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Corresponding Author	Family Name	Quque
	Particle	
	Given Name	Martin
	Suffix	
	Division	
	Organization	CNRS, IPHC UMR 7178, Université de Strasbourg
	Address	Strasbourg, France
	Phone	
	Fax	
	Email	martin.quque@iphc.cnrs.fr
	URL	
Author	ORCID	http://orcid.org/0000-0001-7386-1416
	Family Name	Paquet
	Particle	
	Given Name	Matthieu
	Suffix	
	Division	
	Organization	Swedish University of Agricultural Sciences (SLU)
	Address	Uppsala, Sweden
	Phone	
	Fax	
	Email	
Author	URL	
	ORCID	
	Family Name	Zahn
	Particle	
	Given Name	Sandrine
	Suffix	
	Division	
	Organization	CNRS, IPHC UMR 7178, Université de Strasbourg
	Address	Strasbourg, France
	Phone	
	Fax	
	Email	
	URL	

ORCID

Author	Family Name	Théron
	Particle	
	Given Name	Frank
	Suffix	
	Division	
	Organization	CNRS, CEFE UMR 5175, Université de Montpellier
	Address	Montpellier, France
	Phone	
	Fax	
	Email	
	URL	
	ORCID	

Author	Family Name	Faivre
	Particle	
	Given Name	Bruno
	Suffix	
	Division	Biogéosciences
	Organization	CNRS UMR 6282, Université de Bourgogne Franche-Comté
	Address	Dijon, France
	Phone	
	Fax	
	Email	
	URL	
	ORCID	

Author	Family Name	Sueur
	Particle	
	Given Name	Cédric
	Suffix	
	Division	
	Organization	CNRS, IPHC UMR 7178, Université de Strasbourg
	Address	Strasbourg, France
	Division	
	Organization	Institut Universitaire de France
	Address	Paris, France
	Phone	
	Fax	
	Email	
	URL	
	ORCID	

Author	Family Name	Criscuolo
	Particle	
	Given Name	François
	Suffix	
	Division	

	Organization	CNRS, IPHC UMR 7178, Université de Strasbourg
	Address	Strasbourg, France
	Phone	
	Fax	
	Email	
	URL	
	ORCID	
Author	Family Name	Doutrelant
	Particle	
	Given Name	Claire
	Suffix	
	Division	
	Organization	CNRS, CEFE UMR 5175, Université de Montpellier
	Address	Montpellier, France
	Division	Research Centre On Biodiversity and Genetic Resources
	Organization	CIBIO-InBio, University of Porto
	Address	Porto, Portugal
	Phone	
	Fax	
	Email	
	URL	
	ORCID	
Author	Family Name	Covas
	Particle	
	Given Name	Rita
	Suffix	
	Division	Research Centre On Biodiversity and Genetic Resources
	Organization	CIBIO-InBio, University of Porto
	Address	Porto, Portugal
	Division	Fitzpatrick Institute of African Ornithology, DST-NRF Centre of Excellence
	Organization	University of Cape Town
	Address	Cape Town, South Africa
	Phone	
	Fax	
	Email	
	URL	
	ORCID	
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Keywords (separated by '-')	Sociable weaver - Cross-fostering - Offspring - Early environment - Survival
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Contrasting associations between nestling telomere length and pre and postnatal helpers' presence in a cooperatively breeding bird

Martin Quque¹ · Matthieu Paquet² · Sandrine Zahn¹ · Frank Théron³ · Bruno Faivre⁴ · Cédric Sueur^{1,5} · François Criscuolo¹ · Claire Doutrelant^{3,6} · Rita Covas^{6,7}

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Abstract

Studies on cooperative breeders have addressed the effects of non-breeding 'helpers' on reproduction and parental care, but the consequences for offspring physiology and long-term survival are less understood. Helpers are expected to benefit offspring, but their presence can also lead to decreased pre- or post-natal parental reproductive effort. To examine whether prenatal and postnatal helpers influence offspring condition, we conducted a whole-clutch cross-fostering experiment in sociable weavers (*Philetairus socius*) that altered the nestlings' social environment (presence/absence of helpers). We tested whether relative telomere length (rTL), an indicator of somatic maintenance, was influenced by prenatal and/or postnatal presence of helpers 9 and 17 days after hatching, and whether rTL predicted long-term survival. Nine days after hatching, we found an overall positive effect of postnatal helpers on rTL: for nestlings with prenatal helpers, a reduction in the number of helpers post-hatch was associated with shorter telomeres, while nestlings swapped from nests without helpers to nests with helpers had a larger rTL. However, when prenatal helpers were present, an increased number of helpers after hatching led to shorter telomeres. Nine-day old chicks with longer rTL tended to be more likely to survive over the 5 years following hatching. However, close to fledging, there was no detectable effect of the experiment on rTL and no link between rTL and survival. This experimental study of a wild cooperative breeder, therefore, presents partial support for the importance of the presence of helpers for offspring rTL and the link between early-life telomere length and long-term survival.

Keywords Sociable weaver · Cross-fostering · Offspring · Early environment · Survival

Communicated by Kevin D. Matson.

✉ Martin Quque
martin.quque@iphe.cnrs.fr

¹ CNRS, IPHC UMR 7178, Université de Strasbourg, Strasbourg, France

² Swedish University of Agricultural Sciences (SLU), Uppsala, Sweden

³ CNRS, CEFCE UMR 5175, Université de Montpellier, Montpellier, France

⁴ Biogéosciences, CNRS UMR 6282, Université de Bourgogne Franche-Comté, Dijon, France

⁵ Institut Universitaire de France, Paris, France

⁶ Research Centre On Biodiversity and Genetic Resources, CIBIO-InBio, University of Porto, Porto, Portugal

⁷ Fitzpatrick Institute of African Ornithology, DST-NRF Centre of Excellence, University of Cape Town, Cape Town, South Africa

Introduction

In iteroparous species, individuals are expected to maximize their lifetime reproductive success through trade-offs between the investments in current reproduction vs. survival and future reproduction (Stearns 1977). For egg-laying species, females may vary the allocation of nutrients, antibodies, or other substances to eggs, thereby influencing the environment in which their offspring will develop. This allocation is in turn influenced by the mother's breeding environment, which is expected to be an indication of the environment in which the offspring will develop. In agreement, studies have shown that when females can anticipate the conditions experienced during reproduction they can influence traits such as egg size (e.g. Fox et al. 1997; Taborsky 2006; Vijendravarma et al. 2010), and hormonal investment (Groothuis et al. 2019), and these traits can correlate with

offspring survival or behavior (e.g. Krist 2011; Paquet et al. 2015a).

