RESEARCH ARTICLE

Exercise training has morph-specific effects on telomere, body condition and growth dynamics in a color-polymorphic lizard

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ABSTRACT

Alternative reproductive tactics (ARTs) are correlated suites of sexually selected traits that are likely to impose differential physiological costs on different individuals. While moderate activity might be beneficial, animals living in the wild often work at the margins of their resources and performance limits. Individuals using ARTs may have divergent capacities for activity. When pushed beyond their respective capacities, they may experience condition loss, oxidative stress, and molecular damage that must be repaired with limited resources. We used the Australian painted dragon lizard that exhibits color polymorphism as a model to experimentally test the effect of exercise on body condition, growth, reactive oxygen species (ROS) and telomere dynamics – a potential marker of stress and aging and a correlate of longevity. For most males, ROS levels tended to be lower with greater exercise; however, males with yellow throat patches – or bibs – had higher ROS levels than non-bibbed males. At the highest level of exercise, bibbed males exhibited telomere loss, while non-bibbed males gained telomere length; the opposite pattern was observed in the no-exercise controls. Growth was positively related to food intake but negatively correlated with telomere length at the end of the experiment. Body condition was not related to food intake but was positively correlated with increases in telomere length. These results, along with our previous work, suggest that aggressive – territory holding – bibbed males suffer physiological costs that may reduce longevity compared with non-bibbed males with superior postcopulatory traits.

KEY WORDS: Alternative mating tactics, Telomere lengthening, Reptiles, *Ctenophorus pictus*, Painted dragon lizards

INTRODUCTION

Many behaviors that are crucial for survival and reproductive success rely on performing stressful, intense or sustained levels of physical activity, including foraging, escaping from predators, migration, courtship displays and territorial defense (Arnold,

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1983). The link between these critical activities and the investment in life-history and sexually selected traits can involve the energetics of resource allocation (Van Noordwijk and de Jong, 1986), physiological stress (Zera and Harshman, 2001) and tradeoffs between self-maintenance, growth and reproduction (Monaghan, 2014; Pontzer, 2018; Roff, 1992; Soulsbury and Halsey, 2018; Speakman et al., 2015). In humans, it is well established that moderate regular exercise has a salubrious effect on immunity, reproduction and stress responses (Pontzer, 2018). However, for example, individual humans vary in how they respond to the intensity and duration of exercise training, exhibiting so-called 'exercise phenotypes' that are associated with allelic variants at several genomic loci (e.g. Bouchard et al., 2011; Bray et al., 2009; Nickels et al., 2020). An extreme example of how activity influences the expression of life-history, reproductive and sexually selected traits is hypogonadism, which is common in ultra-endurance and elite athletes (Hackney, 2020; Nickels et al., 2020). It is also generally well established that when humans engage in acute, extremely intense and prolonged exercise, they suffer from increased oxidative damage (Pontzer, 2018; Powers and Jackson, 2008) and shortened telomeres (Borghini et al., 2015; Denham, 2019; Ludlow et al., 2013; Nickels et al., 2020).

Telomeres are the protective endcaps of chromosomes composed of a repeating sequence of nucleotides – TTAGGG – and associated protein complexes (Blackburn, 1991; Palm and de Lange, 2008). Telomeres shorten with successive cellular divisions *in vitro* and *in vivo* (Allsopp et al., 1995; Monaghan and Ozanne, 2018) and are damaged by an excess of reactive molecules (e.g. oxygen-based free radicals, and reactive oxygen and nitrogen species – henceforth ROS for simplicity; von Zglinicki, 2002). ROS are the natural products of metabolic processes such as the oxidative bursts of immune cells, cellular inflammation responses and ATP production during oxidative phosphorylation in mitochondria (Reichert and Stier, 2017; von Zglinicki, 2002). ROS-induced damage (oxidative stress), and the consequent telomere erosion, is associated with metabolism, disease, parasite load and inflammation (Asghar et al., 2015; Monaghan, 2010; Monaghan and Haussmann, 2006; Monaghan et al., 2009; Sudyka et al., 2019), physical and psychosocial stress (Bebbington et al., 2017; Haussmann and Heidinger, 2015), poor nutrition (Noguera et al., 2015), reproductive effort (Sudyka, 2019; Sudyka et al., 2014) and growth (Geiger et al., 2012; Näslund et al., 2015). The activity of the enzyme telomerase can restore telomere length (Gomes et al., 2010) and other alternative lengthening mechanisms (Cesare and Reddel, 2010). However, telomerase activity and telomere maintenance come at an energetic expense (Young, 2018) and may also be suppressed in many tissues because telomerase expression can promote oncogenesis (cancer) (Gomes et al., 2010; Olsson et al., 2017).

A key problem in telomere biology that has received less scrutiny is our lack of understanding of the factors that underpin individual variation in telomere dynamics and how that might affect or interact with other evolutionary processes. Short telomeres and telomere erosion are candidate biomarkers of the accumulated stressors an individual has endured through life and indicate damage not yet repaired (Monaghan et al., 2018; Wilbourn et al., 2018). These accumulated stressors may link shortening of telomeres with mortality risk (Wilbourn et al., 2018). Indeed, relatively short telomeres are often better predictors of early mortality than chronological age in some species (Schultner et al., 2014; Tricola et al., 2018). Furthermore, individuals of some species with longer telomeres tend to have higher relative reproductive fitness (e.g. sand lizards: Olsson et al., 2011; Pauliny et al., 2018). All else being equal, there is some evidence that differences in telomere length and shortening among individuals reflect their quality (e.g. high breeding and immune function performance; e.g. Le Vaillant et al., 2015). When individuals vary in character states, trait-associated telomere erosion suggests a correlated cost of those traits and disparate investment in them at the expense of telomere maintenance. For example, painted dragon lizards exhibit a negative correlation between sexually selected color and telomere maintenance (e.g. Giraudeau et al., 2016; Rollings et al., 2017). Likewise, telomere erosion may be a useful indicator of the cost of intense and sustained activity or behavior (e.g. Sudyka et al., 2014).

Although we may think of wild animals as highly tuned, high-performance athletes (Irschick and Higham, 2015), their activities incur costs. Fish subjected to only two acute bouts of exhaustive exercise exhibit immediate exercise-induced DNA damage (Aniagu et al., 2006); active and aggression-prone phenotypes may also suffer high telomere erosion (Adriaenssens et al., 2016). In birds, migration reduces antioxidants (Cooper-Mullin and McWilliams, 2016) and shortens telomeres (Bauer et al., 2016; Schultner et al., 2014), and even non-migratory activity increases mortality (Daan et al., 1996; Sudyka et al., 2014). Across vertebrates, endurance and high-intensity activities stimulate the release of glucocorticoids to mobilize energy reserves (e.g. reproductive effort; Bauch et al., 2016). Unless energy reserves are replaced, these activities reduce the availability of those resources for protective and maintenance functions. Glucocorticoids are linked to oxidative stress (Costantini et al., 2011) and to shorter telomeres across different animals (Angelier et al., 2018). Thus, activities that increase evolutionary fitness are also likely to incur costs reflected as telomere erosion.

