

Bill size correlates with telomere length in male American Redstarts

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Abstract Telomere length (TL) has been shown to be a potential predictor of survival in wild vertebrates, and, as a consequence, there is growing interest in understanding the causes of inter-individual variability in TL. In that context, developmental conditions deserve a specific attention because they are thought to be a major driver of telomere shortening. Because poor developmental conditions can accelerate telomere shortening and impair growth (resulting in a small adult size), a positive correlation between TL and body size is expected. However, and surprisingly, the relationship between body size and telomere length has rarely been described in wild vertebrates. Here, we specifically examined this question in hatch-year (HY) and after hatch-year (AHY) male wintering American Redstarts (*Setophaga ruticilla*). Although tarsus size was not related to TL, we found a significant positive correlation between bill size and TL in HY male Redstarts, therefore supporting the idea that determinants of some components of

individual size are also important determinants of TL in young birds. Moreover, this positive relationship between bill size and TL was also found for AHY birds, suggesting that adult TL may be, at least partly, explained by the telomere dynamics that occurred during the developmental phase.

Keywords Telomeres · Body size · Development · *Setophaga ruticilla*

Zusammenfassung

Die Schnabelgröße korreliert bei männlichen Schnäpperwaldsängern mit der Telomerlänge

Es ist gezeigt worden, dass die Telomerlänge (TL) ein potenzieller Anzeiger des Überlebens freilebender Wirbeltiere ist, weshalb zunehmendes Interesse besteht, die Ursachen für die individuelle Variabilität der TL zu verstehen. In diesem Zusammenhang gebührt den Bedingungen während der Entwicklung besondere Aufmerksamkeit, weil angenommen wird, dass diese einen Haupteinflussfaktor auf Telomerverkürzung darstellen. Da schlechte Bedingungen während der Entwicklung Telomerverkürzung beschleunigen und das Wachstum beeinträchtigen können (was zu einer geringen Adultgröße führt), ist eine positive Korrelation zwischen TL und Körpergröße zu erwarten. Überraschenderweise ist jedoch die Beziehung zwischen Körpergröße und Telomerlänge bei freilebenden Wirbeltieren bislang kaum beschrieben worden. Hier haben wir diese Frage an männlichen überwinterten Schnäpperwaldsängern (*Setophaga ruticilla*) untersucht, die entweder einjährig oder mehrjährig waren. Obwohl die Tarsuslänge nicht mit der TL in Beziehung stand, fanden wir eine signifikante positive Korrelation zwischen der Schnabelgröße und TL bei

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einjährigen männlichen Schnäpperwaldsängern, was die Idee unterstützt, dass Faktoren, die gewisse Aspekte der individuellen Größe bestimmen, bei jungen Vögeln auch wichtig für die Bestimmung der TL sind. Außerdem fanden wir diese positive Beziehung zwischen Schnabelgröße und TL auch für die mehrjährigen Vögel, was darauf hindeutet, dass die adulte TL zumindest teilweise mit der Telomerdynamik, die während der Entwicklungsphase auftrat, erklärt werden kann.

Introduction

Since the initial paper by Haussmann and Vleck (2002) that linked ecology and telomere biology, the study of avian telomere dynamics has received increasing attention (Mohnaghan 2010; Haussmann and Marchetto 2010; Nussey et al. 2014). Telomeres appear to shorten throughout the life of individuals (Pauliny et al. 2006; Bize et al. 2009; Salomons et al. 2009; Heidinger et al. 2012; Angelier et al. 2013; Barrett et al. 2013; Bauch et al. 2013; Boonekamp et al. 2014) and, importantly, telomere length (TL) has been shown to be a reliable predictor of survival under some circumstances (Haussmann et al. 2005; Pauliny et al. 2006; Bize et al. 2009; Salomons et al. 2009; Heidinger et al. 2012; Angelier et al. 2013; Barrett et al. 2013) but not others (Pauliny et al. 2006; Beaulieu et al. 2011; Caprioli et al. 2013; Boonekamp et al. 2014). Therefore, specific attention has been paid to the determinants of TL in wild vertebrates.

