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1 Flashy male Jamaican anoles (*Anolis grahami*) show accelerated telomere attrition

2

3 **Abstract**

4 Secondary sexual traits have evolved through sexual selection, many species have developed
5 signals that can indicate their level of other fitness-relevant traits such as fight ability.

6 Previous studies have shown that male sexual signals are honest signals about quality in an
7 intrasexual context, demonstrating a direct relationship between the signal's design and the
8 fighting ability of its possessor. However, signals can be costly since conspicuous signals are
9 more likely to attract predators or be energetically expensive. Here we have analysed if

10 dewlap size and colouration were reliable signs of a male's bite force, and the physiological
11 costs associated with larger dewlaps and intense colouration in Jamaican anoles (*Anolis*
12 *grahami*). We analysed dewlap size and colouration against bite force, and telomere attrition.

13 Our results supported the hypothesis that dewlap size and colour intensity were honest
14 predictors of an individual's fighting potential as indicated by bite force. However, we have
15 also found a relationship between colour intensity with higher telomere attrition rates,
16 thereby indicating a possible cost of this trait for the individual.

17 **Keywords:** *Bite-force, Dewlap, Telomere, Sexual selection*

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25 **Introduction**

26 Secondary sexual traits have evolved through sexual selection, by female preference, inter-
27 male competition or, in some cases, both (Zahavi, 1975; Berglund et al., 1996; Lailvaux &
28 Irschick, 2007). In this context, many species have developed signals that can also indicate the
29 level of other fitness-relevant traits such as fight ability (Emlen, 2008; Putman et al., 2018).
30 Males can express this information in the form of colouration or ornamentation. Conspecific
31 males interpret such signals to evaluate possible competitors, and females use this
32 information to evaluate potential mates (Berglund et al., 1996). Traits that honestly signal
33 fighting ability are advantageous as they can predict contest outcomes and, thus, males can
34 avoid unwinnable physical combats and the costs associated with them (Andersson, 1994).
35 To establish whether a signal is reliable, the trait should be evaluated as to whether the
36 size/shape or colouration of a secondary sexual character is predictive of ecologically relevant
37 performance abilities (Perry et al., 2004). Different studies demonstrate that male secondary
38 sexual signals express reliable information, demonstrating a direct relationship between the
39 signal's design (mainly size and colour) and the fighting ability of its possessor expressed as
40 bite force (e.g. Jennions & Backwell, 1996; Lailvaux & Irschick, 2007).
41 Signals inherent involve costs, more conspicuous signals (or more time devoted to signalling)
42 are more likely to attract predators or be energetically costly to develop (Engqvist et al.,
43 2015). One long-standing hypothesis about secondary sexual signals suggests that their
44 honesty or reliability is related to how costly they are to produce and maintain (Lailvaux et
45 al., 2012). An example of this is carotenoid-based colours (i.e. yellow/red spectrum), which
46 are appropriate for honest signalling due to the costs related to pigment acquisition and the
47 trade-offs between energetic allocation in ornaments against other metabolic processes such
48 protection against oxidative DNA damage (de Lanuza et al., 2014).

49 The genus *Anolis* is characterised by having an extendible throat fan called a dewlap. The
50 dewlap is a versatile signal structure being used in different contexts as a fundamental part
51 of sexual/territorial display behaviours (Vanhooydonck et al., 2005). The dewlap extension is
52 used as a threat or challenge to other males and predators (Jenssen et al., 2001) and to attract
53 potential mates. Females show preference for males with certain dewlap characteristics and
54 are more receptive to these males performing dewlap extensions (Greenberg & Noble, 1944;
55 Crews, 1975). Studies have evaluated the relationship between dewlap size and fighting
56 capacity (i.e. bite force) in anoles species with mixed results depending on the species
57 (Vanhooydonck et al., 2005), level of sexual dimorphism (Lailvaux & Irschick, 2007),
58 territoriality (Vanhooydonck et al., 2005) and level of within-population competition
59 (Baeckens et al., 2018).