Among the environmental effects experienced by females and their developing offspring, sociality has been receiving increasing attention (e.g. Russell et al. 2007, 2008; Dixit et al. 2017). In cooperatively breeding species, sexually mature non-breeding individuals—called ‘helpers’—assist in raising the offspring of others by bringing additional food to the nest and performing other tasks such as territory defense (Cockburn 1998). The presence of these helpers is therefore thought to improve the breeding conditions experienced by females and/or offspring, and studies on several species have generally shown that helper presence is associated with improved juvenile condition and survival (e.g. Ridley 2007; Kingma et al. 2010; Brouwer et al. 2012; Preston et al. 2016; Tanaka et al. 2018). Breeding females may respond to this improvement in reproductive conditions by either maintaining their investment in eggs or food provisioning (Clutton-Brock et al. 2001; Doerr and Doerr 2007; Lejeune et al. 2016), or decreasing it (Crick 1992; Santos and Macedo 2011; Dixit et al. 2017), thereby reducing their cost of reproduction and increasing their survival and future reproduction. Reduction in maternal investment should then be compensated by the additional food brought by helpers (Russell and Lummaa 2009). The direction and magnitude of the response are expected to be influenced by the species’ life-history strategy and especially by the effects of maternal investment on mother’s survival prospects and chances of breeding successfully in the future (Russell and Lummaa 2009). In birds, cooperatively breeding species tend to be long-lived (Arnold and Owens 1998; Downing et al. 2015), and for long-lived species, maximization of lifetime reproductive success was suggested to be more efficiently achieved through increasing the number of breeding events in life than through increased investment in each breeding event (Ghalambor and Martin 2001; Drent and Daan 2002; Reid et al. 2003). In agreement, a recent meta-analysis on 10 cooperatively breeding birds highlighted a tendency for mothers to reduce egg size in larger groups in most species studied (Dixit et al. 2017; but see Fortuna et al. 2021).

It is less clear whether such differential maternal investments translate into differences in the condition and survival of offspring and what is the relative influence of the pre- and post-natal environment. For example, in birds, there are indications that larger eggs are positively associated with nestling’s body size, growth and survival (Krist 2011). However, these associations could arise from genetic and hormonal effects of parents (Morrison et al. 2009; Voillemot et al. 2012; Weber et al. 2018), and/or from rearing conditions independently from parental phenotype (Bize et al. 2002; Velando et al. 2005). From the offspring’s perspective, the presence of helpers can be associated with weaker prenatal maternal egg investment

(Russell et al. 2007; Paquet et al. 2013, 2015a; Langmore et al. 2016) but identical or higher total feeding rate, as more carers are present (Sappington 1977; Wilkinson and Brown 1984; Clarke 1984; Hunter 1987). Higher levels of care can lead to increased growth rate and potentially better condition or higher body mass at fledging, and thus increased likelihood to survive the first few months after fledging (Russell et al. 2007; Canestrari et al. 2011; Loock et al. 2017). The prenatal and postnatal effects of helpers’ presence can thus exert opposite influences on nestling fitness. Studies of maternal effects concerning the social environment, therefore, need to investigate the influence of these two distinct environments. This requires (i) identifying meaningful proxies of offspring fitness and (ii) conducting experiments to separate the influence of the pre- and post-natal environments.

Meaningful proxies of offspring condition should strongly correlate with offspring survival. Telomeres are repeated sequences at the ends of eukaryotic chromosomes. Replication leads to the shortening of the telomeric DNA sequence at each cell division, and beyond a certain number of cell division, telomeres become too short, triggering cell replicative senescence, which participates in the senescence of the whole organism (Tchkonia et al. 2013). Consequently, telomeres became increasingly used as predictors of age-related survival. Telomere length (TL) and/or telomere shortening rate have been shown to predict adult survival in numerous studies involving bird species (Pauliny et al. 2006; Bize et al. 2009; Salomons et al. 2009; Heidinger et al. 2012; Barrett et al. 2013; Boonekamp et al. 2014). Both ecological (Geiger et al. 2012; Stier et al. 2014; Salmón et al. 2016; Spurgin et al. 2017) and social (Hall et al. 2004; Nettle et al. 2015; Hammers et al. 2019) environments may increase or decrease TL (see Dugdale and Richardson (2018) for a review of the environment influence on vertebrate telomere length). This influence of ecological and social environment on TL may be effective very early in an individual’s life, even before birth. For example, in birds, unstable incubation temperature (Stier et al. 2020), predator cues during embryonic development (Noguera and Velando 2019), increased clutch size (Noguera and Velando 2020), or embryonic exposure to corticosterone (Haussmann et al. 2012) are all factors associated with shorter telomeres in nestlings. Although not all studies have established a clear link between telomere length and longevity or survival (e.g. Beaulieu et al. 2011; Caprioli et al. 2013; Reichert et al. 2014), the general trend in birds, mammals and reptiles is towards a consistent positive association between long telomeres and survival (Wilbourn et al. 2018). Taken together these studies support the use of telomeres as reliable indicators of longevity and/or individual quality, sensitive to early ecological and social stress, especially when measured during early life in birds (Eastwood et al. 2019).

In this study, we conducted a cross-fostering experiment to investigate how the pre- and post-natal social environments influence offspring condition, measured by relative telomere length (rTL). In addition, we controlled for a potential trade-off suggested in the literature (e.g. reviewed in Monaghan and Ozanne 2018) between telomere length (related to self-maintenance) and mass or body condition (related to growth). We further assessed the relationship between rTL and survival by testing whether rTL predicts juvenile apparent survival as estimated with capture-mark-recapture models.