Telomere shortening is, at least partly, determined by the events that occur during adult life in vertebrates, and the occurrence of stressors is thought to accelerate this shortening (Haussmann and Marchetto 2010; Heidinger et al. 2012; Bauch et al. 2013). Indeed, poor environmental conditions have recently been associated with an acceleration of telomere shortening in two bird species (Angelier et al. 2013; Mizutani et al. 2013). However, adult TL is not only determined by events occurring during adult life but also by the initial TL at the time when individuals enter the adult life stage. TL is at least partly heritable (Olsson et al. 2011; Horn et al. 2011; Reichert et al. 2014) and most of the telomere shortening occurs during development (Foote et al. 2011; Pauliny et al. 2012; Caprioli et al. 2013), suggesting that variation in conditions during the period leading up to adulthood determines variation in telomere length in wild birds (Geiger et al. 2012; Boonekamp et al. 2014; Herborn et al. 2014). Interestingly, poor developmental conditions are associated with impaired growth and, under some circumstances, with reduced adult size (Merilä 1997). One would expect, therefore, to find a positive correlation between TL and body size at the end of the developmental phase, with larger birds having longer telomeres.

Alternatively, adult size could instead be negatively correlated with TL since a large body size requires a large amount of replication processes, which are known to induce telomere shortening. However, this hypothesis remains unlikely since most telomere shortening seems to result from oxidative stress rather than replication processes (Von Zglinicki 2002). On the other hand, the relationship between TL and body size could be complex and hindered by other ecological processes. For instance, Geiger et al. (2012) showed that telomere shortening during early life is mainly accelerated by some transitory phases of accelerated growth that aim at compensating for previous periods of nutritional deficits (catch-up growth). This catch-up growth can result in significant telomere attrition without any effect on final adult body size, leading therefore to a potential disconnection between TL and adult body size.

During adulthood, different individuals experience different environmental conditions and this can result in variable rates of telomere shortening between individuals (Bize et al. 2009; Salomons et al. 2009; Angelier et al. 2013; Barrett et al. 2013). Importantly, and contrary to TL, body size does not change after the developmental phase since birds have determinate growth, suggesting that telomere dynamics will become independent of structural body size in adults. Therefore, TL should be strongly correlated with body size in young individuals, whereas such correlation should attenuate in old individuals.

Surprisingly, the relationship between body size and TL has rarely been examined in birds, appears inconsistent (Pauliny et al. 2006; Foote et al. 2011; Caprioli et al. 2013), and therefore deserves further examination. Pauliny et al. (2006) found a negative relationship between tarsus length and telomere length in adult Dunlins (*Calidris alpina*), whereas Foote et al. (2011) found that telomere length was not correlated with head length in Lesser Black-backed Gull chicks (*Larus fuscus*). Highlighting this inconsistency a bit more, Caprioli et al. (2013) found that telomere length was positively correlated with keel length in male Barn Swallows (*Hirunda rustica*) but not in females. In this study, we tested whether TL is related to body size in known-aged male American Redstarts (*Setophaga ruticilla*) (from less than 1 year old, i.e. hatch-year birds, HY, and from 2 to 7 years old, i.e., after hatch-year birds, AHY). Because poor developmental conditions are known to increase the rate of telomere shortening (Boonekamp et al. 2014; Herborn et al. 2014) and may simultaneously limit growth during the pre-adult period, we predicted that body size should be positively correlated with TL in HY Redstarts (prediction 1). As explained earlier, body size should be disconnected from telomere dynamics during adulthood, and, therefore, we also predicted that the correlation between body size and TL should attenuate in AHY Redstarts (prediction 2).

