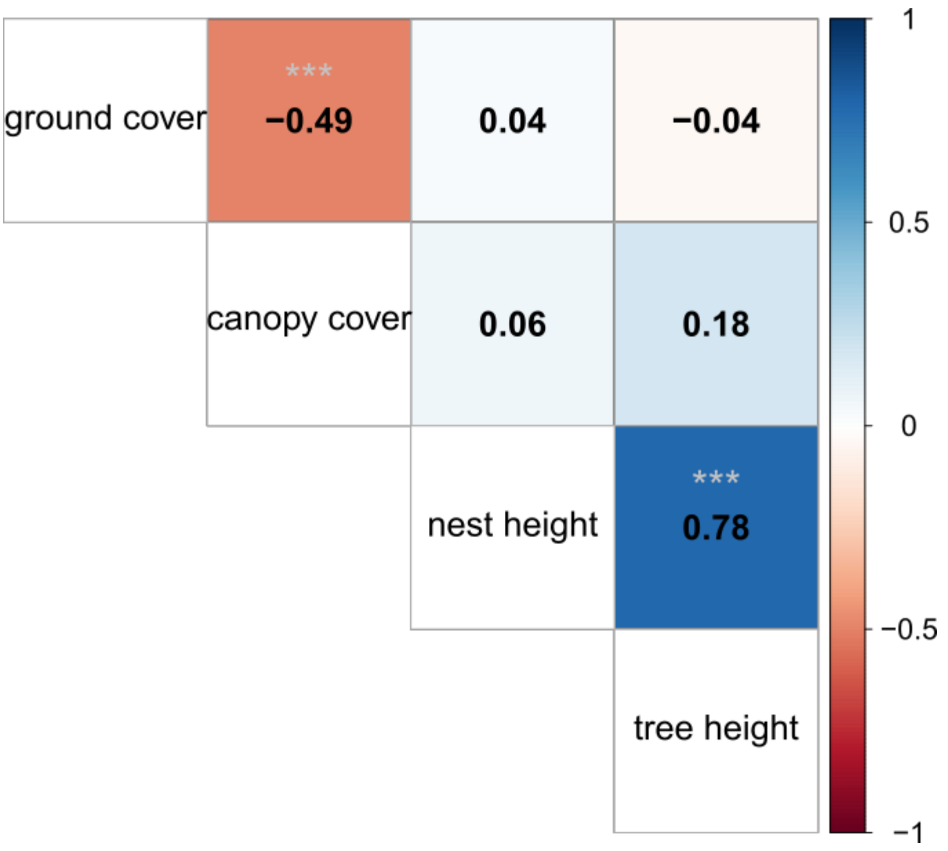
	Conspecific songs per minute
Fixed effects (ß) (95 % CrI)	
Male age	-0.394 (-2.049, 1.310)
Number of neighbouring nests	**1.738 (0.024, 3.470)**
Species (STF against SGF)	5.159 (-3.181, 13.723)
Age * Species	-0.517 (-2.634, 1.574)
Random effects (σ^2) (95 % CrI)	
Nest ID	24.527 (18.993, 32.070)

CrI: credible interval. Statistically meaningful effects are marked in bold. Model (linear mixed-effect model, Gaussian error distribution): Conspecific songs ~ Age * Species + #Nests + (1| NestID)

Table S3: Relation between male age (plumage coloration) to number of conspecific nesting neighbours

n = 55	Number of conspecific nests			
Fixed effects (ß)	slope	St. Error	*z*-value	*p*-value
Male age	**-6.501**	1.445	-4.498	**< 0.001**
Random effects (σ^2)	Variance		St. Deviation	
Nest ID	1162		34.09	

Statistically meaningful effects are marked in bold. Model (generalized mixed-effect model, with binominal distribution and the natural link function): #Conspecific nests ~ Age + (1| NestID)