Our study model was the sociable weaver (*Philetairus socius*), a colonial cooperatively breeding passerine endemic to the semi-arid Kalahari savannahs of southern Africa. These weavers are long-lived among passerines (up to 16 years, Covas 2012) and nest predation by snakes leads to an extremely low reproductive success (Covas et al. 2008). In sociable weavers, egg nutritional and hormonal content were negatively associated with the number of helpers at the nest (Paquet et al. 2013). On the other hand, the overall food load provided to nestlings increases when the number of helpers increases (Covas et al. 2008). In our cross-fostering experiment, we transferred whole clutches to a foster nest (see cross-fostering design in Table 1). The nestlings might thus have been conceived in the presence of helpers but raised in their absence (or vice-versa) and thus their prenatal social environment may differ from the post-natal social environment. Based on the previous knowledge of this species' life-history, and a previous result showing that females with helpers lay smaller eggs with lower levels of steroid hormones than females without helpers (Paquet et al. 2013), we predict: (i) a negative effect of the prenatal presence of helpers on chick rTL; (ii) a positive effect of the postnatal presence of helpers on chick rTL. In addition, we expect an interaction between pre- and post-natal helper presence, and we predict (iii) longer rTL of chicks that benefit from both higher maternal investment in eggs (absence

of pre-hatching helpers) and additional care provided by an increased postnatal helper presence; (iv) a stronger negative impact on chick rTL when the postnatal social environment is unfavorable (decreased presence of postnatal helpers), while prenatal conditions were unfavorable too (presence of prenatal helpers). Finally, we expect that telomere length will be positively associated with survival after fledging.

Material and methods

Species and study area

The study was conducted at Benfontein Game Farm in the Northern Cape Province, South Africa (approx. 28° 53' S, 24° 89' E). The study area covers 15 km² and contains approximately 30 sociable weaver colonies. The vegetation is Kalahari sandveld, consisting of open savannah dominated by *Stipagrostis* grasses and the camelthorn tree *Acacia erioloba*. The area is semi-arid, experiencing low and unpredictable rainfall (average 431 ± 127 mm/year, C.V. = 35.4; Weather Bureau, Pretoria). Most of the precipitation in the study area falls during the summer months, from September to April, when breeding usually takes place.

Sociable weavers are small (ca. 27 g) sexually monomorphic passerine birds endemic to southern Namib and Kalahari regions of Southern Africa. They build a large communal nest made of numerous independent chambers, wherein the birds roost throughout the year and breeding takes place (Maclean 1973a). These weavers are facultative cooperative breeders, with up to eight helpers assisting a breeding pair in raising the chicks, notably by feeding them (Covas et al. 2008). This lighter parental workload may increase the survival of young female breeders (Paquet et al. 2015b) but has no detectable association with clutch size (Covas et al. 2008; Fortuna et al. 2021). Helpers are most often the offspring of one or both breeders (Covas et al. 2006). Younger

Table 1 Cross-fostering procedure design

	Foster nest (postnatal)	
	Without helpers	With helpers
Original nest (prenatal)		
Without helper	Never any helper (9 chicks, 4 nests) EG: 0 (<i>n</i> = 9)	Postnatal helper(s) only (11 chicks, 5 nests) EG: + 1 (<i>n</i> = 11)
With helpers	Prenatal helper(s) only (12 chicks, 5 nests) EG: − 1 (<i>n</i> = 12)	Always at least one helper (18 chicks, 9 nests) EG: + 1 (<i>n</i> = 8)/0 (<i>n</i> = 4)/− 1 (<i>n</i> = 6)

Immediately after hatching, the whole clutch was transferred from its original nest with or without helpers to a foster nest with or without helpers, resulting in chicks with a similar or different pre- and post-hatching social environment. Chicks were swapped within the same colonies. 50 chicks were involved in this procedure, the sample sizes for nestlings and nests where they come from can be read within the brackets in bold font. In bold are also indicated the corresponding experimental groups (EG; + 1: increased number of helpers, 0: no change, − 1: decreased number of helpers)

helpers are both males and females while, when older than one year, helpers are usually males (Doutrelant et al. 2004). There is no extra-pair paternity in this species (Covas et al. 2006; Paquet et al. 2015b). Sociable weavers feed mostly on insects, but also seeds and other plant products (Maclean 1973b).

Data collection

Data were collected between September 2013 and February 2014 (for the variables related to breeding, growth, and telomeres) and until 2019 for chick survival. Unique numbered aluminum ring and color combination are attributed to each adult during the annual captures in winter and to each nestling before fledging, allowing individual identification of each bird. During the breeding season, all chambers in the study colonies are checked every three days, allowing us to identify new clutches and estimate clutch size (in this study, clutch size: mean = 3.5 and SD = 0.57 eggs; brood size before fledging: mean = 2.25 and SD = 0.84 birds). All chambers are visited daily at the end of the incubation period (approximately 15 days), to identify the hatching date. The nestling period usually lasts 21–24 days (Maclean 1973a). Two sets of measurements were performed nine days (D9) and seventeen days (D17) after the first chick hatched in each nest. Hence, chicks were captured only twice, limiting stress. D9 is the earliest moment where all chicks can be ringed and sampled for blood and D17 was chosen to have a measure as late as possible before fledging (as nestlings will fledge prematurely if handled from day 18 onwards). At these two dates, we measured brood size (number of chicks) and nestling mass, and we took blood samples from the brachial vein for sex determination and telomere analysis. This procedure was conducted on a total of 132 nestlings distributed among 15 colonies (containing approximately 400 chambers). In our study, we observed that approximately 39% of the individual nests (chambers) lacked helpers, whereas 61% had helpers. Individual nests harbored from 0 to 4 helpers and the average group size (parents + potential helpers) was 3.2 birds (median = 3, SD = 1.2).

Blood samples at D9 were stored in 95% ethanol. In contrast, because of use in other experiments, blood samples at D17 were centrifuged immediately upon collection and red blood cells were stored frozen. Because different storage conditions may affect rTL measured via quantitative polymerase chain reaction (qPCR, Reichert et al. 2017), we restricted our analysis to the same nestling age comparisons, storage conditions within samples from the same nestling age being strictly identical and could not affect the outcomes.

Tarsus length at D17 was also recorded and used as a proxy for body size. The body condition of a chick was calculated as the residual value from the regression between

tarsus length and mass at D17 (regression plot and statistics available in Electronic Supplementary Material, ESM 1). Tarsus length was not measured at D9. The 15 colonies from where the 132 chicks in this study originated are monitored annually, allowing us to analyze the relationship between the early rTL and survival from birth to the present (6 years).