In lizards, the males of many species patrol and aggressively defend territories (Olsson, 1993; Olsson and Madsen, 1998; Stamps, 1983). Both natural and sexual selection generate directional selection for improved physical performance, such as endurance or sprint speed (Husak and Fox, 2008; Irschick et al., 2008). Faster males are better at defending territories and sire more offspring (Husak et al., 2006, 2008), but performance comes at a cost. Aggressive territorial behavior is energetically expensive and stressful, reducing survival (Marler and Moore, 1988, 1989; Marler et al., 1995). Resource supplementation mitigates some of these effects, suggesting that resource allocation tradeoffs may be an essential factor to consider (Marler and Moore, 1991). However, juvenile lizards fed ad libitum and experimentally trained for endurance show reduced immune function (Husak et al., 2017). Endurance-trained lizards also have diminished survival versus sedentary controls when released into the wild (Husak and Lailvaux, 2019).

Color-polymorphic species are a valuable tool in resolving the interplay between sexually selected and life-history traits. The polymorphism is often a convenient visual code for an individual's associated behaviors and physiology in the otherwise similar genetic background (Stuart-Fox et al., 2021). Here, we tested whether the costs of mating strategies can be evaluated by experimentally manipulating activity levels and measuring telomere erosion in an Australian color-polymorphic lizard, painted dragons (Ctenophorus pictus). Male painted dragons are polymorphic for head color: red, orange, yellow and blue (i.e. the same as body color) (Olsson et al., 2007b). The presence or absence of a yellow gular patch, or 'bib', is also a male-polymorphic trait (Olsson et al., 2009a). Maintaining coloration is costly, and color fades over the breeding season, at least partly in response to oxidative stress (Giraudeau et al., 2016; Olsson et al., 2012). These color traits correspond with alternative reproductive tactics (Friesen et al., 2016; Healey et al., 2007; McDiarmid et al., 2017; Olsson et al., 2007a, 2009b) and telomere length, which may be mediated by metabolism and oxidative stress (Friesen et al., 2017a; Olsson et al., 2018a; Rollings et al., 2017). In these dragons, both color and oxidative status are at least in part determined by genetics (Olsson et al., 2007b, 2009c, 2008). In the lab, mitochondrial superoxide (SOx) levels (an indicator of oxidative status) are negatively correlated with body condition and endogenous antioxidant activity (Friesen et al., 2019, 2017b).

We tested whether activity level and food consumption may explain morph-specific differences in telomere length and the loss of body condition observed in wild-caught animals (Healey and Olsson, 2009; Olsson et al., 2009a). We measured telomere erosion in response to manipulated activity (two levels of enforced exercise and a control treatment) over a month. We predicted that the more aggressive morphs (i.e. red-headed males and bibbed males of any head color) would have higher ROS and suffer more significant telomere erosion than the other morphs (i.e. orange, yellow and blue males and non-bibbed males of any color) as a result of exercise treatment (Olsson et al., 2018b, 2017). We predicted that telomere attrition would be most pronounced at the highest level of exercise but would also be mediated negatively by ROS levels and positively by body condition and food consumption. A simple negative relationship between growth and telomere erosion is unlikely given the potentially complex relationships between condition, food intake and morph-types, and the fact that lizards have indeterminate growth (Shine and Charnov, 1992); nevertheless, cellular replication and energy expenditure are often associated with growth and telomere loss (Casagrande and Hau, 2019; Monaghan and Ozanne, 2018).

MATERIALS AND METHODS
Animal collection
The Animal Ethics Committee at the University of Sydney authorized this work (AE20136050), and the lizards were collected under NSW National Parks and Wildlife Service Scientific license (SL100352). Australian painted dragons, Ctenophorus pictus (W. Peters 1866), are small (adult snout–vent length, SVL, 65–95 mm; mass 8–16 g) diurnal lizards of sandy habitats and low vegetation, with a range covering central New South Wales to Western Australia (Cogger, 2014). Ctenophorus pictus are annuals, with over 90% dying within 1 year in this population (Olsson et al., 2007b). We caught 56 mature (~9 months old) male lizards by noose or hand at Yathong Nature Reserve, NSW, Australia (145°35′E, 32°35′S) during the Australian spring (ca. mid-October, early in the breeding season). We exhaustively sampled with daily repeated passes along a ~15 km transect over 7 days; hence, our sample should approximately represent natural head color and bib morph frequencies in the wild at the time – head color: red $n=15$ (26.8%), orange $n=13$ (23.2%), yellow $n=17$

(30.4%), blue n=11 (19.6%); bib-morphs: bibbed n=20 (35.7%), non-bibbed n=36 (62.3%). The animals were held in facilities at the University of Sydney, where they were housed individually in opaque plastic enclosures (330×520×360 mm) with a sandy substrate and exposed to a 12 h:12 h light cycle. We fed each lizard exactly four mealworms (of the same size class) lightly dusted with calcium and multivitamins every other day. We misted the enclosures with water once per day. Before each feeding, we removed and tallied the number and proportion of uneaten worms, which allowed us to calculate food consumption throughout the experiment. Heat lamps and ceramic hides allowed the lizards to thermoregulate (preferred body temperature ∼35–36°C; Melville and Schulte, 2001).

Exercise treatments
Head color and bib morphs were distributed among one of three endurance exercise treatment groups: no exercise (0X, N=18), light exercise (1X, N=19) and heavy exercise (3X, N=19). Endurance exercise was similar to a previous protocol (Tobler et al., 2012; Uller and Olsson, 2003, 2006), which consisted of letting the lizards swim in a water bath (60 cm×60 cm and 20 cm deep) of constant temperature (34–36°C, monitored using a thermometer). Lizards were individually transferred directly from their home enclosures into the water, where they naturally began to swim using an undulatory motion. When a lizard stopped swimming, he was persuaded to continue with a light tap to the tail. If, after three consecutive taps, the lizard did not resume swimming, he was considered to be exhausted and returned to his home enclosure. Light exercise males (1X) swam once to exhaustion before removal to their home enclosure. Heavy exercise males (3X) swam to exhaustion 3 times with 30 min recovery periods spent in their home enclosure between swims. No-exercise males (0X) were used to control for handling effects: each was caught, picked up and placed in a water bath (60×60 cm and 2 cm deep; 34–36°C) for 3 min (∼average of an exhaustive swim), and returned to their cage. All treatments (0X, 1X, 3X) were administered 3 days per week for approximately 4 weeks, beginning 4 November and ending 3 December. This period corresponds to the mid-to-late period of the breeding season.

