Evidence for multiple functions in a sexually selected ornament

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In gregarious animals, social interactions frequently take the form of dominance hierarchies that maintain stable relationships between individuals, and settle disputes without extra costs. Traits that function as signals of status can play an important role in mediating interactions among individuals, both in social and in sexual contexts. Carotenoid ornaments are more generally assumed to be sexually selected and not so relevant to general social contexts. However, it is possible for them to function in social contexts if they signal socially relevant aspects. Here we experimentally analysed social dominance and resource control in male groups of a gregarious species, the European serin, Serinus serinus, in relation to a sexual ornament. We tested whether yellow carotenoid-based plumage coloration, age, body size and testosterone were predictors of social dominance over a nonsexual resource (i.e. feeding context). We showed that dominance hierarchies were steep and were related to testosterone levels and ornamental coloration, particularly the male yellow carotenoid-based crown patch. Our results suggest that carotenoid-based colour and testosterone levels can be reliable predictors of social status in agonistic encounters in groups of male serins. Moreover, together with previous work on the sexual function of male coloration, this study provides evidence that male serin yellow coloration has a dual function in both sexual and nonsexual contexts. These results raise the possibility that this ornament may have evolved and be maintained via social selection over social competition/cooperation for reproductive opportunities and ecological resources.

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signal an individual’s fighting ability and, as such, predict the outcome of conflicts or the position of individuals within dominance hierarchies. In contrast to melanin pigmentation, there has been much less research on the function of carotenoid-based traits in status-signalling contexts, but studies suggest they are widespread among taxa such as reptiles (Hamilton, Whiting, & Pryke, 2013), fish (Evans & Norris, 1996) and birds (Griggio, Serra, Licheri, Monti, & Pilastro, 2007). Whether or not they have a sexual function, carotenoid-based signals have the potential to convey information in competitive contexts. Variation in carotenoid coloration is associated with an individual’s ability to forage, assimilate and process carotenoids (reviewed in Blount, 2004; Olson & Owens, 1998). Also, since these pigments are vital nutrients, important as immunoenhancers and antioxidants (reviewed in Lozano, 1994; Olson & Owens, 1998; see also Hill & Johnson, 2012), it is often the case that these signals are indicators of individual health condition. In such cases, high-quality individuals should exhibit increased ornamentation and thus advertise their superior competitive ability, irrespective of whether carotenoid coloration is dependent on trade-offs for different functions (Lozano, 1994) or is a direct indicator of both physiological and metabolic capacity, as well as immune condition (Hill & Johnson, 2012).

A positive relation between carotenoid-based plumage and fighting ability has been demonstrated for several bird species, for both red (e.g. widowbirds, Euplectes ardens and Euplectes axillaris, Pryke, Lawes, & Andersson, 2001; Pryke & Andersson, 2003) and yellow feathers (e.g. rock sparrow, Petronia petronia, Griggio et al., 2007; yellow warbler, Setophaga petechia, Studd & Robertson, 1985). A recent experimental study with golden-crowned sparrows, Zonotrichia atricapilla, has shown that multiple signals of carotenoid and melanin were independently related with social dominance in mixed-sex dominance trials (Chaine, Roth, Shizuka, & Lyon, 2013). In the Gouldian finch, Erythrura gouldiae, a genetically based colour-polymorphic species, both red-headed males and females are more aggressive and dominant towards black and yellow colour morphs (Pryke, 2007; Pryke & Griffith, 2006). While all these studies were directed to carotenoid-based status signals, in most cases dominance was only assessed in a sexual competitive context, without considering a social selection perspective.

Our study species, the European serin, Serinus serinus, is a gregarious, nonterritorial, socially monogamous finch that exhibits male mate-guarding behaviour (Mota & Hoi-Leitner, 2003). Male European serins display a sexually dichromatic yellow carotenoid-based breast and crown, resulting from a single annual moult 6–8 months before breeding. Male coloration has been shown to be a sexually selected trait preferred by females (Leitão, Monteiro, & Mota, 2014). In this study, we investigated whether male serin yellow carotenoid-based coloration plays a role in male social dominance over nominating resources. Since testosterone is known to modulate a set of behaviours such as courtship, parental and aggressive behaviours (Adkins-Regan, 2005), we also measured testosterone levels in order to determine its relation to male dominance, and to assess whether it was related to male ornamentation.