Cross-fostering procedure

The detailed methods can be found in Paquet et al. (2015a), with the difference that here we focused on the reproduction period from September 2013 to February 2014. In brief, when two clutches from the same colony and of the same size were laid synchronously (or within a 1-day interval), both whole clutches were swapped on the day after the last egg was laid. Group sizes after hatching (*i.e.* parents + number of postnatal helpers) were established by counting the number of birds seen feeding the chicks. Observations and counting took place from under a hide placed at 3–5 m from the colony. The group size within a nest usually remains stable during the breeding cycle (from nest building to offspring fledging; Paquet et al. 2016), allowing us to infer the number of helpers before cross-fostering retrospectively. Within the 132 nestlings sampled during this study, 72 were involved in the cross-fostering protocol, among them, the presence (or absence) of helpers was known for 50 of them (18 broods). The pre- and post-natal social environments for these 50 chicks are detailed in Table 1.

Telomere length measurements

To assess the prenatal and postnatal effect of helpers on chick rTL, we measured early relative telomere length at D9 and just before fledging at D17 in chicks using the qPCR procedure. This protocol was first developed by Cawthon (Cawthon 2002) and thereafter popularized in birds' studies (Criscuolo et al. 2009; Herborn et al. 2014; Nettle et al. 2015; Meillère et al. 2015; Costanzo et al. 2017). The qPCR provides a non-absolute measure of an individual's TL, a relative telomere length as it is expressed relatively to one specific sample that is given arbitrarily the value of 1 (see Nussey et al. 2014; Lai et al. 2018) for a comparison between TL measurement methods). Shortly, after genomic DNA extraction from red blood cells (nucleated in birds) using silica-membrane columns (Nucleospin Blood QuickPure, Macherey–Nagel, Düren, Germany), DNA quantity and quality were assessed based on spectrophotometer absorbance (Nanodrop 1000 Thermo Scientific, ratios A260/280 and A260/230) and gel-migration (on a sub-sample randomly chosen of 30 samples, see ESM 2). Dilutions of extracted DNA (at 2.5 ng/μL) were prepared using sterile distilled water and were amplified using telomere and control gene primers with the BRYT Green fluorescent dye (GoTaq qPCR

Master Mix, Promega Charbonnières-les-Bains, France). We used recombination activating gene RAG1 as our control gene for weavers, designed to be non-variable among the individuals of our population (as advised by Smith et al. 2011; see ESM 2). The forward and reverse primers for the control gene were: SOWEA-F: 5'-TGCAAAGAGATTTTCG ATATGATG-3', SOWEA-R: 5'-TCACTGACATCTCCC ATTCC-3'. Tel1b: 5'-CGGTTTGTGGGTTTGGGTT TGGGTTTGGGTTTGGGTT-3', Tel2b: 5'-GGCTTGCCT TACCCTTACCCTTACCCTTACCCTTACCCT-3' for the telomere amplification. An automated thermocycler (CFX 384 Biorad Hercules, USA) was used, with reaction conditions set at 95 °C for 2 min, followed by 40 cycles of data collection at 95 °C for 1 min and a 60 °C annealing–extension step for 1 min for RAG1. For the telomeric sequence, the conditions were set at 95 °C for 2 min followed by 30 cycles of data collection for 15 s at 95 °C, 30 s at 56 °C, and 1 min at 72 °C. The 132 weaver samples used in the present study were part of 504 samples that were measured in duplicates on 5 different runs. Each run includes 1 plate of telomere sequence amplification and 1 plate of control gene sequence amplification, due to the differences in qPCR temperature conditions. On each plate, we ran a dilution curve (20–0.313 ng) to check that the efficiency of amplification did not vary among plates, and a melting curve to check for amplification artifacts (like primer-dimer signal, see ESM 2). The mean qPCR amplifying efficiencies were 99.8% (99.4–99.9) for telomere and 99.9% (99.7–100.1) for the control gene (100% reflect a doubling of the DNA sequence at each amplification step). Samples were randomly distributed over the plates, and 40 were repeated to assess interplate variation. As advised by Eisenberg (2016), rather than coefficients of variation, we reported the interplate and intraplate intra-class correlation coefficients for T/S ratio, respectively, 0.895 and 0.767.

The rTL is then calculated from the T/S ratio, where 'T' is the copy number of the telomeric sequence and 'S' is the copy number of the control sequence. We took into account the slight variation of efficiency between telomere and RAG1 amplifications by calculating the T/S ratio accordingly to Pfaffl's recommendation (Pfaffl 2001):

$$\left[\left(1 + E_{(\text{telomere})} \right)^{\Delta Cq_{(\text{telomere})}} \right] / \left[\left(1 + E_{(\text{RAG1})} \right)^{\Delta Cq_{(\text{RAG1})}} \right]$$

where 'E' is the amplification efficiency and 'ΔCq' the difference in time required to reach the fluorescence detectability threshold between control and sample (Cqcontrol – Cqsample).

Statistical analysis

Categorical variables were tested through ANOVA (package 'stats' v.3.6, R Core Team 2019). Post-hoc comparisons

were done using the *multcomp* R package with Tukey contrasts corrections (Hothorn et al. 2008). Quantitative variables including the T/S ratio were first z-scored and then tested directly through the t statistics provided by default by the function 'lmer'. Statistical tests were performed by the R software (R Core Team 2019) at the significance threshold $\alpha = 5\%$.

Effects of helpers on chick telomere length: definition of variables

In our analysis, we considered the effects of (i) the natural presence of helper in the nest of origin (hereafter referred to as 'prenatal presence') and (ii) the postnatal change in helper presence induced by the cross-fostering (hereafter referred to as 'postnatal helper change'). The prenatal presence of helpers was coded 0 (no helpers) and 1 (presence of helpers) while the postnatal helper change was coded 0 (no change), – 1 (reduced number of helpers) and + 1 (presence or increased number of helpers).

