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Abstract

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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 (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

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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.

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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

41 offspring survival or behavior (e.g. Krist 2011; Paquet et al.
42 2015a).

43 Among the environmental effects experienced by females
44 and their developing offspring, sociality has been receiving
45 increasing attention (e.g. Russell et al. 2007, 2008; Dixit
46 et al. 2017). In cooperatively breeding species, sexually
47 mature non-breeding individuals—called ‘helpers’—assist
48 in raising the offspring of others by bringing additional
49 food to the nest and performing other tasks such as terri-
50 tory defense (Cockburn 1998). The presence of these help-
51 ers is therefore thought to improve the breeding conditions
52 experienced by females and/or offspring, and studies on
53 several species have generally shown that helper presence
54 is associated with improved juvenile condition and survival
55 (e.g. Ridley 2007; Kingma et al. 2010; Brouwer et al. 2012;
56 Preston et al. 2016; Tanaka et al. 2018). Breeding females
57 may respond to this improvement in reproductive conditions
58 by either maintaining their investment in eggs or food provi-
59 sioning (Clutton-Brock et al. 2001; Doerr and Doerr 2007;
60 Lejeune et al. 2016), or decreasing it (Crick 1992; Santos
61 and Macedo 2011; Dixit et al. 2017), thereby reducing their
62 cost of reproduction and increasing their survival and future
63 reproduction. Reduction in maternal investment should then
64 be compensated by the additional food brought by helpers
65 (Russell and Lummaa 2009). The direction and magnitude
66 of the response are expected to be influenced by the species’
67 life-history strategy and especially by the effects of mater-
68 nal investment on mother’s survival prospects and chances
69 of breeding successfully in the future (Russell and Lum-
70 ma 2009). In birds, cooperatively breeding species tend
71 to be long-lived (Arnold and Owens 1998; Downing et al.
72 2015), and for long-lived species, maximization of lifetime
73 reproductive success was suggested to be more efficiently
74 achieved through increasing the number of breeding events
75 in life than through increased investment in each breeding
76 event (Ghalambor and Martin 2001; Drent and Daan 2002;
77 Reid et al. 2003). In agreement, a recent meta-analysis on
78 10 cooperatively breeding birds highlighted a tendency for
79 mothers to reduce egg size in larger groups in most species
80 studied (Dixit et al. 2017; but see Fortuna et al. 2021).

81 It is less clear whether such differential maternal invest-
82 ments translate into differences in the condition and sur-
83 vival of offspring and what is the relative influence of the
84 pre- and post-natal environment. For example, in birds,
85 there are indications that larger eggs are positively asso-
86 ciated with nestling’s body size, growth and survival
87 (Krist 2011). However, these associations could arise
88 from genetic and hormonal effects of parents (Morrison
89 et al. 2009; Voillemot et al. 2012; Weber et al. 2018), and/
90 or from rearing conditions independently from parental
91 phenotype (Bize et al. 2002; Velando et al. 2005). From
92 the offspring’s perspective, the presence of helpers can be
93 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; Looch
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) iden-
tifying 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. Replica-
tion 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 repli-
cative senescence, which participates in the senescence of
the whole organism (Tchkonina 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 ver-
tebrate 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 (Hausmann 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 tel-
omeres and survival (Wilbourn et al. 2018). Taken together
these studies support the use of telomeres as reliable indica-
tors of longevity and/or individual quality, sensitive to early
ecological and social stress, especially when measured dur-
ing 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)

217 helpers are both males and females while, when older than
218 one year, helpers are usually males (Doutrelant et al. 2004).
219 There is no extra-pair paternity in this species (Covas et al.
220 2006; Paquet et al. 2015b). Sociable weavers feed mostly
221 on insects, but also seeds and other plant products (Maclean
222 1973b).