Methods

Study species, morphometric measurements, and telomere analyses

American Redstarts are migratory passerines that begin arriving in the wintering area in September and remain on their non-breeding territories for 6–8 months until they depart on spring migration (Marra 2000). Our study was conducted in 2008 (February–April) at the Font Hill Nature Preserve, Jamaica, where Redstarts have been banded and aged (HY, AHY) every year since 1993, allowing us to know the exact age of many birds. Sixty-one male Redstarts (21 HY and 40 AHY; 38 of known age, from less than 1 to 7 years old) were captured using mist-nets. Specifically, 21 birds were less than 1 year old, and 9, 1, 2, 3 and 2 birds were respectively 2, 3, 4, 5 and 7 years old. A small blood sample (50–100 μ l) was collected from the brachial vein for DNA collection. All new birds were banded and then aged (HY, AHY) by plumage characteristics (retix patterns and shapes, growth bars, presence of incoming black feathers, breast and wing axillary coloration, and color transition on upperparts) as detailed in Marra et al. (1993). In addition, all Redstarts were measured to assess their body size (tarsus length, bill length, bill width and bill depth to the nearest 0.1 mm). We did not focus on body mass in this study because body mass is known to fluctuate quickly in response to short-term changes in rainfall abundance in the non-breeding grounds (Angelier et al. 2011), and it could therefore not be used to reliably assess body size. Following methods previously described (Angelier et al. 2013), DNA was extracted and telomeres were measured using a real-time quantitative PCR technique validated for birds (Crisuolo et al. 2009) and American Redstarts (Angelier et al. 2013). Morphometric measures were correlated and, therefore, we used a principal component analysis to calculate the body size of Redstarts: most of the variance was explained by two uncorrelated axes (PC1, PC2) that respectively explained 49.02 and 25.91 % of the variance. PC1 was significantly correlated with bill length ($r = 0.780$), width ($r = 0.847$) and depth ($r = 0.783$), whereas PC2 was significantly correlated with tarsus length only ($r = 0.959$). Therefore, PC1 represents a measure of bill size whereas PC2 represents a measure of tarsus length.

Statistical analyses

All statistical analyses were conducted with SAS (v.9.3). We used generalized linear models (normal distribution, identity link function) to test (1) whether TL of all Redstarts ($n = 61$) was explained by ‘age class’ (HY vs. AHY), ‘PC1’, ‘PC2’ and interactions; and (2) whether TL

of known-aged birds ($n = 38$) was explained by ‘age’, ‘PC1’ and ‘PC2’. In addition, we tested whether bill size (PC1) and tarsus length (PC2) differed between HY and AHY birds ($n = 61$). Finally, we tested whether these variables (PC1 and PC2) were correlated with individual age by using linear regressions (known-aged birds, $n = 38$).

Results

Telomere length, bill size and tarsus length

PC1 was significantly and positively correlated with TL in male American Redstarts: a higher PC1 score was associated with longer telomeres ($F_{1,58} = 6.43$, $p = 0.014$; Fig. 1a). Moreover, HY birds had shorter telomeres than AHY birds ($F_{1,58} = 4.11$, $p = 0.047$). There was no significant effect of the ‘PC1 \times age class’ interaction on TL ($F_{1,55} = 0.01$, $p = 0.943$; Fig. 1a), indicating that the relationship between TL and PC1 did not differ between HY and AHY birds (Fig. 1a). There was no significant effect of PC2 or the ‘PC2 \times age class’ interaction on TL (PC2: $F_{1,57} = 0.86$, $p = 0.357$, interaction: $F_{1,56} = 0.12$, $p = 0.727$; Fig. 1b).

When considering only known-aged birds ($n = 38$), TL was significantly and positively related to PC1 ($F_{1,36} = 4.83$, $p = 0.034$). However, there was no significant effect of PC2 or the age of individuals on TL (PC2: $F_{1,34} = 0.37$, $p = 0.547$; age: $F_{1,35} = 0.29$, $p = 0.591$).

Age, bill size and tarsus length

PC1 did not significantly differ between HY and AHY Redstarts ($F_{1,59} = 0.90$, $p = 0.348$; Fig. 2a). However, AHY Redstarts had a higher PC2 score than HY Redstarts ($F_{1,59} = 14.28$, $p < 0.001$; Fig. 2b). When considering only known-aged birds ($n = 38$), neither PC1 nor PC2 were significantly correlated with age (PC1: $F_{1,36} = 1.77$, $p = 0.192$; PC2: $F_{1,36} = 2.06$, $p = 0.160$).

