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Sex-dependent spatial structure of telomere length in a wild long-lived scavenger

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Abstract. Sex-related divergences in many phenotypic traits, such as morphology, physiology, and behavior, have widely been described in animals. These asymmetries may adapt the sexes to different subniches, but also may produce sex-specific optima for life-history traits, as well as different costs. In birds, long movements in search of food and intraspecific competition may entail important metabolic costs that can be predicted to be unequal if both sexes perform somehow differently. However, the extent to which sex-specific individual movements, foraging strategies and social dominance relationships are correlated with physiological costs has rarely been evaluated. The effects of prolonged exposure to stressors can be mirrored in accelerated cellular damage and aging as well as in the by-products resulting from the activation of the stress response machinery. Both indicators, measured as telomere length and the concentration of feather corticosterone ($CORT_f$), respectively, would reflect physiological costs at different time frames. Here, on the basis of information provided by GPS-tagged Andean condors, a sexually dimorphic scavenger with a highly despotic social system, we determined whether sex-specific movement patterns correlated to variation in telomere length and $CORT_f$ levels. We found a striking pattern of spatial structure of telomere length that was, in addition, sex-specific; males breeding farther from feeding grounds exhibited longer telomeres, while the opposite pattern was found in females. Nevertheless, telomere length was not related to the range of movements performed by condors. We also found that females displayed higher $CORT_f$ values than males, regardless of the location of their nests, which is likely related to social dominance hierarchy and sexual size dimorphism. Sex-specific optima for trade-offs associated with ecological factors might underlie the fact that populations are spatially structured from a telomere-length perspective, which has never been described before.

Key words: feather corticosterone; long-lived birds; movement patterns; social environment; telomere length.

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Introduction

Within-species sex-related differences in morphology, behavior, and longevity are widespread in the animal kingdom (Promislow 2003, Fairbairn et al. 2007). In birds, sexes usually differ in size and coloration, which has largely been thought to be driven by sexual selection and distinct parental roles (Andersson 1994). Likewise, differences in foraging strategies have been observed in a number of both sexually size-dimorphic and size-monomorphic species, which have been related to reduction in intersexual competition for food and foraging niches (Newton 1979, Lewis et al. 2002, Weimerskirch et al. 2006). Besides morphological asymmetries that may confer one sex competitive advantages over the other while feeding, sexual differences in energy or nutritional requirements could also explain the observed differences in foraging behavior (Stauss et al. 2012). Sexual divergence may have ecological significance in adapting the sexes to different subniches, but also may produce sex-specific optima for life-history traits, including investment in longevity and somatic maintenance (Bonduriansky et al. 2008).

One of the most distinctive features of birds is the ability to fly, which represents a clear advantage that also entails important metabolic costs (Norberg 1990). Long-lived avian species, such as seabirds and scavengers that exploit spatially unpredictable food sources, often cover enormous ranges to forage (Fritz et al. 2003, Ruxton and Houston 2004). The flying performance of these large-sized species strongly relies on the dynamic of local climatic conditions, like the availability of winds and thermals (Weimerskirch et al. 2000, Duriez et al. 2014), so that movements under adverse weather conditions may became extremely difficult and even impossible (Shepard and Lambertucci 2013). Moreover, sexual size dimorphism may result in differences in flight efficiency and competitive abilities between sexes (Wearmouth and Sims 2008). During the breeding season, both longer movements and increased habitat exploitation intensify energy demands, and thus, resource allocation tradeoffs and physiological costs potentially affecting lifetime fitness are expected to occur (Amélineau et al. 2014). However, the extent to which sex-specific individual movements, foraging strategies, and dominance relationships are correlated with physiological costs remains virtually unexplored.

The Andean condor (*Vultur gryphus*) is a top scavenger living in the Andean range, from Colombia to Tierra del Fuego, Argentina, and Chile. Andean condors are unique among birds of prey because they show a strong direct sexual size dimorphism, with males being 30–40% heavier than females (del Hoyo et al. 1994). The species is highly despotic with adult males being at the top of the hierarchy and clearly dominant in conspecific interactions, particularly at feeding places (Donázar et al. 1999). Andean condors are specialized for highly efficient gliding flight, but their huge body size and mass (wingspan about 3 m and body mass up to 16 kg) represent a major challenge when weather conditions are adverse (Shepard and Lambertucci 2013). Here, we took advantage of the data obtained by GPS-tracked Andean condors in the Argentinean Patagonia. In this region, most individuals share common feeding grounds in the Andean piedmont steppes (Fig. 1), but whereas some pairs breed close to the steppe, others do so in the Cordillera and along the Pacific slope and are thus forced to make long daily trips and crosses over the mountain range to access feeding grounds (Lambertucci et al. 2014). Previous research showed that although both sexes forage in similar areas (Lambertucci et al. 2014), intersexual competition determines that sexes segregate at a mesohabitat scale, so that larger males are more prone to exploit carcasses in rugged slopes, whereas females are more frequently observed on food resources found in more humanized plains (Donázar et al. 1999, Lambertucci et al. 2012).

On the basis of this scenario, we hypothesize that physiological cost will be related to foraging movement patterns, yet unequally for males and females if they perform somehow differently. To test this hypothesis, we used two different evaluators providing long- and medium-term perspectives on individual physiology, that is, telomere length and feather corticosterone ($CORT_f$) levels, respectively, and related them to the movement patterns of GPS-tagged condors.

