**Parental telomere length predicts offspring sex ratio in the Seychelles warbler**

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**Abstract**

A major puzzle in evolutionary biology is when and why mothers should modify the sex of their offspring to maximise their own fitness. Theory suggests that mothers should bias sex ratios towards the sex with the highest fitness gains when in good condition; however, empirical support for this hypothesis is equivocal. This is likely due to i) a lack of the detailed life-history data that is required to predict whether and in what direction sex ratio bias should occur, and ii) a lack of a robust measure of parental condition. Cooperatively breeding Seychelles warblers (*Acrocephalus sechellensis*) adaptively modify the sex of their offspring, producing an excess of females in good conditions to maximise the direct and inclusive fitness benefits of having related helpers in their territories. Here we show that sex ratio modification in the Seychelles warbler is mediated by parental telomere length. Telomeres are protective caps on the ends of chromosomes that shorten in response to stress, and are excellent biomarkers of individual condition. Mothers and fathers with long telomeres produced 77% daughters, while parents with short telomeres produced 67% sons. Furthermore, we found a positive association between parental and offspring telomere length, suggesting that condition is passed on from parents to offspring. Finally, we found that longer telomeres in juvenile females, but not males, was strongly associated with increased survival. This suggests that female offspring are disproportionately affected by parental investment, and that parents produce female offspring when in good condition to maximise their own fitness.

**Introduction**

In many organisms females produce offspring with skewed sex ratios, despite the fact natural selection operates against deviations from unity in a frequncy-dependent manner (Fisher 1930). In a seminal paper, Trivers and Willard proposed that when maternal condition affects offspring fitness, and when fitness of males is affected more than females, mothers in good condition should produce more sons in order to maximise their own fitness (Trivers and Willard 1973). More recent theoretical work has shown that natural selection may favour either sons or daughters, depending on the quality of the rearing environment (Charnov et al. 1981), paternal attractiveness (Burley 1981), and depending on the life-history and sex-specific demography of the populaiton being studied (Leimar 1996; Schindler et al. 2015).

Given that theory predicts a range of relationships between parental condition and offspring sex ratio, it is perhaps not surprising that results from empirical studies in natural populations have been highly varied (reviewed in West 2009; Booksmythe et al. 2015). When in good condition or a high quality environment, mothers can produce an excess of sons (e.g. Ellegren et al. 1996; Nager and Monaghan 1999; Pryke and Griffith 2009), an excess of daughters (e.g. Komdeur et al. 1997; Hewison et al. 2005), or neither (e.g. Brown and Silk 2002; Postma et al. 2011; MacLeod and Clutton-Brock 2013). However, it has proved difficult to tell whether the patterns observed in natural populations match theoretical expectations (Komdeur and Pen 2002; Abe et al. 2014). A major reason for this is that in many species the life-history data required to generate predictions about sex allocation are lacking. In such cases it is very difficult to tell whether observed relationships (or lack thereof) are consistent with evolutionarily plausible scenarios, or whether they reflect type I and II error (Leimar 1996; Schindler et al. 2015).

A second problem with sex allocation studies is that of measuring parental condition. The majority of studies of parental condition and offspring sex ratio have used a measure of body condition based on body fat (e.g. Whittingham and Dunn 2000; Hewison et al. 2005), or a measure of social rank (e.g. Clutton-Brock et al. 1984; MacLeod and Clutton-Brock 2013). However, morphological measures of condition may be related to resource availability in variety of ways, making them a poor measure of condition (discussed in Sheldon and West 2004). Social rank appears to be a better measure of resource availability (Sheldon and West 2004), but its efficacy as a measure of condition is will to vary among species according to social structure, and in many cases (i.e. in species with no obvious distinctions between dominant and subordinate individuals) is unmeasurable. Thus a robust, widely applicable measure of condition is needed to understand sex allocation, but such a measure is currently lacking.