We ensured that none of the exercise treatment groups had an overabundance of 'high-endurance' exercise phenotype lizards, by timing all males during exercise to exhaustion the day before allocating them to a group (there was no difference pre-allocation between treatment groups in the time until exhaustion, $F_{2,53}$=1.803, P=0.175). We collected blood samples and recorded body mass (to 0.01 g) and SVL (to 1 mm) before the experiment commenced (late October) and immediately after the experiment (early December). The blood samples were used for telomere and ROS measurements. The same trained, experienced and repeatable operator took the SVL measurements (±<1 mm). Three males died (one from 3X and two from 0X) at different points in the experimental period (no significant effect of treatment), leaving 53 survivors. This mortality rate (∼5%) is typical in the lab for this short-lived dragon (C.R.F. and M.O., personal observation).

Sample collection
Blood sampling
We sampled blood (∼100 µl) from each lizard before and after the treatment period by using a capillary tube and gently perforating the vena angularis (in the corner of the mouth). An aliquot of peripheral blood (10 µl) from each male was diluted with nine volumes of phosphate-buffered saline (PBS; 137 mmol l⁻¹ NaCl, 2.7 mmol l⁻¹

KCl, 1.5 mmol l⁻¹ KH$_2$PO$_4$, 8 mmol l⁻¹ Na$_2$HPO$_4$, pH 7.4) and stored on ice prior to ROS analysis (see below). The remaining blood was centrifuged, the plasma removed, and the remaining pellet of nucleated red blood cells was resuspended in 200 µl of PBS and stored immediately at −80°C for later use in qPCR quantification of telomeres (we avoided the top layer or 'buffy coat' of the pellet that sits above the red blood cells, as it contains the white blood cells and may affect telomere length measurement; Olsson et al., 2020).

Quantifying relative telomere length (rTL)
These methods have been described in detail elsewhere (Rollings et al., 2017, 2014). In brief, we purified DNA from 50 µl blood using a DNeasy Blood and Tissue Kit (Qiagen), according to the manufacturer's instructions. RNase A (Qiagen) was added at the recommended concentration. The DNA concentration (ng µl⁻¹) of each sample was measured in duplicate using a Pherastar FS (BMG, Labtech, Germany) and aliquots diluted to 10 ng µl⁻¹ using the AE buffer provided in the DNA extraction kit. Telomere length was measured using real-time quantitative PCR (qPCR) and a SensiMix SYBR No-ROX Kit (Bioline, Sydney, Australia). The telomere primers used were Tel1b (5′-CGGTTTGTTTGGGTTTGGGTTT-GGGTTTGGGTTTGGGTT-3′) and Tel2b (5′-GGCTTGCCTTA-CCCTTACCCTTACCCTTACCCTTACCCT-3′) (Criscuolo et al., 2009). The 18S ribosomal RNA (*18S*) gene (92 bp amplicon in *Anolis*) was selected as the reference gene, as it had previously been validated in a reptile (Plot et al., 2012) including this species (Rollings et al., 2017). The primer sequences used were 18S-F (5′-GAGGTGAAATTCTTGGACCGG-3′) and 18S-R (5′-CGAACC-TCCGACTTTCGTTCT-3′). The melt curves produced for both telomere and 18S after amplification by qPCR displayed a single peak, indicating specific amplification of the target DNA sequence. qPCR was performed in a final volume of 20 µl for both telomeres and 18S. A 10 ng sample of DNA was used per reaction, and the primers were used at a concentration of 250 nmol l⁻¹. For each reaction, 11.25 µl SensiMix SYBR No-ROX Master Mix (Bioline) was added, and MgCl$_2$ was added for a reaction concentration of 1.7 mmol l⁻¹. Reactions were run in triplicate for each sample. Amplifications were carried out in a Rotor-Gene 6000 thermocycler (Qiagen) using an initial Taq activation step at 95°C for 10 min, and a total of 40 cycles of 95°C for 15 s, 60°C for 15 s and 72°C for 15 s. A melt curve was created over the temperature range of 60 to 95°C after each run to ensure no non-specific product amplification. No-template control reactions were run in triplicate for each primer set during every qPCR run to ensure no contamination. Standard curves were created using the blood of a randomly selected lizard, for both telomeres and 18S, to ensure consistent rates of amplification over a wide range of DNA concentrations. The reaction was considered consistent when a straight line with an R^2 value exceeding 0.985 could be fitted to the values obtained. The efficiency of the telomere amplification was 1.05, and the efficiency of the 18S amplification was 0.96. LinRegPCR 2015.2 (Ruijter et al., 2009a,b,c; Tuomi et al., 2010) was used to analyze the qPCR data.

Quantifying SOx and other ROS
Mitochondrial SOx and general ROS analyses were completed within 4 h of sampling blood. Before staining, diluted blood was diluted a further 50-fold with PBS and then centrifuged (300 **g** for 5 min) to pellet cells; each cell pellet corresponded to 10 µl of whole blood. Cells were resuspended in 100 µl of PBS containing no additions (unstained control), 5 µmol l⁻¹ MitoSOX Red (MR; Thermofisher; detects SOx) or 0.1 mmol l⁻¹ dihydrorhodamine 123

(DHR; Thermofisher; detects reactive intermediates such as peroxide and peroxynitrite).

The fluorescence from these probes can be used to detect, respectively, SOx ions (MR) and hydrogen peroxide and peroxynitrite (DHR). MR and DHR were added from stock solutions in dimethylsulfoxide (DMSO); the final concentration of DMSO was 0.2% (v/v) or less. Cells were subsequently incubated at 36°C for 30 min, then washed with PBS by centrifugation as described above, and held on ice until analysis by flow cytometry. A total of 50,000 events were acquired for all samples. Flow cytometry was performed using a Becton Dickinson LSRFortessa X20, with excitation at 488 nm for both MR and DHR, and emitted fluorescence was collected using bandpass filters of 575±13 nm for MR and 515±10 nm for DHR. Data were acquired and analyzed using FACSDiva v4.0.1 (Becton Dickinson, Sydney, Australia) and FloJo (v9.1; TreeStar Inc.) software, respectively. On the basis of forward angle laser scatter and side angle laser scatter, a number of blood cell populations were discerned; the results obtained were similar for all these populations. For each sample, the arithmetic mean fluorescence for all 50,000 cells acquired was determined using FloJo software and used to compare between samples and treatments. The accuracy and consistency within a sample period of flow cytometry results have been validated in our previous work ($r=0.97$, $P<0.001$; see Olsson et al., 2009c, for further details).

Data preparation and statistical analyses

Body condition index (BCI) was calculated as the residuals from a regression analysis of mass as a function of SVL, which renders BCI independent of body length ($r=-0.138$, $P=0.325$). BCI is useful because it positively correlates with energy reserves and the endogenous antioxidant superoxide dismutase (SOD) (Friesen et al., 2019; Friesen et al., 2017b). SOx and general ROS measurements were collected on successive days within both sampling periods (late October and early December); thus, we standardized measurements (z-transformation) within the day the measurements were taken to account for potential batch effects (Friesen et al., 2019; Nakagawa et al., 2017).