Telomeres are evolutionarily conserved caps consisting of repeated DNA sequences that protect eukaryotic linear chromosome ends (Zakian 1995). Telomere attrition is thought to play a key

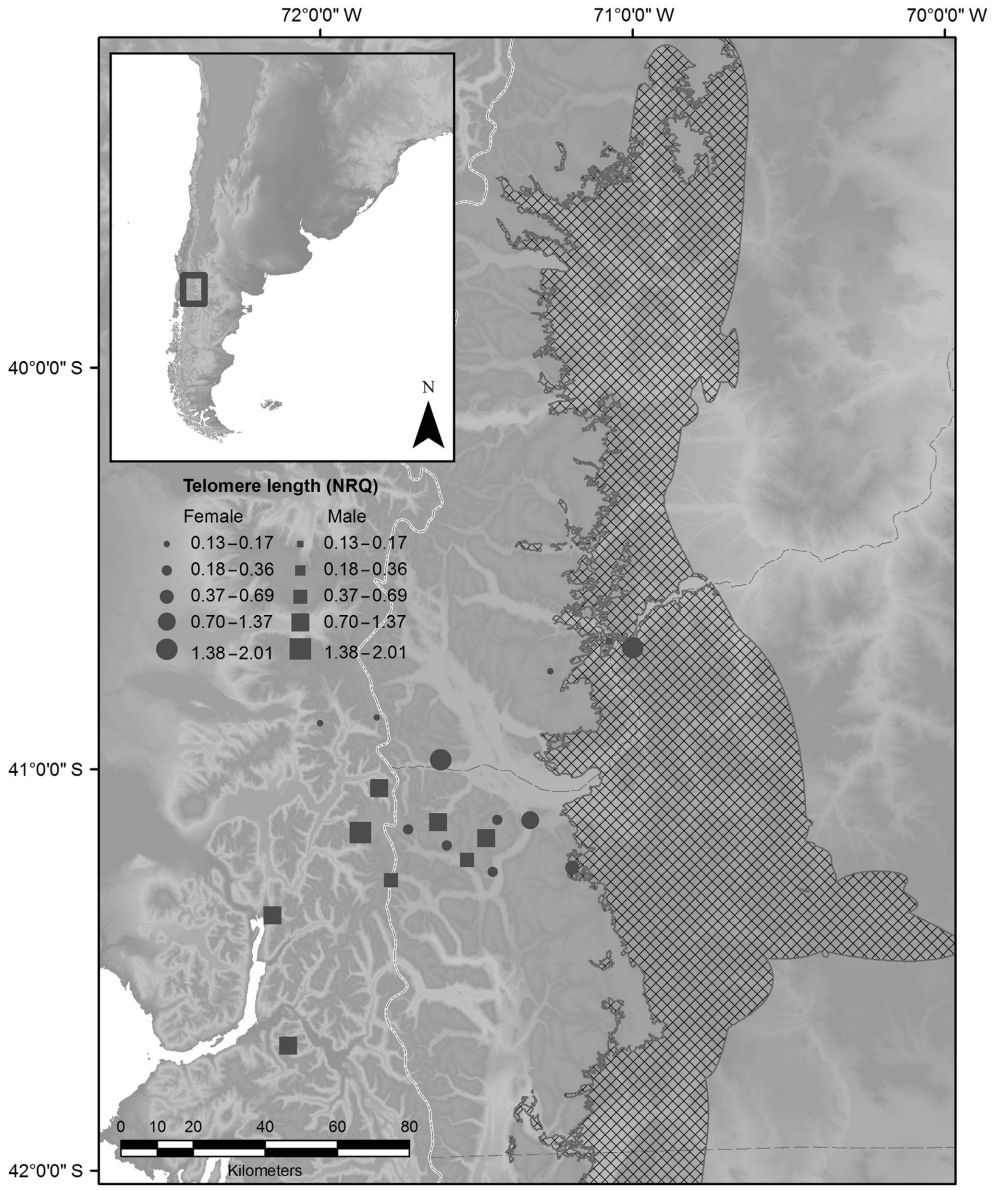

Fig. 1. Map of the study site showing the location of the study area (in a square top left) and the distribution of nesting sites and telomere length associated with each female (circles) and male (squares) breeding condors. The area represented by a reticulated texture delimits the steppe feeding grounds.

role in organismal senescence given that, in the absence of telomerase-driven restoration, they gradually shorten during each cellular division to a critical threshold that triggers chromosome instability and cell death (Armanios and Blackburn 2012). In general, telomeres shorten predictably with age, particularly in short-lived birds (Haussmann et al. 2003, but see Hall et al. 2004), although it has been recognized that the amount of shortening greatly depends on accumulated oxidative damage affecting both the telomere sequence and the restorative ability of the enzyme telomerase (von Zglinicki 2002). Additionally, we evaluate physiological response to the cost of movement and foraging strategies by means of the glucocorticoid corticosterone (CORT) in feathers. Recent evidence suggests that glucocorticoids modulate oxidative stress

balance and telomere dynamics (Haussmann and Marchetto 2010, Costantini et al. 2011). Birds release CORT into the bloodstream as a mediator of allostasis (maintaining homeostasis through change), combining the energetic costs related to sudden life-threatening challenges with daily life-history stages (McEwen and Wingfield 2003). CORT is an important metabolic regulator, and its baseline level can increase during energetically demanding situations (Landys et al. 2006, Angelier et al. 2008). The concentration of CORT in blood denotes the bird's physiological status at a particular moment, while the amount of CORT deposited in feathers ($CORT_f$) represents an integrated measure of the hypothalamus–pituitary–adrenal axis activity during the feather growth period (Bortolotti et al. 2008). $CORT_f$ levels have been positively correlated with both baseline and acute CORT levels in blood (Bortolotti et al. 2008, Fairhurst et al. 2013, Jenni-Eiermann et al. 2015). Taking into account these evaluators, we specifically predict that condors breeding farther from the foraging area and thus performing longer-distance foraging movements will have shorter telomeres and higher $CORT_f$ levels than those breeding close to the feeding grounds. In addition, females will have even shorter telomeres and higher $CORT_f$ levels than males as a consequence of their pervasive subordinate status. Finally, we predict that trade-offs will occur between self-maintenance and longevity and that the specific optima will differ between sexes.

