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**Structural complexity of hunting habitat and territoriality
increase the reversed sexual size dimorphism in diurnal
raptors**

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Keywords:	Body size, life-history traits, sexual size dimorphism (SSD)
Abstract:	<p>Despite numerous efforts and many hypotheses to explain the selective pressures that may have favoured reversed sexual dimorphism (RSD) in raptors - i.e. that the female is larger than the male - some drivers of RSD are still unknown.</p> <p>Here we analyse how much variation in RSD is explained by hunting habitat structure, territoriality or territory size. We do so using data on diurnal raptors from the New World and the Western Palearctic - i.e. Cathartidae, Pandionidae, Accipitridae and Falconidae, the largest bird group showing RSD - taking into account the phylogenetic relationships among species.</p> <p>Our results identify the type of the main prey as a major factor explaining RSD in raptors. We also found RSD to increase with increasing structural complexity in the hunting habitat from open or semi-open habitats to forest interior. RSD also increased with increasing degree of territoriality of the species (non-territorial < facultative < territorial). Finally, for territorial species RSD increased with increasing size of nesting territory. A model comprising only three predictor variables (prey type, structural complexity of hunting habitat and territoriality) explained up to 50% of the variation in RSD of European and American diurnal raptor species, and up to 40% of the variation in RSD when only territorial species were considered.</p> <p>Our results highlight the relevance of spatial facets of the niche - e.g. hunting habitat, territoriality and territory size - in exerting selective pressures on the body size of diurnal raptors. These selective pressures, joint with already known trophic factors - e.g. diet - are decisive for the evolution of the RSD, a key trait in the functional ecology of raptors. Our findings open up new perspectives in the study of sexual size divergence in birds.</p>

1 **Abstract**

2 Despite numerous efforts and many hypotheses to explain the selective pressures that may have
3 favoured reversed sexual dimorphism (RSD) in raptors - i.e. that the female is larger than the
4 male - some drivers of RSD are still unknown.

5 Here we analyse how much variation in RSD is explained by hunting habitat structure,
6 territoriality or territory size. We do so using data on diurnal raptors from the New World and the
7 Western Palearctic – i.e. Cathartidae, Pandionidae, Accipitridae and Falconidae, the largest bird
8 group showing RSD - taking into account the phylogenetic relationships among species.

9 Our results identify the type of the main prey as a major factor explaining RSD in raptors. We
10 also found RSD to increase with increasing structural complexity in the hunting habitat from
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13 species RSD increased with increasing size of nesting territory. A model comprising only three
14 predictor variables (prey type, structural complexity of hunting habitat and territoriality)
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18 territoriality and territory size - in exerting selective pressures on the body size of diurnal raptors.

19 | These selective pressures, joint with already known trophic factors – e.g. diet ~~preference~~- are
20 decisive for the evolution of the RSD, a key trait in the functional ecology of raptors. Our
21 findings open up new perspectives in the study of sexual size divergence in birds.

22 **Keywords:** Body size, life-history traits, sexual size dimorphism (SSD).

23 **Introduction**

24 Understanding the selective pressures that cause sex differences in life history is a fundamental
25 question in ecology (Sutherland et al. 2013). Among most of diurnal raptors (Cathartidae,
26 Pandionidae, Accipitridae and Falconidae), body size is one of the most notable differences
27 between males and females. Raptors generally show female-biased sexual size dimorphism, an
28 opposite trend to what is observed in most bird and mammal species, thus usually termed
29 reversed sexual dimorphism (hereafter RSD) (Amadon 1959; Andersson and Norberg 1981;
30 Székely et al. 2007). Even so, RSD varies widely among different species of raptors. While some
31 species show barely noticeable differences between sexes, in others, females are twice as heavy
32 as their partners (Newton 1979).

33 Numerous hypotheses have been proposed to explain what selective pressures may cause RSD in
34 raptors (Massemin et al. 2000; Ferguson-Lees and Christie 2001; ~~and~~ Krüger 2005; Slagsvold
35 and Sonerud 2007; Sonerud et al. 2013). However, despite the abundant literature on RSD, the
36 mechanisms favouring this trait remain elusive (Ferguson-Lees and Christie 2001; Sonerud et al.
37 2013; Friedman and Remeš 2016) partly because several potential drivers of RSD are yet to be
38 evaluated. For instance, the relationships between RSD and relevant raptor characteristics such
39 as the structural complexity of the hunting habitat, the degree of territoriality, and territory size
40 have received little attention (Snyder and Wiley 1976; Walter 1979; Pérez-Camacho et al. 2015;
41 Table 1). Novel empirical evidence on the causal factors of RSD is required to better understand
42 the evolution of body size, not only in diurnal raptors, but also in other groups of birds showing
43 RSD (Jehl and Murray 1986; Székely et al. 2000; Sonerud et al. 2014a).