60 Here we aimed to analyse, if dewlap size and dewlap colouration were reliable signs of a
61 male's bite force and if there is any physiological cost associated with these signals (using
62 telomere attrition) in captive Jamaican anoles (*Anolis grahami*, Gray 1845). Consistent with
63 previous studies, we expected dewlap size to be a good predictor of bite force, more
64 importantly we predicted that there would be a biological cost associated with more intense
65 coloured dewlaps.

66 **Methods**

67 *Subjects*

68 During this experiment 10 adult males, of unknown age, were used for data collection. All
69 animals were hand caught in Nonsuch Island, Bermuda and transported by air to Chester
70 Zoo, under licence 16-07-05-46, after clearance from a veterinary surgeon. The Jamaican
71 anole (*Anolis grahami*), despite being an invasive species in Bermuda is the most observed
72 lizard on the island (Bacon et al. 2011). Subject animals weighted on average 10.20 ± 2.12 g

73 and had a snout-ventral length of 6.65 ± 0.30 cm and all individuals experiment exhibited
74 breeding behaviour over the course of this study.

75 All the experimental methods described here were approved by the Chester Zoo's Ethics
76 Committee, UK and conform to all regulations and laws in all relevant countries in relation
77 to care of experimental animal subjects. Additionally, we can confirm, from our post-
78 experimental monitoring that no animals suffered any injuries, became ill or had their
79 survivorship negatively affected as a result of this study.

80 *Lizard housing*

81 Lizards were kept as a group of one male and two females in ExoTerra 60 cm x 45 cm x 90 cm
82 screen terrariums inside an isolated and temperature-controlled room at Chester Zoo, UK. A
83 12 hour photoperiod was maintained with an average temperature of 30 °C during the day
84 and 24° C at night. Temperature and humidity (around 60%) were monitored with a
85 thermometer/hygrometer. Each terrarium was supplied with a basking lamp, soil substrate,
86 and a potted plant. The terraria were sprayed daily with water, and lizards were fed live
87 crickets 3 times a week. The side of the terrariums were covered with black plastic between
88 adjacent terrariums to avoid visual contact between different lizards groups.

89 *Dewlap area*

90 To obtain a reliable measure of dewlap size, lizards were positioned sideways side against a
91 1-cm² gride paper and the base of the second ceratobranchial was carefully pulled forward
92 with a pair of tweezers until completely extended (Figure 1). Before taking a digital picture,
93 animals were placed in such a manner that the extended dewlap was parallel to the lens of
94 the camera (Canon PowerShot SX520HS digital camera). All measurements were made in an
95 identical manner using the same settings on the camera. We calculated the total dewlap area
96 for each individual using ImageJ software (Schneider et al., 2012).

97 *Dewlap colouration*

98 We used a USB-2000 portable diode-array spectrometer and a PX-2 xenon strobe light source
99 (both from Ocean Optics, Dunedin, USA) to perform spectrophotometric measurements.
100 Spectral analyses were conducted in the 300 and 700 nm range. Spectral reflectance
101 measurements were always taken of each male from the centre of the dewlap, three
102 measurements per lizard. Spectralon white standard measurements were taken between
103 each individual to account for lamp drift. We calculated the colorimetric parameters using
104 the Pavo package (Maia et al, 2013) for R studio (R Studio Team, 2015): brightness (mean
105 reflectance across 320–700nm), hue (wavelength corresponding to $[(\max \text{ reflectance} - \min$
106 $\text{ reflectance})/2]$), and red chroma (sum of reflectance from 605–700 divided by brightness).

107 *Bite force*

108 We induced the lizards to bite a force transducer by tapping them gently on the side of
109 the mouth, this method resulted in a characteristic threat response where the jaws are
110 opened maximally. Lizards were held by the researcher for immobilisation and then
111 encouraged to bite a force sensitive resistor connected to force a transducer and charge
112 amplifier (Kistler Inc., Winterthur, Switzerland). When the free end of the holder (i.e. bite
113 plates) was placed between the jaws of the animal, prolonged and repeated biting resulted.
114 The force resistor placement on the lizards' mouth was standardised for all animals. For more
115 detailed descriptions of setup and biting procedure, see Herrel et al. (1999). The bite force
116 of all lizards were measured five times and only the maximum value was used for analysis.