Telomeres are being increasingly recognised as excellent biomarkers of individual condition, reflecting acccumulating costs experienced over an individuals' lifetime (Monaghan and Haussmann 2006; Asghar et al. 2015). These protective caps on the ends of chromosomes shorten with age, and in response to oxidative stress caused by poor environmental and/or social conditions (Von Zglinicki 2002; Epel et al. 2004). Telomere shortening is also directly involved in cellular senescence and cell death, and telomere length and dynamics have been linked to survival and lifespan in a number of species (Cawthon et al. 2003; Heidinger et al. 2012; Barrett et al. 2013).Telomeres therefore present an ideal biomarker to test the hypothesis that parental condition is linked to offpsring sex ratio. However, to our knowledge no studies have looked at parental telomere length in relation to offspring sex ratio.

In this study we use telomeres to test the hypothesis that parental condition is related to offspring sex ratio in the Seychelles warbler(*Acrocephalus sechellensis*). This species constitutes a textbook example of adaptive sex ratio modification (Komdeur et al. 1997; Frank 1998). The Seychelles warbler is a facultative cooperative breeder; in good environmental conditions, daughters often remain on their natal territory to help rear their siblings (Komdeur 1996). Females on high quality territories produce an excess of daughters in order to retain co-breeders and maximise inclusive fitness (Komdeur 1996; Komdeur et al. 1997). Follow up work has shown that there are both direct and indirect fitness benefits of producing daughters on high quality territories (Komdeur 1998; Richardson et al. 2002), suggesting that this is an adaptive trait. However, until now we have never tested whether adaptive sex ratio allocation in the Seychelles warbler is mediated by maternal or paternal condition.

We first test the hypothesis that parents with longer telomeres produce more females. We then then test the hypothesis that parental condition is passed onto offspring by testing for a positive relationship between telomere length in parents and offspring. Finally, we analyse sex-specificrelationships between telomere length and offspring survival to test the hypothesis that survival of daughters, but not sons, is condition dependent. We discuss our results in the context of realised direct and inclusive fitness benefits to parents.

**Methods**

##### Study species and sampling

We utilised a long-term study of Seychelles warblers on Cousin Island, which has been monitored since 1986, intensively so since 1997 (Richardson et al. 2003; Spurgin et al. 2014). Individuals are usually ringed at less than one year old, and then followed throughout their lives. As they do not disperse to or from Cousin (Komdeur et al. 2004), a biannual census of birds on Cousin during each breeding season gives accurate measures of social status, age and survival (Crommenacker et al. 2011; Barrett et al. 2013). Seychelles warblers are highly territorial and all territories are mapped during the breeding seasons using detailed observational data of foraging and territorial defence behaviour, and surveyed for territory quality (Komdeur 1992; Richardson et al. 2003). Full details of catching and monitoring methods can be found in Brouwer *et al.* (2012).

Each time a bird is caught on Cousin body mass and tarsus length are measured (to the nearest 0.1g and 0.1mm, respectively), and age is confirmed on the basis of eye colour (Komdeur 1991) and previous captures (Richardson et al. 2003). A blood sample (*ca* 25 l) is taken via brachial venipuncture, and stored in 1 ml of absolute ethanol in a 1.5 ml screw-cap microfuge tube, at room temperature.

##### Molecular methods and parentage

For each sample, genomic DNA was extracted from a ~2 mm2 flake of preserved blood using the DNeasy Blood and Tissue Kit (Qiagen), following the manufacturer's protocol, with the modification of overnight lysis at 37oC and a final DNA elution volume of 80 l. DNA concentration and purity were quantified using a NanoDrop 8000 Spectrophotometer (ThermoScientific), and DNA integrity was validated by visualization with ethidium bromide after electrophoresis on a 1.2% agarose gel. Sex was determined using the molecular method outlined by Griffiths *et al.* (1998).

All samples were genotyped at 30 polymorphic microsatellite loci arranged into four multiplex reactions (see Spurgin et al. 2014 for details). Using these data, parentage was assigned using MasterBayes (HANNAH TO DO).

Telomeres were measured from a total of 1386 samples, using a qPCR method with absolute standards (full details provided in Barrett et al. 2012). Of these, 209 were from juvenile birds between 1 and 12 months old for which we had telomere length measurements available from at least one parent. We excluded nestlings less than one month old from this analysis as telomere length at this stage is expected to feflect inheritance, whereas telomere length in fledgling birds is expected to reflect early life experiences.Because adult birds are not caught every year, we did not have samples available from parents at the year each juvenile was born. As an overall measure of parental condition, therefore, we calculated an average telomere length for each parent by calculating the mean of all telomere measurements for each adult sample.