44 A widely accepted hypothesis for RSD posits that it responds to differentiated sex roles during
45 the breeding season (Storer 1966; Reynolds 1972; Andersson and Norberg 1981; Slagsvold and

46 Sonerud 2007; Sonerud et al. 2014a). It is well known that in raptors, the female usually
47 incubates, broods and feeds the nestlings, until they can feed themselves unassisted, while the
48 male provides food for the family (Newton 1979). Greater difference in sex roles implies a
49 greater potential for differential selection on male and female body size. Sonerud et al. (2014a)
50 showed that prey size conditions the period of time in which chicks have to be fed by the
51 females~~should eat female-assisted~~. Large preys cannot be managed by the chicks until they reach
52 an advanced age, delaying the time at which females resume to hunting (Sonerud et al. 2014a, b).
53 As a result, males would need to provide a frequent and abundant supply of food for the whole
54 family, especially after the eggs hatch (Newton 1979; del Hoyo et al. 1994). Selective pressures
55 would have driven males to increase their hunting efficiency by hunting smaller prey, which are
56 often more abundant than larger prey (Storer 1966). If true, male raptor size would decrease
57 because smaller prey species are usually more agile than larger prey and, because smaller
58 predators are more agile and more efficient at capturing small prey (Reynolds 1972; Andersson
59 and Norberg 1981; Ferguson-Lees and Christie 2001; Dial et al. 2008; Tornberg et al. 2014).
60 Male size reduction, would ultimately improve reproductive success (Ydenberg and Forbes
61 1991) by increasing efficiency at hunting smaller prey.

62 Prey type and size is recurrently utilised as a proxy for mechanisms underlying the variation in
63 RSD among species of raptors. For example, several works have documented the effect of prey
64 type, as a surrogate for prey agility, on RSD, suggesting that the higher the speed and agility of
65 the main prey of the raptor, the greater its RSD (Hill 1944; Reynolds 1972; Newton 1979;
66 Wheeler and Greenwood 1983; Temeles 1985; Paton et al. 1994). Additionally, Sonerud et al.
67 (2014a, 2014b) showed that prey type can act as a proxy for prey handling time given the
68 positive correlation between prey agility and prey handling time (Sonerud et al. 2014a). The

69 longer the handling time, the longer the female is confined to the nest, which would in turn lead
70 to greater RSD values.

71 Other explanatory factors for RSD variation have received much less attention. For example,
72 there is little information on how the structural complexity of the habitat affects hunting success,
73 male raptor size and RSD. We hypothesise that structurally complex habitats such as forest
74 interiors, where many obstacles must be avoided during hunting, would exert an additional
75 pressure on males to become smaller in order to increase their agility, akin to the pressure due to
76 prey agility. This hypothesis predicts that RSD is greater among forest-dwelling raptors than
77 among raptors inhabiting open habitats such as steppes, savannahs and deserts, which present
78 few obstacles to hunting.

79 Another little-studied factor that may affect RSD is territoriality. Territoriality is an extreme case
80 of intra-specific competition in which certain individuals are able to breed by controlling a
81 portion of the habitat, while those that fail to occupy a territory often do not contribute offspring
82 to the next generation (Brown 1964). Most raptor species (75% of the genera) are territorial
83 during the breeding season (Newton 1979; del Hoyo et al. 1994; Ferguson-Lees and Christie
84 2001; Rebollo et al. 2017). If territorial disputes are resolved based on aerial agility, territoriality
85 should promote a reduction in the size of competing individuals. That is, smaller male size would
86 translate into greater aerial agility and thus, into greater likelihood of gaining access to nesting
87 territories through effective flight displays (Andersson and Norberg 1981; Widén 1984;
88 Hakkarainen et al. 1996; Székely et al. 2007). Alternatively, if territorial disputes are resolved
89 through force, territoriality may promote an increase in body size, i.e the larger the female, the
90 greater its effectiveness in competing with other females for the best males and their nesting
91 territories (Olsen and Olsen 1987; McDonald et al. 2005; Sergio et al. 2007; Pérez-Camacho et

92 al. 2015). These hypotheses propose that territorial species could experience extra selective
93 pressures related to nesting in relation to non-territorial raptors. These additional pressures may
94 promote RSD.

95 There are few data to test whether territoriality promotes an increase in RSD and, if so, whether
96 RSD increases through an increase in female size, a reduction in male size, or both (Olsen and
97 Olsen 1987; McDonald et al. 2005; Sergio et al. 2007; Pérez-Camacho et al. 2015). The same
98 can be said of the potential effect of nesting territory size on RSD, which is tightly linked to
99 territoriality. For a territorial species, the size of the nesting territory determines the number of
100 reproductive pairs in a given area (Patterson 1980; Newton 2003). Therefore, if two species have
101 the same population size but occupy territories of different sizes, then the proportion of breeding
102 adults should be smaller in the species occupying the larger territories. As a result, the selective
103 pressures on traits that promote access to breeding territories should increase with increasing size
104 of nesting territory. Whether and how this increased pressure affects RSD is yet to be examined.