We established male groups under laboratory conditions to determine whether male yellow ornamentation was related to aggressive interactions and social dominance, testing the possibility that social competition over nonreproductive resources also influences the evolution of this trait.

**METHODS**

**Housing and Morphological Measurements**

We captured 28 male European serins, using mist nets, in the surroundings of Coimbra (40°11‘25" N 8°33‘35" W, Portugal), in the winter (February) of 2012, after moult and before breeding. Individuals were housed in an indoor aviary in the Laboratory of Ethology at the University of Coimbra (40°12‘26"N 8°25‘21"W, Portugal), where we divided them into seven groups of four males, and housed them in cages (118 × 50 cm and 50 cm high) with ambient temperature of 20 ± 2 °C and natural lighting. Birds had ad libitum access to a commercial seed mixture (canary seed 46%, rapeseed 22%, niger seed 7%, linseed 7%, peeled oats 6%, hempseed 5%, wild seeds 5%, radish seed 1% and spinach seed 1%; European Finches Prestige, Versele-Laga, Deinze, Belgium), tap water and mixed grit with crushed oyster shell. We minimized the opportunity for dominant males to monopolize food resources in the groups by placing multiple food and water receptacles in each cage.

We ringed birds with numbered black plastic rings (A. C. Hughes, Hampton Hill, U.K.), which were replaced by plastic colour rings just before the experiments to allow visual identification during video analysis. Ring colour was not related to any variables analysed (Pearson correlations: P > 0.10 for all tests). We also aged birds (first year or adult birds) using plumage marks according to Svensson (1992). We measured morphological parameters including wing (±1 mm), tarsus (±0.01 mm) and mass (±0.5 g) immediately before the experiments. Body size was estimated from the PC1 of a principal component analysis using these variables, which explained 50.8% of variance, had high loadings for tarsus (0.80) and mass (0.88) and a medium loading for wing (0.31). The crown and breast yellow patches were measured by the same person (S. T.) by overlaying a transparent grid on these areas and estimating the number of squares they covered, as described by Hill (1992).

**Spectral Analysis**

During the month of capture, we performed spectral analysis of males’ plumage reflectance, taking into account the passerine bird vision perception range (320–700 nm), using an Ocean Optics USB4000 spectrophotometer, a MikropackMini-DT-2-GS light source (Ocean Optics, Dunedin, FL, U.S.A.) and an optical fibre reflectance probe (Ocean Optics R400-7 UV/VIS), held vertically, attached to a rigid black holder to standardize the distance between probe and sample (distance of 3 mm, providing a sampling area of 28 mm²). All measurements were standardized using white (Ocean Optics, WS-1-SS) and dark standards. We measured the crown, throat, breast and belly of each male by taking three readings from each area, which were then averaged for each region. We then quantified coloration as perceived by birds, by applying avian visual models (Vorobyev & Osorio, 1998; Vorobyev, Osorio, Bennett, Marshall, & Cuthill, 1998). We calculated cone quantum catches for each of the five cone types present in the avian retina (Bownaker, Heath, Wilkie, & Hunt, 1997), four single cones and the double cone (using equation 1 in Vorobyev et al., 1998), integrating cone sensitivity, irradiance light and reflectance spectrum of the plumage. Since cone sensitivity data are unavailable for our species, we considered the cone sensitivities of another ultraviolet-sensitive (UVS) representative species, the blue tit, Cyanistes caeruleus, for single and double cones (Hart, Partridge, Cuthill, & Bennett, 2000). As a measure of irradiance we used D65, the spectrum of standard daylight. Plumage coloration was quantified using the short-wavelength-sensitive (SWS) ratio and the double cone, representing chromatic and achromatic indices of plumage reflectance (Evans, Hinks, Wilkin, & Sheldon, 2010). We assumed double cones are responsible for achromatic differentiation, since experimental data suggest that they are responsible for luminance vision (Hart, 2001; Jones & Osorio, 2004; Vorobyev & Osorio, 1998). As carotenoid-based plumage coloration results from the pigment absorption of wavelengths otherwise typical of white feathers.
(Shawkey, Hill, McGraw, Hood, & Huggins, 2006), we used the same measure as Evans et al. (2010) to quantify yellow pigment concentration, which we perceive as saturation. The SWS ratio compares the SWS cone to the mean quantum cone catch of the other three single cones (UVs, MWS and LWS) so that SWS ratio = 3−1/(UVs+MWS+LWS)/SWS. We first used an average across all body parts, and in a later analysis, we split the measurement to determine which body regions were more socially relevant. Visual models were applied using the pavo package (Maia, Eliason, Bitton, Doucet, & Shawkey, 2013), running in R (R Development Core Team, 2015).