*Statistical analyses*

All statistical analyses were carried out using R version 3.2.2 (R Development Core Team 2011). Mixed models were carried out using the lme4 package [Pinheiro2012].

We first calulated sex ratio variation over our 16 year dataset using all available catch data from Cousin. All juveniles caught in their first year of life sexed and sex ratio was calulated separately for each year. We calculated 95% confidence limits for each year using a bootstrapping approach; 1000 populations of males and females were simulated for each year based on observed sample sizes and a 50% chance each offpring being female, and from this 5% and 95% quantiles were extracted.

We used generalized linear mixed effects models (GLMMs) with a binomial error structure to test how parental TL is related to offspring sex ratio. Offspring sex was included as a binary response variable, and territory quality and the number of helpers were included as covariates, as both of these variables have been previously demonstrated to predict offspring sex ratio (Komdeur et al. 1997). We also included parental age as a covariate to control for potential confounding effects of senescence on offspring sex ratio. As our dataset spanned many years, and contained multiple juveniles from the same parents, we included birth year, maternal ID and paternal ID as random factors.

We used linear mixed effects models (LMMs) to test for a relationship between parental and offspring telomere length. Juvenile telomere was entered as the response variable, age class as a fixed factor, and as covariates we included maternal and paternal TL, maternal and paternal age, territory quality and the number of helpers present in the natal territory. Random effects were specified as with the GLMMs, above.

Finally, we used GLMMs to test whether parental telomere length was related to survival to adulthood. Survial to adulthood (yes/no) was included as the response variable, and offspring telomere length and offspring sex were included as covariates. Random effects were specified as above.

**Results**

Overall, sex ratio in our Seychelles warbler dataset did not differ from 50:50 (49% of all juveniles were male; binomial test, P = 0.94). There was variation in sex ratio among years (Fig. 1); of the 17 years we observed an excess of males in two years, and an excess of females in one year.

Maternal and paternal telomere length were positively, but non-signficantly, related (Pearson correlation, estimate = 0.18; CIs, = -0.03, 0.37; Fig. 1A). Therefore while it is possible that offspring with high quality mothers also had high quality fathers, this relationship is very weak. Generalised linear mixed models controlling for maternal age (Table S1) showed that offspring sex ratio was significantly related to maternal telomere length (estimate = -0.62, CIs = -1.09, -0.16; Fig. 1B). There was also a tendency for fathers with longer telomeres to have more female offspring, although this was not significant (estimate = -1.17, CIs = -2.78, 0.43; Fig. 1C). Interestingly, we found that the average telomere length of both mother and father had the strongest effect on offspring sex ratio (estimate = -0.65, CIs = -1.04, -0.25; Fig. 1D). Pairs with short telomeres (<4kb) produced on average 67% males, while pairs with long telomeres (>6kb) produced 77% females. We found no effect of territory quality or the number of helpers on offspring sex ratio (Table S1).

We then tested whether parental condition was passed on to offspring by testing for relationships between parental and offspring telomere length (Table S2). Offspring telomere length not related to maternal telomere length (estimate = 0.14, CIs = -0.20, 0.48; Fig. 3A), but was positively related to paternal telomere length (estimate = 0.48, CIs = 0.08, 0.88; Fig. 3B). Again, however, the strongest relationship was found with mean parental telomere length (estimate = 0.77, CIs = 0.21, 1.33; Fig. 3C). The relationship between parental and offpring telomere length was stronger for females (Fig. 3C; R2 from linear regression = 0.13) than for males (R2 < 0.01); however, the interaction between parental telomere length and sex was not significant (estimate = -0.67, CIs = -1.62, 0.28; Fig. 3C).

Finally, we tested how juvenile telomere length in each was related to survival (Table S3). In a model not including telomere length, we found no difference between sexes in probability of survival to adulthood (est = 0.58; CI = -0.31, 1.47). However, when telomere length was included in the model we found that survival was significantly higher in males (est = 3.81; CI = 1.43, 6.19), and positively related to telomere length (est = 0.52; CI = 0.11, 0.93). Importantly, there was a significant interaction effect between sex and telomere length on survival (est = -0.75; CI = -1.26, -0.23). Telomere length in female juveniles was positively related to juvenile survival, while no such relationship was observed in males (Fig. 3D).