105 Here, we test the relative ability of four hypotheses to explain interspecific variation in RSD of
106 diurnal raptors from the New World and the Western Palearctic (see Table 1 for a summary).
107 First, the *prey agility hypothesis*, which poses that prey agility influences male size because
108 smaller males are more effective at capturing agile prey. This hypothesis predicts a positive
109 correlation between raptor RSD and the agility of the prey, measured by the taxonomic grouping
110 to which the main prey belongs. Second, the *habitat complexity hypothesis* states that complexity
111 may induce RSD in raptors because forest interiors would favour hunting of smaller males. The
112 prediction is for male size to decrease with increasing structural complexity of the hunting
113 habitat during the breeding season. Third and fourth, the *territoriality* and *territory size*
114 | *hypotheses*, respectively, which expect territoriality to affect RSD through larger females ~~and/or~~

115 smaller males being more effective at establishing nesting territories when there is a spatial
116 constraint on nesting. The derived prediction is that territorial species and, within territorial
117 species those defending the largest territories, will show higher values of RSD. We take into
118 account the phylogenetic non-independence among raptor species, both when we explore
119 bivariate relationships of RSD against each proxy and when we test these hypotheses in a
120 multiple regression setting.

121

122 **Materials and methods**

123 **Data collection**

124 We collated data on New World and Western Palearctic diurnal raptor species from numerous
125 data sources (see Supplementary material Appendix 1); the data encompassed a wide range of
126 habitats and life histories. RSD was calculated for each species using the arithmetic midpoint
127 between the minimal and maximal body masses given in each sex (mid-range) and the following
128 index based on Storer (1966): $RSD\ Index = 100 \times [(female\ mass - male\ mass) / (0.5 \times (female$
129 $mass + male\ mass))]$. In parallel, the RSD index was calculated using the mid-range of the cubed
130 wing length, in order to compare our results with previous studies on RSD that used wing length
131 as a surrogate for body mass (Ferguson-Lees and Christie 2001 and Krüger 2005).

132 We assessed the ability of fFour factors linked to our hypotheses (see above) were assessed for
133 their ability to predict-explain the variation in RSD for raptors: (1) prey agility, which was scored
134 according to each species' main prey (mainly based on the diet description found in Ferguson-
135 Lees and Christie 2001 and del Hoyo et al. 1994), following a 6-point scale in ascending order of
136 prey agility [1 = carrion (including eggs, nestlings and injured prey), 2 = invertebrates, 3 =
137 reptiles and amphibians, 4 = fish, 5 = mammals, 6 = birds] (sensu Temeles 1985, but including

138 carrion and amphibians + reptiles); further studies should refine the prey agility index when
139 accurate data on the proportional composition of the diet becomes available for each of the
140 studied species; (2) structural complexity of hunting habitat, (mainly based on the habitat
141 description found in Ferguson-Lees and Christie 2001 and del Hoyo et al. 1994) which was
142 assessed on a 3-point scale [1 = open habitat (e.g. hunting takes place exclusively or mainly in
143 open landscapes such as desert, savanna, or over the tree canopy), 2 = semi-open habitat (e.g.
144 mosaic of fields and forests or the ecotone between them), 3 = closed habitat (e.g. hunting takes
145 place exclusively or mainly inside forests)]; (3) territoriality, characterised as the average extent
146 of nesting territorial behaviour during the breeding season on a 3-point scale [0 = non-territorial
147 (species that breed in colonies or loose colonies), 1 = facultative (breeding behaviour varies
148 between non-territorial and territorial among different populations of the same species), 2 =
149 territorial (solitary species that defend an area containing the nest and usually some food
150 resources as well)] (for data sources see Supplementary material Appendix 1); and (4) territory
151 size (for the subset of territorial species), expressed as an index reflecting the territory size per
152 unit body mass:

153 Territory size index = mean nearest neighbour nest distance / \log_{10} (mid-range of male body
154 mass)

155 This index takes into account the relationship between territory size and species body mass
156 among the species studied here (data not shown; $r = 0.611$, $p < 0.001$; Schoener 1968; Newton
157 1979; Palmqvist et al. 1996). Male body mass was used to calculate the territory size index
158 because it explained more variation in RSD than female body mass or the mean body mass of
159 both sexes (Supplementary material Appendix 2. Figure A1). Data on distances among nests
160 were extracted from a literature review conducted by searching the databases of the Web of

161 Science, Zoological Record and Wildlife and Ecology Studies Worldwide. The following search
162 terms were used: *nest distance* OR *distribution* OR *spacing* OR *dispersion* OR *territory*, *spatial*
163 *pattern* OR *distribution* OR *nearest neighbour* AND *raptor* OR *< the name of each raptor group*
164 *>*. Of the more than 850 papers identified, we retained 123 (see Supplementary material
165 Appendix 1) and extracted distance data for territorial species, allowing us to calculate the
166 territory size index.