In the Results, we report analyses based on the UVS visual system. We assumed that S. serinus has the same visual system as its close relative Serinus canaria, which is known to have the UVS visual system (Das, Wilkie, Hunt, & Bowmaker, 1999). However, since the actual visual system is not known for S. serinus, we also conducted similar analyses based on the violet-sensitive (VS) visual system (see Appendix Tables A1–A3). Results were similar to those obtained using the UVS visual system.

Testosterone Assays

Blood samples from each bird were taken early in the breeding season (April), to obtain individual testosterone levels. We could not take another sample immediately before the experiments, owing to constraints on the amount of blood we could take from a bird of this size, as well as the fact that these birds were later used in another experiment (Trigo & Mota, 2014). Therefore, testosterone levels, as measured in this study, must be taken as baseline for breeding conditions and are not directly related to the social groups, since they were measured before the groups were formed. The present study was conducted before Trigo and Mota (2014) experiment, with several months separating them.

Samples were taken in the morning with individuals being handled for 2–4 min. Blood was collected from the brachial vein (approximately 100 μl), using a heparinized capillary tube. After centrifugation, the plasma samples (5–50 μl) were stored at −20 °C until hormonal analysis.

Testosterone concentrations were measured by radioimmunoassay in ISPA (Lisbon, Portugal), following a previously described method (Canário & Scott, 1989). Samples were assayed in duplicate for testosterone, using an antibody for testosterone (Fitzgerald, assay in ISPA (Lisbon, Portugal), following a previously described until hormonal analysis.

Statistical Analysis

We first tested for possible group differences in activity, aggressiveness (number of individual attacks and displays) and time spent in the feeder with a one-way analysis of variance (ANOVA). Within-individual repeatability was calculated for aggressiveness and time spent in the feeder across the 5 days from the variance analysis ANOVA (Lessells & Boag, 1987). When we found repeatability, we averaged variables across the 5 days of tests, in order to have a single measurement for each individual. The relationship between dominance index (David’s score), average of time spent in the feeder across all individuals was examined using Pearson correlations.

We tested which factors were predictors of social dominance using generalized linear mixed models (GLMM), with dominance index as the dependent variable and group as a random factor,
assuming normal distribution of error terms. The models incor-
porated all possible combinations of variables that could be related
to dominance, namely plumage chromaticity (SWS ratio) and
plumage achromaticity (double cone), as well as age, body size, and
crown and breast patch size. We report the results (F and P values)
for the fixed effects. The model did not include variables that were
correlated to avoid problems of collinearity (Pearson correlations: 
P > 0.10 for all variables included).

Having found a significant effect of SWS ratio (plumage chro-
maticity) over dominance index (see Results), we performed a
GLMM focusing on plumage chromaticity of each individual body
part as predictors (crown, throat, breast and belly SWS ratio; vari-
bles were not correlated with Pearson correlations: all P > 0.05) in
order to partition the trait signal and assess its components.

We performed a third model analysis, with the same specifica-
tions as the other models, to test for testosterone as a predictor
variable of dominance index. This model was made separately due
to the smaller sample size, since we only had a subsample of birds
with measured testosterone levels (N = 18). The correlation be-
tween testosterone and other variables that could explain social
dominance (total SWS ratio, crown SWS ratio and body size) was
analysed using Pearson correlations.