The dependent variables, rTL, BCI, SVL, body mass, SOx and general ROS (ROS, hereafter), were tested for the effects of exercise on the change from the beginning to the end of the experimental period (Δ=final/end−initial/beginning value), e.g. ΔrTL, ΔBCI and ΔSVL values, but we also tested for correlations among the Δ variables, such as ΔrTL versus ΔBCI, as well as correlations such as ΔrTL versus food intake and SOx and general ROS.

We first tested for correlations between variables to explore how variables might interact to explain changes in ΔrTL. We used both Kendall's tau and Spearman's rho non-parametric tests (using their congruence as a sensitivity test) when either variable in a correlation test failed normality as determined by Kolmogorov–Smirnov tests. Both Spearman's rho and Kendall's tau correlations are reported when they gave different results in terms of significance at $\alpha \leq 0.05$. Otherwise, Pearson correlations are reported when both variables passed tests of normality. We also used non-parametric tests to explore differences in the dependent variables between morphs (Kruskal–Wallis, k number of groups >2; and Mann–Whitney, k=2) and exercise regimes (Jonckheere–Terpstra post hoc test for ordered differences in treatment effects, i.e. levels of exercise).

We conducted GLM analyses to investigate the effect of exercise treatment on ΔrTL, ΔBCI, ΔSVL, ΔROS and ΔSOx, as well as the associations of these variables with head color and bib morphs and morph×exercise interactions. We did not include a three-way

interaction because of the sample size. We constructed initial 'full' GLM models with exercise, head color, bib, exercise×head-color, and exercise×bib as fixed factors. To avoid drawing inferences from an over-fitted model, we reduced the full model by only retaining variables that improved model fit as indicated by a ΔAICc (Akaike information criterion for small sample sizes) of ≤ 2.0, stopping when the model was not improved by removing variables (Konishi and Kitagawa, 2008). If an interaction was retained, then we also included both fixed terms of the interaction regardless of their statistical significance. We omitted initial rTL as a covariate to control of regression of the mean effects because adding this covariate can bias or erroneously inflate differences between groups (Bateson et al., 2019). Pairwise post hoc analyses employed the Benjamini–Hochberg procedure to control false discovery rates, but the full tables are available from Dryad (dryad.z8w9ghxbx). In the figures, we present standardized (mean=0, s.d.=1) GLM-estimated means and 95% confidence intervals (CI) as error bars (Nakagawa et al., 2017; Verhulst, 2020). We also include a dashed line on the z-score scale that indicates '0', or no change, on the original scale.

With the exception of ΔSVL, all of the Δ response values adhered to assumptions of normality (Kolmogorov–Smirnov tests, all $P>0.200$: ΔSVL Kolmogorov–Smirnov distance=0.196, $P<0.001$). ΔSVL was further evaluated by visual inspection (histogram Q–Q and P–P plots) and by generating the kurtosis (1.6197) and skewedness statistics (0.7833, s.e.=0.3274:). Positive kurtosis greater than zero indicated that the ΔSVL data exhibited more extreme outliers than a normal distribution. This distribution of ΔSVL had a long right tail and significant positive skewness (skewedness >2×s.e.). Q–Q plots generated by fitting ΔSVL to a gamma distribution indicated a good fit, so we modeled ΔSVL with a GLM (gamma distribution, log-link function) after adding 2 mm to each ΔSVL measurement to eliminate zeros from the dataset to conform with the assumptions of a gamma distribution GLM, but we plot raw values including 'negative growth' in SVL. We note that while measurement error may in part explain why we have 'negative growth' in ∼20% of the males, there is a precedent for shrinkage in lizards (Wikelski and Thom, 2000); the same experienced person measured all lizards, and intra-operator measurement error tends to be small in lizards (Bulakhova et al., 2011). In any case, the error should be randomly distributed across telomere lengths (and morphs). We report the median, range, and percentage change of initial SVL and the GLM estimated means and 95% confidence intervals in original units.

All statistical analyses were performed in SPSS 25.0 (IBM, Armonk, NY, USA) and Sigma Plot 13.0 (Systat Software Inc. San Jose, CA, USA). The dataset can be accessed from Dryad (dryad.z8w9ghxbx; Friesen et al., 2021).

RESULTS

Morph-specific changes in rTL

rTL was rank consistent between an individual's measurement before and after exercise treatment [Spearman's ρ=0.714, $P<0.001$; intraclass correlation coefficient (ICC)=0.880, 95% CI 0.800–0.929, $P<0.001$].

The patterns of ΔrTL depended significantly on the interaction between exercise treatment and each morph type (Table 1). Non-bibbed males exhibited telomere erosion at the 0X level of exercise but gained telomere length at the 1X and 3X levels of exercise. Bibbed males exhibited the opposite relationship (Fig. 1A; see Table S1 in Dryad, dryad.z8w9ghxbx). The interaction of exercise and head color was significant but not straightforward (Fig. 1A).

Condition and growth

Food consumption

Males ate most of the food offered to them (median 91.1%, excluding one male that ate only 26.7% of his food; the food eaten by the remainder of the males ranged from 66.7% to 100%). There was no difference in the percentage of food consumed across exercise treatments (Jonckheere–Terpstra test: $z_{d.f.3}=-1.487$, $P=0.137$). There was weak evidence of a difference among morphs (Kruskal–Wallis
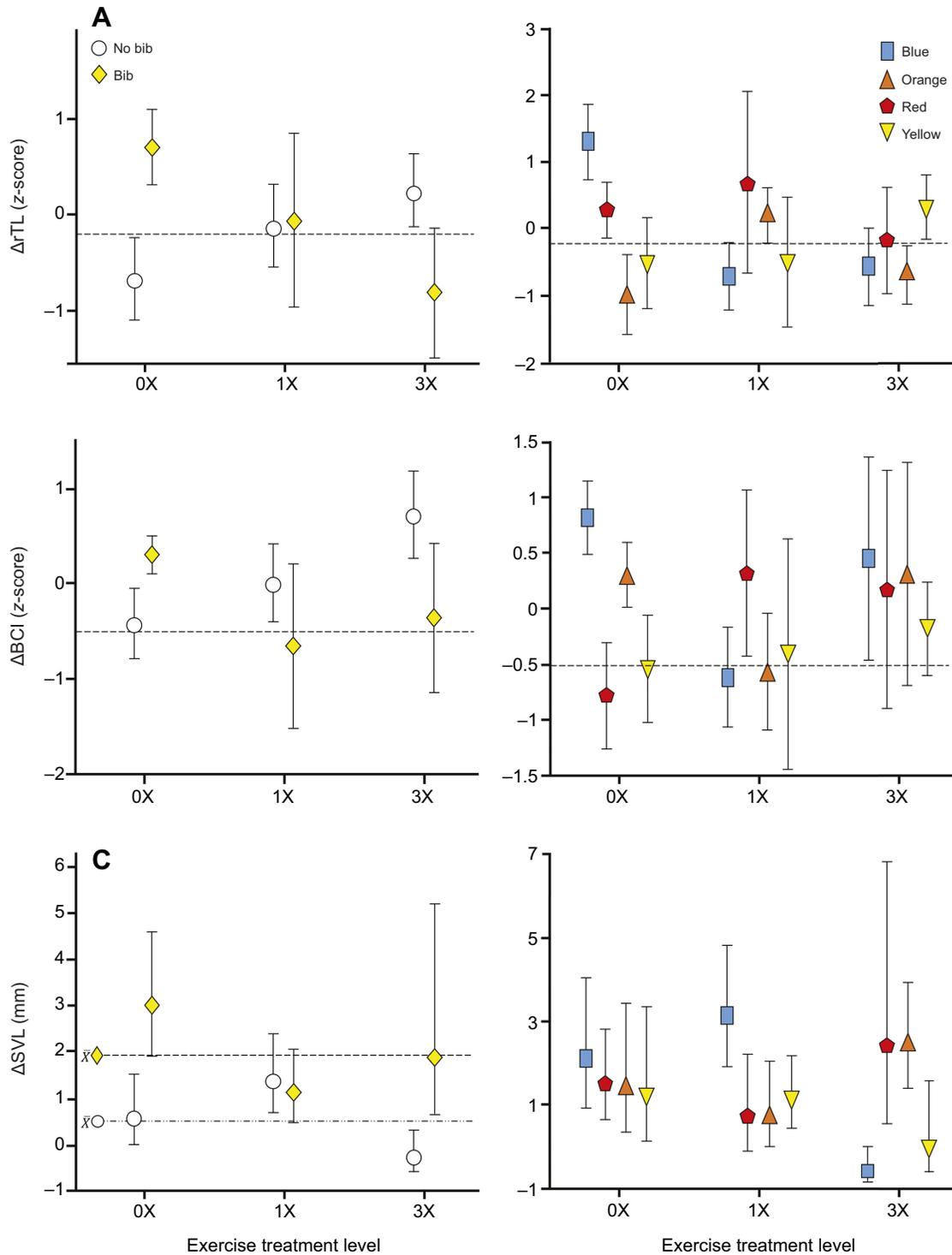