167 Our goal is to test a parsimonious model, i.e. with few variables of high explanatory power^{high}
168 ~~explanatory variables~~, which have not been examined to date (with the exception of prey type),
169 rather than a comprehensive model with many variables, most of them with poorly explanatory
170 power, which has already been tested (e.g. Krüger 2005).

171 **Statistical analyses**

172 Since our goal was not to build accurate predictive models but rather to understand the
173 relationships between RSD and predictor variables, we followed a two-pronged approach.
174 Firstly, we inspected the bivariate relationships between RSD and each of our predictor
175 variables, each of them supported by a well-founded hypothesis. Secondly, we used saturated
176 ordinary least squares (OLS) models to analyse the associations of RSD with the four predictors
177 (prey agility, hunting habitat, territoriality or territory size). Standardised regression coefficients
178 and the associated *p*-values were used to approximate the strength with which variables were
179 associated with RSD. To evaluate the extent to which collinearity among predictors affected our
180 models, we calculated their condition number; a condition number greater than five indicates
181 unstable regression coefficients (Belsley 1991). We also performed OLS partial regressions to
182 calculate the amount of variation in RSD explained by each predictor either independently or
183 jointly with the other predictors.

184 We repeated all analyses for two sets of species. Of the approximately 135 species inhabiting the
185 study regions (del Hoyo et al. 1994; Ferguson-Lees and Christie 2001), the first set comprised 75
186 territorial, facultative and non-territorial species for which we had complete data on all variables,
187 including phylogenetic data. The distribution of RSD across studied raptor species was normal
188 without any signs of skewness (Supplementary material Appendix 3. Figure A4). Future studies
189 should seek to determine whether our results are also valid for a global set of diurnal raptor
190 species. The second set focused on the 36 territorial species for which we also had data on
191 territory size. This procedure allowed us to investigate our hypotheses not only for a
192 comprehensive set of species to assess the extent to which territoriality associates with RSD, but
193 also for the subset of territorial species to infer whether species defending larger territories show
194 greater RSD. A percentage response variable such RSD should be modelled using GLS models
195 with logit link function for the residuals. However, the statistical distribution of RSD, analogous
196 to a continuous response variable allowed us modelling it using OLS. First, RSD is normally
197 distributed as supported by Shapiro-Wilk normality tests for both the 75 ($P = 0.504$) and the 36
198 ($P = 0.652$) species subsets. Second, most of RSD data fall within the linear section of the
199 sigmoidal logistic curve (i.e. between 0.2 and 0.8) and thus, all predicted values are within 0 and
200 100%.

201 **Phylogenetic analyses**

202 To account for phylogenetic autocorrelation, we compared the results of the abovementioned
203 OLS models with those of phylogenetic generalized least squares (PGLS) models (Freckleton et
204 al. 2002). PGLS models are a special type of generalized least squares model that accounts for
205 phylogenetic correlation structure in model residuals, represented by a phylogenetic variance-
206 covariance matrix. We fitted PGLS models by making maximum likelihood-based adjustments

207 to the evolutionary scaling parameters λ and δ (Pagel 1999). The parameter λ indicates the fit of a
208 trait to a Brownian evolutionary model; in other words, the parameter assesses the extent to
209 which evolutionary relatedness leads to patterns of trait similarity. It ranges from zero (absence
210 of phylogenetic signal) to one (perfect fit to Brownian motion). The parameter δ is the power to
211 which the elements of the variance-covariance matrix are raised and it characterises the tempo of
212 evolution. Whereas a default value of $\delta=1.0$ indicates linear change in the trait that is
213 proportional to branch length, values of $\delta < 1.0$ suggest an early evolution of the trait, while
214 values of $\delta > 1.0$ suggest a more recent evolution (Pagel 1999). This analysis allows us to
215 determine whether model residuals contain phylogenetic signal, and it also indicates the extent to
216 which we can rely on the significance of OLS regression coefficients. We extracted data on the
217 phylogenetic relationships for the set of 75 species of raptors considered, and for the subset of 36
218 territorial species from the recent avian phylogeny published by Jetz et al. (2012). We computed
219 the phylogenetic variance-covariance matrices that allowed calculation of λ , δ and PGLS models.
220 We accounted for non-phylogenetic independence between species also in the bivariate analyses
221 of RSD with predictor variables.