All variables fulfilled the statistical assumptions. Statistical
analysis were performed with R using packages nlme (Pinheiro,
Bates, DebRoy, & Sarkar, 2011), MuMIn (Barton, 2009) and Hmisc
(Harrell, 2012).

Ethical Note

This work was performed in accordance with the Portuguese
National Authority for Animal Health (DGAV). Permits for animal
capture, transport, maintenance, handling and experiments were
carried out under I.C.N.B. licences (49/2012/CAPT) to P.G.M. ac-
cording to Portuguese legislation.

Birds were captured and transported to the aviary in small
groups in cages (70 × 35 cm and 50 cm high), and upon arrival
moved to their housing cages. In the aviary, the birds’ status was
checked daily, and they were maintained with care to ensure their
health and wellbeing. The veterinary surgeon also checked the
birds’ general state and housing conditions. During experiments,
agonistic physical interactions (pecking) were rarely observed, and
when they occurred never caused physical injury. After experi-
ments and before release, birds were transferred to a large indoor
aviary for a 5-day period of flight training, to improve flight per-
formance and reach normal activity. Individuals were then released
in their capture locations where they joined groups of conspecifics.

RESULTS

Male groups did not differ in aggressiveness (F6,21 = 1.697, 
P = 0.171), time spent in the feeder (F6,21 = 0.508, P = 0.796) or
general activity (F6,21 = 1.680, P = 0.175).

Within groups, the traits defining dominance were consistent
across days (time spent in the feeder: t5 = 0.356, F27/108 = 3.775,
P < 0.001; aggressiveness: t5 = 0.268, F27/108 = 2.839, P < 0.001).
Also, these behavioural variables were correlated with the domi-
nance index: individuals that retained control of the feeder for
longer were also more aggressive (t5 = 0.569, N = 28, P = 0.002)
and had a higher dominance index (David score and aggressiv-
ness: r = 0.681, N = 28, P < 0.001). The dominance relationship
between members of each group was found to be steep (mean ±
SE = 0.70 ± 0.063; Fig. 1), which is indicative of strong hierarchies.

Only plumage chromaticity was a significant predictor of
dominance score (Fig. 2), while plumage achromaticity, age, body
size, and crown and breast patch size were not significantly related
to social dominance (Table 1).

When we separately analysed the effects of plumage chroma-
ticity in each of the males’ yellow body parts, only the crown SWS
ratio showed a significant effect over dominance (F1,17 = 9.977,
P = 0.005; Fig. 3), whereas throat (F1,17 = 0.793, P = 0.385), breast
(F1,17 = 0.820, P = 0.379) and belly SWS ratio (F1,17 = 0.001,
P = 0.990) did not.

Testosterone levels positively affected social dominance, with
males with higher levels of testosterone also showing higher
dominance rank (F10,10 = 7.620, P = 0.020; Fig. 4). However, the
difference between individuals in testosterone was not correlated
with male ornamentation, either SWS ratio of all body parts
(t5 = 0.190, N = 18, P = 0.443) or crown SWS ratio (t5 = 0.100,
N = 18, P = 0.705). It was also not correlated with body size (r =
0.040, N = 18, P = 0.868).

Similar results were found when we used the VS visual system
in visual models (see Appendix Tables A1, A2 and A3).
Individuals with higher plumage chromaticity and higher levels of testosterone were more aggressive and dominant. Other factors might affect the outcome of contests and the achievement of dominance, such as body size or age. However, our analysis did not reveal such correlation: neither different body size nor age variation seem to have an effect on social dominance, which could indicate that age differences and variation in size do not actually give an advantage in social dominance in serins.

Our results support the growing evidence that carotenoid coloration is involved in status signalling (Evans & Norris, 1996; Griggio et al., 2007; Hamilton et al., 2013; Young, Cain, Svedin, Backwell & Pryke, 2015), and can be important in social competition. Moreover, we demonstrated that the same sexually selected signal (Leitão et al., 2014) can similarly be used as a status signal in the context of social competition over nonreproductive resources (food). These results are indicative of a dual function of the yellow coloration, and suggest that this ornamentation may have evolved and be maintained not only via competition for reproductive opportunities (sexual selection), but also via competition for access to other resources in nonsexual contexts, that is, social selection.