Discussion

Bill size and telomere length in HY males

Congruent with prediction 1, we found that TL was positively correlated with bill size (PC1) in HY male American Redstarts. This confirms that specific components of body size and TL are correlated in young birds (Caprioli et al. 2013), and supports the idea that the determinants of some components of body size are also important determinants of TL. This correlation probably results from

Fig. 1 Relationship between body size and telomere length (TL) in hatch-year (HY) and after hatch-year (AHY) male American Redstarts (*Setophaga ruticilla*) (solid line HY birds, dashed line AHY birds). **a** TL and principal component 1 (PC1, bill size). **b** TL and principal component 2 (PC2, tarsus size)

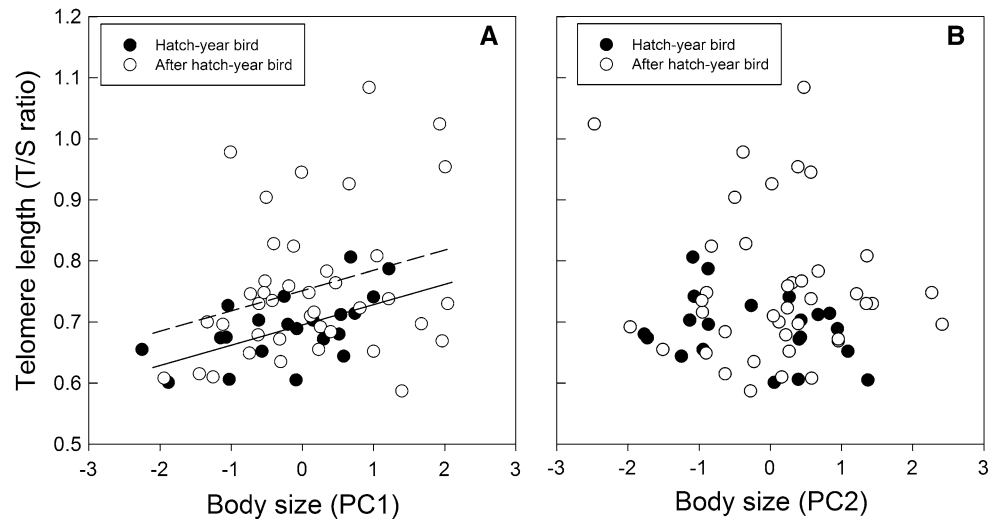
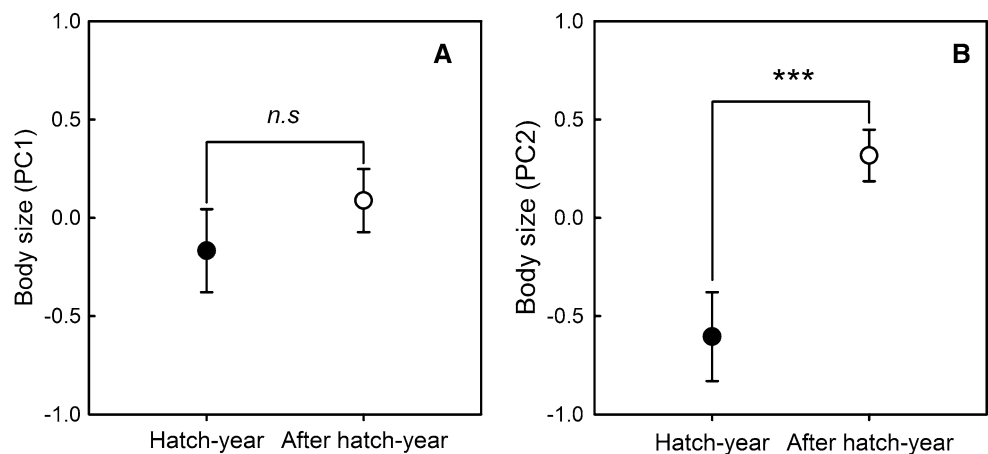