222 To compare our models against models lacking the assumptions made by PGLS - i.e. Brownian
223 Motion as the model of reference - we fitted a Generalized Mixed Model in a Bayesian
224 framework using Markov Chain Monte Carlo (MCMC) (Hadfield and Nakagawa 2010). In this
225 modelling framework, phylogenetic relationships are included as a random effect rather than as a
226 variance-covariance matrix expressing the phylogenetic structure in model residuals (see
227 Appendix 4. Table A1).

228 We calculated the significance of correlations after correcting the number of degrees of freedom
229 using Dutilleul's (1993) method implemented in SAM 4.0 (Rangel et al. 2010) and using a

230 phylogenetic ANOVA (Garland et al. 1993). Phylogenetic analyses were performed in R 3.3.0
231 (R Development Core Team) using the packages ‘ape’ (Paradis et al. 2004), ‘caper’ (Orme et al.
232 2013), ‘MCMCglmm’ (Hadfield 2010) and ‘phytools’ (Revell 2012). Figures depicting partial
233 regressions were generated using the eulerAPE area-proportional Euler diagram application
234 (Micallef and Rodgers 2014). Data available from the Supplementary material Appendix 1,
235 Table A1.

236

237 **Results**

238 Analysis of bivariate relationships between RSD and predictors revealed that diurnal raptors that
239 hunt more agile prey had higher RSD than raptors that hunt less agile or immobile prey ($r =$
240 0.658 , corrected- $p < 0.001$; Fig. 1a). Species that hunt in forest interiors showed greater RSD
241 than species hunting in open or semi-open habitats ($r = 0.328$, corrected- $p = 0.017$; Fig. 1b).
242 Species that are territorial during the breeding season showed the greatest RSD, followed by
243 facultative species, and finally by non-territorial species, which showed the smallest RSD ($r =$
244 0.400 , corrected- $p = 0.002$; Fig. 1c). Among the subset of 36 territorial raptors, RSD positively
245 correlated with mean territory size index ($r = 0.434$, corrected- $p = 0.011$; Fig. 2). The strength
246 and significance of bivariate associations between RSD and the predictors were virtually
247 identical when analysed based according to a phylogenetic ANOVA (Garland et al. 1993; see
248 Fig. 1). Further, we obtained similar results regardless of whether RSD was calculated using
249 body mass or cubed wing length, though RSD calculated with body mass was higher ($F = 9.31$; p
250 $= 0.003$) and more sensitive to the explanatory variables used in this study than the RSD
251 calculated using cubed wing length (Figs. 1 and 2, and Supplementary material Appendix 3,
252 Figs. A1-A3).

253 Strength of the associations of RSD with the four predictors, as measured by standardised
254 regression coefficients, were consistent across OLS and PGLS models and across both sets of
255 species (Table 2). Prey agility was associated with the highest standardised regression
256 coefficients, followed by hunting habitat; these coefficients were significant for OLS and PGLS
257 models. Territoriality and territory size showed the smallest coefficients, which in no case
258 achieved statistical significance in a multiple linear modelling framework. Collinearity among
259 predictors did not affect the stability of regression coefficients since condition numbers were < 5
260 (i.e. 1.662 for the full set of 75 species and 2.027 for the subset of 36 territorial species). To
261 check for the robustness of our prey agility classification, we run sensitivity analyses slightly
262 modifying the classification of prey types whose agility may be more dubious – e.g. fish being
263 more agile than reptiles and vice versa or merging amphibians, reptiles and fish into a single
264 lower-vertebrate category. Sensitivity analyses yielded virtually identical model coefficients and
265 significations in both OLS and PGLS models (results not shown to avoid redundancy),
266 confirming that our results are robust to subtle changes in our classification of prey agility.

267 To fit the PGLS models, we performed maximum likelihood-based adjustment of the
268 evolutionary parameters λ and δ ; for both species sets, λ was greater than 0.8 and δ was greater
269 than 1.0. These values suggest that the unexplained portion of RSD still contains non-random
270 phylogenetic signal, with closely related species tending to share similar RSD. Besides, RSD of
271 closely related species probably evolved non-linearly, with differences in RSD across species
272 accumulating over relatively recent times (i.e. $\delta > 1.0$). Taking the phylogenetic non-
273 independence of species into account in the PGLS analysis did not appreciably affect the ranking
274 of standardised coefficients for each predictor (Table 2).