Materials and Methods

Study area, bird tagging, and sampling

Our study was conducted on the northwestern Patagonia of Argentina and Chile (Fig. 1). The western part includes the Andes mountains where terrain is steep and dominated by the Valdivian Forest. Toward the east, there is a transitional area (ecotone) followed by the Patagonian steppe where a less steep relief and vegetation dominated by grasses and shrub predominates. Weather is characterized by a mean annual precipitation that declines from ca. 4000 mm on the west to ca. 500 mm on the east and is largely concentrated during autumn and winter (March to August). In this area, Andean condors eat introduced herbivores, mainly livestock (Lambertucci et al. 2009). Larger abundances of those herbivores are concentrated in the steppe where most of the condors forage (Lambertucci et al. 2014).

Between 2010 and 2011, 20 adult breeding condors (11 females and nine males) were captured using cannon-net traps baited with ungulate carcasses. The breeding status of condors was verified when handled at the time of capture, by confirming the presence of a brood patch in all individuals. All birds were weighed using a Pesola scale, and wing length was measured to the nearest millimeter.

We tagged condors with GPS devices (2010: 10 patagial PTT-100 50 g Solar Argos/GPS tags (Microwave Telemetry Inc., Columbia, Maryland, USA); 2011: 10 backpack 100 g Solar GPS–GSM CTT-1070-1100 tags (CellTrack Tech, LLC, Somerset, Pennsylvania, USA). These devices were cycled to transmit as much as possible, which resulted in different device performance. Thus, Microwave PTT-tags were able to record one GPS location every one hour, while CellTrack CTT-1070-1100 tags recorded one location every 15 min. Additionally, a greater covert feather, that is, those on the outer wing, which overlay the primary flight feathers, was collected from every individual for hormone analyses. We chose this particular feather because it is easily identifiable, which guarantees that the same feather was taken from all individuals, and has a sufficiently large size, despite not being an essential flight feather. Finally, 5 mL of blood from the brachial or medial metatarsal vein was collected from every individual and preserved in ethanol 96% until molecular analyses were performed, that is, telomere length determined (see details in *Determination of telomere length* below).

Spatial analyses

Our analyses included individual movement data from a six-month period (spring–autumn seasons from the Southern Hemisphere). From a total of 49,022 GPS locations, we computed fixed kernel density estimators for each individual and defined the home-range sizes as the areas encompassed within 95% isopleths using ABODE (beta v5) tool (Laver 2005) for ArcGIS 9.3 (ESRI Inc., Redlands, California, USA; see Lambertucci et al. 2014). We used a least-squares cross-validation method (Seaman and Powell 1996) to select the smoothing parameter (h). We estimated the daily distance (km) flown by a condor by first summing

the straight-line distance between consecutive locations along a day. Then, for each bird, we estimated the mean value of daily distance as the average of the sum of the straight-line distance between each pair of sequential fixes along a day, for all monitoring days. We used the steppe, which concentrates the highest livestock and other large herbivores density that currently represents the main food source for condors in Patagonia to delimit the foraging area (see Lambertucci et al. 2009). In addition, we delineated breeding areas as places with the highest concentration of locations (coordinates) in an area of 2 km radius, with most later corroborated in the field.

Determination of telomere length

We used DNA extracted from erythrocytes to evaluate telomere length. In birds, nucleated erythrocytes have a high turnover rate, leading to the expectation of telomere-length loss in these blood cells over time (Nussey et al. 2014). Due to their high turnover rate, blood cell telomere lengths may shorten at a greater rate than telomere lengths in other tissues (e.g., leukocytes, skin), which may give rise to significant within-individual differences in telomere length among tissues (Friedrich et al. 2000). In long-lived birds, as the Andean condor, a large telomere loss with chronological age seems not to be the rule (Haussmann et al. 2003, Hall et al. 2004, Foote et al. 2011). Indeed, telomere loss occurs more rapidly in the early stages of life, and once an individual reaches the adult status, the shortening rate is much slower (Barrett and Richardson 2011). Therefore, although the biological age of each free-ranging condor was unknown, the fact that all samples came from the same tissue (whole blood) and all sampled birds were adult breeders facilitated the comparison of telomere length among them (Nussey et al. 2014).

We estimated telomere length by a quantitative PCR assay (qPCR) (Cawthon 2002) adapted to measure relative telomere length in birds (Criscuolo et al. 2009). qPCR provides an estimate of the amount of telomere sequence present in the sample relative to the amount of a specified non-telomeric reference sequence that is autosomal and non-variable in copy number (Cawthon 2002). We measured relative telomere length by determining the ratio of telomere repeat copy number to single control gene copy number in target samples when compared with a reference sample. qPCR assay measures both terminal and interstitial telomeric repeats (ITSs) (Nakagawa et al. 2004). Although ITSs do not vary with age (Delany et al. 2003), substantial variation between species as well as between individuals of the same species has been reported (Foote et al. 2013). The inclusion of ITSs in telomere-length estimations always underestimates telomere length because most ITSs are shorter than most telomeres (Foote et al. 2013). However, it is so far unclear whether or not this variation is problematic, since it depends on the extent of ITSs in the study species. Unfortunately, the extent to which ITSs are present and vary among individual condors, as for most bird species, is completely unknown. Nonetheless, within-species estimates of telomere length obtained through different methods that avoid or include ITSs in calculations are positively and significantly correlated (Criscuolo et al. 2009, Foote et al. 2013). Consistent relationships between telomere length measured through different methods and fitness components have been reported (Pauliny et al. 2006, Bize et al. 2009, Salomons et al. 2009, Foote et al. 2011, Barrett et al. 2013) which suggest that the potential negative effects of both intra- and interspecific variations in ITSs on telomere-length estimation do not necessarily confound those connections found between telomere dynamics and life-history traits. Consequently, although our approach presents some drawbacks, such as the generalized underestimation of telomere length (Foote et al. 2013) and the likelihood to not detecting slight differences that may exist between groups (see Young et al. 2013), qPCR assay is an appropriate method for studies aimed at investigating intraspecific variation in relative telomere length and erosion rate (Cawthon 2002, Criscuolo et al. 2009, Reichert et al. 2014, Badás et al. 2015).

