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

Lewis G. Spurgin1,2, Hannah, L. Dugdale3,4, Kat Bebbington1, Eleanor A. Fairfield1, Jan Komdeur3, Terry Burke4 and David S. Richardson1,5,.

1. School of Biological Sciences, University of East Anglia, Norwich Research Park, NR4 7TJ, United Kingdom
2. Department of Zoology, Edward Grey Institute, University of Oxford, Oxford, UK
3. Groningen Institute for Evolutionary Life Sciences, University of Groningen, Groningen, The Netherlands
4. Department of Animal and Plant Sciences, University of Sheffield, Sheffield, UK
5. Nature Seychelles, Roche Caiman, Mahé, Republic of Seychelles

**Correspondence**: Lewis Spurgin - [lewisspurgin@gmail.com](mailto:lewisspurgin@gmail.com); David Richardson - [david.richardson@uea.ac.uk](mailto:david.richardson@uea.ac.uk)

**Key words**: Life-history, Sex allocation, sex ratio, Telomeres, Trivers-Willard hypothesis

**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 that provide them 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 to adulthood. This suggests that female offspring are disproportionately affected by variation in parental condition, and that mothers produce female offspring when they and their mates are in good condition, in order 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 frequency-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 sex ratio bias towards an excess of 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 population being studied (Leimar 1996; Schindler et al. 2015).

Given that theoretical work predicts that a range of relationships between parental condition and offspring sex ratio can occur, it is unsurprising that results from empirical studies of sex ratios have been highly varied (reviewed in West 2009; Booksmythe et al. 2015). When in good condition or in 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 concerns 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 will vary among populations and 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 increasingly recognised as excellent biomarkers of individual condition, reflecting accumulating costs experienced over individual lifetimes (Monaghan and Haussmann 2006; Asghar et al. 2015). Telomeres are protective caps on the ends of chromosomes that 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 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 (Frank 1998; Davies et al. 2012). 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 (Komdeur 1996; Komdeur et al. 1997), and 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 a direct response to territory quality, or instead whether it is mediated by maternal or paternal condition.

We study parental condition and sex ratio over 16 years on an isolated island population. First, we test the hypothesis that parents with longer telomeres produce more females. We then then test whether parental condition is passed onto offspring, by testing for a positive relationship between telomere length in parents and offspring. Finally, we analyse sex-specific relationships between telomere length and offspring survival to test the hypothesis that survival of daughters, but not sons, is condition-dependent.

**Methods**

##### Study species and sampling

We utilised a long-term study of Seychelles warblers on Cousin Island, which has been studied since 1986, and intensively monitored 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 birds do not disperse to or from Cousin (Komdeur et al. 2004), a biannual census on the island 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 each breeding season and territory quality is calculated based on territory size and food availability (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 DNeasy Blood and Tissue Kits (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 aged 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 analyses involving offspring telomere length, as telomerel ength very early in life is expected to reflect inheritence whereas telomere length in fledgling birds is expected to incorporate the effects of 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 calculated juvenile sex ratio variation over time in our 16 year dataset using all available catch data from Cousin (N = 2546). Sex ratio was calculated separately for each year, using all juveniles born and caught in that 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 probability each offspring being female of P = 0.5, giving us a null distribution of sex ratios for each year. From this 5%, and 95% quantiles were extracted for comparison against observed values.

We used generalized linear mixed effects models (GLMMs) with a binomial error structure to test how parental telomere length 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. Because for many juveniles we only had telomere length measurements for one parent, we ran separate models for maternal and paternal telomere length. We also ran a third model, including the mean telomere length of both parents as an explanatory variable. 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 in all models.

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

Finally, we used GLMMs to test whether parental telomere length was related to survival to adulthood. Survival to adulthood (yes/no) was included as the response variable, and offspring telomere length, offspring sex and a sex x telomere length interactions were included as explanatory variables. 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-significantly, 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 offspring 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**

Komdeur *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 conditions, producing females in good conditions is an adaptive strategy. Here we apply this analysis to a 16 year dataset, and use telomeres as biomarkers of individual condition to test the long-standing hypothesis that parents adjust the sex of their offspring according to their condition (Trivers and Willard 1973). We find that sex ratio varies over time, but that this is mostly within the expeced range of fluctations given the population and sample sizes on Cousin. However, we show very clearly that mothers and fathers 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.