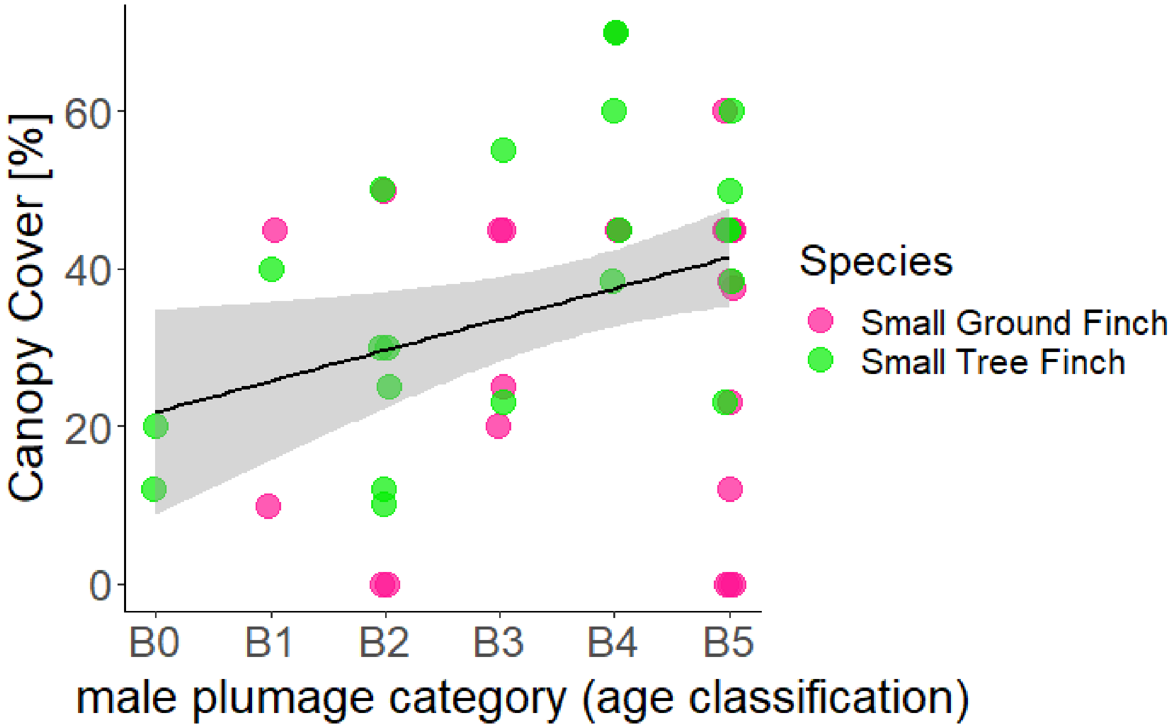


Supplement Figure 1*: **Correlation matrix of the vegetation characteristics**.* Canopy and ground cover are negatively correlated, which is expected because under conditions of high canopy cover, less sun reaches the ground, and vegetation is less likely to grow to great heights in shady environments. Tree height is strongly correlated with nesting height in the tree (both in m)