275 OLS partial regressions confirmed that prey agility explained a larger proportion of RSD
276 variation than the other three predictors, which independently explained proportions of RSD
277 variation according to the ranking of their OLS and PGLS regression coefficients (multiple
278 regression models; Fig. 3). Interestingly, territoriality and territory size explained a greater total
279 amount of RSD variation than hunting habitat. However, the variation explained by these two
280 territorial predictors partially overlapped with the variation in RSD explained by prey agility,
281 which was 14.1% for the complete set of 75 species and 16.7% for the subset of 36 territorial
282 species (Fig. 3 and Supplementary material Appendix 3, Table A1). For this reason, both
283 territorial variables are less important than hunting habitat within a multiple modelling context.
284 These results were qualitatively identical to those from PGLMM where phylogenetic
285 relationships were modelled as a random effect (see Appendix 4 for details).

286

287 **Discussion**

288 Our results, for the first time, provide empirical evidence that RSD in diurnal raptors positively
289 correlates with the structural complexity of the hunting habitat, as well as with territoriality.
290 Notably, these results encompass a broad range of raptor species and the large geographical
291 extent. The associations we find do not seem to be affected by the evolutionary relatedness
292 among species; they seem more likely to have appeared as an adaptive response to the ecological
293 factors on which this study focused.

294 **Relative importance of ecological factors**

295 The relationships between RSD and the predictors hold regardless the evolutionary relationships
296 among species, and despite the fact that raptor RSD is a strongly phylogenetically structured
297 trait. This means that closely related raptor species may have evolved RSD in response to similar

298 selective pressures (Paton et al. 1994; Krüger 2005), some of which are analysed here. No more
299 thanOnly three predictor variables together explain up to 50% of the variation in RSD across the
300 entire set of New World and Western Palearctic diurnal raptor species; up to 40% of RSD
301 variation when only territorial species are considered. That is, a reduced number of mechanisms
302 (i.e. 3) would suffice to largely explain the evolution and maintenance of RSD in birds of prey
303 (for reviews, see Massemin et al. 2000; Ferguson-Lees and Christie 2001; Krüger 2005; and
304 Slagsvold and Sonerud 2007).

305 That RSD increases with increasing prey agility is widely accepted (Hill 1944; Storer 1966;
306 Reynolds 1972; Newton 1979; Temeles 1985; Ydenberg and Forbes 1991; Tornberg et al. 1999;
307 Massemin et al. 2000; Krüger 2005), and the prey agility hypothesis is supported by our results
308 based on a relatively large number of species distributed over a large geographical area.

309 Alternatively, our measurement of prey agility based on taxonomic grouping can also be seen as
310 a proxy for ingestion rate *sensu* Slagsvold and Sonerud (2007). Avian prey would take longer to
311 ingest than mammalian prey, mammals would take longer to ingest than reptiles, and reptiles
312 longer than insects (Slagsvold and Sonerud 2007, Slagsvold et al. 2010, Sonerud et al. 2014a, b).
313 Consequently, ingestion rate would explain RSD in the same direction as prey agility does, at
314 least when prey agility is measured based on taxonomy.

315 Our work identifies new ecological factors that influence RSD both jointly with prey agility and
316 independently of it. For example, the structural complexity of the hunting habitat, an overlooked
317 variable so far, explains 11% of the variation in RSD mostly independent of its association with
318 prey agility. This result suggests that, species feeding on agile prey inside complex habitats may
319 show the greatest RSD, and thus, that the selective pressures exerted by prey agility and habitat
320 complexity may be cumulative. Note that habitat preference (for example, used by Krüger 2005)

321 is not equivalent to the structural complexity of the hunting habitat. For example, some raptor
322 species breeding in forests hunt over the canopy or in the forest edges. In fact, Krüger (2005) did
323 not find support for habitat preference as a driver of RSD.

324 The association between RSD and prey agility partially overlaps with the association between
325 RSD and species territoriality. In other words, part of the variation in RSD is explained jointly by
326 both predictors. This is not entirely surprising in the case of diurnal raptors, since species of this
327 group that capture more agile prey are more likely to show territorial behaviour than species
328 capturing more vulnerable prey (Nilsson et al. 1982; Martínez-Hesterkamp et al. [in press 2018](#)).
329 Territorial behaviour and prey type could increase RSD in a species through different
330 mechanisms. The scarcity of studies analysing the relationships between RSD and territoriality
331 and territory size may have led researchers to overestimate the effects of prey-type based
332 mechanisms on RSD. Territoriality and territory size explained more absolute RSD variation in
333 partial regressions than did the structural complexity of hunting habitat (Fig. 3), even though
334 their regression coefficients were non-significant in multiple linear models. These findings,
335 together with the significant correlation between RSD and territoriality and territory size (Figs.
336 1c, 2), advise to take these spatial factors into account, yet few studies have done so (Snyder and
337 Wiley 1976; Walter 1979; Widén 1984).