An unanswered question in the study of sex ratios is whether mothers adjust offspring sex in response to their own condition, or directly in response to the environment (Pryke and Rollins 2012). Our results suggest that sex allocation is mediated predominantly by parental condition. We found no evidence that the result of Komdeur *et al.* (1997), showing that Seychelles warblers in high quality territories produced an excess of females [Tables S1-S3], has persisted over time. 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). In accordance with this, we found a stronger relationship between maternal telomere length and territory quality in early years (R2 = 0.11, estimate = 3.04,CIs = -0.49, 6.57), compared to the entire dataset (linear regression, R2 = < 0.01, estimate = 0.43,CIs = -0.40, 1.25; Table S1), although neither were significant. That parental telomere length, and not territory quality, predicts offspring telomere length is also instructive in this respect.

Parental condition is ultimately driven by a combination of variation in genes, and 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 the many different experiences an individual faces. A major advantage of studying telomeres in natural populations is that no matter how multifaceted and complex social and ecological environment, the effects of 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. S2). The difficulty of measuring parental condition 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 often be correlated. We found that 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, despite that fact that maternal and paternal telomere length were only very weakly related. 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 the Seychelles warbler, 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). Whether the parental effects in this study reflect genetic effects, or instead reflect a relationship between parental condition and the quality of parental care, is not yet clear. Regardless, we suspect that combined maternal and paternal effects on sex allocation are common [e.g. Pryke2009], and will become more apparent as more long-term studies combine parentage and telomere data to test hypotheses relating to sex allocation.

Previous research suggested that Seychelles warblers on low quality territories produced an excess of males 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 environmental 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 damage (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.

**Acknowledgements**

We thank Nature Seychelles for facilitating the long-term Seychelles warbler project. The Seychelles Bureau of Standards and Department of Environment gave permission for sampling and fieldwork. We thank Emma Barrett for her work on this project, everyone who has helped in the field, and the current Seychelles warbler research group for useful discussions. This work was funded by two Natural Environment Research Council (NERC) grants to DSR (NE/F02083X/1 and NE/K005502/1). LGS is supported by an Edward Grey Institute fellowship, and HLD was funded by a NERC fellowship.

**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.

**References**

Abe, J., Y. Kamimura, and S. a. West. 2014. Inexplicably female-biased sex ratios in melittobia wasps. Evolution 2709–2717.

Asghar, M., D. Hasselquist, B. Hansson, P. Zehtindjiev, H. Westerdahl, and S. Bensch. 2015. Hidden costs of infection: Chronic malaria accelerates telomere degradation and senescence in wild birds. Science 347:436–438.

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.

Barrett, E. L. B., T. Burke, M. Hammers, J. Komdeur, and D. S. Richardson. 2013. Telomere length and dynamics predict mortality in a wild longitudinal study. Molecular Ecology 22:249–259.

Booksmythe, I., B. Mautz, J. Davis, S. Nakagawa, and M. D. Jennions. 2015. Facultative adjustment of the offspring sex ratio and male attractiveness: a systematic review and meta-analysis. Biological Reviews, doi: [10.1111/brv.12220](http://dx.doi.org/10.1111/brv.12220).

Brouwer, L., I. Barr, M. van de Pol, T. Burke, J. Komdeur, and D. S. Richardson. 2010. MHC-dependent survival in a wild population: evidence for hidden genetic benefits gained through extra-pair fertilizations. Molecular Ecology 19:3444–3455.

Brouwer, L., J. Komdeur, and D. S. Richardson. 2007. Heterozygosity-fitness correlations in a bottlenecked island species: A case study on the Seychelles warbler. Molecular Ecology 16:3134–3144.