Fig. 2 Difference in body size between hatch-year (HY) and after hatch-year (AHY) male American Redstarts. **a** Age and principal component 1 (PC1, bill size). **b** Age and principal component 2 (PC2, tarsus size)



developmental conditions that affect simultaneously growth and developmental telomere dynamics (Boonekamp et al. 2014; Herborn et al. 2014), but it might also result from genetic factors that might concomitantly govern bill size and telomere length.

In vertebrates, telomere shortening is accelerated by oxidative stress, which is the balance between reactive oxygen species and antioxidant defences (Von Zglinicki 2002; Haussmann and Marchetto 2010). During the development, environmental constraints are known to, respectively, increase oxidative stress and reduce growth (Alonso-Alvarez et al. 2007; Costantini 2010; Kim et al. 2011; Bourgeon et al. 2011), suggesting that the specific conditions of this developmental phase may be responsible for a potential relationship between adult body size and telomere length (Geiger et al. 2012). Indeed, growth is slowed down and individuals usually reach small adult size when reared under poor conditions. Moreover, growth is also made at the expense of antioxidant defences (Kim et al. 2011), suggesting the existence of a trade-off between maintenance and growth when chicks are developing under

such conditions. This trade-off is thought to be mediated by the glucocorticoids that are known to play a vital role in developmental processes (Haussmann et al. 2012; Monaghan 2014). For instance, glucocorticoids secretion increases in response to food shortages, and this triggers begging behavior in developing chicks (Loiseau et al. 2008), which is also associated with increased oxidative stress (Moreno-Rueda et al. 2012). Although we did not have access to the developmental phase of Redstarts and could not test the link between glucocorticoids levels, oxidative stress, and growth in this study, oxidative stress and glucocorticoid regulation are probably the functional mechanisms linking telomere length and adult size in wild vertebrates. In birds, developmental conditions can have a strong impact on both adult bill size and telomere dynamics. For instance, Sockman (2012) showed that hatching order, and thus sibling competition, was associated with bill morphology in Lincoln's Sparrow (*Melospiza lincolnii*). In addition, laying order is also known to affect yolk oxidative status, and, potentially, the telomere length of developing nestling (Rubolini et al. 2006). This

emphasizes that developmental conditions, such as sibling competition, may simultaneously account for inter-individual variations in TL and morphology (bill morphology: Sockman 2012; telomeres: Boonekamp et al. 2014; Herborn et al. 2014).

Bill size and telomere length in AHY males

The relationship between bill size (PC1) and TL was also present for older birds (AHY), whereas we were expecting bill size to become disconnected from TL in AHY birds, since telomere dynamics of adult birds should be relatively independent of bill size (prediction 2). There are two potential explanations for this. First, bill size could be functionally connected to telomere dynamics in adult Redstarts. Birds with large bills may be better able to cope with their environment (e.g., better foraging ability) or they may adopt different strategies than birds with small bills and this could result in slower telomere shortening. Although a previous study reported that non-breeding habitat occupancy affects adult telomere dynamics (Angelier et al. 2013), habitat occupancy is not related to body size in Redstarts (Marra 2000), suggesting that bill size is disconnected from telomere dynamics in adults. If bill size and telomere shortening were connected, most of the Redstarts with short bills should be found in the habitat where telomere shortening is the fastest (i.e., dry scrubs), but this is not the case (Marra 2000). Moreover, we did not find any difference in bill size between HY and AHY birds, suggesting that a large bill does not provide obvious survival benefits to male Redstarts. Therefore, this explanation is unlikely. Second, the influence of adult life on TL could be minor relative to the impact of developmental conditions on TL (Pauliny et al. 2012). If so, most variation in adult TL would still be explained by the telomere dynamics that had occurred during the developmental phase when adult size is determined. Indeed, there is increasing evidence that most telomere shortening occurs early in life (Salomons et al. 2009; Foote et al. 2011; Heidinger et al. 2012; Herborn et al. 2014). This explanation could also explain why age is not related to TL in AHY Redstarts. Of course, adult telomere dynamics still surely affects TL (Angelier et al. 2013; Mizutani et al. 2013), and this probably explains why bill size better explains a larger part of the variability in TL of HY Redstarts relative to that of AHY Redstarts (Fig. 1).