We tested if the prenatal presence of helpers and the postnatal helper change, as well as their interaction had an impact on early telomere length (i) nine days after hatching and (ii) later, just before fledging, at seventeen days after hatching. Telomere length and dynamics are known to be affected by individual characteristics, such as sex (Barrett and Richardson 2011; Young et al. 2013) or growth rate (Ringsby et al. 2015; Monaghan and Ozanne 2018; Vedder et al. 2018), as well as by the social environment (Hall et al. 2004; Nettle et al. 2015; Dugdale and Richardson 2018; Hammers et al. 2019). Hence, in addition to the prenatal presence and the postnatal helper change, we tested the influence of the following explanatory variables: sex, breeding period (different climatic conditions), brood size (intra-nest social competition), and body condition (an indicator of chick growth). The breeding period had two levels: the first between October and November 2013 (sparse rains) and the second between December 2013 and January 2014 (abundant rains). The prenatal presence of helpers and the postnatal helper change were not correlated: ($\chi^2 = 0.040$, $P = 0.842$), which validates the randomness of the cross-fostering procedure. Moreover, there was no evidence for collinearity between all other variables (Variance Inflation Factors were less than three: $VIF_{\max} = 1.49$).

Effects of helpers on chick telomere length: model fitting and selection

For the tests conducted either on day 9 or day 17, we built separated mixed linear models (LMM) with 'nest' as a random factor nested in 'colony' to control for non-independence of chicks in a nest. Due to the relatively low sample size ($n = 50$), we decided not to include more than five

explanatory variables to avoid over fitting (Harrison et al. 2018). We applied a model selection procedure with the ‘MuMIn package on R, based on the lowest Aikake’s information criterion corrected for small sample sizes (AIC; v. 1.43 Barton 2013). The procedure was adjusted to provide models containing no more than five variables, including the two main effects we wanted to test, *i.e.*, prenatal presence and postnatal variation in the number of helpers. We chose models as complete as possible with a maximum Δ AIC of 2. Then, depending on the selection procedure, the interaction term ‘prenatal presence x postnatal helper change’ may not be included in the lowest AIC model. All proposed and selected models involving telomere length are available in the electronic supplementary material (ESM 3, Table S1). We graphically ensured that model residuals did not significantly differ from a Gaussian distribution and related Anderson–Darling’s tests had P value > 0.05 for rTL both 9 and 17 days after hatching, respectively, $A = 0.25$, $P = 0.72$ and $A = 0.33$, $P = 0.51$, indicating that the model residuals fitted a normal distribution.

A Pearson’s correlation test was conducted to test for correlation of intra-individual values of chick telomere lengths repeatedly measured at day 9 and day 17 post-hatch.

Chick body condition and body mass growth vs. telomere length

Chick body condition was calculated as the residuals of the regression of body mass vs. tarsus length both measured at D17. Using the same statistical procedure as for telomere length, we tested whether the effect of helpers could be reflected in the body condition of chicks through mixed linear models with mass at D9 and body condition at D17 as dependent variables. Full models used in the model selection procedure included brood sizes at D9 or D17, chick sex and season, as well as nest/colony as random factors. Furthermore, we used the same statistical approach to examine the link between body condition at D17, body mass at D17 or body mass gain between D9 and D17 and chick telomere length at D17.

Telomere length and apparent survival

To estimate whether rTL predicted apparent survival we fitted Cormack–Jolly–Seber (CJS) models (Gimenez et al. 2007) on six years of capture-mark-recapture history of 132 fledglings (59 females and 73 males from cross-fostered as well as non-cross-fostered nests). We measured apparent survival, which does not allow us to differentiate dead individuals from those that permanently dispersed beyond the area studied. However, both sexes are philopatric (Dijk et al. 2015), and the 15–20 colonies in the study area are captured yearly, allowing us to re-capture birds dispersing between

colonies (usually less than 10%; Covas 2011). Furthermore, by considering detectability values lower than one, CMR models offer a reliable and explicit way to perform survival analysis in the wild (Gimenez et al. 2008). The CJS model is composed of apparent survival probability ϕ (defined as the probability to survive and not permanently emigrate the next year) and recapture probability p (defined as the probability of an individual apparently alive in a year to be recaptured with mist nets that year). We set ϕ to vary linearly with rTL (scaled) on the logit scale. We also allowed both ϕ and p to vary with the sex of the individuals as we expected them to be lower for females (Dijk et al. 2015; Paquet et al. 2015b) and to make sure that any relationship between rTL and apparent survival was not solely due to sex differences. We found an average recapture probability of 0.722 (min = 0.568, max = 0.854) for females and of 0.826 for males (min = 0.738, max = 0.900).

We specified both capture-recapture models using JAGS, version 4.2.0 (Plummer 2015) run using the rjags package (Plummer 2013) in Program R, version 3.4.3 (see ESM 4 for JAGS code). We estimated parameters using vague priors (see ESM 4 for priors and initial values). We used 3000 posterior samples from three Markov Chain Monte Carlo (MCMC) chains based on 3000 iterations after an adaptation period of 5000, a burn-in of 10,000 and thinning interval of 3. We assessed model convergence both visually and by using the ‘‘R hat’’ Gelman–Rubin statistic (Gelman and Rubin 1992) and found the 95% upper limits of potential scale reduction factors to equal 1 for all estimated parameters, indicating that convergence was achieved. We assessed the fit of our two models to the data (*i.e.* posterior predictive checks) by simulating capture recaptures histories from our two models at each iteration and comparing the number of simulated recaptures for the 3000 posterior samples with the number of observed recaptures. Simulated values systematically lower or higher than observed values would indicate a lack of fit [*i.e.* p (simulated < observed) close to 0 or 1]. We obtained p (simulated < observed) = 0.47 and 0.49 for models looking at rTL at D9 and D17, respectively, indicating a good fit to the data.

Ethical statement

All experiments were conducted with permission from the Northern Cape Department of Tourism Environment and Conservation (permit FAUNA 942/2012) and the approval of the Ethics Committee of the University of Cape Town (2009/V12/RCREN). Our procedures involved the capture, confinement, handling, and blood sampling of the birds in the field, with the time elapsed between extracting the birds from the nets until the last bird was released ranging from 2 to 3 h. While queuing to be processed, birds rested in individual bird bags and were placed in a

quiet, ventilated and shaded area. The sampling volume (ca. 75 μ l) remained well below the prescribed limits for the percentage of the total blood volume of this passerine. After handling, the adult birds could recover for a few minutes before being released in small groups. Any birds that showed signs of fatigue or injury were taken to an indoor aviary to recover and were subsequently released. This happened for less than 1% of the birds handled. To decrease handling times, captures were conducted with a team of 8–12 experienced ringers that were allocated specific tasks to streamline the procedures conducted.