223 Data collection

224 Data were collected between September 2013 and Febru-
225 ary 2014 (for the variables related to breeding, growth, and
226 telomeres) and until 2019 for chick survival. Unique num-
227 bered aluminum ring and color combination are attributed to
228 each adult during the annual captures in winter and to each
229 nestling before fledging, allowing individual identification
230 of each bird. During the breeding season, all chambers in
231 the study colonies are checked every three days, allowing
232 us to identify new clutches and estimate clutch size (in this
233 study, clutch size: mean = 3.5 and SD = 0.57 eggs; brood
234 size before fledging: mean = 2.25 and SD = 0.84 birds). All
235 chambers are visited daily at the end of the incubation period
236 (approximately 15 days), to identify the hatching date. The
237 nestling period usually lasts 21–24 days (Maclean 1973a).
238 Two sets of measurements were performed nine days (D9)
239 and seventeen days (D17) after the first chick hatched in each
240 nest. Hence, chicks were captured only twice, limiting stress.
241 D9 is the earliest moment where all chicks can be ringed and
242 sampled for blood and D17 was chosen to have a measure
243 as late as possible before fledging (as nestlings will fledge
244 prematurely if handled from day 18 onwards). At these two
245 dates, we measured brood size (number of chicks) and nest-
246 ling mass, and we took blood samples from the brachial vein
247 for sex determination and telomere analysis. This procedure
248 was conducted on a total of 132 nestlings distributed among
249 15 colonies (containing approximately 400 chambers). In
250 our study, we observed that approximately 39% of the indi-
251 vidual nests (chambers) lacked helpers, whereas 61% had
252 helpers. Individual nests harbored from 0 to 4 helpers and
253 the average group size (parents + potential helpers) was 3.2
254 birds (median = 3, SD = 1.2).

255 Blood samples at D9 were stored in 95% ethanol. In con-
256 trast, because of use in other experiments, blood samples
257 at D17 were centrifuged immediately upon collection and
258 red blood cells were stored frozen. Because different stor-
259 age conditions may affect rTL measured via quantitative
260 polymerase chain reaction (qPCR, Reichert et al. 2017),
261 we restricted our analysis to the same nestling age com-
262 parisons, storage conditions within samples from the same
263 nestling age being strictly identical and could not affect the
264 outcomes.

265 Tarsus length at D17 was also recorded and used as a
266 proxy for body size. The body condition of a chick was cal-
267 culated 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 + num-
ber 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 off-
spring 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' stud-
ies (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 re-
lative telomere length as it is expressed relatively to one spe-
cific sample that is given arbitrarily the value of 1 (see Nus-
sey et al. 2014; Lai et al. 2018) for a comparison between TL
measurement methods). Shortly, after genomic DNA extrac-
tion from red blood cells (nucleated in birds) using silica-
membrane columns (Nucleospin Blood QuickPure, Mach-
erey–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

317 Master Mix, Promega Charbonnières-les-Bains, France). We
 318 used recombination activating gene RAG1 as our control
 319 gene for weavers, designed to be non-variable among the
 320 individuals of our population (as advised by Smith et al.
 321 2011; see ESM 2). The forward and reverse primers for the
 322 control gene were: SOWEA-F: 5'-TGCAAGAGATTTTCG
 323 ATATGATG-3', SOWEA-R: 5'-TCACTGACATCTCCC
 324 ATTCC-3'. Tel1b: 5'-CGGTTTGTGGGTTTGGGTT
 325 TGGGTTTGGGTTTGGGTT-3', Tel2b: 5'-GGCTTGCCT
 326 TACCCTTACCCTTACCCTTACCCTTACCCT-3' for the
 327 telomere amplification. An automated thermocycler (CFX
 328 384 Biorad Hercules, USA) was used, with reaction condi-
 329 tions set at 95 °C for 2 min, followed by 40 cycles of data
 330 collection at 95 °C for 1 min and a 60 °C annealing–exten-
 331 sion step for 1 min for RAG1. For the telomeric sequence,
 332 the conditions were set at 95 °C for 2 min followed by 30
 333 cycles of data collection for 15 s at 95 °C, 30 s at 56 °C,
 334 and 1 min at 72 °C. The 132 weaver samples used in the
 335 present study were part of 504 samples that were measured
 336 in duplicates on 5 different runs. Each run includes 1 plate of
 337 telomere sequence amplification and 1 plate of control gene
 338 sequence amplification, due to the differences in qPCR tem-
 339 perature conditions. On each plate, we ran a dilution curve
 340 (20–0.313 ng) to check that the efficiency of amplification
 341 did not vary among plates, and a melting curve to check for
 342 amplification artifacts (like primer-dimer signal, see ESM
 343 2). The mean qPCR amplifying efficiencies were 99.8%
 344 (99.4–99.9) for telomere and 99.9% (99.7–100.1) for the
 345 control gene (100% reflect a doubling of the DNA sequence
 346 at each amplification step). Samples were randomly distrib-
 347 uted over the plates, and 40 were repeated to assess inter-
 348 plate variation. As advised by Eisenberg (2016), rather than
 349 coefficients of variation, we reported the interplate and
 350 intraplate intra-class correlation coefficients for T/S ratio,
 351 respectively, 0.895 and 0.767.