Age and telomere length

Our study was cross-sectional, and, thus, we were not able to measure telomere dynamics. Longitudinal studies are usually required to find a relationship between telomere length and age for two main reasons. First, this relationship

is usually masked by the large inter-individual variation in telomere length in cross-sectional studies (Pauliny et al. 2012; Heidinger et al. 2012; Barrett et al. 2013; Boonekamp et al. 2014). Second, selection processes may hide the progressive shortening of telomere with advancing age in cross-sectional studies because young birds with short telomeres disappear quickly from the population and only birds with long telomeres remain in the population (Hausmann and Mauck 2008). Therefore, cross-sectional studies usually require a very large sample size and multiple years of data to detect the expected negative relationship between age and TL, and the sample size was certainly too limited in our study to detect this relationship ($n = 38$). Accordingly, we did not find this negative correlation between age and telomere length, but, more surprisingly, we found that HY birds had overall shorter telomeres than AHY birds. Specific poor developmental conditions may have resulted in short telomeres in the 2008 cohort explaining this unexpected result. On the other hand, HY birds with very short telomeres may be selected against so that they do not reach older ages (Hausmann and Mauck 2008). This could also explain that HY Redstarts had, on average, shorter telomeres than AHY Redstarts. Importantly, we found a significant relationship between bill size and telomere length despite having only conducted a cross-sectional study, suggesting that the functional relationship linking bill size and telomere length is robust. This interpretation is indeed supported by a recent study that found a negative effect of poor developmental conditions on telomere length (Herborn et al. 2014). Further studies are now necessary to understand whether cohort effects could explain unexpected patterns in cross-sectional studies of telomere length in wild animals.

Tarsus length and telomere length

In this study, we found that TL is significantly correlated with bill size (PC1) but not with tarsus length (PC2). The causes of this discrepancy remain to be determined. Although bill size may better reflect developmental conditions than tarsus size, there is currently little information on the causes of inter-individual variation in bill or tarsus size in American Redstarts. Developmental constraints and oxidative stress could have major effect on bill growth and minor or no effect on tarsus growth. Indeed, bill size may mainly depend on developmental conditions whereas tarsus size may be mainly determined by a genetic component in Redstarts, as previously found in another passerine species (Keller et al. 2001). Supporting the idea that tarsus length may not be primarily determined by developmental conditions, Bourgeon et al. (2011) found that wing length, but not tarsus length, reach smaller size when European Starling (*Sturnus vulgaris*) chicks are bred under poor

developmental conditions (enlarged brood and strong sibling competition). Interestingly, we found that AHY birds had larger tarsus, but not bill, than HY birds. This suggests that birds with short tarsus disappear quickly from the population and that only Redstarts with large tarsus can reach old ages. Since telomere length is positively linked with survival in this species (Angelier et al. 2013), one would logically expect a positive relationship between telomere length and tarsus length. However, we did not find such a relationship in our study. Because most telomere shortening occurs during development (Boonekamp et al. 2014; Herborn et al. 2014), adult telomere length—HY and AHY birds—are certainly mainly determined by developmental conditions that seem disconnected from tarsus length. Therefore, future studies should rely on multiple sampling of the same individuals to properly test whether telomere dynamics is connected to tarsus length or not.