Results

We present for each result below the estimate $\pm$ standard error in brackets. In Table 2 (telomere-related models) and Table 3 (body mass-related models), we present in addition 95% confidence interval (CI95%), test statistics and *P* values. After the model selection procedure (detailed in ESM 3, Table S1), all models contained the following independent variables: prenatal presence, postnatal helper change and the random effect of the nest nested in the colony. The interaction between pre- and post-natal helpers (prenatal presence $\times$ postnatal helper

Table 2 Effect of the prenatal and postnatal presence of helpers on chick relative telomere length (rTL, z-transformed)

Predictors	rTL D9				
	Estimates	Std. error	CI	Statistic	<i>P</i>
(a)					
Intercept	−0.08	0.55	−1.17–1.00	−0.15	0.880
Prenatal presence of helpers	0.29	0.45	−0.58–1.17	0.65	0.513
Postnatal helper change	1.18	0.50	0.20–2.16	2.36	0.018
Brood size D9	0.09	0.17	−0.24–0.43	0.54	0.587
Chick sex	−0.43	0.25	−0.91–0.05	−1.74	0.082
Prenatal presence $\times$ postnatal helper change	−1.76	0.54	−2.81 to −0.70	−3.27	0.001
Random effects					
σ^2	0.46				
τ_{00} (nest:colony_id)	0.50				
τ_{00} (colony_id)	0.39				
ICC	0.66				
N (nest)	18				
N (colony_id)	3				
Observations	50				
Marginal R^2 /conditional R^2	0.177/0.718				
(b)					
Intercept	1.91	0.17	1.57–2.25	11.04	<0.001
Prenatal presence of helpers	−0.13	0.21	−0.53–0.28	−0.61	0.542
Postnatal helper change	−0.06	0.12	−0.29–0.18	−0.48	0.635
Breeding season	0.12	0.18	−0.23–0.46	0.66	0.508
Random Effects					
σ^2	0.39				
τ_{00} (nest:colony_id)	0.00				
τ_{00} (colony_id)	0.00				
N nest	18				
N (colony_id)	3				
Observations	50				
Marginal R^2 /conditional R^2	0.017/NA				

The following tables list the estimates ('est.'), 95% confidence interval ('CI 95%'), standard error ('SE'), test statistics ('stat.', *t* or *F*, respectively, for continuous or categorical variables) and *P* values ('*P*') from linear mixed models. We only consider the variables retained after the model selection procedure (ESM 3). Continuous variables have been scaled and transformed into z-scores. Lines in bold indicate a significant test with $\alpha=0.05$ as a threshold. Results are given for chick telomere length at 9 (a) and 17 (b) days after hatching. In this latter case, random effects did not explain a significant part of the variance

Table 3 Effect of the prenatal and postnatal presence of helpers on the chick mass at day 9 (a) and chick body condition at day 17 (b) post-hatch (linear mixed models)

Predictors	Body mass D9 (g)				
	Estimates	Std. error	CI	Statistic	<i>P</i>
(a)					
Intercept	2.01	0.99	0.06–3.96	2.02	0.044
Prenatal presence of helpers	0.51	0.43	–0.32–1.35	1.20	0.231
Postnatal helper change	0.14	0.59	–1.00–1.29	0.24	0.808
Brood size D9	–0.88	0.23	–1.34 to –0.42	–3.77	<0.001
Chick sex	0.51	0.26	–0.01–1.02	1.94	0.053
Prenatal presence × postnatal helper change	0.35	1.09	–1.79–2.49	0.32	0.752
Random Effects					
σ^2	0.62				
τ_{00} (nest:colony_id)	0.11				
τ_{00} (colony_id)	0.46				
ICC	0.48				
N (nest)	18				
N (colony_id)	3				
Observations	50				
Marginal R^2 /conditional R^2	0.255/0.611				
(b)					
Intercept	–0.99	0.50	–1.97–0.00	–1.95	0.051
Prenatal presence of helpers	0.36	0.40	–0.42–1.15	0.90	0.367
Postnatal helper change	0.90	0.44	0.04–1.77	2.04	0.041
Breeding season	0.55	0.28	–0.00–1.11	1.95	0.051
Chick sex	0.16	0.21	–0.26–0.58	0.76	0.450
Brood size D17	–0.51	0.15	–0.80 to –0.21	–3.37	0.001
Random effects					
σ^2	0.34				
τ_{00} (nest:colony_id)	0.59				
τ_{00} (colony_id)	0.00				
ICC	0.63				
N (nest)	18				
N (colony_id)	3				
Observations	50				
Marginal R^2 /conditional R^2	0.257/0.728				

None shows a significant effect of helpers. Testing body mass at D17 or body mass gain between D9 and D17 led to similar non-significant effects (data not shown)

change), as well as chick sex and brood size were kept only for the presence of helpers at D9. Only the breeding season was kept as an additional fixed factor for the model testing individual variability in rTL at D17. The original data sets regarding both the effect of helpers on chick rTL and the effect of rTL on survival are available online as distinct tables in ESM5. Chicks rTL measured at D9 and D17 were found to be significantly correlated—even if the correlation is not high ($r = 0.27$, $t = 2.64$, $P = 0.009$, $n = 93$, Pearson's correlation).

Effect of the prenatal and postnatal presence of helpers on chick rTL

The detailed statistics are given in Table 2 and related plots are Fig. 1a for D9 and 1b for D17.

Nine days after hatching, we found a significant interaction between the prenatal helpers' presence and the postnatal helpers' presence (-1.76 ± 0.54). The Tukey contrasts post-hoc comparisons showed that for the chicks from nests without helpers during the prenatal stage, obtaining