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

$$358 \left[\left(1 + E_{(\text{telomere})} \right)^{\Delta Cq_{(\text{telomere})}} \right] / \left[\left(1 + E_{(\text{RAG1})} \right)^{\Delta Cq_{(\text{RAG1})}} \right]$$

359 where 'E' is the amplification efficiency and 'ΔCq' the
 360 difference in time required to reach the fluorescence
 361 detectability threshold between control and sample
 362 (Cq_{control} – Cq_{sample}).
 363

364 Statistical analysis

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

were done using the *multcomp* R package with Tukey con- 367
 trasts corrections (Hothorn et al. 2008). Quantitative vari- 368
 ables including the T/S ratio were first z-scored and then 369
 tested directly through the t statistics provided by default by 370
 the function 'lmer'. Statistical tests were performed by the R 371
 software (R Core Team 2019) at the significance threshold 372
 $\alpha = 5\%$. 373

Effects of helpers on chick telomere length: definition 374 of variables 375

In our analysis, we considered the effects of (i) the natural 376
 presence of helper in the nest of origin (hereafter referred 377
 to as 'prenatal presence') and (ii) the postnatal change in 378
 helper presence induced by the cross-fostering (hereafter 379
 referred to as 'postnatal helper change'). The prenatal pres- 380
 ence of helpers was coded 0 (no helpers) and 1 (presence of 381
 helpers) while the postnatal helper change was coded 0 (no 382
 change), – 1 (reduced number of helpers) and + 1 (presence 383
 or increased number of helpers). 384

We tested if the prenatal presence of helpers and the 385
 postnatal helper change, as well as their interaction had an 386
 impact on early telomere length (i) nine days after hatching 387
 and (ii) later, just before fledging, at seventeen days after 388
 hatching. Telomere length and dynamics are known to be 389
 affected by individual characteristics, such as sex (Barrett 390
 and Richardson 2011; Young et al. 2013) or growth rate 391
 (Ringsby et al. 2015; Monaghan and Ozanne 2018; Ved- 392
 der et al. 2018), as well as by the social environment (Hall 393
 et al. 2004; Nettle et al. 2015; Dugdale and Richardson 394
 2018; Hammers et al. 2019). Hence, in addition to the pre- 395
 natal presence and the postnatal helper change, we tested 396
 the influence of the following explanatory variables: sex, 397
 breeding period (different climatic conditions), brood size 398
 (intra-nest social competition), and body condition (an indi- 399
 cator of chick growth). The breeding period had two levels: 400
 the first between October and November 2013 (sparse rains) 401
 and the second between December 2013 and January 2014 402
 (abundant rains). The prenatal presence of helpers and the 403
 postnatal helper change were not correlated: ($\chi^2 = 0.040$, 404
 $P = 0.842$), which validates the randomness of the cross- 405
 fostering procedure. Moreover, there was no evidence for 406
 collinearity between all other variables (Variance Inflation 407
 Factors were less than three: $VIF_{\max} = 1.49$). 408

Effects of helpers on chick telomere length: model fitting 409 and selection 410

For the tests conducted either on day 9 or day 17, we built 411
 separated mixed linear models (LMM) with 'nest' as a 412
 random factor nested in 'colony' to control for non-inde- 413
 pendence of chicks in a nest. Due to the relatively low sam- 414
 ple size ($n = 50$), we decided not to include more than five 415