Fig. 1. Interaction plots of exercise and morph types of painted dragons. (A–C) Change in (A) relative telomere length (ΔrTL), (B) body condition index (ΔBCI) and (C) growth (snout–vent length; ΔSVL) for lizards in the three exercise conditions: 0X, no exercise; 1X, light exercise; 3X, heavy exercise. Plots on the left are of bib morphs, and those on the right are head color morphs. ΔrTL and ΔBCI were standardized (z-transformation), and ΔSVL is plotted as the raw untransformed difference in SVL. All symbols are centered on the estimated mean, and the bars represent 95% confidence interval estimates of the mean from generalized linear models. The dashed horizontal lines in A and B represent '0' or 'no change' on the original unstandardized scale. The dashed horizontal lines in C for bib morphs represent the overall mean of each morph as indicated by the symbol to the left.

Table 1. ΔrTL

Source	Likelihood ratio χ^2	d.f.	P-value
Full model vs intercept-only model	25.356	14,38	**0.031**
Test of model effects	Wald χ^2	d.f.	Type III
Exercise treatment	1.341	2,38	0.512
Head color morph	5.408	3,38	0.144
Bib	0.059	1,38	0.808
Exercise treatment×head color morph	47.532	6,38	**<0.001**
Exercise treatment×bib	19.330	2,38	**<0.001**

The change in relative telomere length (ΔrTL; end−beginning) was analyzed by GLM (normal, identity link function). Bold indicates significance at $P \leq 0.05$.

Table 2. ΔBCI

Source	Likelihood ratio χ^2	d.f.	P-value
Full model versus intercept only model	36.906	14,38	**0.001**
Test of model effects	Wald χ^2	d.f.	Type III
Exercise treatment	2.777	2,38	0.250
Head color morph	4.612	3,38	0.203
Bib	2.060	1,38	0.151
Exercise treatment×head color morph	21.402	6,38	**0.002**
Exercise treatment×bib	18.777	2,38	**<0.001**

The change in body condition index (ΔBCI; end−beginning) was analyzed by GLM (normal, identity link function). Bold indicates significance at $P \leq 0.05$.

$H=7.752$, $P=0.051$, but group medians ranged from 86.7% to 97.8%). There was no evidence of a difference between bib-morphs (Mann–Whitney $U=346.5$, $P=0.661$). Food consumption was not significantly correlated with ΔrTL (Spearman's $\rho=-0.214$, $P=0.124$) or ΔBCI (Spearman's $\rho=0.046$, $P=0.741$) but was positively correlated with ΔSVL (Spearman's $\rho=0.295$, $P=0.032$). There was mixed evidence that ΔSOx (see below) and ΔROS were positively correlated with food consumption depending on the statistical test used (ΔSOx, Spearman's $\rho=0.262$, $P=0.058$; Kendall's $\tau=0.201$, $P=0.041$; ΔROS, Spearman's $\rho=0.263$, $P=0.058$).

ΔBCI
BCI rank was consistent between an individual's measurement before and after exercise treatment (Spearman's $\rho=0.723$, $P<0.001$; ICC=0.661, 95% CI 0.414–0.806, $P<0.001$).

Overall, across all males, body condition tended to increase through the treatment period (paired t-test; $t_{52}=3.705$, $P<0.001$); however, visual inspection of the data indicated some males lost condition while others gained it. ΔBCI was positively correlated with ΔrTL ($r=0.316$, $P=0.021$; Fig. 2).

ΔBCI was also affected by exercise treatment through interactions with head color and bib morph (Table 2). The patterns of ΔBCI across exercise treatments in both bibbed and non-bibbed males were congruent with the patterns in ΔrTL. That is, the trend in ΔBCI was 0X>1X>3X for bibbed males, but 0X<1X<3X for non-bibbed males (Fig. 1B). Similarly, the patterns of ΔBCI and ΔrTL were congruent across exercise treatments in blue morphs, but there was no clear pattern of ΔBCI across exercise treatments in the other three morphs (Fig. 1B).