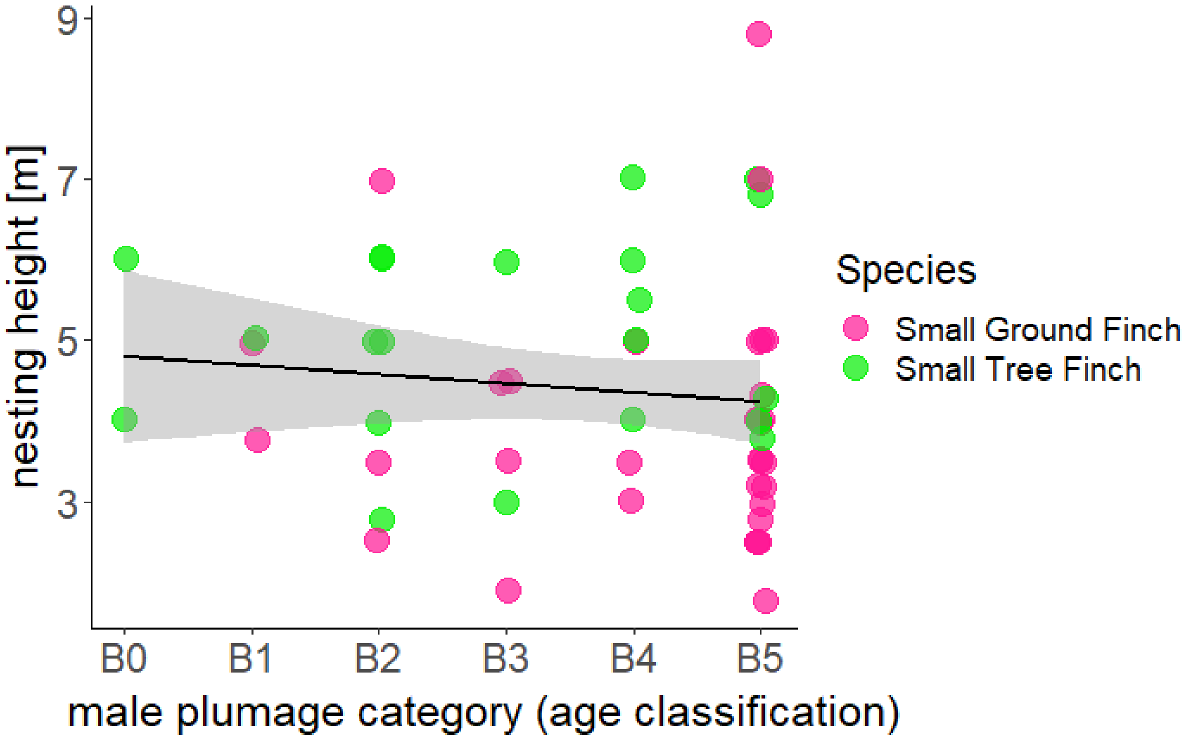
Table S4: Relation between male age (plumage coloration) and vegetation characteristics

n = 55		**Canopy cover [%]**
Fixed effects (ß)	*slope*	*p-value*
Male age	**3.927**	**0.017**
Male age*Species	2.980	0.376
		Nesting height [m]
Male age	-0.112	0.399
Male age*Species	0.126	0.642

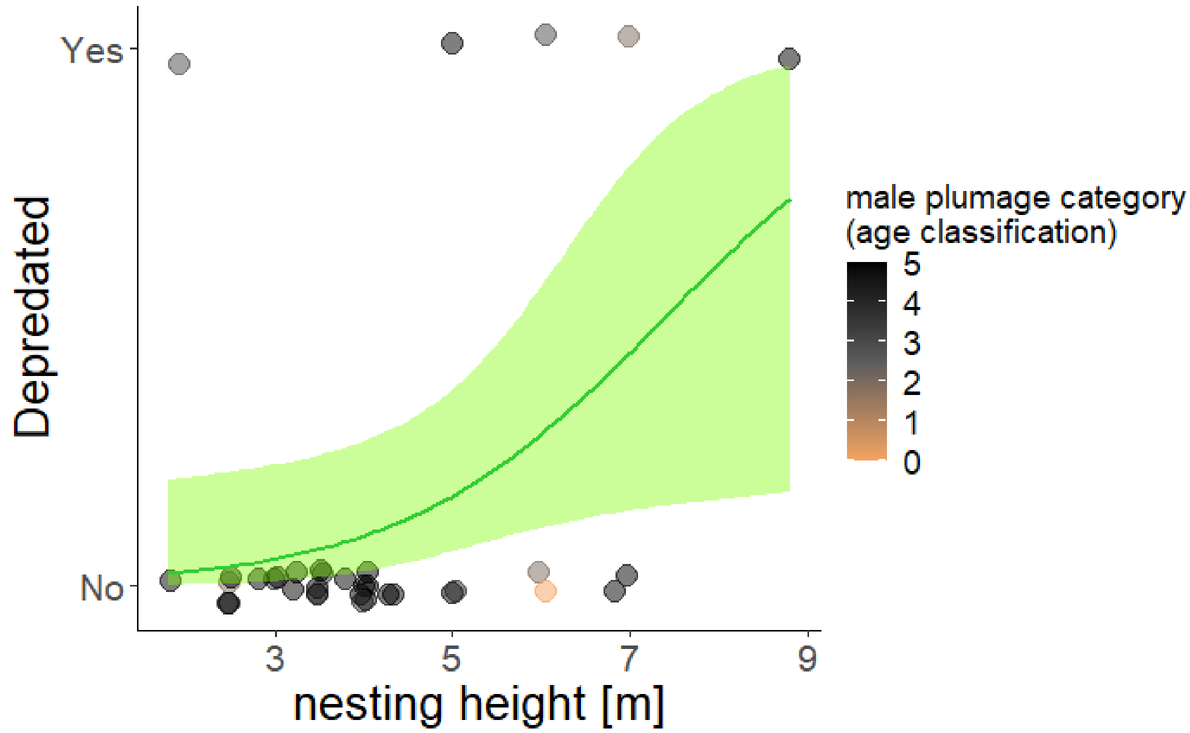
Statistically meaningful effects are marked in bold. Model (linear regression models): 1)CanopyCover ~ Age; 2)CanopyCover ~ Age*Species; 3)NestingHeight ~ Age; 4)NestingHeight ~ Age*Species