117 *Telomere erosion*

118 To analyse telomere erosion, animals were swabbed using a buccal swab twice over a six
119 months interval. Swabs were placed in tubes with dry capsules for stabilisation until
120 laboratory analysis. After a DNA extraction using a DNeasy Blood and Tissue Kit (Qiagen,

121 Australia), a real-time quantitative PCR (qPCR) allowed the measurement of telomere length.
 122 Telomere primers to used were: Telb1 (5'-
 123 CGGTTTGTTGGGTTGGGTTGGGTTGGGTTGGGTT-3') and Telb2 (5'-
 124 GGCTTGCCTTACCCTTACCCTTACCCTTACCCTTACCCT-3'). The 18S ribosomal RNA (18S) gene
 125 (92 bp in *Anolis*) was selected as the reference gene as it had previously been successfully
 126 used in a reptile (Plot et al., 2012). The primer sequences used were 18S-F (5'-
 127 GAGGTGAAATTCTTGGACCGG-3') and 18S-R (5'-CGAACCTCCGACTTTCGTTCT-3'). The qPCR
 128 was performed in a final volume of 20 µl for both telomeres and 18S. 10 ng of DNA was used
 129 per reaction, and the primers at a concentration of 250 nM. Reactions were run in triplicate
 130 for each sample. The measurement of the relative telomere length was calculated by using
 131 an adaptation of the qPCR method described by performed following protocol described by
 132 Giraudeau et al. (2016) and Dutra et al. (2020). The relative telomere length calculation
 133 consisted of the ratio of telomere repeat copy (T) to the reference gene (S; 18S) copy number
 134 (S); T/S.

135 *Statistical analysis*

136 Prior to statistical analyses, data on bite force was log₁₀ transformed to meet the assumptions
 137 of normality and homoscedascity (Shapiro-Wilk's test with $W \geq 0.95$). To remove the influence
 138 of body size on the variables, we used analyses of covariance (ANCOVAs) with SVL as
 139 covariate. To test if dewlap size and colour were a good predictor of a male's bite-force and
 140 telomere attrition we used ANCOVA with size as a covariate. We used RStudio version
 141 1.2.5033 (R Studio Team, 2015) for all statistical analyses.

142

143 **Results**

144 The ANCOVA analysis showed that dewlap size was positively significant for bite force
145 ($F_{1,8}=5.6$, $p=0.05$). The dewlap colouration analysis was positively significant for brightness
146 against bite force ($F_{1,8}=10.6$, $p=0.01$), and telomere attrition ($F_{1,8}=7.17$, $p=0.03$). Yellow
147 chroma ($F_{1,8}=8.09$, $p=0.02$), red chroma ($F_{1,8}=6.26$, $p=0.03$), and hue ($F_{1,8}=5.67$, $p=0.04$) were
148 positively significant for telomere attrition. All other analyses did not result in statistically
149 significant relationships.

150 **Discussion**

151 Our results show that dewlap size and colour intensity were honest predictors of an
152 individual's bite force. Our analysis also demonstrated that intense dewlap colouration is
153 associated with higher telomere attrition rates, thereby indicating a possible cost of this trait
154 for the individual.

155 *Anolis grahami* are highly territorial lizards, with males defending their territories with visual
156 displays, including dewlap extensions (Vanhooydonck et al., 2005). The reliability of such
157 display could avoid the costly interactions physical combats may impose through bites during
158 male-male competition (Andersson, 1994). Our results agree with previous studies showing
159 that dewlap size is a reliable sign of combat performance, as measured by bite force. Previous
160 studies have shown a relationship between bite-force and combat success, especially in *Anolis*
161 species with high sexual dimorphism (Lailvaux & Irschick, 2007), such as *A. grahami*. This study
162 reinforces the idea that dewlaps, among other signals, can act as a reliable indicator of combat
163 ability to rival individuals; thereby, avoiding potentially physically damaging fights (Lailvaux &
164 Irschick, 2007) .