Status signalling can be particularly relevant in gregarious birds (West-Eberhard, 1983) such as the serin, since they can reveal information regarding an individual’s competitive ability to others and mediate conflict situations. At the group level, individual differences in coloration might arise as a result of trade-off mechanisms that maintain this variation in coloration. Living in groups conveys several advantages for more subordinate (less colourful) males, as they can benefit from the presence of other group members through protection and social information use (e.g. follow better foragers, Toth & Griggio, 2011). Although this can increase competition for food, more colourful males can also benefit from attracting individuals to the group by decreasing the risk of predation (group size effect on vigilance and dilution effect; Alexander, 1974). At the individual level, if more dominant individuals achieve more control over food resources (from which the pigments are derived), they could be more efficient at expressing coloration, which can directly signal their superior competitive ability to others.

Our experiment also demonstrates that social dominance is positively associated with the difference between individuals in testosterone level, indicating that dominance status is hormonally mediated in male serins. It is generally recognized that testosterone is correlated with aggressive displays, at least during periods of male – male competition (high testosterone levels are associated with high levels of aggression; Wingfield, Ball, Dufty, Hegner, & Ramenofsky, 1987). Our results show that the difference between individuals in testosterone level attained 2 months before we established the experimental groups predicted future social dominance, which is an indication that it relates in a stable way to dominance. Basal testosterone levels could be indicative of high testosterone production during aggressive interactions, as individuals can vary consistently in their androgen production (reviewed in Kempenaers, Peters, & Foerster, 2008). Still, our results show no correlation between testosterone levels and the males’ colour traits. Sex-steroid hormones such as testosterone can modulate the expression of sexual traits by favouring the allocation of pigments to ornaments, as in melanin-based coloration (Andersson, 1994; Mougeot, Perez-Rodriguez, Martinez-Padilla, Leckie, & Redpath, 2007). Regarding carotenoids, the majority of studies suggest that testosterone can stimulate carotenoid transport and increase carotenoid availability (Blas, Perez-Rodriguez, Bortolotti, Vithubuela, & Marchant, 2006; Peters, 2007), while others did not find a direct link between testosterone and colour expression (Day, McBroom, & Schlinger, 2006; Peters, Roberts, Kurvers, & Delhey, 2012). In a recent experiment with serins, Trigo and Mota

**Table 1**

<table>
<thead>
<tr>
<th>Variables</th>
<th>Estimate</th>
<th>SE</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plumage chromaticity (SWS ratio)</td>
<td>5.475</td>
<td>2.432</td>
<td>5.069</td>
<td>0.039</td>
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<tr>
<td>Plumage achromaticity (double cone)</td>
<td>-3.429</td>
<td>23.270</td>
<td>0.222</td>
<td>0.885</td>
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<tr>
<td>Breast patch size</td>
<td>0.028</td>
<td>0.056</td>
<td>0.246</td>
<td>0.627</td>
</tr>
<tr>
<td>Crown patch size</td>
<td>0.153</td>
<td>0.440</td>
<td>0.120</td>
<td>0.734</td>
</tr>
<tr>
<td>Body size</td>
<td>-0.088</td>
<td>0.658</td>
<td>0.018</td>
<td>0.895</td>
</tr>
<tr>
<td>Age</td>
<td>0.592</td>
<td>1.610</td>
<td>0.135</td>
<td>0.718</td>
</tr>
</tbody>
</table>

Predictors were plumage chromaticity (SWS ratio), plumage achromaticity (double cone), breast patch size, crown patch size, body size, age. 'Group' was also included as a random factor, to control for differences between experimental groups.

**DISCUSSION**

Our results show that male serins in captive groups form steep dominance hierarchies, which is indicative of strong consistent differences between individuals in their agonistic interactions. We also demonstrated that plumage coloration and testosterone levels can independently predict social dominance in a feeding context.
(2014) reported a moderate negative effect of implanted testoster-
one on the satiation and size of yellow coloration of males. Still, the relationship between testosterone and carotenoid-based plumage coloration is unclear, and needs further research.