Growth
Growth in length (ΔSVL) was not correlated with ΔBCI (Spearman's $\rho=-0.171$, $P=0.222$) nor with change in body mass (ΔMass: Spearman's $\rho=-0.091$, $P=0.516$). ΔSVL and ΔrTL were not correlated (Spearman's $\rho=0.010$, $P=0.975$); however, ΔSVL was negatively correlated with rTL at the beginning of the experiment (initial rTL, Spearman's $\rho=-0.341$, $P=0.012$) and
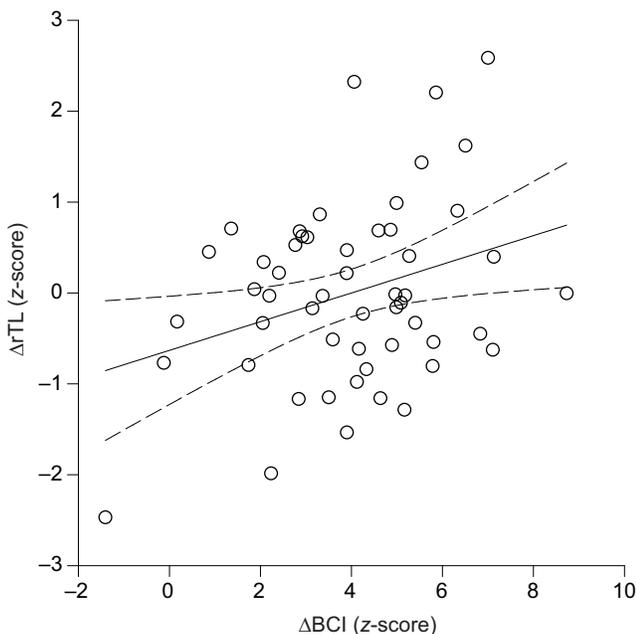
Fig. 2. Relationship between ΔrTL and ΔBCI of painted dragons from the beginning to the end of the exercise period. ΔBCI was positively correlated with ΔrTL ($r=0.316$, $F_{1,51}=5.654$, $P=0.021$). Both variables were standardized (z-transformation). The dashed lines represent the 95% confidence limits of the slope of the regression line.
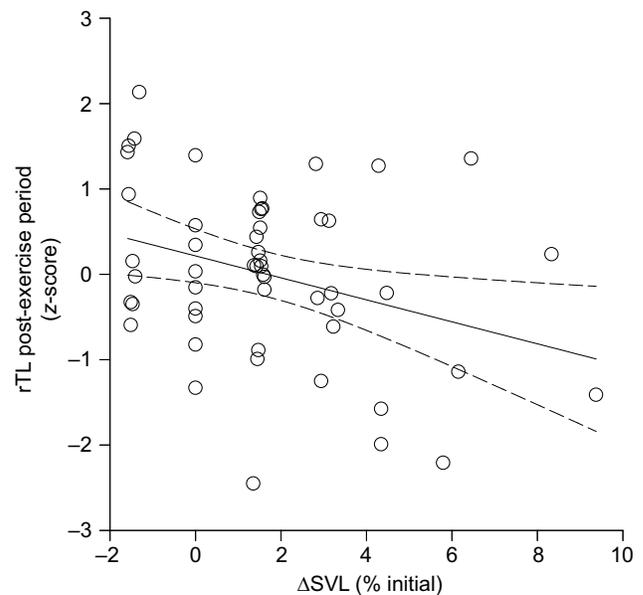
Fig. 3. Relationship between rTL measured at the end of the exercise period and ΔSVL in painted dragons. rTL data were z-transformed. Transforming the raw change in SVL (Δmm) to a percentage of the initial SVL improved normality of the residuals, satisfying assumptions of linear regression (Kolmogorov–Smirnov test, $P=0.777$, $r=0.326$, $F_{1,51}=6.079$, $P=0.017$). The dashed lines represent the 95% confidence limits of the slope of the regression line.

Table 3. ΔSVL

Source	Likelihood ratio χ^2	d.f.	P-value
Full model versus intercept only model	25.212	14,38	**0.033**
Test of model effects	Wald χ^2	d.f.	Type III
Exercise treatment	5.605	2,38	0.061
Head color morph	3.489	3,38	0.322
Bib	10.103	1,38	**0.001**
Exercise treatment×head color morph	27.388	6,38	**<0.001**
Exercise treatment×bib	9.658	2,38	**0.008**

The change in snout–vent length (ΔSVL; end−beginning) was analyzed by GLM (gamma, log link function). Deviance value=36.639, d.f.=38, Deviance/d.f.=0.964, indicating that the model is not over-dispersed. Bold indicates significance at $P \leq 0.05$.

Table 4. SOx

Source	Likelihood ratio χ^2	d.f.	P-value
Full model versus intercept only model	14.082	6,46	**0.029**
Test of model effects	Wald χ^2	d.f.	Type III
Exercise treatment	6.018	2,46	**0.049**
Head color morph	8.775	3,46	**0.032**
Bib	4.294	1,46	**0.038**

Superoxide (SOx) levels at the end (final SOx, standardized by sample date and then z-transformed across all sample dates) were analyzed by GLM (normal, identity link function). Backward elimination of interaction terms between head color morph×exercise (P=0.263) and bib×exercise (P=0.511) reduced the model to main effects only. ΔAICc of reduced (AICc: 153.24) versus full model (AICc: 176.76)=−23.41. Bold indicates significance at $P \leq 0.05$.

with rTL at the end of the exercise treatment period (final rTL, Spearman's ρ=−0.278, P=0.044; Fig. 3).

Across males, 10 individuals were 1 mm shorter, nine did not grow in length, but the majority (N=34) gained SVL through the treatment period (Wilcoxon signed-rank test, $SVL_2−SVL_1$: W=746, Z=4.396, P<0.001); the distribution was right-skewed towards higher values (median ΔSVL=1 mm, range of 7 mm (−1 to 6 mm; −1.59% to 9.38% of initial length). Overall, bibbed males exhibited greater growth in length than non-bibbed males (Mann–Whitney rank-sum test, ΔSVL: U=198, T=638, P=0.018). Eight of the 10 males that reduced in length were non-bibbed males (head color morphs: 3 blue, 3 red, 0 orange, 4 yellow). In addition, 10 males

(head color morphs: 3 blue, 1 red, 3 orange, 3 yellow) had ≥4% increases in SVL, and 8 of these males had bibs.