We used glyceraldehyde-3-phosphate dehydrogenase (GAPDH) as a control single copy gene, which was amplified using the forward and reverse primers GAPDH-F (5′-AACCAG CCAAGTACGATGACAT-3′) and GAPDH-R (5′-CCATCAGCAGCAGCCTTCA-3′). We used the telomere forward and reverse primers: Tel1b (5′-CGGTTTGTTTGGGTTTGGGTTTGGGTTT GGGTTTGGGTT-3′) and Tel2b (5′-GGCTTGCC TTACCCTTACCCTTACCCTTACCCTTACCCT

-3′). We carried out telomere and GAPDH real-time amplifications on two different plates. Each reaction for the telomere (or GAPDH) plates was performed using 20 ng/μL of DNA per well with sets of primers Tel1b/Tel2b (or GAPDH-F/GAPDH-R), each used at a concentration of 200 nM/200 nM, in a final volume of 20 μL containing 10 μL of Fast Start Universal SYBR Green Brilliant Master (Roche, Diagnostics GmbH, Mannheim, Germany). PCR conditions for the telomere portion of the assay were 10 min at 95°C followed by 30 cycles of 1 min at 56°C and 1 min at 95°C, while conditions for the GAPDH portion of the assay were 10 min at 95°C followed by 40 cycles of 1 min at 60°C and 1 min at 95°C.

We performed PCRs in a Light Cycler 480 RT-PCR System (Roche). To test the efficiency of each PCR, a standard curve was produced in every plate by serially diluting one sample (160, 40, 10, 2.5, and 0.66 ng/μL of DNA per well) and by running it in triplicate. The slopes of the standard curves ranged from −3.01 to −3.67 with a R^2 value between 0.98 and 1.00; efficiencies ranged from 87% and 114% (mean $\text{efficiency}_{\text{telomere}}$ = 95.5%; mean $\text{efficiency}_{\text{GAPDH}}$ = 106.5%), thus falling within the acceptable range of efficiencies for qPCR assays (see review in Horn et al. 2010). The coefficients of variation (CV) of the quantification cycle (Cq) values for the GAPDH and telomere amplifications were <5% in all samples following Criscuolo et al. (2009). Sample level repeatability within and across plates was ≥97.9% for telomere and GAPDH RT-PCR. To be able to compare measurements among plates, one individual was used as a reference and run in triplicate on every plate. We then calculated the threshold C_t of this reference sample for each plate; the C_t of a DNA sample is the fractional number of PCR cycles to which the sample must be subjected in order to accumulate enough products to cross a set threshold of magnitude of fluorescent signal. All other samples were run in duplicate on the plates, and mean values per plate were used to calculate relative ratios of target individual relative to the reference individual. qPCRs were performed a minimum of two times (i.e., two telomere and two GAPDH plates) for each sample. Mean intra- and interplate CV were 0.71% and 2.32%, respectively, for the C_t values of GAPDH assays, while intra- and interplate CV were 0.41% and 0.97%, respectively, for the C_t values of telomere assays. To take into account the variation of efficiencies between telomere and GAPDH amplifications, we calculated relative telomere length by transforming quantification cycle values (C_t) into normalized relative quantities (NRQs) following Hellemans et al. (2007).

Determination of $CORT_f$ concentration

We extracted CORT from each covert feather using a methanol-based extraction technique following the protocol described in Bortolotti et al. (2008) with some modifications. We used half of the feather (cutting the feather longitudinally and including the rachis) for hormone analyses. The length of each feather was first weighed and measured excluding the calamus, which was discarded. We then cut each feather into pieces of less than 5 mm^2 and placed in a glass vial with 10 mL of methanol (HPLC grade; VWR International, Mississauga, Ontario, Canada). The capped vials were sonicated in a water bath at room temperature for 30 min, followed by incubation at 50°C overnight in a shaking water bath. The methanol containing the hormones was separated from the feather bits using vacuum filtration, washing the vial and feather remains with an additional 10 mL of methanol, and adding it to the original methanol extract. When the evaporation of the samples was completed in the fume hood, the extract residues were reconstituted with 1200 μL of phosphate buffer (PBS; 0.05 M, pH 7.6) and frozen at −20°C until CORT was measured by radioimmunoassay (RIA). Since it is not possible to incorporate tritium into the growing feathers, we evaluated what percentage of CORT extracted from the feather and contained in the methanol is recovered by spiking the feathers with a known amount of H^3-CORT. Antiserum and purified CORT for standards were purchased from Sigma Chemicals, Oakville, Canada (Anti-Corticosterone product no. C8784, lot no. 090M4752; purified CORT product no. C-2505, lot no. 22K1439). All samples were extracted in one single batch and assessed the recovery efficiency of the methanol extraction by including feather samples spiked with approximately 5000 DPM of ^{3}H-CORT (Amersham Bioscience, Baie d'Urfe, Quebec). Ninety-one percentage of the radioactivity was recoverable in the reconstituted samples. $CORT_f$ concentration (pg/mm) was determined using RIA as in previous studies (Bortolotti et al. 2008). Antiserum and purified