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References

- Alonso-Alvarez C, Bertrand S, Faivre B, Sorci G (2007) Increased susceptibility to oxidative damage as a cost of accelerated somatic growth in Zebra finches. *Funct Ecol* 21:873–879
- Angelier F, Tonra CM, Holberton RL, Marra PP (2011) Short-term changes in body condition in relation to habitat and rainfall abundance in American redstarts *Setophaga ruticilla* during the non-breeding season. *J Avian Biol* 42:335–341
- Angelier F, Vleck CM, Holberton RL, Marra PP (2013) Telomere length, non-breeding habitat and return rate in male American redstart. *Funct Ecol* 27:342–350
- Barrett ELB, Burke TA, Hammers M, Komdeur J, Richardson D (2013) Telomere dynamics predict mortality in a life-long longitudinal wild study. *Mol Ecol* 22:249–259
- Bauch C, Becker PH, Verhulst S (2013) Telomere length reflects phenotypic quality and costs of reproduction in a long-lived seabird. *Proc R Soc Lond B* 280:20122540
- Beaulieu M, Reichert S, Le Maho Y, Ancel A, Criscuolo F (2011) Oxidative status and telomere length in a long-lived bird facing a costly reproductive event. *Funct Ecol* 25:577–585
- Bize P, Criscuolo F, Metcalfe NB, Nasir L, Monaghan P (2009) Telomere dynamics rather than age predict life expectancy in the wild. *Proc R Soc Lond B* 276:1679–1683
- Boonekamp JJ, Mulder GA, Salomons HM, Dijkstra C, Verhulst S (2014) Nestling telomere shortening, but not telomere length, reflects developmental stress and predicts survival in the wild. *Proc R Soc Lond B* 281:20133287
- Bourgeon S, Guindre-Parker S, Williams TD (2011) Effects of sibling competition on growth, oxidative stress, and Humoral immunity: a two-year brood size manipulation. *Physiol Biochem Zool* 84:429–437
- Caprioli M, Romano M, Romano A, Rubolini D, Motta R, Folini M, Saino N (2013) Nestling telomere length does not predict longevity, but covaries with adult body size in wild barn swallows. *Biol Lett* 9:20130340
- Costantini D (2010) Effects of diet quality on growth pattern, serum oxidative status, and corticosterone in pigeons (*Columbia livia*). *Can J Zool* 88:795–802
- Criscuolo F, Bize P, Nasir L, Metcalfe NB, Foote CG, Griffiths K, Gault EA, Monaghan P (2009) Real-time quantitative PCR assay for measurement of avian telomeres. *J Avian Biol* 40:342–347
- Foote CG, Gault EA, Nasir L, Monaghan P (2011) Telomere dynamics in relation to early growth conditions in the wild in the lesser black-backed gull. *J Zool* 283:203–209
- Geiger S, Le Vaillant M, Lebard T, Reichert S, Stier A, Le Maho Y, Criscuolo F (2012) Catching-up but telomere loss: half-opening the black box of growth and ageing trade-off in wild king penguin chicks. *Mol Ecol* 21:1500–1510
- Hausmann MF, Marchetto NM (2010) Telomeres: linking stress and survival, ecology and evolution. *Curr Zool* 56:714–727
- Hausmann MF, Mauck RA (2008) Telomeres and longevity: testing an evolutionary hypothesis. *Mol Biol Evol* 25:220–228
- Hausmann MF, Vleck CM (2002) Telomere length provides a new technique for aging animals. *Oecologia* 130:325–328
- Hausmann MF, Winkler DW, Vleck CM (2005) Longer telomeres associated with higher survival in birds. *Biol Lett* 1:212–214
- Hausmann MF, Longenecker AS, Marchetto NM, Juliano SA, Bowden RM (2012) Embryonic exposure to corticosterone modifies the juvenile stress response, oxidative stress and telomere length. *Proc R Soc Lond B* 279:1447–1456
- Heidinger BJ, Blount JD, Boner W, Griffiths K, Metcalfe NB, Monaghan P (2012) Telomere length in early life predicts lifespan. *Proc Natl Acad Sci USA* 109:1743–1748
- Herborn KA, Heidinger BJ, Boner W, Noguera JC, Adam A, Daunt F, Monaghan P (2014) Stress exposure in early post-natal life reduces telomere length: an experimental demonstration in a long-lived seabird. *Proc R Soc Lond B* 281:20133151
- Horn T, Robertson BC, Will M, Eason DK, Elliott GP, Gemmill NJ (2011) Inheritance of telomere length in a bird. *PLoS ONE* 6:e17199
- Keller LF, Grant PR, Grant BR, Petren K (2001) Heritability of morphological traits in Darwin's Finches: misidentified paternity and maternal effects. *Heredity* 87:325–336
- Kim S-Y, Noguera JC, Morales J, Velando A (2011) Quantitative genetic evidence for trade-off between growth and resistance to oxidative stress in a wild bird. *Evol Ecol* 25:461–472
- Loiseau C, Sorci G, Dano S, Chastel O (2008) Effects of experimental increase of corticosterone levels on begging behavior, immunity and parental provisioning rate in house sparrows. *Gen Comp Endocrinol* 155:101–108
- Marra PP (2000) The role of behavioral dominance in structuring patterns of habitat occupancy in a migrant bird during the non-breeding season. *Behav Ecol* 3:299–308
- Marra PP, Sherry TW, Holmes RT (1993) Territorial exclusion by a long-distance migrant warbler in Jamaica: a removal experiment with American redstarts (*Setophaga ruticilla*). *Auk* 110:565–572
- Merila J (1997) Expression of genetic variation in body size of the collared flycatcher under different environmental conditions. *Evolution* 51:526–536
- Mizutani Y, Tomita N, Niisuma Y, Yoda K (2013) Environmental perturbations influence telomere dynamics in long-lived birds in their natural habitat. *Biol Lett* 9:20130511