ΔSVL was also affected by exercise treatment alone (*post hoc* Jonckheere–Terpstra test: $z_{d.f.3}$=−2.121, P=0.034; ΔSVL 0X=1X<3X) and through interactions with head color and bib morph (Table 3). The pattern of ΔSVL across exercise treatments in bibbed males was qualitatively similar to the pattern of ΔrTL. Bibbed males grew the most in the 0X treatment, in which rTL also increased, but grew much less in the 1X and 3X treatments. Non-bibbed males grew the least, with some males losing length in the 3X treatment, in which they gained the most in rTL. ΔSVL and
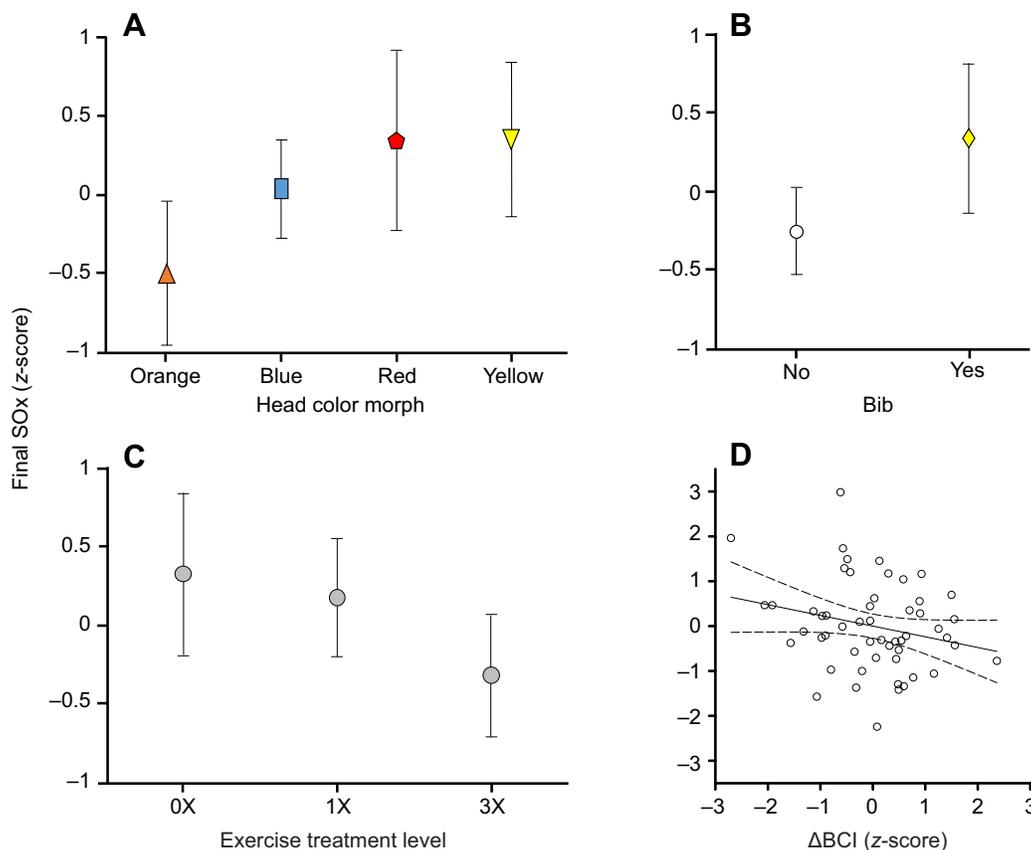
Fig. 4. The relationship of superoxide (SOx) at the end of the exercise period and morph types and exercise condition of painted dragons. Final SOx data were z-transformed and plotted against (A) head color morph, (B) bib morph, (C) exercise treatment and (D) ΔBCI (z-transformed) (r=−0.239, $F_{1,51}$=3.077, P=0.085). All symbols are centered on the estimated mean, and the bars represent 95% confidence estimates of the mean from generalized linear models.

ΔrTL exhibited qualitatively opposite patterns across exercise treatments in blue morphs, but no clear pattern for ΔSVL was apparent in the other three morphs (Fig. 1C).

Across all males, body mass did not systematically change through exercise treatment period (paired *t*-test; t_{52}=1.115, *P*=0.270); likewise, exercise treatment, morph-type nor their interaction were associated with ΔMass (all *P*>0.087) nor was ΔrTL associated with ΔMass (*r*=−0.130, *P*=0.353).

ROS
SOx
SOx was not consistent between an individual's measurement before and after exercise treatment (ICC=−0.069, 95% CI −0.331–0.202, *P*=0.691), and ΔSOx throughout the exercise treatment period was not related to head color or bib morph or their interaction with exercise (all *P*>0.109). However, SOx at the end of exercise treatment (final SOx) depended on exercise treatment, head color and bib morph (Table 4, Fig. 4) but not the interactions between exercise treatment and either of the morph types (backward eliminated, *P*>0.230). Bibbed males had higher final SOx than non-bibbed males (bib *P*=0.038); final SOx was significantly lower in the highest exercise (3X) group than in the no-exercise (0X) group (exercise *P*=0.049); and orange males had lower final SOx than all other morphs (head color morph *P*=0.032; all pairwise *P*<0.048), which was the only difference among head color morphs.

Other ROS
ROS was weakly consistent between an individual's measurement before and after exercise treatment (Spearman's ρ=0.263, *P*=0.058, ICC=0.299, 95% CI 0.033–0.525, *P*=0.014).

The ROS after exercise treatment and ΔROS were not affected by exercise treatment, and neither variable was related to initial or post-treatment BCI, ΔBCI, rTL, ΔrTL, head color, bib morph or their interactions with exercise (all *P*>0.172).

DISCUSSION
This experiment, which was inspired by differential condition loss of bib morphs in field studies (Healey and Olsson, 2009; Olsson et al., 2009a), was designed to test the effect of physical exercise and the resultant energy/resource allocation tradeoffs on morph-specific telomere dynamics. We manipulated activity levels through enforced exercise treatments to test for morph-specific responses in telomere dynamics in painted dragons (*Ctenophorus pictus*). This experimental approach revealed morph-specific, activity-related elongation and erosion of telomeres. Telomere dynamics were related to body condition and growth, the latter of which was positively associated with food intake, as might be predicted by the metabolic telomere attrition hypothesis (sensu Casagrande and Hau, 2019). The differences in telomere dynamics were most evident between bib morphs.

The telomere dynamics of bibbed and non-bibbed males suggest the potential for further longevity tradeoffs through the breeding season in this species. The interaction of head color morph with exercise treatment was primarily driven by the increase in telomere length in blue morphs with no exercise and the reduction in telomere length when they were exercised at any level, while the other morphs mostly maintained or lost telomere length. Blue morphs only appeared relatively recently in the sampled population, so we know little about their biology or mating tactics (Olsson et al., 2007b), which limits the scope for interpretation of these results. We do know from previous work that bibbed males and blue males have similarly short telomeres (Rollings et al., 2017) and lower endurance

than the other morphs (Tobler et al., 2012), so it is possible that patterns in bibbed males may be relevant for future work on blue males. We therefore restrict our discussion to the broader relationships among variables and the differences among bib morphs because their mating tactics are known, and the analyses of bib versus non-bib morphs have higher power than those of the four head color morphs.

Endurance and physiological performance in lizards are likely to be a polygenic trait, as in humans, where allelic variation at over 20 loci contributes to endurance performance phenotype (Williams and Folland, 2008) and the ability to respond to training (Mann et al., 2014). It seems likely such allelic variation is differentially aggregated in bibbed and non-bibbed morphs as a result of morph-specific correlated selection. Differential energy strategies are likely to underpin different reproductive tactics of all morphs. However, in the lab, animals usually do not have the same opportunity for activity as in the wild, where they must forage for food, escape predators, and find and defend territories. In our no-exercise (0X) treatment, bibbed males maintained or increased telomere length and body condition and length simultaneously. With increasing energetic demands of exercise, bibbed males exhibited reduced growth and condition, and lost telomere length, while those without the bib showed the opposite pattern.

Across all males, body condition and telomere dynamics were correlated (Fig. 2). Positive changes in body condition across exercise treatments and morphs were qualitatively associated with increases in telomere length, a trend especially apparent in bib morphs (Fig. 1A,B). The behavior of bibbed males matches their territorial role, as they are the first to be aggressive during territorial contests and have faster reaction times than non-bibbed males (McDiarmid et al., 2017; Tobler et al., 2012). Non-bibbed males have better endurance, tend to copulate for shorter periods, but inseminate more and faster sperm than bibbed males (Friesen et al., 2020), suggesting that non-bibbed males employ an alternative, sneaker/satellite male strategy rather than monopolizing females (*sensu* Smith, 1982; Smith and Price, 1973), all of which may increase their fitness by lowering the need for energetically expensive aggressive territorial and mate-guarding behavior.