CORT for standards were purchased from Sigma Chemicals. Samples were duplicated and randomly measured in the RIA. A parallel relationship was found between serial dilutions of reconstituted feather extracts and the standard curve. Assay variability was determined as the percentage of CV resulting from six samples of internal standard. Samples were measured in one single RIA with CV of 6% and limit of detection (ED 80) of 24.55 pg/assay tube. We corrected data by length because CORT deposition in growing feathers is hypothesized to be time dependent (see Bortolotti et al. 2008, 2009, Bortolotti 2010, Jenni-Eiermann et al. 2015).

Statistical procedure

We analyzed variation in the response variables NRQ and $CORT_f$ by means of linear models. The response variables were log-normalized, and multicollinearity between explanatory variables was assessed (VIF values <2 in all cases) prior to performing models in R software v 3.1.0 (R Development Core Team 2014). In each case, we included year, sex, home-range size (km^2), position (longitude coordinate) of each nest site, and a body condition index (residuals from the regression of body mass against wing length) as explanatory variables. Because the longitude coordinate was strongly correlated to the distance from the nest to the steppe ($r = -0.981$, $P < 0.001$), it was clear that this variable, but not the latitude, represents a good surrogate of distance from breeding to feeding areas. We included the longitude coordinate instead of the distance of the nest site to the feeding grounds in our models because some nests are located inside the steppe and, although they are located at variable distances from the feeding grounds, the distance values approach zero in all cases. We fitted alternative models by including single variables and also the two- and three-term additive combinations plus two-term interactions between the different explanatory variables.

Model selection was made on the basis of the Akaike's information criterion (AICc) corrected for small sample sizes to find the most parsimonious model (lowest AICc) and rank the remaining models (Burnham and Anderson 2002). Delta AICc (ΔAICc) was calculated as the difference in AICc between each model and the best model in the set. Following Burnham and Anderson (2004), we computed the Akaike weights (AICcω) to assess the mass of evidence in favor of each candidate model.

Results

Andean condor breeding sites were located from the west side of the Andean mountains (Chile) to the east part (Argentina), and even occurred inside the steppe in some cases, thus ranging from zero to 83 km (linear distances) from feeding areas (Fig. 1). The number of days we monitored individuals with a GPS device ranged from 65 to 174, with variation due to the device type (see *Materials and methods*), the performance of the device, as well as the date of deployment. Likewise, the number of fixes per individual varied from 899 to 6394. Birds moved between the breeding and feeding areas an average of 83 km/d (range 46–152 km, skewness = 0.99, kurtosis = 3.45, median = 54.54), covering an average home-range size of 7368 km^2 (kernel 95%, range 745–26,264 km^2).

Movement patterns differed between sexes. Thus, home ranges and maximum daily distances (but not mean distances) were significantly larger in males than in females (Table 1). A detailed inspection of the data indicated that, in general, males performed larger mean daily distances than females, yet with highly variable values that also included very short distances, which overlapped with those of females in some cases. These patterns might explain the lack of statistical differences in mean distances travelled between sexes. Within each sex, the values of these three variables were independent of the longitude position of the nest site (Spearman correlations, $P > 0.20$ in all cases).

Average telomere length (NRQ) of males (mean = 0.98 ± 0.18 standard error (SE) was longer than that of females (mean = 0.63 ± 0.19 SE), yet not significantly (Mann–Wilcoxon $\chi^2 = 2.19$, df = 1, $P = 0.15$). With regard to the variation in telomere length (log-NRQ), our information-theoretic approach yielded only one model with ΔAICc < 2 (see Table 2). This model showed that variation in telomere length was only explained by the longitude coordinate of the nest site, which represents the distance of the nest to the feeding areas (longitude: estimate [est]: 0.74 ± 0.33 SE), the sex (est: −101.12 ± 32.84 SE), plus the interaction between the two variables (est: −1.41 ± 0.46 SE).

Table 1. Summary statistics and comparison between sexes of the explanatory variables defining movement patterns of GPS-tagged individual Andean condors.

		Males	Females	Mann–Whitney *U* test	
Variable	Sample size	9	11	*Z*	*P*-value
Home range km^2	Maximum	53,254	27,231.8	−2.925	0.002
	Minimum	10,580	2670.7		
	Mean	25,230	8964.3		
	SD	16,371.87	6852.9		
Maximum distance km	Maximum	349.5	310.8	−2.469	0.012
	Minimum	238.3	197.2		
	Mean	292.3	248.3		
	SD	29.5	36.1		
Mean distance km	Maximum	152.3	117.8	−0.912	0.370
	Minimum	46.6	53.1		
	Mean	90.9	76.7		
	SD	32.2	21.3		

Note: Home ranges were computed as fixed kernel density estimators, with sizes defined as the areas encompassed within 95% isopleths.

None of the 95% confidence intervals (CI) for the parameter estimates included zero (sex: −170.73, −31.51; distance to the feeding areas: 0.03, 1.44; sex × distance: −2.39, −0.44), indicating that all these predictors significantly influenced variation in telomere length. As predicted, results for this model indicate that females showed shorter telomeres than males. In addition, variation in telomere length was strongly related to the location of the nest site (longitude), but in opposite directions for both sexes and with a stronger effect (steeper slope) in the case of males (Fig. 2). Thus, males breeding toward the Pacific coastal areas of Andean mountains showed longer telomeres than those breeding close to the steppe, while females breeding near to the coast showed shorter telomeres than those breeding in the steppe.