338 **Hunting habitat structure**

339 Our results identify that hunting habitats with high structural complexity affect RSD in raptors.
340 This supports our initial hypothesis that agility needed to catch prey effectively in an
341 environment with obstacles (i.e. forest interior) selects for the most agile males, which should be
342 smaller. Such selective pressure should increase the RSD of species that hunt within closed
343 habitats, while negligibly affecting the RSD of species that hunt in habitats with fewer obstacles

344 (i.e. open habitats such as savannahs, steppes or deserts). On the other hand, we observed similar
345 RSD for species hunting in open as for species hunting in mixed habitats. This may indicate that
346 only habitats of greater structural complexity exert sufficient selective pressure to drive RSD.

347 If highly complex habitats select for smaller body size, it could in principle lead to a size
348 reduction in both sexes. Instead, we observed higher RSD in forest hunters, suggesting that the
349 size reduction occurred primarily or exclusively in males. This likely reflects the fact that raptor
350 RSD is influenced by hunting efficiency specifically during the early stages of the breeding
351 season, including the pre-breeding period, egg-laying, incubation, and first half of the nestling
352 period (Newton and Marquiss 1984; Pérez-Camacho et al. 2015). During this period the male
353 bears nearly sole responsibility for hunting, leading the male to be more strongly selected for
354 small size than the female (Ferguson-Lees and Christie 2001; Sonerud et al. 2014a, b). Our
355 findings are consistent with previous research advocating for greater selective pressures on male
356 size than on female size. For example, Pérez-Camacho et al. (2015) showed that in a Spanish
357 population of a forest raptor, the northern goshawk *Accipiter gentilis*, L., small breeding males
358 had more fledglings than larger males, while the reproductive success of females remained
359 unaffected. The net result suggests an intensified sex role differentiation and therefore RSD.

360 **Territoriality and territory size**

361 RSD is positively associated with increasing degree of territoriality in diurnal raptor species of
362 the New World and the Western Palearctic. This finding extends previous evidence, derived
363 from only a few species, that raptor RSD may have evolved by sexual selection through
364 competition among males for a territory (Widén 1984), or among females for the best males or
365 territories (Sergio et al. 2007; McDonald et al. 2005; Pérez-Camacho et al. 2015). Our study
366 provides modern, large-scale confirmation of the observations, first reported nearly four decades

367 ago, that colonial and semi-colonial species show lower RSD than territorial species (Snyder and
368 Wiley 1976; Walter 1979), and that RSD increases with increasing size of the territory defended
369 (Walter 1979). Those works failed to propose mechanisms to explain how intra-sexual
370 competition for a territory may have influenced the body size of both sexes. Our results inspire
371 the following proposal for how territoriality and territory size may have exerted selective
372 pressures on males, females or both, leading to increased RSD. As "owners" of the nesting
373 territory, males are responsible for defending it and defining its boundaries against other males
374 (Newton 1979; Olsen and Olsen 1987). Disputes between males for ownership and delimitation
375 of the territories are solved by aerial displays and, ultimately, air fights (Cade 1960; Andersson
376 and Norberg 1981; Widén 1984). In species equipped with harmful weapons like talons, agility is
377 more important than size and strength, where agility is defined as manoeuvrability and the ability
378 to ascend rapidly in order to take up an advantageous position above the opponent (Widén 1984).
379 Consequently, smaller and more agile males should outcompete their congeners due to their
380 higher probability of obtaining a territory to breed and leave offspring.

381 Females, occupy and defend from other females a small portion of the nesting territory near the
382 nest; this "territory" is usually limited to the area where the male brings food and transfers it to
383 the female (Olsen and Olsen 1987). We suggest that these disputes between females, which take
384 place near the ground over smaller areas than the entire nesting territory, are resolved through
385 aggressive displays with or without physical contact. In this case, size and strength should be
386 most important for intimidating and expelling competitors from the feeding area, which would
387 favour larger females. Studies for three diurnal raptor species (Northern goshawk and Black kite
388 in Spain and Brown falcon in Australia) have shown that larger females are more likely to be
389 recruited as breeders than smaller ones (McDonald et al. 2005; Sergio et al. 2007; Pérez-

390 Camacho et al. 2015). Contrary to what is observed in males, larger and stronger females should
391 have a competitive advantage in acquiring territories, increasing their chances of breeding. In
392 this way, selective pressures from territoriality in both males and females may increase RSD.

393 Our finding that raptor RSD increases with increasing size of the territory defended echoes the
394 results of one study conducted nearly four decades ago by Walter (1979) in Eleonora's Falcon
395 *Falco eleonora*, Gené. We propose that for territorial species similar in size, males and females
396 of species defending smaller nesting territories experience weaker competitive pressures to breed
397 than species defending larger nesting territories. The former species should have access to a
398 greater density of suitable breeding sites where they experience weaker selective pressures, so
399 they should show lower RSD than species defending larger nesting territories. Another non-
400 exclusive reason for increasing RSD with increasing territory size would select for small male
401 (provider of prey) body size due to energetic costs, i.e., longer movements during foraging in the
402 larger territories.