165 The red colouration observed on dewlap of adult male *A. grahami* is associated with
166 carotenoids (Macedonia et al., 2000) which are commonly obtained through diet and they are
167 an important antioxidant defence against reactive oxygen radicals (McGraw, 2005; Freeman-

168 Gallant et al.,2011). Pigment allocation to increase brightness of colourful ornaments could
169 reduce the availability of carotenoids for use as antioxidants and, thereby, could increase DNA
170 damage (McGraw & Ardia, 2003), leading to telomere attrition. A pioneering study on
171 Australian painted dragons (*Ctenophorus pictus*) demonstrated this trade-off between
172 telomere attrition and colour maintenance for signalling in a lizard species (Giraudeau et al.,
173 2016), similar evidence has also been found in birds (Taff & Freeman-Gallant 2017). Our
174 results support these findings suggesting that the maintenance of carotenoid-based
175 colouration could lead to telomere shortening.

176 A central idea of life-history theory is that investment in present reproduction reduces
177 survivorship and, consequently, future reproduction (Cox & Calsbeek 2009; Cox et al., 2010).
178 The foundation for this hypothesis is that organisms that prioritise breeding over cellular
179 maintenance (such as antioxidant production) often age quicker, having shorter life spans and
180 higher rates of telomere attrition (Ricklefs & Wikelski, 2002). Physiological explanations for
181 the trade-off are grounded in the notion that these two components compete for limited
182 energy and nutrients (Zera & Harshman, 2001). Laboratory and field manipulations have
183 demonstrated this prediction with respect to different physiological processes including DNA
184 repair and resistance to oxidative stress using different species, including *Anolis* lizards (Cox
185 et al., 2010). Our results support this hypothesis with male anoles investing in reproduction
186 now at the cost of accelerated telomere attrition. Male anoles, by investing in an intense
187 dewlap colouration, increase their chances of reproduction, as it has been shown that females
188 have a preference for intense coloured dewlaps (Sigmund, 1983). If telomere attrition is, in
189 fact, associated with increased senescence in anole lizards, then maintaining dewlap
190 coloration with the associated benefits in terms of reproductive success but at the expense
191 of longevity may be favoured by increasing reproductive output. Within a polygynous mating

192 system, males can maximise reproductive success by monopolising females through male-
193 male contests such as dewlap displays (Orrell & Jenssen, 2001). The breeding strategy Anolis
194 consists of females laying multiple clutches of single eggs during a prolonged season (Cox &
195 Calsbeek, 2010), giving males the opportunity to sire multiple batches of offspring in one
196 breeding season.

197 In summary our results support previous studies showing that dewlap size and colouration
198 are honest signals of bite force, but that these come with physiological costs. More studies
199 using free-ranging animals and larger sample sizes are necessary to better understand this
200 trade-off, including additional measurements such as circulating carotenoids and reactive
201 oxygen radicals to fully understand the link between carotenoid-based colouration and
202 telomere attrition (i.e., longevity).

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207 authors have no conflicts of interest to declare that are relevant to the content of this
208 article.

209 **Availability of data and material**

210 Data is available as Passos, Luiza (2022), "Jamaican Anoles Dewlap data", Mendeley Data,
211 V1, doi: 10.17632/2vphhkcrjj.1

212 **References:**

213 Andersson, M. (1994). *Sexual Selection*. Princeton, New Jersey: Princeton University Press.

214 Bacon, J.P., Gray, J.A., & Kitson, L. (2011). Status and conservation of the reptiles and
215 amphibians of the Bermuda Islands. *Conservation of Caribbean Island Herpetofaunas*,
216 1, 161–182. <https://doi.org/10.1163/ej.9789004183957.i-228>

217 Baeckens, S., Driessens, T., Huyghe, K., Vanhooydonck, B., & Van Damme, R. (2018).
218 Intraspecific variation in the information content of an ornament: Why relative dewlap
219 size signals bite force in some, but not all island populations of *Anolis sagrei*.
220 *Integrative and Comparative Biology*, 58(1), 25–37. <https://doi.org/10.1093/icb/icy012>

221 Berglund, A., Bisazza, A., & Pilastro, A. (1996). Armaments and ornaments: an evolutionary
222 explanation of traits of dual utility. *Biological Journal of the Linnean Society*, 58, 385–
223 399.

