



Telomere length and dynamics of spotless starling nestlings depend on nest-building materials used by parents



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Nest materials used by animals can have profound effects on developing offspring. They can modify the bacterial and parasitic environment of the nest, and can influence parental investment through sexual signalling processes. In spotless starlings, *Sturnus unicolor*, green plants and feathers are known nest materials with such functions. The aim of our study was to experimentally assess their influence on nestlings' telomere length and attrition, which are good predictors of their survival prospects. In a full-factorial experiment, we explored these effects in two different populations, together with the potential effects of hatching date, ectoparasitism, bacterial environment and nestling growth. Telomere length and attrition largely depended on population identity and hatching date. After correcting for these effects, the addition of feathers resulted in higher rates of telomere attrition. The addition of plants did not affect nestling telomeres in general, but did in interaction with location: in Hueneja, the experimental addition of green plants resulted in longer telomeres. Feather pigmentation also did not affect telomere length or attrition in general, but did in interaction with location: in Hueneja, the experimental addition of unpigmented feathers resulted in nestlings with longer telomeres and lower attrition rates. Moreover, prevalence of staphylococci on the skin of 8-day-old nestlings was negatively related to telomere lengths of fledglings. Taken together, these results suggest a direct link between nest material composition and nestling telomere length and dynamics. This relationship could be partially mediated by the antimicrobial and/or antiparasitic properties of nest materials or by sexual signalling processes. We discuss possible roles of maternal effects, parasites, immunity and nestling growth in explaining these experimental effects.

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Environmental conditions that offspring experience during growth have important consequences for their survival and reproductive prospects (Monaghan, 2008). These environmental conditions include indirect genetic effects of parents on offspring phenotypes through parental behaviours that in birds include, among others, nest building, nest defence against predators, nest sanitation, incubation, brooding and feeding effort (Mousseau & Fox, 1998). From an evolutionary perspective, research on the effects of nest-building behaviour on offspring survival prospects and recruitment is of particular interest because nests are extended

phenotypes of builders (Dawkins, 1982) on which natural and sexual selection operate (Collias & Collias, 1984; Hansell, 2000; Moreno, 2012; Palomino, Martín-Vivaldi, Soler, & Soler, 1998; Soler, Møller, & Soler, 1998). On the one hand, nest-building behaviour may have indirect consequences for developing offspring because nests may signal the phenotypic quality of builders (Collias, 1964; Moreno, 2012). This would affect reproductive decisions of their mates through differential investment (Burley, 1986; Sheldon, 2000) in a typical postmating sexual selection process (Soler et al., 1998). On the other hand, nests may directly influence nestling phenotypes by their structures and materials having thermoregulatory, antipredator, antimicrobial or antiparasitic properties (Dubiec, Gózd, & Mazgajski, 2013; Heenan, 2013; Moreno, 2012).

The use of nest materials with antimicrobial and/or antiparasitic properties is considered a form of self-medication (Clayton & Wolfe,

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1993; de Rooze, Lefèvre, & Hunter, 2013). Most green plants used for nest building are aromatic plants that contain volatile compounds or essential oils with repellent or toxic effects on blood-sucking arthropods and microorganisms and, therefore, could play a role in minimizing the effects of pathogenic bacteria and nest parasites on developing offspring (Clark, 1990; Clark & Mason, 1985; Tomás et al., 2012). Evidence of green plants reducing the risk of bacterial and parasitic infection of nestlings is compiled in Dubiec et al. (2013). More recently, the use of feathers as nest material has also been proposed to have antimicrobial effects (Soler, Martín-Vivaldi, Peralta-Sánchez, & Ruiz-Rodríguez, 2010). Evidence of this function has accumulated during the last few years. We know, for instance, that bacterial colonies from unpigmented feathers have higher antimicrobial activity than those from pigmented feathers in some nest environments (Peralta-Sánchez et al., 2014). This property would explain the reduced bacterial loads and hatching failures of barn swallow, *Hirundo rustica*, eggs in nests with experimentally supplied unpigmented feathers (Peralta-Sánchez, Møller, Martín-Platero, & Soler, 2010; Peralta-Sánchez, Møller, & Soler, 2011). More recently, experimental addition of feathers led to a reduction in eggshell bacterial loads in nests of spotless starlings, *Sturnus unicolor*, and in artificial nests without parental influence (Ruiz-Castellano, Tomás, Ruiz-Rodríguez, Martín-Gálvez, & Soler, 2016). Thus, effects related to the antimicrobial and antiparasitic properties of nest materials are key candidates to explain the expected associations between nest-building behaviour of parents and variables related to survival prospects of nestlings (Dubiec et al., 2013; Gwinner & Berger, 2005; Mennerat, Mirleau et al., 2009a; Mennerat, Perrat et al., 2009b; Polo, Rubalcaba, & Veiga, 2015).