Levels of $CORT_f$ were negatively correlated with NRQ values (Spearman $\rho = -0.48$, $P = 0.03$), with those individuals showing higher $CORT_f$ levels having shorter telomeres. When analyzing sexes separately, this pattern was only statistically significant for females ($r = -0.69$, $P = 0.02$), but not for males ($r = -0.45$, $P = 0.22$). Again, we predicted a negative association between $CORT_f$ and distance from the nest site to the feeding grounds and foraging movement patterns. However, variation in log-$CORT_f$ levels was mainly explained by sex. We obtained three models with $\Delta AICc < 2$ (Table 2). The first model included only sex (est: −0.31 ± 0.10 SE) with females showing higher $CORT_f$ levels than males (Fig. 3). This model received much higher support (double Akaike weight) than the other two (see Table 2). Also, the 95% CI for the parameter estimates of this model did not include zero (−0.53, −0.09). The second model included sex (est: −0.30 ± 0.10 SE) and year (est: −0.13 ± 0.10 SE) with females exhibiting higher levels than males and slightly, yet not significant, higher $CORT_f$ values in 2010 than in 2011. In fact, the 95% CI did not include zero for sex (−0.51, −0.08), but they did for year (−0.34, 0.09) indicating a very low influence of this latter variable. The third model included sex (est: −0.32 ± 0.98 SE) and body condition (est: $-8.27 \times 10^{-05} \pm 7.38 \times 10^{-05}$ SE). Likewise, the 95% CI did not include zero for sex (−0.53, -9.50×10^{-02}), but they did for body condition (-0.00, 7.30×10^{-05}). Therefore, the most important variable explaining variation in feather corticosterone was the sex and thus the model with only this variable the best.

Discussion

To our knowledge, this is the first study reporting a spatial structure of telomere length in a wild long-lived vertebrate population. This pattern was, in addition, sex-specific; male condors breeding within the Andean mountain range and far from steppe feeding areas had longer telomeres, while females showed the opposite pattern. Although our cross-sectional approach only

Table 2. AICc-based model selection to assess the effect of individual and environmental variables on telomere length (logNRQ) and feather corticosterone ($logCORT_f$) values.

Model	AICc	ΔAICc	AICcω	R^2 adj
Telomere length				
Sex × long	20.47	0	1.00	0.37
Sex	23.04	2.57	0.28	0.10
Intercept	23.53	3.06	0.22	
Year	25.03	4.56	0.10	0.01
HR	25.06	4.59	0.10	0.01
Sex + year	25.11	4.64	0.10	0.10
Sex × BCI	25.32	4.85	0.09	0.20
Long	25.92	5.45	0.07	−0.03
Sex + BCI	26.17	5.70	0.06	0.05
Sex + HR	26.18	5.71	0.06	0.05
Sex + long	26.20	5.73	0.06	0.05
BCI	26.30	5.83	0.05	−0.05
Sex × HR	27.85	7.38	0.02	0.09
Sex × year	28.16	7.69	0.02	0.07
Sex + year + long	28.56	8.09	0.02	0.05
Sex + year + BCI	28.70	8.23	0.02	0.05
Sex + year + HR	28.73	8.26	0.02	0.05
Year × long	29.05	8.58	0.01	0.03
Year × HR	29.73	9.26	0.01	−0.00
Year + HR + long	30.26	9.79	0.01	−0.03
Year × BCI	30.55	10.08	0.01	−0.04
Year + HR + BCI	30.94	10.47	0.01	−0.07
HR × long	31.37	10.90	0.00	−0.09
HR + long + BCI	31.47	11.00	0.00	−0.09
HR × BCI	31.51	11.04	0.00	−0.10
Long × BCI	32.59	12.12	0.00	−0.16
Feather corticosterone				
Sex	3.11	0	1.00	0.30
Sex + year	4.49	1.38	0.50	0.32
Sex + BCI	4.85	1.74	0.42	0.31
Sex + HR	5.33	2.22	0.33	0.29
Sex + long	5.67	2.56	0.28	0.28
Sex + year + HR	6.41	3.30	0.19	0.34
Sex × BCI	6.62	3.51	0.17	0.33
Sex + year + BCI	7.41	4.30	0.12	0.30
Sex × long	7.78	4.67	0.10	0.29
Sex + year + long	7.98	4.87	0.09	0.28
Sex × year	8.05	4.94	0.08	0.28
Intercept	8.51	5.40	0.07	
Sex × HR	8.63	5.52	0.06	0.26
Year	9.49	6.38	0.04	0.04
BC	10.37	7.26	0.03	−0.01
HR	10.57	7.46	0.02	−0.02
Long	11.20	8.09	0.02	−0.05
Year × long	15.20	12.09	0.00	−0.03
Year + HR + BCI	15.29	12.18	0.00	−0.03
Year + HR + long	15.48	12.37	0.00	−0.04
HR × BCI	15.52	12.41	0.00	−0.04
Year × BCI	15.70	12.59	0.00	−0.05
Year × HR	15.88	12.77	0.00	−0.06
HR + long + BCI	15.90	12.79	0.00	−0.06
HR × long	16.66	13.55	0.00	−0.11
Long × BCI	16.84	13.73	0.00	−0.12

Notes: Akaike's second-order corrected information criterion (AICc) values, AICc differences (ΔAICc) with the highest ranked model (i.e., the one with the lowest AICc), Akaike weights (AICcω), and adjusted R^2 are shown. Explanatory variables: sex, year; long, longitude coordinate; HR, home range; BCI, body condition index. The symbol "×" denotes the independent effect of two variables plus their interaction.

shows a fixed picture, the negative relationship between nest site longitude and telomere length is extremely suggestive and leads to a suite of alternative interpretations.