It is difficult to say whether the exercise treatment we employed better represents the energy expenditure of a territorial or a sneaker strategy. Nevertheless, the exercise levels represent incremental increases in energy expenditure, which may have forced and exposed allocation tradeoffs in the lab. The association of BCI and telomere loss across exercise treatments within bib morphs is congruent with patterns of greater-than-average mass loss of bibbed males in the wild (Healey and Olsson, 2009; Olsson et al., 2009a) where territorial defense gives bibbed males a paternity advantage (Olsson et al., 2009a). Displaying a bib seems to incur a 'social cost' from more frequent challenges to and by rivals and higher energetic expenditure, resulting in poorer condition (Olsson et al., 2007b). Bibbed males have higher resting metabolic rates than non-bibbed males (Friesen et al., 2017a), lower endogenous antioxidant protection (Friesen et al., 2019), and higher SOx levels (this study), which along with decreasing body condition may also contribute to telomere loss in high-activity bibbed males. These various 'social' and physiological costs may, in part, explain decreases in the frequency of bibbed morphs across some years (Healey and Olsson, 2009).

Among lizards, body size and aggressiveness are generally positively associated with contest success (Olsson and Madsen, 1998), but growth rate and aggression are often negatively correlated with survival (Olsson and Shine, 2002; Stamps, 2007).

In this study, across all males (regardless of treatment), growth correlated with shorter final telomeres, while those males that showed a reduction in size or did not grow tended to maintain or even increase telomere length – the bibbed males invested in higher growth rates overall. Investment in a size advantage when using aggressive tactics is associated with reproductive fitness. Bibbed males maintained body condition while they also maximized growth rate with no exercise (0X), which is probably a lower level of activity and energy expenditure than free-living lizards, but at higher levels of activity it is likely to have affected their survival in the wild. Non-bibbed males represented the majority of the males that did not grow. The growth rate and final telomere length are likely interrelated and probably reflect morph-specific strategies on a fast–slow pace of life continuum (Giraudeau et al., 2019).

Longevity is predicted to be influenced by oxidative stress (Kirkwood, 2017); however, although we know that annual mortality is ~90%, the variation of within-season longevity has not been investigated in the field for these painted dragons. We found no direct link between either SOx or other ROS and telomere erosion (highest correlation coefficient |0.192|, all $P<0.168$), but males that grew more tended to have higher SOx and other ROS levels, which we know is correlated with DNA damage (Olsson et al., 2018a). As a group, bibbed males grew significantly more and had higher SOx, suggesting indirect links between telomere length and growth, energy utilization patterns and ROS levels.

These results imply different energy pathways for growth and bodily maintenance, possibly extending to telomerase expression, alternative lengthening mechanisms, activity and antioxidant protection (which we did not measure). We predicted a negative relationship between growth and telomere dynamics. Approximately 36% of the males decreased in length or did not grow. Growth was negatively related to telomere length at both the beginning and end of the experiment but not to ΔrTL, suggesting that an individual's prior investments in maintenance, early in the breeding season or earlier in life, set up growth and telomere length trajectories (e.g. Nettle et al., 2015; Parolini et al., 2015). Growth was positively related to food consumption, suggesting that energy and critical resources (e.g. calcium or vitamins dusted on mealworms) limit growth. However, food consumption was not related to increased body condition (i.e. residual body mass that is independent of body length) or telomere dynamics. Indeed, across all males, ignoring exercise treatments, telomere length was negatively correlated with growth but positively correlated with improved body condition, suggesting a tradeoff in energy storage/ maintenance versus skeletal growth. This result may, in part, be explained by the weak evidence of a negative correlation between BCI and SOx ($r=-0.239$, one-tailed $P=0.043$), suggesting a mechanistic link between BCI and telomere protection from oxidative damage (Barnes et al., 2019; von Zglinicki, 2002).

In this species, Friesen et al. (2019) demonstrated a significant, indirect negative link between SOx and body condition by describing a negative relationship between SOx levels and SOD (the enzyme that quenches SOx) activity, and a positive relationship of SOD with BCI. These relationships were also bib-morph specific, with bibbed males showing lower SOD activity and sperm that were more sensitive to SOx than non-bibbed males (Friesen et al., 2019). Interestingly, in this study, we also found tentative evidence that food consumption may be positively related to ROS, which, if true, might be due to the high-fat content of mealworms (~32% fat; Ravzanaadii et al., 2012), providing more substrate for lipid peroxidation and concomitant free-radical cascade (Halliwell and Gutteridge, 2015). However, others have found that simply eating and digesting food comes at an oxidative cost (Butler et al., 2016). Mitochondrial function and ROS production are complex and depend on substrates (Castro et al., 2015; Martos-Sitcha et al., 2017) that may differentially affect the fitness of different mitochondrial haplotypes (Aw et al., 2018; Ballard and Youngson, 2015). In ectotherms, shifts from aerobic to anaerobic metabolism may also reduce ROS production in mitochondria, relieving oxidative stress (Pérez-Jiménez et al., 2012). We found no evidence of an interaction between food consumption and bib morph on ROS (all $P>0.187$), but the link between energy use, diet and oxidative stress may have important implications for life-history and reproductive strategies.

Ours is one of a growing number of studies that have observed rTL elongation in ectothermic animals (e.g. Hatakeyama et al., 2016; McLennan et al., 2018; Ujvari et al., 2016). Despite acknowledging multiple mechanisms in which they can be elongated (Blackburn et al., 2006; Cesare and Reddel, 2010), we typically think of telomere attrition as a one-way street after development to sexual maturity. Telomere elongation is especially surprising in painted dragons, which are annuals and were ~70– 90% through their expected lifespan at the end of this experiment. We need to examine environmental factors and metabolic mechanisms that may explain the regulation of attrition and elongation more carefully in post-embryonic individuals from wild populations (Casagrande and Hau, 2019), particularly in ectotherms.

Author contributions
Conceptualization: C.R.F., M.O.; Methodology: C.R.F., M.W., N.R., M.G., M.O.; Validation: N.R., C.M.W.; Formal analysis: C.R.F., M.W., N.R., J.S., C.M.W.; Investigation: C.R.F., M.W., J.S., M.G., C.M.W., M.O.; Resources: C.R.F., M.W., J.S., C.M.W., M.O.; Data curation: C.R.F.; Writing - original draft: C.R.F.; Writing - review & editing: C.R.F., M.W., N.R., J.S., M.G., C.M.W., M.O.; Visualization: C.R.F.; Supervision: C.R.F., M.W., C.M.W., M.O.; Project administration: M.O.; Funding acquisition: C.R.F., M.O.

Data availability
Data are available from the Dryad digital repository (Friesen et al., 2021): dryad. z8w9ghxbx

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