- Monaghan P (2010) Telomeres and life histories: the long and the short of it. *Ann NY Acad Sci* 1206:130–142
- Monaghan P (2014) Organismal stress, telomeres and life histories. *J Exp Biol* 217:57–66
- Moreno-Rueda G, Redondo T, Trenzado CE, Sanz A, Zuniga JM (2012) Oxidative stress mediates physiological costs of begging in Magpie (*Pica pica*) nestlings. *PLoS ONE* 7:e40367
- Nussey DH, Baird D, Barrett E, Boner W, Fairlie J, Gemmill N, Hartmann N, Horn T, Hausmann MF, Olsson M, Turbill C, Verhulst S, Zahn S, Monaghan P (2014) Measuring telomere length and telomere dynamics in evolutionary biology and ecology. *Methods Ecol Evol* 5:299–310
- Olsson M, Pauliny A, Wapstra E, Uller T, Schwartz T, Blomqvist D (2011) Sex differences in Sand lizard telomere inheritance: paternal epigenetic effects increases telomere heritability and offspring survival. *PLoS ONE* 6:e17473
- Pauliny A, Wagner RH, Augustin J, Szép T, Blomqvist D (2006) Age-independent telomere length predicts fitness in two bird species. *Mol Ecol* 15:1681–1687
- Pauliny A, Larsson K, Blomqvist D (2012) Telomere dynamics in a long-lived bird, the barnacle goose. *BMC Evol Biol* 12:257
- Reichert S, Rojas ER, Zahn S, Robin JP, Criscuolo F, Massemin S (2014) Maternal telomere length inheritance in the king penguin. *Heredity* 114:10–16
- Rubolini D, Roman M, Bonisoli AA, Saino N et al (2006) Early maternal genetic and environmental components of antioxidant protection, morphology and immunity of yellow-legged gull. *J Evol Biol* 19:1571–1584
- Salomons HM, Mulder GA, van de Zande L, Hausmann MF, Linskens MHK, Verhulst S (2009) Telomere shortening and survival in free-living corvids. *Proc R Soc Lond B* 276:3157–3165
- Sockman KW (2012) Hatching order and seasonal timing of development predict bill morphology of nestling and adult Lincoln's Sparrows. *Condor* 114:645–653
- Von Zglinicki T (2002) Oxidative stress shortens telomeres. *Trends Biochem Sci* 27:339–344