Fig. 1 Relative telomere length (rTL, T/S ratio) 9 days (**a**) and 17 days (**b**) after hatching in relation to helpers' presence in sociable weavers. We compared the rTL of 50 cross-fostered individuals according to (i) the presence of helpers before the cross-fostering and (ii) after the cross-fostering. This latter experimental factor is categorised as increased number of helpers (+1, blue); no change in helpers' presence (0, green) and decreased number of helpers (−1, red). **a** Post-hoc significant differences (Tukey contrasts) concerned: longer

rTL in chicks that started with no helpers but get experimental helpers' presence ($P=0.010$); decreased rTL in chicks that started with helper presence but thereafter experienced no helpers ($P=0.042$); shorter rTL in chicks that started with helpers and experienced increased helpers presence after hatching compared to chicks that had helpers only after hatching ($P=0.043$). **b** no significant differences were found at D17. See text for statistics. Error bars represent standard errors. White numbers inside the bars give the sample size

postnatal helpers was associated with larger rTL nine days after hatching (Fig. 1a, 0/1 vs 0/0, post-hoc: 1.54 ± 0.49 , $z=3.13$, $P=0.01$). For chicks that had prenatal helpers, a decrease in the number of helpers was associated with a shorter rTL (1/−1 vs 1/0, post-hoc: -1.21 ± 0.44 , $z=-2.75$, $P=0.042$). However, the rTL of chicks swapped from nests with helpers to nests with more helpers was not affected by the increase in helper number after hatching (1/+1 vs 1/0 and 1/−1, post-hoc: respectively, -1.23 ± 1.20 , $z=-1.03$, $P=0.83$ and 1.20 ± 0.51 , $z=2.35$, $P=0.12$). Among the chicks experiencing additional helpers, those with prenatal helpers had shorter telomeres on average (0/+1 vs 1/+1, post-hoc: -1.18 ± 0.44 , $z=-2.73$, $P=0.043$). The effect of chick sex and brood size were not significant (respectively, -0.43 ± 0.25 and 0.09 ± 0.17). When measured at D17 post-hatch, neither the prenatal presence or the postnatal helper change nor their interaction term were found to be significantly related to offspring's rTL (Fig. 1b, Table 2b). The breeding season, while kept in the selected model, had no significant effect (0.12 ± 0.18).

Effects of helpers on chick body mass and body condition

Neither the prenatal or the postnatal presence of helpers were associated with a change in chick body mass at D9, or chick body condition at D17 (Table 3). Only brood sizes (D9 and D17) negatively affected body mass at D9 and body condition at D17, respectively. Testing body mass at D17 or

the gain in body mass between D9 and D17 did not shown any significant relationships (data not shown). There was no relationship between body mass gain (D17–D9) and chick rTL at D17 (ESM 6, Table S2).

Chick telomere length and apparent survival rate

We found that sociable weaver chicks with longer rTL at D9 tended to have a higher apparent survival rate the following five years although the 95% credible interval overlapped zero [estimate (95% credible interval) = $0.21 (-0.072, 0.52)$,

Fig. 2 Relation between relative telomere length (rTL, T/S ratio) 9 days after hatching and apparent survival. 132 birds were annually captured from 2014 to the present (6 years). Estimate and 95% Credibility Interval = $0.21 (-0.07; 0.52)$, p (estimate > 0) = 0.928

p (estimate > 0) = 0.928, Fig. 2]. We found no clear association between rTL at D17 and apparent survival [estimate = -0.013 (-0.24, 0.22), p (estimate > 0) = 0.458].

Discussion

We investigated the influence of the prenatal and postnatal presence of helpers on rTL and the link between rTL and survival in nestlings of the sociable weaver, a cooperatively breeding bird. Early-life rTL (*i.e.* measured nine days after hatching) was overall positively associated with the presence of post-natal helpers but was also influenced by an interaction of the presence of pre- and post-natal helpers. Specifically, we found that for chicks coming from nests without prenatal helpers, rTL was longer when postnatal helpers were added after hatching. For the chicks coming from nests that already had prenatal helpers, telomere length was shorter when the number of helpers decreased after hatching. For those chicks, however, an increase in the number of postnatal helpers had no significant effect on offspring rTL. The interaction between the prenatal presence and postnatal helper change showed that the increase in postnatal helpers was associated with a greater offspring rTL only when no prenatal helper was present. The effects observed nine days after hatching (D9) were not observed at the end of the nestling period (D17; but see below). Finally, the CMR analysis conducted to assess the link between early rTL and post-fledgling survival showed a tendency for rTL at D9 to be positively related to survival up to five years after hatching, but this relationship was no longer present at D17.

Contrasting effects of pre- and post-natal helpers on offspring's telomeres

Nestlings from original nests without helpers had greater rTL at D9 when raised with postnatal helpers than without. On the other hand, reducing the number of postnatal helpers (*i.e.* concerned nests with prenatal helpers) was associated with shorter chicks' rTL. These two findings support a beneficial effect of post-hatching helpers on offspring rTL in sociable weaver. Such positive postnatal influence is thought to be mediated by the enhancement of developmental conditions that nestlings experience through the additional care provided (Covas et al. 2008; Bebbington et al. 2018). This additional care may also contribute to decreasing sibling competition in larger broods, which has been shown as a modulating mechanism of rTL in chicks from different species (Voillemot et al. 2012; Boonekamp et al. 2014; Nettle et al. 2015; Young et al. 2017). A negative effect of sibling competition on offspring development was also suggested here through a negative effect of brood size on body mass. Nevertheless, this beneficial effect appears to be limited,

since the addition of postnatal helpers in nests already harboring prenatal helpers had no significant effect.

We found in addition an interaction between the prenatal presence and postnatal helper change indicating that the positive effect of postnatal helpers on chick rTL is dependent on the presence of prenatal helpers. Indeed, adding helpers after hatching was negatively associated with chick's rTL if those chicks had experienced prenatal helpers (*i.e.* they had on average shorter rTL than those without prenatal helpers); the effect persisted even when removing the two extreme values for the 0/1 condition (Fig. 1a). This outcome is expected if there is a prevalent negative prenatal effect resulting from a reduced maternal investment during egg production in presence of prenatal helpers, compared to the benefits of being raised with post-natal helpers. In fact, previous studies have shown that the conditions experienced during embryonic life may alter telomere length at birth (Entringer et al. 2011; Haussmann et al. 2012; Vedder et al. 2018; Noguera and Velando 2019, 2020; Stier et al. 2020). Sociable weavers females were found to lay smaller eggs with lower steroid hormone content (Paquet et al. 2013). Telomere shortening may thus arise from this weaker maternal investment in the presence of pre-hatching helpers. Our results suggest that such initial telomere handicap may not be reversed by the beneficial effects of post-natal helpers. Still, our sample size does not allow us to draw definitive conclusions, and the pre/post-natal helpers interaction effects deserve further study.