Telomeres have been usually related with the biology of aging, and hence, they have been shown to shorten with age in many vertebrate species (Haussmann et al. 2003, Müezzinler et al. 2013). Accordingly, our results may imply that males breeding toward the Pacific coast are younger (having longer telomere length) than those breeding close to the steppe, while females showed the opposite, yet less evident, pattern. The trend found within males agrees with the largely known evidence that high quality, often older, raptors usually breed close to feeding areas (e.g., Sergio et al. 2007). The fact that the known highest breeding densities of Andean

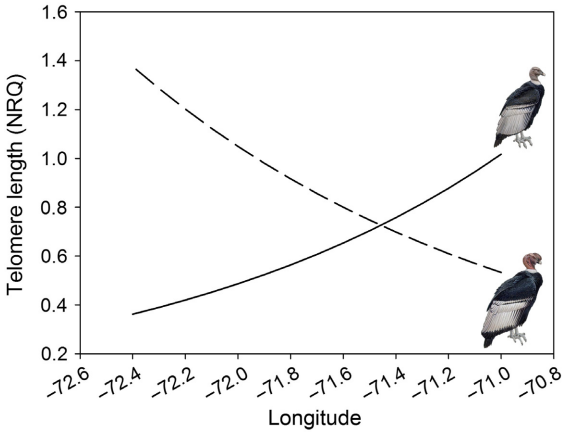

Fig. 2. Relationship between the telomere length (normalized relative quantity [NRQ]) and the longitude coordinate of the nest site for female (solid line) and male (dashed line) Andean condors. Condor drawings were modified from Sanchez et al. (1998).

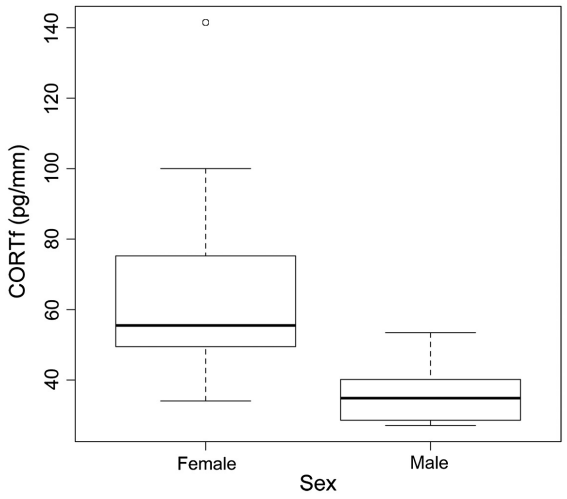

Fig. 3. Feather corticosterone ($CORT_f$) levels (pg/mm) of male and female Andean condors. The line within boxes indicates the median, the edges of the boxes indicate the first (Q1) and third (Q3) quartiles, and the whiskers extend 1.5 times the interquartile range.

condors are located near the steppe, in the eastern slopes of the Cordillera (S. Lambertucci, *unpublished data*), further supports that this area is of high quality. It seems clear that breeding in central or western slopes of the cordillera, and far from the steppe main foraging area, should impose important constraints linked to the necessity of crossing important topographical barriers and facing inclement weather (annual rainfall is up to 4000 mm), especially to a large-sized bird with very limited capacity for flapping flight (Pennycuick and Scholey 1984). These circumstances would decrease the quality of the mountainous areas for breeding, thus favoring their occupation by young and subordinate individuals. Nonetheless, it is surprising that those variables describing the daily range of movements performed by individual condors are unrelated to the variability in telomere length. However, an examination of the intrasexual variability of these movement patterns revealed that they were independent from the position (longitude coordinate) of the nest site relative to the foraging areas. In other words, condors breeding in areas far from the steppe foraging grounds do not perform longer daily movements than those breeding close. Actually, some Andean condors breeding within the steppe showed patterns of north–south foraging movements that covered the same or even larger areas than those covered in the east–west axis by the condors breeding in the Pacific coast, although the latter should necessarily face higher physiological costs when crossing the cordillera.

Following this reasoning, the question arises as to why female Andean condors do not follow a similar spatial structure of telomere length to that of males, but the opposite? This can be motivated by intersexual foraging niche differentiation and social dominance relationships, ultimately promoting human-induced female-biased mortality near the foraging steppe areas. During the last few decades, the Patagonian steppe has experienced an increased anthropization and, consequently, condors have been increasingly subject to direct and indirect persecution through shooting and poisoning, as well as casualties involving man-made structures (Lambertucci 2007, Lambertucci et al. 2011). Donázar et al. (1999) found that, due to intraspecific competition and social hierarchy, condors segregate at mesohabitat scale within the steppe, with adult females being relegated to scavenge in flatter and more humanized areas, while adult males forage mainly on the steep and safer slopes. Therefore, the observed structure of telomere length might be the outcome of asymmetric mortality events and higher turnover rates of those females breeding in this area, where new (and young) females would recruit into the breeding population. Indeed, sex-biased mortality toward female condors determines a skewed sex ratio in the adult fraction of the studied population with important consequences in its long-term viability (Lambertucci et al. 2012).