416 explanatory variables to avoid over fitting (Harrison et al.
417 2018). We applied a model selection procedure with the
418 ‘MuMIn package on R, based on the lowest Aikake’s infor-
419 mation criterion corrected for small sample sizes (AIC; v.
420 1.43 Bartoń 2013). The procedure was adjusted to provide
421 models containing no more than five variables, including the
422 two main effects we wanted to test, *i.e.*, prenatal presence
423 and postnatal variation in the number of helpers. We chose
424 models as complete as possible with a maximum Δ AIC of
425 2. Then, depending on the selection procedure, the interac-
426 tion term ‘prenatal presence x postnatal helper change’ may
427 not be included in the lowest AIC model. All proposed and
428 selected models involving telomere length are available in
429 the electronic supplementary material (ESM 3, Table S1).
430 We graphically ensured that model residuals did not sig-
431 nificantly differ from a Gaussian distribution and related
432 Anderson–Darling’s tests had P value > 0.05 for rTL both 9
433 and 17 days after hatching, respectively, $A = 0.25$, $P = 0.72$
434 and $A = 0.33$, $P = 0.51$, indicating that the model residuals
435 fitted a normal distribution.

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

439 Chick body condition and body mass growth vs. telomere 440 length

441 Chick body condition was calculated as the residuals of the
442 regression of body mass vs. tarsus length both measured at
443 D17. Using the same statistical procedure as for telomere
444 length, we tested whether the effect of helpers could be
445 reflected in the body condition of chicks through mixed lin-
446 ear models with mass at D9 and body condition at D17 as
447 dependent variables. Full models used in the model selection
448 procedure included brood sizes at D9 or D17, chick sex and
449 season, as well as nest/colony as random factors. Further-
450 more, we used the same statistical approach to examine the
451 link between body condition at D17, body mass at D17 or
452 body mass gain between D9 and D17 and chick telomere
453 length at D17.

454 Telomere length and apparent survival

455 To estimate whether rTL predicted apparent survival we
456 fitted Cormack–Joly–Seber (CJS) models (Gimenez et al.
457 2007) on six years of capture–mark–recapture history of 132
458 fledglings (59 females and 73 males from cross-fostered as
459 well as non-cross-fostered nests). We measured apparent
460 survival, which does not allow us to differentiate dead indi-
461 viduals from those that permanently dispersed beyond the
462 area studied. However, both sexes are philopatric (Dijk et al.
463 2015), and the 15–20 colonies in the study area are captured
464 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 lin-
early 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 adapta-
tion period of 5000, a burn-in of 10,000 and thinning inter-
val 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 param-
eters, 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 systemati-
cally 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 mod-
els 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 cap-
ture, confinement, handling, and blood sampling of the
birds in the field, with the time elapsed between extract-
ing 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

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

Results

527
 528 We present for each result below the estimate \pm standard
 529 error in brackets. In Table 2 (telomere-related models)
 530 and Table 3 (body mass-related models), we present in
 531 addition 95% confidence interval (CI95%), test statis-
 532 tics and *P* values. After the model selection procedure
 533 (detailed in ESM 3, Table S1), all models contained the
 534 following independent variables: prenatal presence, post-
 535 natal helper change and the random effect of the nest
 536 nested in the colony. The interaction between pre- and
 537 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)

538 change), as well as chick sex and brood size were kept
 539 only for the presence of helpers at D9. Only the breeding
 540 season was kept as an additional fixed factor for the model
 541 testing individual variability in rTL at D17. The original
 542 data sets regarding both the effect of helpers on chick rTL
 543 and the effect of rTL on survival are available online as
 544 distinct tables in ESM5. Chicks rTL measured at D9 and
 545 D17 were found to be significantly correlated—even if
 546 the correlation is not high ($r = 0.27$, $t = 2.64$, $P = 0.009$,
 547 $n = 93$, 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