Brouwer, L., D. Richardson, and J. Komdeur. 2012. Helpers at the nest improve late-life offspring performance: evidence from a long-term study and a cross-foster experiment. PLoS ONE 7:e33167.

Brown, G. R., and J. B. Silk. 2002. Reconsidering the null hypothesis: Is maternal rank associated with birth sex ratios in primate groups? Proceedings of the National Academy of Sciences of the United States of America 99:11252–11255.

Burley, N. 1981. Sex Ratio manipulation and selection for attractiveness. Science 211:722–725.

Cawthon, R. M., K. R. Smith, E. O’Brien, A. Sivatchenko, and R. A. Kerber. 2003. Association between telomere length in blood and mortality in people aged 60 years or older. Lancet 361:393–395.

Charnov, E. L., R. L. Los-den Hartogh, W. T. Jones, and J. van den Assem. 1981. Sex ratio evolution in a variable environment. Nature 289:27–33.

Clutton-Brock, T. H., S. D. Albon, and F. E. Guinness. 1984. Maternal dominance, breeding success and birth sex ratios in red deer. Nature 308:358–360.

Crommenacker, J. van de, J. Komdeur, and D. S. Richardson. 2011. Assessing the cost of helping: the roles of body condition and oxidative balance in the Seychelles warbler (Acrocephalus sechellensis).

Davies, N. B., J. R. Krebs, and S. West. 2012. An Introduction to Behavioural Ecology. 3rd ed. WIley-Blackwell, Chichester.

Ellegren, H., L. Gustafsson, and B. C. Sheldon. 1996. Sex ratio adjustment in relation to paternal attractiveness in a wild bird population. Proceedings of the National Academy of Sciences of the United States of America 93:11723–11728.

Epel, E. S., E. H. Blackburn, J. Lin, F. S. Dhabhar, N. E. Adler, J. D. Morrow, and R. M. Cawthon. 2004. Accelerated telomere shortening in response to life stress. Proceedings of the National Academy of Sciences of the United States of America 101:17312–17315.

Fisher, R. A. 1930. The Genetical Thoery of Natural Selection. Oxford University Press.

Frank, S. 1998. Foundations of social evolution. Princeton University Press.

Giordano, M., D. Costantini, and B. Tschirren. 2015. Sex-specific effects of prenatal and postnatal nutritional conditions on the oxidative status of great tit nestlings. Oecologia 177:123–31.

Griffiths, R., M. C. Double, K. Orr, and R. J. Dawson. 1998. A DNA test to sex most birds. Molecular Ecology 7:1071–5.

Heidinger, B. J., J. D. Blount, W. Boner, K. Griffiths, N. B. Metcalfe, and P. Monaghan. 2012. Telomere length in early life predicts lifespan. Proceedings of the National Academy of Sciences of the United States of America 109:1743–8.

Hewison, J. M., J. M. Gaillard, P. Kjellander, C. Toïgo, O. Liberg, and D. Delorme. 2005. Big mothers invest more in daughters - Reversed sex allocation in a weakly polygynous mammal. Ecology Letters 8:430–437.

Jones, K. S., S. Nakagawa, and B. C. Sheldon. 2009. Environmental Sensitivity in Relation to Size and Sex in Birds: Meta-Regression Analysis. American Naturalist 174:122–133.

Komdeur, J. 1991. Cooperative breeding in the Seychelles warbler. PhD Thesis, Cambridge University.

Komdeur, J. 1996. Facultative Sex Ratio Bias in the Offspring of Seychelles Warblers.

Komdeur, J. 1992. Importance of habitat saturation and territory quality for evolution of cooperative breeding in the Seychelles warbler. Nature 358:493–495.

Komdeur, J. 1998. Long-term fitness benefits of egg sex modification by the Seychelles warbler. Ecology Letters 1:56–62.

Komdeur, J., and M. D. Pels. 2005. Rescue of the Seychelles warbler on Cousin Island, Seychelles: The role of habitat restoration. Biological Conservation 124:15–26.

