**Adaptive sex ratio allocation is linked to maternal TL in the Seychelles warbler**

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**Abstract**

**Introduction**

The Seychelles warbler (*Acrocephalus sechellensis*) constitutes a textbook example of adaptive sex ratio modification (**???**; Komdeur 1996). 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 *et al.* (**???**) showed that

In this study we combine telomere data with the long-term Seychelles warbler data set to test the hypothesis parental condition is related to offspring sex ratio. Specifically, we test the hypothesis that mothers and fathers with longer telomerers produce more females.

**Methods**

*Study species and sampling*

*Molecular methods*

*Statistical analyses* We used linear mixed effects models (LMMs) to test for a relationship between parental and juvenile TL. Juvenile TL was entered as the response variable, age class as a fixed factor, and as covariates we included maternal and paternal TL, seasonal food availability, territory quality and the number of helpers present in the natal territory. As our dataset spanned many breeding seasons, and contained multiple juveniles from the same parents, we included an index of the breeding season, maternal ID and paternal ID as random factors. In order to differentiate between parental quality and parental condition, we partitioned parental TL into 'juvenile parental TL' and 'adult parental TL'. Juvenile TL is related to later-life survival, and is thus a biomarker of individual quality, whereas adult TL is expected to reflect the stresses encountered over their adult life, and is thus a marker of condition. Because juvenile and adult parental TL are correlated, we ran separate models for these two variables, keep all other variables the same.

We then separately tested whether parental age was related to offspring TL, again using LMMs. These were constructed as above, but with parental age and parental lifespan added as covriates in place of parental (adult and juvenile) TL. We chose to run these models separately from the models including parental TL due to collinearity issues between TL and age (Barrett et al. 2012). We compared models containing parental TL to those containing parental age using AICc values.

Finally, we used generalized linear mixed effects models (GLMMs) with a binomial error structure to test how parental TL is related to offspring sex ratio. These models were constructed exactly as the LMMs above, but with offspring sex as the response variable.

**Results**

Seychelles warbler juvenile TL was not related to maternal juvenile TL (estimate = 303.07, CIs = -1968.03, 2574.16; Fig. 1A), but was positively related to maternal adult TL (estimate = 1912.57, CIs = 168.11, 3657.04; Fig. 1B). Conversely, juvenile TL was positively related to paternal juvenile TL (estimate = 1637.53, CIs = 195.94, 3079.13; Fig. 1C), but was not related to paternal adult TL (estimate = 241.54, CIs = -1609.71, 2092.79; Fig. 1D). Juvenile TL was not related to maternal age (estimate = 238.22, CIs = -1111.69, 1588.13; Fig. 2A), but was positvely associated with maternal lifespan (estimate = 1975.02, CIs = 401.60, 3548.45; Fig. 2B). Finally, juvenile TL was not associated with paternal age (estimate = 750.06, CIs = -724.76, 2224.88; Fig. 2C) or paternal lifespan (estimate = 863.47, CIs = -714.40, 2441.34; Fig. 2D).

Offspring sex ratio was not related to maternal juvenile TL (estimate = 0.80, CIs = -1.28, 2.89; Fig. 3A), but longer maternal adult TL was significantly related to offspring sex ratio (estimate = -1.31, CIs = -2.62, 0.01); mothers with longer telomeres as adults had more females offspring compared to mothers with shorter telomeres (Fig. 3B). A similar result was found for patenral TL: offspring sex ratio was not related to paternal juvunile TL (estimate = -0.94, CIs = -2.69, 0.81; Fig. 3C), but fathers with longer telomeres as adults had significantly more females (estimate = -1.51, CIs = -2.85, -0.17; Fig. 3D).

Offspring sex ratio was not related to either maternal age (estimate = 0.03, CIs = -1.02, 1.07; Fig. 4A) or maternal lifespan (estimate = -0.02, CIs = -1.23, 1.19; Fig. 4B). However, older fathers had significantly more female offspring (estimate = -1.34, CIs = -2.64, -0.05; Fig. 4C). There was no relationship between paternal lifespan and offspring sex ratio (estimate = -0.07, CIs = -1.24, 1.10; Fig. 4D).

To tease apart whether parental age or telomere effects were most importand driving offspring telomere length, we used an information theoretic approach. The best model with offspring telomere length as the response variable was the one containing parental adult telomere lengths as predictors (AICc = 1164.15), which was a better fit than the model containing parental age (AICc = 1214.80) and parental lifespan (AICc = 1207.55). The same result was found when offspring sex raito was the response variable: the model with parental telomere length as predictors had a lower AICc (98.16) than models containing parental age (AICc = 110.65) or parental lifespan (AICc = 115.81).

**Discussion**

Barrett, E. L. B., W. Boner, E. Mulder, P. Monaghan, S. Verhulst, and D. S. Richardson. 2012. Absolute standards as a useful addition to the avian quantitative PCR telomere assay. Journal of Avian Biology 43:571–576.

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