Although coloration and testosterone were not correlated, they both predicted male dominance. This could result from reduced power of the test due to a small sample size in relation to effect sizes or derive from complex relationships between testosterone and coloration with dominance. Actually, while testosterone may cause the dominant behaviour (Adkins-Regan, 2005) coloration is, in this case, signalling it. In spite of these possible differences, both relate significantly to dominance, which underlies the robustness of colour signalling. More tests are needed to understand the different physiological mechanisms underlying carotenoid coloration and testosterone and their possible difference in functional pathways in relation to dominance status.

Overall, our experiment reveals that yellow carotenoid-based coloration and testosterone levels in the European serin predict social dominance in a nonsexual, feeding context. These results, together with previous research, show that yellow coloration is sexually preferred by females (Leitão et al., 2014), indicating that a dual function of a carotenoid ornament is possible. These results also highlight the importance of considering contexts other than sexual contexts when studying armament — ornament signal processes, which can be more appropriately framed within social selection.

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References


### Appendix

#### Table A1

Summary of generalized linear mixed models (GLMM) of the David’s score (social dominance), using violet-sensitive (VS) spectral sensitivity in the visual model

<table>
<thead>
<tr>
<th>Variables</th>
<th>Estimate</th>
<th>SE</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plumage chromaticity (SWS ratio)</td>
<td>10.706</td>
<td>5.229</td>
<td>4.129</td>
<td>0.058</td>
</tr>
<tr>
<td>Plumage achromaticity (double cone)</td>
<td>−5.809</td>
<td>23.720</td>
<td>0.048</td>
<td>0.809</td>
</tr>
<tr>
<td>Breast patch size</td>
<td>0.022</td>
<td>0.056</td>
<td>0.071</td>
<td>0.701</td>
</tr>
<tr>
<td>Crown patch size</td>
<td>0.113</td>
<td>0.446</td>
<td>0.205</td>
<td>0.804</td>
</tr>
<tr>
<td>Body size</td>
<td>0.159</td>
<td>0.669</td>
<td>0.056</td>
<td>0.816</td>
</tr>
<tr>
<td>Age</td>
<td>0.616</td>
<td>1.658</td>
<td>2.255</td>
<td>0.716</td>
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</table>

Predictors were plumage chromaticity (SWS ratio), plumage achromaticity (double cone), breast patch size, crown patch size, body size, age. ‘Group’ was also included as a random factor, to control for differences between experimental groups.

#### Table A2

Summary of generalized linear mixed models (GLMM) of the David’s score (social dominance), for the effects of plumage chromaticity using violet-sensitive (VS) spectral sensitivity in the visual model

<table>
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<td>SWS ratio for crown</td>
<td>10.706</td>
<td>5.229</td>
<td>4.129</td>
<td>0.058</td>
</tr>
<tr>
<td>SWS ratio for throat</td>
<td>−5.809</td>
<td>23.720</td>
<td>0.048</td>
<td>0.809</td>
</tr>
<tr>
<td>SWS ratio for throat</td>
<td>0.022</td>
<td>0.056</td>
<td>0.071</td>
<td>0.701</td>
</tr>
<tr>
<td>SWS ratio for breast</td>
<td>0.113</td>
<td>0.446</td>
<td>0.205</td>
<td>0.804</td>
</tr>
<tr>
<td>SWS ratio for belly</td>
<td>0.159</td>
<td>0.669</td>
<td>0.056</td>
<td>0.816</td>
</tr>
</tbody>
</table>

#### Table A3

Correlation between testosterone levels and social dominance, coloration (SWS ratio for all body parts and SWS for crown) and body size

<table>
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<th>Variables</th>
<th>Statistics</th>
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<td>David’s score (social dominance)</td>
<td>$r_s=0.569$, $P=0.014$</td>
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<tr>
<td>Plumage chromaticity (SWS ratio)</td>
<td>$r_s=0.165$, $P=0.512$</td>
</tr>
<tr>
<td>SWS ratio for crown</td>
<td>$r_s=0.118$, $P=0.641$</td>
</tr>
<tr>
<td>Body size</td>
<td>$r_s=0.143$, $P=0.570$</td>
</tr>
</tbody>
</table>

$N = 18$ for each variable.