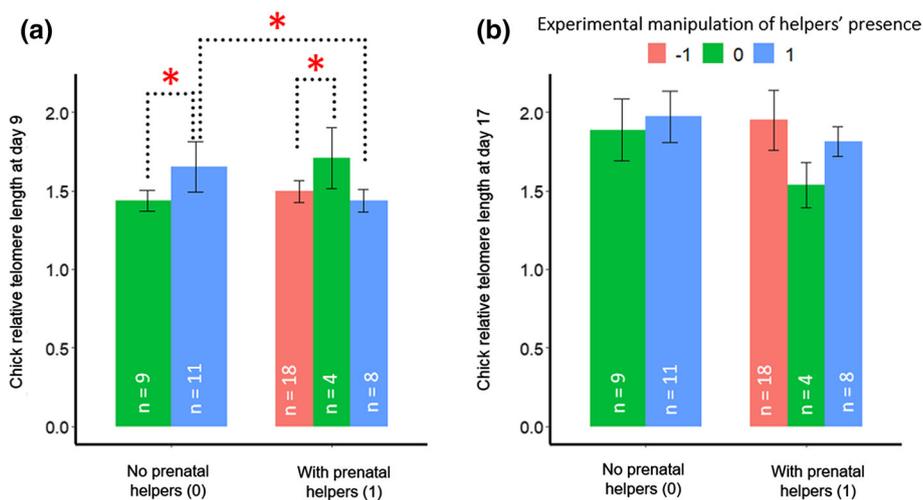


Fig. 1 Relative telomere length (rTL, T/S ratio) 9 days (a) and 17 days (b) after hatching in relation to helpers' presence in sociable weavers. We compared the rTL of 50 cross-fostered individuals according to (i) the presence of helpers before the cross-fostering and (ii) after the cross-fostering. 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

557 postnatal helpers was associated with larger rTL nine days
 558 after hatching (Fig. 1a, 0/1 vs 0/0, post-hoc: 1.54 ± 0.49 ,
 559 $z=3.13$, $P=0.01$). For chicks that had prenatal helpers, a
 560 decrease in the number of helpers was associated with a
 561 shorter rTL (1/-1 vs 1/0, post-hoc: -1.21 ± 0.44 , $z=-2.75$,
 562 $P=0.042$). However, the rTL of chicks swapped from nests
 563 with helpers to nests with more helpers was not affected by
 564 the increase in helper number after hatching (1/+1 vs 1/0
 565 and 1/-1, post-hoc: respectively, -1.23 ± 1.20 , $z=-1.03$,
 566 $P=0.83$ and 1.20 ± 0.51 , $z=2.35$, $P=0.12$). Among the
 567 chicks experiencing additional helpers, those with prenatal
 568 helpers had shorter telomeres on average (0/+1 vs 1/+1,
 569 post-hoc: -1.18 ± 0.44 , $z=-2.73$, $P=0.043$). The effect
 570 of chick sex and brood size were not significant (respec-
 571 tively, -0.43 ± 0.25 and 0.09 ± 0.17). When measured at
 572 D17 post-hatch, neither the prenatal presence or the postna-
 573 tal helper change nor their interaction term were found to be
 574 significantly related to offspring's rTL (Fig. 1b, Table 2b).
 575 **AQ5** The breeding season, while kept in the selected model, had
 576 no significant effect (0.12 ± 0.18).

Effects of helpers on chick body mass and body condition

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

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

Chick telomere length and apparent survival rate

588 We found that sociable weaver chicks with longer rTL at D9
 589 tended to have a higher apparent survival rate the follow-
 590 ing five years although the 95% credible interval overlapped
 591 zero [estimate (95% credible interval) = $0.21 (-0.072, 0.52)$,
 592 $p(\text{estimate} > 0) = 0.928$]