224 Cox, R. M., & Calsbeek, R. (2010). Severe costs of reproduction persist in *Anolis* lizards
225 despite the evolution of a single-egg clutch. *Evolution*, 64(5), 1321–1330.
226 <https://doi.org/10.1111/j.1558-5646.2009.00906.x>

227 Cox, R. M., Parker, E. U., Cheney, D. M., Liebl, A. L., Martin, L. B., & Calsbeek, R. (2010).
228 Experimental evidence for physiological costs underlying the trade-off between
229 reproduction and survival. *Functional Ecology*, 24(6), 1262–1269.
230 <https://doi.org/10.1111/j.1365-2435.2010.01756.x>

231 Crews, D. (1975). Effects of different components of male courtship behaviour on
232 environmentally induced ovarian recrudescence and mating preferences in the lizard,
233 *Anolis carolinensis*. *Animal Behavior*, 23, 349–356.

234 De Lanuza, G. P. i, Carazo, P., & Font, E. (2014). Colours of quality: structural (but not
235 pigment) coloration informs about male quality in a polychromatic lizard. *Animal*
236 *Behaviour*, 90, 73–81. <https://doi.org/10.1016/j.anbehav.2014.01.01>

237 Dutra, L., Souza, F.S., Friberg, I.M., Araújo, M., Vasconcellos, A.S & Young, R.Y. (2020).
238 Validating the use of oral swabs for telomere length assessment in dogs. *Journal of*
239 *Veterinary Behaviour*, 40, 16-20

240 Emlen, D.J. (2008). The evolution of animal weapons. *Annual Review of Ecology, Evolution*
241 *and Systematics*. 39, 387–413.

242 Engqvist, L., Cordes, N., & Reinhold, K. (2015). Evolution of risk-taking during conspicuous
243 mating displays. *Evolution*, 69(2), 395–406. <https://doi.org/10.1111/evo.12591>

244 Giraudeau, M., Friesen, C. R., Sudyka, J., Rollings, N., Whittington, C. M., Wilson, M. R., &
245 Olsson, M. (2016). Ageing and the cost of maintaining coloration in the Australian
246 painted dragon. *Biology Letters*, 12(7), 734–738.
247 <https://doi.org/10.1098/rsbl.2016.0077>

248 Greenberg, B., & Noble, G.K. (1944). Social behaviour of the American chameleon (*Anolis*
249 *carolinensis* Voigt). *Physiological Zoology*, 17, 392–439.

250 Gray, J. E. (1845). Catalogue of the Specimens of Lizards in the Collection of the British
251 Museum. London: Trustees of the British Museum.

252 Herrel, A., Aerts, P., Fret, J., & De Vree, F. (1999). Morphology of the feeding system in agamid
253 lizards: ecological correlates. *The Anatomical Record*, 254, 496–507.

254 Freeman-Gallant, C. R., Amidon, J., Berdy, B., Wein, S., Taff, C. C., & Hausmann, M. F.
255 (2011). Oxidative damage to DNA related to survivorship and carotenoid-based sexual
256 ornamentation in the common yellowthroat. *Biology Letters*, 7(3), 429–432.
257 <https://doi.org/10.1098/rsbl.2010.1186>

258 Jennions, M.D., & Backwell, P.R.Y. (1996). Residency and size affect fight duration and
259 outcome in the fiddler crab *Uca annulipes*. *Biological Journal of the Linnean Society*, 57,
260 293–306.

261 Janssen, T. A., Lovern, M. B., & Congdon, J. D. (2001). Field-testing the protandry-based
262 mating system for the lizard, *Anolis carolinensis*: Does the model organism have the
263 right model? *Behavioral Ecology and Sociobiology*, 50(2), 162–172.
264 <https://doi.org/10.1007/s002650100349>

265 Lailvaux, S. P. & Irschick, D. J. (2007) The evolution of performance-based male fighting
266 ability in Caribbean *Anolis* lizards. *The American Naturalist*, 170, 573-586.