Komdeur, J., and I. Pen. 2002. Adaptive sex allocation in birds: the complexities of linking theory and practice. Philosophical transactions of the Royal Society of London. Series B, Biological sciences 357:373–380.

Komdeur, J., S. Daan, J. Tinbergen, and C. Mateman. 1997. Extreme adaptive modification in sex ratio of the Seychelles warbler’s eggs. Nature 385:522–525.

Komdeur, J., T. Piersma, K. Kraaijeveld, F. Kraaijeveld-Smit, and D. S. Richardson. 2004. Why Seychelles warblers fail to recolonize nearby islands: unwilling or unable to fly there? Ibis 146:298–302.

Leimar, O. 1996. Life-history analysis of the Trivers and Willard sex-ratio problem. Behavioral Ecology 7:316–325.

MacLeod, K. J., and T. H. Clutton-Brock. 2013. No evidence for adaptive sex ratio variation in the cooperatively breeding meerkat, Suricata suricatta. Animal Behaviour 85:645–653.

Monaghan, P., and M. F. Haussmann. 2006. Do telomere dynamics link lifestyle and lifespan? Trends in Ecology and Evolution 21:47–53.

Nager, R., and P. Monaghan. 1999. Experimental demonstration that offspring sex ratio varies with maternal condition. Proceedings of the ….

Postma, E., F. Heinrich, U. Koller, R. J. Sardell, J. M. Reid, P. Arcese, and L. F. Keller. 2011. Disentangling the effect of genes, the environment and chance on sex ratio variation in a wild bird population. Proceedings. Biological sciences / The Royal Society 278:2996–3002.

Pryke, S. R., and S. C. Griffith. 2009. Genetic incompatibility drives sex allocation and maternal investment in a polymorphic finch. Science 323:1605–1607.

Pryke, S. R., and L. a. Rollins. 2012. Mothers adjust offspring sex to match the quality of the rearing environment. Proceedings of the Royal Society B: Biological Sciences 279:4051–4057.

R Development Core Team. 2011. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing; R Foundation for Statistical Computing.

Richardson, D. S., T. Burke, and J. Komdeur. 2002. Direct benefits and the evolution of female-biased cooperative breeding in Seychelles warblers. Evolution 56:2313–2321.

Richardson, D. S., T. Burke, and J. Komdeur. 2003. Sex-specific associative learning cues and inclusive fitness benefits in the Seychelles warbler. Journal of Evolutionary Biology 16:854–861.

Richardson, D. S., J. Komdeur, and T. Burke. 2004. Inbreeding in the Seychelles warbler: environment-dependent maternal effects. Evolution 58:2037–2048.

Schindler, S., J.-M. Gaillard, A. Grüning, P. Neuhaus, L. W. Traill, S. Tuljapurkar, and T. Coulson. 2015. Sex-specific demography and generalization of the Trivers-Willard theory. Nature 526:249–252. Nature Publishing Group, a division of Macmillan Publishers Limited. All Rights Reserved.

Schulte-Hostedde, A. I., B. Zinner, J. S. Millar, and G. J. Hickling. 2005. Restitution of mass-size residuals: Validating body condition indices. Ecology 86:155–163.

Sheldon, B. C., and S. A. West. 2004. Maternal dominance, maternal condition, and offspring sex ratio in ungulate mammals. The American Naturalist 163:40–54.

Spurgin, L. G., D. J. Wright, M. van der Velde, N. J. Collar, J. Komdeur, T. Burke, and D. S. Richardson. 2014. Museum DNA reveals the demographic history of the endangered Seychelles warbler. Evolutionary Applications 7:1134–1143.

Trivers, R., and D. Willard. 1973. Natural selection of parental ability to vary the sex ratio of offspring. Science 179:90–92.

Von Zglinicki, T. 2002. Oxidative stress shortens telomeres. Trends in Biochemical Sciences 27:339–344.

West, S. 2009. Sex Allocation. Princeton University Press 482.

Whittingham, L. a, and P. O. Dunn. 2000. Offspring sex ratios in tree swallows: females in better condition produce more sons. Molecular Ecology 9:1123–9.