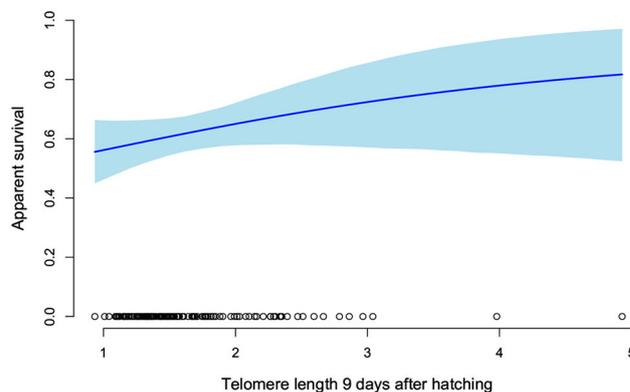


Fig. 2 Relation between relative telomere length (rTL, T/S ratio) 9 days after hatching and apparent survival. 132 birds were annually captured from 2014 to the present (6 years). Estimate and 95% Credibility Interval = $0.21 (-0.07; 0.52)$, $p(\text{estimate} > 0) = 0.928$

593 p (estimate > 0) = 0.928, Fig. 2]. We found no clear asso-
 594 ciation between rTL at D17 and apparent survival [esti-
 595 mate = -0.013 (-0.24, 0.22), p (estimate > 0) = 0.458].

596 Discussion

597 We investigated the influence of the prenatal and postnatal
 598 presence of helpers on rTL and the link between rTL and
 599 survival in nestlings of the sociable weaver, a cooperatively
 600 breeding bird. Early-life rTL (*i.e.* measured nine days after
 601 hatching) was overall positively associated with the presence
 602 of post-natal helpers but was also influenced by an interac-
 603 tion of the presence of pre- and post-natal helpers. Specifi-
 604 cally, we found that for chicks coming from nests without
 605 prenatal helpers, rTL was longer when postnatal helpers
 606 were added after hatching. For the chicks coming from
 607 nests that already had prenatal helpers, telomere length was
 608 shorter when the number of helpers decreased after hatch-
 609 ing. For those chicks, however, an increase in the number of
 610 postnatal helpers had no significant effect on offspring rTL.
 611 The interaction between the prenatal presence and postnatal
 612 helper change showed that the increase in postnatal help-
 613 ers was associated with a greater offspring rTL only when
 614 no prenatal helper was present. The effects observed nine
 615 days after hatching (D9) were not observed at the end of
 616 the nestling period (D17; but see below). Finally, the CMR
 617 analysis conducted to assess the link between early rTL and
 618 post-fledgling survival showed a tendency for rTL at D9 to
 619 be positively related to survival up to five years after hatch-
 620 ing, but this relationship was no longer present at D17.

621 Contrasting effects of pre- and post-natal helpers 622 on offspring's telomeres

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

since the addition of postnatal helpers in nests already har-
 boring prenatal helpers had no significant effect.

We found in addition an interaction between the prenatal
 presence and postnatal helper change indicating that the pos-
 itive 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 pres-
 ence 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 nest-
 lings 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 pre-
 vious 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 inter-
 pretation 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 help-
 ers 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.

694 2015; Mizutani et al. 2016) or food availability (Spurgin
695 et al. 2017) might have blurred possible helper effects at
696 D17. For example, in black-tailed gull chicks (*Larus cras-*
697 *sirostris*), the effect of sibling competition on telomeres was
698 weak on the first day after hatching and became stronger
699 30 days after hatching, potentially concealing the effect of
700 other factors (Mizutani et al. 2016). In European starlings
701 (*Sturnus vulgaris*), the effect of sibling rivalry on telomere
702 attrition was also dependent on nestling age: not detectable
703 at 3 days after hatching (D3), detectable at D12 and faded
704 at D24 (Nettle et al. 2015). In the same study, the effect on
705 oxidative status was detectable at D3 but no longer at D12.
706 Those studies and ours seem to indicate that the effect of
707 different environmental factors might vary with individual
708 age and species.