**Discussion**

Komder *et al.* (1997) found that Seychelles warblers modify the sex ratio of their offspring according to their territory quality. Because females are more likely to remain on the natal territory and help in good environmental condtions, producing females in good conditions is an adaptive strategy. Here, using telomeres as biomarkers of individual condition, we show that this result is likely to be mediated by parental condition. Parents with longer telomeres produce more females and have offspring with longer telomeres. Additionally, we found that female, but not male, survival to adulthood is dependent on telomere length.

Our results suggest that parental condition, rather than environmental conditions *per se.*, is behind adaptive sex ratio modification in the Seychelles warbler. Using a much larger temporal dataset, we were unable to replicate the finding that pairs in high quality territories produced an excess of females [Komdeur et al. (1997); Tables S1-S3]. At the time Komdeur *et al.* carried out their original study, average conditions on Cousin Island were poor, and highly variable across territories. Since then, thanks to conservation efforts, overall conditions have improved dramatically, and variance in territory quality has decreased (Komdeur and Pels 2005). Thus, it appears that territory quality is no longer the main driver of adult condition in Seychelles warblers.

Parental condition is ultimately driven by variation in the social and ecological environment. However, in many instances this can be very difficult to capture as it is impossible to assess the costs of different experiences. A major advantage of studying telomeres in natural populations is that no matter how multifaceted and complex an individual's social and ecological environment, this can be reduced down to a single measure of individual condition. Telomeres are therefore likely to prove much more informative for understanding the relationship between parental condition and offspring sex ratios than measures of condition based on morphometrics or social rank, as they directly reflect the ecological stress experienced by individuals (Monaghan and Haussmann 2006; Asghar et al. 2015). In our study, when we replaced parental telomere length with a measure of body condition based on body mass controlled for tarsus length (Schulte-Hostedde et al. 2005), we found that while relationships between parental condition and sex ratio were in the predicted direction, they were weak and not significant (Table S4; Fig. S1). The difficulty of measuring parental condtion is a key factor affecting variation in results of sex allocation studies (Sheldon and West 2004), and telomeres offer considerable promise for addressing this issue.

Teasing apart maternal and paternal effects on sex allocation is a difficult task (see Booksmythe et al. 2015 for a recent discussion), not least because maternal and paternal condition may correlated. Although we detected only a very weak relationship between maternal and paternal condition in Seychelles warblers, averaging maternal and paternal telomere lengths was a better predictor of both sex ratio and offspring telomere length than maternal or paternal telomere length alone. This suggests that offspring condition, and thus sex allocation, is the product of combined maternal and paternal effects. This is in accordance with previous research in this species, which has shown that offspring fitness is affected by both maternal inbreeding (Richardson et al. 2004; Brouwer et al. 2007), and the genetic quality of males chosen by mothers (Richardson2005; Brouwer et al. 2010). We suspect that combined maternal and paternal effects on sex allocation are common, although few studies have investigated this.

Finally, we found an interaction between sex and juvenile telomere length on survival to adulthood. We previously thought that Seychelles warblers on low quality territories prodiced an excess of males predominantly because females are less likely to stay and help in poor conditions, negating the fitness benefits gained from producing an excess of daughters (Komdeur et al. 1997; Komdeur 1998). Here we show that in addition to this, females are less likely to survive to adulthood when in poor condition. Hence the fitness gains for producing males when in poor condition are greater than previously thought. In general, a greater sensitivity of females to variation in condition is surprising as most studies find that males are more sensitive to envieonmental variation (Jones et al. 2009). Interestingly, however, recent research in birds has shown that prenatal and postnatal variation in food availability has disproportionate effects on female offspring due to increased oxidative damagae (Giordano et al. 2015). Future research on the relationship between telomeres, provisioning and sex ratios will provide insights into the mechanistic basis of sex allocation.

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**Author contributions** LGS and DSR developed the ideas for this paper, and DSR initiated telomere research in this species. DSR, HLD, JK and TB managed the overall Seychelles warbler project. EAF, KLB and LGS carried out the sample preparation and lab work. HLD conducted the parentage analyses. LGS conducted the remaining analyses and drafted the manuscript, with input from DSR. All authors contributed to the final manuscript.

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