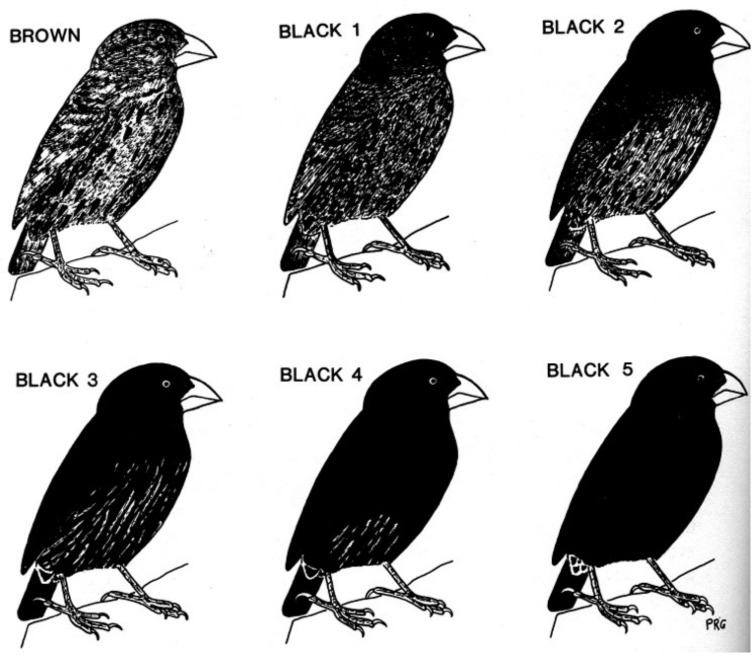
Supplement Figure 2a: **Relation between male age (plumage coloration) and canopy cover**. Showing that older males nest in areas with a higher percentage of vegetation canopy cover (n = 55, slope = 3.927, p = 0.017). Dots represent raw data, pink representing Small Ground Finch and green Small Tree Finch; black line the mean estimate and grey ribbon representing the 95 % CrI.



Supplement Figure 2b*: ***Relation between male age (plumage coloration) and nesting height**. No effect of male age on nesting height (n = 55, slope = -0.126, p = 0.642). Dots represent raw data, pink representing Small Ground Finch and green Small Tree Finch; black line the mean estimate and grey ribbon representing the 95 % CrI.



Supplement Figure 3**: Increased depredation events with increased nesting height**. The depredation risk increases with nests that are placed higher in the trees (n = 35, slope = 0.776, p = 0.049). No effect of male age or general soundscape activity. Dark green line represents the mean estimate, green ribbon the 95% CrIs and dots the raw data. Colour of the dots represents the male age category increasing from sandy brown (B0) to black (B5+).



Supplement Figure 4: **Changes in plumage coloration in male Small Ground Finches with each annual moult**. Males require, on average, 5 years to attain a fully black head. Brown-Black 5 correspond to the colour and age categories 0–5 used, with 0 being yearling males and 5 including 5 year- and older males. (Figure used with permission Grant and Grant 1987)