709 **Body mass growth, telomeres, and survival**

710 The suggestion that offspring's early rTL is a proxy of sur-
711 vival rate has been supported in other species (Geiger et al.
712 2012; Heidinger et al. 2012; Stier et al. 2014; Young et al.
713 2017; Eastwood et al. 2019; Chatelain et al. 2020); but see
714 (Boonekamp et al. 2014) or (Wood and Young 2019) for a
715 critical view on telomere shortening and survival. Although
716 the 95% credible interval slightly overlapped zero, our study
717 tends also to suggest that chick rTL early after hatching
718 might predict post-fledging apparent survival, at least up
719 to 5 years after hatching. In this species, a previous study
720 showed that helpers had a negative effect on offspring sur-
721 vival but only during the first year after fledging, after that,
722 this negative effect disappeared (Covas et al. 2011). Even
723 if in the medium term (five years here) the presence of
724 postnatal helpers seems to be rather positive for offspring
725 apparent survival, the consequences of helpers could be
726 more complex especially in the very first years of life. This
727 adds another level of complexity in understanding the evo-
728 lutionary advantages and disadvantages of social structure
729 involving cooperative breeding.

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

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

species in showing the ability of helpers to compensate for
745 the differential maternal investment in eggs so that, on aver-
746 age, fledglings have the same body condition. Since, in our
747 study, chicks varied in their day 9 rTL but not body con-
748 dition, it seems that for the chicks that do not have help-
749 ers, allocation of energy is toward growth at the expense
750 of their telomeres. Such a trade-off between growth and
751 telomere maintenance has been shown in numerous verte-
752 brate species (Tarry-Adkins et al. 2009; Geiger et al. 2012;
753 Stier et al. 2014; Pauliny et al. 2015; Ringsby et al. 2015;
754 Vedder et al. 2017, 2018). A quicker post-hatching growth
755 ensures a higher success rate at fledging (Kersten and Bren-
756 ninkmeijer 1995; Harris et al. 2008; Canestrari et al. 2011;
757 Looock et al. 2017; Hipfner and Gaston 1999) and an earlier
758 fledging date may decrease predation risk in sociable weav-
759 ers (Ferreira 2015). As a result, there could be a stronger
760 evolutionary pressure on body growth rather than telomere
761 length; in other words, short-term survival by avoiding
762 predation rather than long-term survival through somatic
763 maintenance. Alternatively, resource-investment trade-offs
764 may be reflected not in body condition or mass, but in tissue
765 maturation rate, which could be reflected in shorter telom-
766 eres (Crisuolo et al. 2019).
767

768 **Conclusions**

769 Here, we set to investigate the effect of the social environ-
770 ment (presence of helpers) before and after hatching on off-
771 spring rTL. Our results suggest an overall positive effect
772 of postnatal helpers on the offspring rTL early in life, but
773 our study did not provide evidence that this relationship is
774 conserved until fledging. Furthermore, the positive postnatal
775 effect of helper presence was dependent on prenatal condi-
776 tions, being stronger in nests that did not have pre-natal
777 helpers. Thus, the presence of helpers may induce opposite
778 effects depending on whether helpers are present before or
779 after hatching and that the interaction between the prenatal
780 and postnatal environment is essential to understand the con-
781 sequences of the social environment on offspring. In addition
782 to the social environment, the ecological context (*e.g.*, tem-
783 perature, food availability) may also affect rTL, both before
784 and after hatching, but this was not investigated here. This
785 calls for data over longer periods spanning different climatic
786 conditions, to decipher the interaction between social and
787 ecological environment. According to our results, the chicks
788 with the shortest telomeres in their early life might also be
789 less likely to survive the first years of life. Although other
790 factors influence rTL, such as genetics or the quality of care
791 provided, our study suggests that social context, has a poten-
792 tial important role to play in influencing individual develop-
793 ment and survival in cooperatively breeding birds. However,
794 the mechanisms that sustain these pre- and post-natal social
795 effects on rTL remain to be identified and further studies

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

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809 study. CD, FT, MP and RC collected the data in the field. CD, FT,
810 MP, MQ and RC organized the database. MQ performed the statistical
811 analysis, MP the survival analysis and SZ the laboratory analyses. MQ
812 wrote the first draft of the manuscript. CD, CS, FC, MP, RC and SZ
813 wrote sections of the manuscript. All authors contributed to manuscript
814 revision, read and approved the submitted version.

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824 Declarations

825 **Conflict of interest** The authors declare that the research was con-
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