267 Lailvaux, S. P., Gilbert, R. L., & Edwards, J. R. (2012). A performance-based cost to honest
268 signalling in male green anole lizards (*Anolis carolinensis*). *Proceedings of the Royal*
269 *Society B: Biological Sciences*, 279(1739), 2841–2848.
270 <https://doi.org/10.1098/rspb.2011.2577>

271 Maia, R., Eliason, C. M., Bitton, P. P., Doucet, S. M., & Shawkey, M. D. (2013). pavo: An R
272 package for the analysis, visualization and organization of spectral data. *Methods in*
273 *Ecology and Evolution*, 4(10), 906–913. <https://doi.org/10.1111/2041-210X.12069>

274 McGraw, K. J. (2005). The antioxidant function of many animal pigments: Are there
275 consistent health benefits of sexually selected colourants? *Animal Behaviour*, *69*(4),
276 757–764. <https://doi.org/10.1016/j.anbehav.2004.06.022>

277 McGraw, K. J., & Ardia, D. R. (2003). Carotenoids, Immunocompetence, and the Information
278 Content of Sexual Colors: An Experimental Test. *American Naturalist*, *162*(6), 704–712.
279 <https://doi.org/10.1086/378904>

280 Orrell, K. S., & Jenssen, T. A. (2002). Male mate choice by the lizard *Anolis carolinensis*: A
281 preference for novel females. *Animal Behaviour*, *63*(6), 1091–1102.
282 <https://doi.org/10.1006/anbe.2002.3013>

283 Perry, G., Levering, K., Girard, I., & Garland, T. Jr. (2004). Locomotor performance and
284 dominance in male *Anolis cristatellus*. *Animal Behaviour*, *67*, 37–47.

285 Plot, V., Criscuolo, F., Zahn, S., & Georges, J. Y. (2012). Telomeres, age and reproduction in a
286 long-lived reptile. *PLoS ONE*, *7*(7), 1–6. <https://doi.org/10.1371/journal.pone.0040855>

287 Putman, B. J., Azure, K. R., & Swierk, L. (2018). Dewlap size in male water anoles associates
288 with consistent inter-individual variation in boldness. *Current Zoology*, *65*(2), 189–195.
289 <https://doi.org/10.1093/cz/zoy041>

290 R Studio Team. (2015). RStudio: Integrated Development for R. RStudio, Inc., Boston, MA.
291 <http://www.rstudio.com>

292

293 Ricklefs, R.E., & Wikelski, M. (2002). The physiology/life-history nexus. *Trends in Ecology &*
294 *Evolution*, *17*, 462–468.

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305
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312
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Schneider, C.A., Rasband, W.S., & Eliceiri, K.W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, 9, 671-675.

Sigmund, W. R. (1983). Female preference for *Anolis carolinensis* males as a function of dewlap color and background coloration. *Journal of Herpetology*, 17(2), 137–143.
<https://doi.org/10.2307/1563454>

Taff, C. C., & Freeman-Gallant, C. R. (2017). Sexual signals reflect telomere dynamics in a wild bird. *Ecology and Evolution*, 7(10), 3436–3442. <https://doi.org/10.1002/ece3.2948>

Vanhooydonck, B., Herrel, A. Y., Van Damme, R., & Irschick, D. J. (2005). Does dewlap size predict male bite performance in Jamaican *Anolis* lizards? *Functional Ecology*, 19(1), 38–42. <https://doi.org/10.1111/j.0269-8463.2005.00940.x>

Zahavi, A. (1975). Mate selection—a selection for a handicap. *Journal of Theoretical Biology*, 53:205–214.

Zera, A.J., & Harshman, L.G. (2001). The physiology of life history trade-offs in animals. *Annual Review of Ecology, Evolution, and Systematics*, 32, 95–12

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321 Figure 1. Jamaican anole (*Anolis grahami*) having its dewlap fully extended with the use of
322 tweezers for total area measurement.

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