Nest building, however, is a costly activity (Mainwaring & Hartley, 2013) and, thus, nest-building effort should be adjusted to environmental characteristics. Selection pressure due to parasitism varies greatly both geographically (Ardia, 2007; Freeman-Gallant, O'Connor, & Breuer, 2001; Martin II, Pless, Svoboda, & Wikelski, 2004; Møller, Garamszegi, Peralta-Sánchez, & Soler, 2011; Møller, Martín-Vivaldi, Merino, & Soler, 2006) and temporally (i.e. laying date; Merino, Møller, & de Lope, 2000; Sorci, Soler, & Møller, 1997) and, thus, antiparasitic and antimicrobial effects of experimental manipulations of nest material will also depend on geographical and temporal variation in selection pressures. In fact, the expected beneficial effects of nest materials in terms of probability of nestling recruitment (e.g. body mass, immunocompetence) have not been detected in several experimental studies (see review in Dubiec et al., 2013).

Recently, telomere length and dynamics have been proposed as measures that encapsulate the effects of stressful environmental conditions on nestlings' development and survival prospects (Monaghan, 2014; Monaghan & Haussmann, 2006). Telomeres are specialized structures at the end of the chromosome, consisting of short repeats of the noncoding DNA sequence TTAGGG, which protect the integrity of genetic information during cell division (Blackburn, 1991). Recent studies have reported negative associations between telomere length and baseline corticosterone levels (Quirici, Guerrero, Krause, Wingfield, & Vásquez, 2016), oxidative stress (Badás et al., 2015; Kim & Velando, 2015) and parasite infection (Asghar, Hasselquist et al., 2015). Moreover, early life telomere length has strong maternal effects (Asghar, Bensch, Tarka, Hansson, & Hasselquist, 2015) and telomere dynamics depend on abiotic (e.g. altitude, laying date, Soler et al., 2015; Stier et al., 2016) and biotic environmental conditions (e.g. nestling competition for food, Nettle et al., 2015; Reichert et al., 2014; Soler et al., 2015), including those related to parental behaviour (Sudyka et al., 2014). Thus, telomere length and dynamics in nestlings are appropriate target variables for testing the effects of nest-building behaviour (e.g. nest material used) on nestling development.

Here, we experimentally explored the effects of green plants and/or feathers on telomere length and dynamics in spotless starling nestlings, while considering temporal and geographical variation. We expected to detect the beneficial effects of these nest materials in terms of telomere length and reduced telomere attrition in nestlings from nests with experimentally added plants and/or feathers, especially in the area with higher ectoparasitism. We also quantified ectoparasitism and bacterial loads on the skin of nestlings, and explored the expected negative relationship with telomere length and positive relationship with telomere shortening in nestlings close to fledging.

METHODS

Study Area and Species

The study was performed in Hoya de Guadix, southeast of Spain, a high-altitude plateau 1000 m above sea level with a semiarid climate, during the 2012 breeding season. The spotless starling populations under study breed in cork nestboxes (internal dimensions: 180 × 210 mm and 350 mm high, 240 mm from the bottom to the hole) attached to tree trunks or walls 3–4 m above ground. The two populations breed in the old railway stations of La Calahorra (37°15'N, 3°01'W) and Hueneja (37°13'N, 2°56'W), 8 km apart. Ecological conditions of the study areas are similar except for colony size and ectoparasitism level (see Results). Approximately 80 pairs breed per year at La Calahorra and 35 pairs in Hueneja. Ectoparasitism by the fly *Carnus hemapterus* and occupation of nestboxes was higher in La Calahorra than in Hueneja, although empty nestboxes were available in both populations during the study.

The hole-nesting spotless starling mostly breeds in colonies and uses a variety of nesting materials, including feathers and green plants, for both the structural and the lining layer of the nest (Peralta-Sánchez et al., 2012; Ruiz-Castellano et al., 2016; Veiga, 2002). In the studied populations, starlings usually lay four or five eggs per clutch in mid-April. Full incubation starts with the penultimate egg resulting in asynchronous hatching, which usually takes place from early May onwards (Soler, Navarro, Pérez-Contreras, Avilés, & Cuervo, 2008). At the beginning of April, before breeding started, nestboxes were checked every second or third day until eggs were detected. Only first breeding attempts were considered in this study. Hatching date (age 0), defined as the day when half or more of the brood was hatched (Tomás, 2015), was established by visiting nestboxes daily close to the expected dates (incubation lasts for 7–12 days after clutch completion). The nestling period ranges from 18 to 25 days (Veiga, 2002).

Experimental Design

Our experiment followed a full-factorial design with feather or plant treatments (see below) starting on day 3 of nestling age. We first recorded the number of feathers and whether plants were present in nests and, subsequently, all plants and feathers were removed. Each nest was randomly assigned to one treatment. Since feathers of different colours may also differ in antimicrobial properties (Peralta-Sánchez et al., 2010), the feather treatment consisted of adding (1) 15 pigmented or (2) 15 unpigmented feathers to the nest or (3) leaving the nest without feathers. This number of feathers is within the range and close to the modal interval of number of feathers found in starling nests in the study area (from 55 nests, 17%, 33% and 17% of nests had 0–10, 10–20 and 20–30 feathers, respectively). Feathers were marked on the quill with a permanent marker to distinguish them from feathers introduced by the parents. The plant treatments consisted of (1) adding 1.6 g of a

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