Telomere length might alternatively be reflecting biological, but not chronological age (Aviv 2002, Bize et al. 2009). Telomere damage is associated with internal metabolic processes, as well as external factors, causing oxidative stress (Kotrschal et al. 2007, Houben et al. 2008). Thus, the rate of telomere loss may be a useful biomarker of chronic oxidative stress (Houben et al. 2008, Young et al. 2015). Our results showed that female Andean condors had shorter telomeres than males (except at the eastern extreme distribution area), which would be reflecting that females, in general, experience higher levels of oxidative stress. Apart from potential genetic and endocrine causes (Horn et al. 2011), sex-specific

telomere loss rates have been proposed to be driven by different environmental conditions, physiological stress, and reproductive history experienced by each sex and not by chronological age (Pauliny et al. 2006, Reed et al. 2008, Young et al. 2013). The pattern of telomere length found within females agrees with that predicted. Therefore, females breeding farther from the feeding grounds would experience higher physiological costs associated with longer movements and adverse weather conditions than those breeding near this area. Furthermore, the subordinate status that yields to frequent intraspecific aggressions, the use of lower quality habitats, and lower access to food resources would result in increased loss of telomere lengths in females.

Accordingly, female condors had much higher levels of $CORT_f$ than males, regardless of nest location. Circulating CORT levels play a role in the regulation of parental care and have been positively correlated with foraging effort and provisioning rate in birds (Angelier et al. 2008, Bonier et al. 2011). However, in condors, both sexes share parental care, although we found they perform dissimilar foraging trips. Home-range sizes of male condors, as well as maximum daily distances, were larger than those of females. Carrete et al. (2013) reported that the Egyptian vulture (*Neophron percnopterus*), also a scavenger, showed higher levels of $CORT_f$ and larger home-range sizes when overwintering in Africa as compared to levels and home-range sizes measured during breeding in Europe. In addition, females had the largest home ranges at wintering quarters and higher $CORT_f$ than males (Carrete et al. 2013). We found, however, that female condors had comparatively smaller home ranges and higher $CORT_f$ than males. In a scenario of social conflict and competition for resources, concentrations of CORT will vary depending on how physiologically costly is to acquire and maintain dominant and subordinate status (see review in Goymann and Wingfield 2004). Subordinate females could elevate circulating CORT levels in response to physical and physiological threats from more dominant males (Abbott et al. 2003). Given that we measured the integrated amount of $CORT_f$, increased levels in females could be due to higher baseline concentrations and/or higher frequency of stressors. The high $CORT_f$ levels found in females may thus be mirroring recurrent stressful episodes, likely associated with social dominance hierarchy (Goymann and Wingfield 2004). In contrast, male condors would exploit larger areas in search of food, and the increased physiological costs of these long movements would be counterbalanced by a reduction in agonistic interactions through avoidance of intraspecific encounters at carcasses.

Alternatively, this pattern may be related to sexually dimorphic constraints and resolutions in trade-off associated with size differences between the sexes. Comparatively small females may have higher metabolic demands than males (Glazier 2008), and thus, higher $CORT_f$ levels as a by-product of increased mobilization of metabolic fuel during breeding and increased foraging effort needed to maintain homeostatic balance (McEwen and Wingfield 2003). Both chronic stress and elevated CORT are associated with increased oxidative stress and short telomeres (Epel et al. 2004), a pattern that precisely matches with the general trend of higher $CORT_f$ levels and shorter telomere length we found in females as compared to males. Interestingly, within-species negative associations between body size and telomere length have been recently shown in wild house sparrows (*Passer domesticus*) (Ringsby et al. 2015) and proposed as a feasible mechanism underlying the apparent trade-off between body size and longevity often found within vertebrate species (e.g., Kraus et al. 2013). Our results, however, seem to contradict this trend. Male Andean condors are larger than females, while showing longer telomeres. It is important to note that selective pressures could act in a reversed manner in this species as compared to other raptors, mainly due to the atypical direct sexual size dimorphism. Although we do not know how the long-term costs associated with larger size are incurred, these could be linked to changes in telomere dynamics. These changes either as a correlated trait or a consequence of larger size could reduce potential longevity of larger individuals (Ringsby et al. 2015). Thus, our results would imply that older males, even if they are of the same chronological age than females, could have died already. Alternatively, the long-lasting stressful conditions experienced by females could mask the actual pattern of telomere length attributable to their lower body size. Therefore,

females would invest more in traits that increase immediate survival, such as circulating CORT, even if they come at a cost to traits associated with longevity, such as telomere length.

Studies aimed at exploring connections between physiological stress and cellular aging in non-human or model organisms are still scarce. Haussmann et al. (2011) reported that embryonic exposure to experimentally increased CORT resulted in higher levels of reactive oxygen metabolites and an overrepresentation of short telomeres compared with control birds, thus hastening aging and ultimately increasing mortality. Therefore, telomere length can be viewed as an integrative measure of both telomere dynamics and glucocorticoid-induced oxidative stress, and all are thought to influence longevity (Haussmann and Marchetto 2010, Haussmann et al. 2011). Furthermore, recent evidence suggests that exposure to stressors experienced by the parental generation can have long-term, cross-generational effects for offspring health, a relationship mediated in part by telomere dynamics (see review in Haussmann and Heidinger 2015). The conserved nature of both the glucocorticoid stress response and telomeres suggests that the links found between exposure to stressors and telomere dynamics in a few species, mostly humans and model organisms, are likely to occur in all vertebrates (Haussmann and Heidinger 2015).

Our study highlights that parallel variations in telomere length and concentrations of CORT may appear in a sexually dimorphic species with a highly despotic social system and divergent sex-specific foraging strategies. Sexual differences in the optimal resolution of trade-offs associated with food acquisition and the social environment might underlie the fact that populations are spatially structured from a telomere-length perspective, which has never been described before. This novel finding gives rise to stimulating questions for evolutionary and ecological studies, such as the potential links between environmental conditions, physiological-oxidative stress, and aging, and how they impact performance and life-history trajectories of long-lived organisms.

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