A non-exclusive explanation for the lack of a positive effect of an increased number of postnatal helpers for nestlings with prenatal helpers might be that, above an optimal threshold, adding more helpers would have no benefits, or could even become detrimental for offspring rTL. A previous study in the same species has actually shown that larger group sizes may result in a weaker offspring survival likelihood (Covas et al. 2011, but see Wood 2017 chap. 3). When analyzing only the effect of group size before and after hatching, we found that the number of helpers had no effect on telomere length at either D9 or D17 (ESM 7). This confirms the results presented here and supports the interpretation that, in our case, a larger number of helpers does not provide greater benefits for the offspring, whatever their age. In addition, a previous study on this population found that the positive effect of helpers on chicks after hatching is mostly detected under adverse environmental conditions (Covas et al. 2008). If fewer helpers provide sufficient help under usual climatic conditions, this may explain why we found no significant effect of an increased number of helpers post-hatch when prenatal helpers were already present (1/+1 vs 1/0 and 1/-1). Given the association between helpers' presence and rTL at day 9, it may be surprising to find no association at day 17. However, in addition to the presence of helpers, several environmental factors such as climate (Mizutani et al. 2013), sibling rivalry (Nettle et al.

2015; Mizutani et al. 2016) or food availability (Spurgin et al. 2017) might have blurred possible helper effects at D17. For example, in black-tailed gull chicks (*Larus crassirostris*), the effect of sibling competition on telomeres was weak on the first day after hatching and became stronger 30 days after hatching, potentially concealing the effect of other factors (Mizutani et al. 2016). In European starlings (*Sturnus vulgaris*), the effect of sibling rivalry on telomere attrition was also dependent on nestling age: not detectable at 3 days after hatching (D3), detectable at D12 and faded at D24 (Nettle et al. 2015). In the same study, the effect on oxidative status was detectable at D3 but no longer at D12. Those studies and ours seem to indicate that the effect of different environmental factors might vary with individual age and species.

Body mass growth, telomeres, and survival

The suggestion that offspring's early rTL is a proxy of survival rate has been supported in other species (Geiger et al. 2012; Heidinger et al. 2012; Stier et al. 2014; Young et al. 2017; Eastwood et al. 2019; Chatelain et al. 2020); but see (Boonekamp et al. 2014) or (Wood and Young 2019) for a critical view on telomere shortening and survival. Although the 95% credible interval slightly overlapped zero, our study tends also to suggest that chick rTL early after hatching might predict post-fledging apparent survival, at least up to 5 years after hatching. In this species, a previous study showed that helpers had a negative effect on offspring survival but only during the first year after fledging, after that, this negative effect disappeared (Covas et al. 2011). Even if in the medium term (five years here) the presence of postnatal helpers seems to be rather positive for offspring apparent survival, the consequences of helpers could be more complex especially in the very first years of life. This adds another level of complexity in understanding the evolutionary advantages and disadvantages of social structure involving cooperative breeding.

Heidinger et al. (2012) have shown that rTL measured within the first month in zebra finches predicted lifespan better than subsequent measurements. Our results are in line with this finding, as we did not detect an association between rTL and apparent survival for older chicks (before fledging). However, the exact reasons for why earlier telomere length is a better predictor of survival than later telomere length remain elusive (Ingles and Deakin 2016; Lieshout et al. 2019).

The improved rearing conditions induced by postnatal helpers could have led also to improve body condition. However, and similarly to a previous study in the same species (Paquet et al. 2013), both mass at D9 and fledglings' body condition (D17) did not vary with the presence of helpers. These results support previous suggestions on this and other

species in showing the ability of helpers to compensate for the differential maternal investment in eggs so that, on average, fledglings have the same body condition. Since, in our study, chicks varied in their day 9 rTL but not body condition, it seems that for the chicks that do not have helpers, allocation of energy is toward growth at the expense of their telomeres. Such a trade-off between growth and telomere maintenance has been shown in numerous vertebrate species (Tarry-Adkins et al. 2009; Geiger et al. 2012; Stier et al. 2014; Pauliny et al. 2015; Ringsby et al. 2015; Vedder et al. 2017, 2018). A quicker post-hatching growth ensures a higher success rate at fledging (Kersten and Breninkmeijer 1995; Harris et al. 2008; Canestrari et al. 2011; Loock et al. 2017; Hipfner and Gaston 1999) and an earlier fledging date may decrease predation risk in sociable weavers (Ferreira 2015). As a result, there could be a stronger evolutionary pressure on body growth rather than telomere length; in other words, short-term survival by avoiding predation rather than long-term survival through somatic maintenance. Alternatively, resource-investment trade-offs may be reflected not in body condition or mass, but in tissue maturation rate, which could be reflected in shorter telomeres (Criscuolo et al. 2019).

Conclusions

Here, we set to investigate the effect of the social environment (presence of helpers) before and after hatching on offspring rTL. Our results suggest an overall positive effect of postnatal helpers on the offspring rTL early in life, but our study did not provide evidence that this relationship is conserved until fledging. Furthermore, the positive postnatal effect of helper presence was dependent on prenatal conditions, being stronger in nests that did not have pre-natal helpers. Thus, the presence of helpers may induce opposite effects depending on whether helpers are present before or after hatching and that the interaction between the prenatal and postnatal environment is essential to understand the consequences of the social environment on offspring. In addition to the social environment, the ecological context (e.g., temperature, food availability) may also affect rTL, both before and after hatching, but this was not investigated here. This calls for data over longer periods spanning different climatic conditions, to decipher the interaction between social and ecological environment. According to our results, the chicks with the shortest telomeres in their early life might also be less likely to survive the first years of life. Although other factors influence rTL, such as genetics or the quality of care provided, our study suggests that social context, has a potential important role to play in influencing individual development and survival in cooperatively breeding birds. However, the mechanisms that sustain these pre- and post-natal social effects on rTL remain to be identified and further studies

on the underlying molecular mechanisms (e.g. hormones, oxidative stress, metabolic pathways) are now needed.

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Author contribution statement BF, CD, MP and RC designed the study. CD, FT, MP and RC collected the data in the field. CD, FT, MP, MQ and RC organized the database. MQ performed the statistical analysis, MP the survival analysis and SZ the laboratory analyses. MQ wrote the first draft of the manuscript. CD, CS, FC, MP, RC and SZ wrote sections of the manuscript. All authors contributed to manuscript revision, read and approved the submitted version.

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Declarations

Conflict of interest The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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