403 Based on our present findings, we can hypothesise that the selective pressures induced by all the
404 predictors analysed here favour a strong reduction in male size, which would explain the
405 evolution of RSD in raptors. These results agree with Krüger's (2005) who found strong support
406 for male reduction and little support for female enlargement in a comparative study comprising
407 510 species of diurnal raptors and owls. However, territoriality can also promote an increase in
408 female size, as evidenced by previous studies (McDonald et al. 2005; Sergio et al. 2007; Pérez-
409 Camacho et al. 2015) and by our results. We propose that the evolution of RSD in diurnal raptors
410 reflects primarily a strong reduction in male size, together with a possible weaker enlargement of
411 females in some species.

412 In conclusion, this study shows how ~~the hunting strategy of raptors~~ (prey agility and hunting
413 habitat) ~~may~~ have influenced their RSD: the greater the prey agility and structural complexity of
414 the hunting habitat in the breeding season, the greater the RSD. A substantial proportion of the
415 well-established influence of prey agility (or prey type) on raptor RSD may also be linked to
416 evolutionary pressures related to territoriality and territory size. In sum, our results show how
417 intricate relationships amongst both eltonian (trophic) and grinnellian (spatial) aspects of diurnal
418 raptors' niches may have acted as selective pressures leading to the evolution of RSD. The
419 substantial amount of variation in raptor RSD explained by prey agility, habitat complexity and
420 territoriality advises future studies to consider these factors.

421

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438 *Authors' contributions* – LP, SM, SR and GG conceived the ideas and designed methodology.
439 SM and LP collected the data. IM and SM analysed the data. LP, SM and IM led the writing of
440 the manuscript. All authors contributed critically to the drafts and gave final approval for
441 publication.

442 *Conflicts of interest* – The authors declare that they have no conflict of interest.

443

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- 562
- 563 Supplementary material (Appendix XXXXX (insert manuscript number) at LÄNK). Appendix
564 1–4.

565 **Tables**

566 Table 1. Summary of the hypotheses proposed here to explain RSD variation in diurnal raptors. The selective pressures, responses, competitive
 567 advantages and outcomes derived from each hypothesis are outlined.

Hypothesis	Selective pressure	Response	Competitive advantage	Outcome for RSD
Prey agility	Agility of the main prey during breeding season	Increased male agility	Hunting efficiency during breeding season	♀♂ → ♀♂
Hunting habitat structure	Structural complexity of the hunting habitat during breeding season	Increased male agility	Hunting efficiency during breeding season	♀♂ → ♀♂
Territoriality or Territory size	Territoriality during breeding season or Nesting territory size	Increased female strength and volume	Female competition for male and his territory	♀♂ → ♀♂
		Increased male agility	Male competition for territory via acrobatic flight displays	♀♂ → ♀♂

568

569 Table 2. Multiple regression models of diurnal raptor RSD in the New World and Western Palearctic.

Model	Prey agility			Hunting habitat			Territoriality			Territory size index			λ	δ	R^2_{adj}	CN
	β_2	t	$P \leq$	β_1	t	$P \leq$	β_3	t	$P \leq$	β_3	t	$P \leq$				
OLS (75 sp.)	0.591	6.482	<.001	0.254	3.013	0.004	0.103	1.112	0.27				0.000	1.000	0.500	1.662
PGLS (75 sp.)	0.574	5.877	0.000	0.250	2.838	0.006	0.133	1.450	0.152				0.950	14.407	0.462	
OLS (36 sp.)	0.429	2.619	0.014	0.353	2.578	0.015				0.266	1.591	0.122	0.000	1.000	0.398	2.027
PGLS (36 sp.)	0.433	2.626	0.013	0.349	2.524	0.017				0.241	1.430	0.162	0.890	15.981	0.365	

Note. OLS, ordinary least squares; PGLS, phylogenetic generalized least squares; sp., species. Results for OLS and PGLS models are shown with their corresponding adjusted coefficients of determination (R^2_{adj}) and the standardised regression coefficients of the predictors included in these models. Phylogenetic PGLS models include the evolutionary parameters λ and δ (Pagel 1999), which were estimated using maximum likelihood methods. [These parameters, and which fitted for model residuals](#), indicate that the evolution of RSD has been slow and subject to evolutionary inertia, with closely related species showing RSD values more similar than can be expected at random. Condition number (CN) was calculated for OLS models; values smaller than five indicate that collinearity among predictors does not affect regression coefficients (Belsley 1991).

570 **Figures**

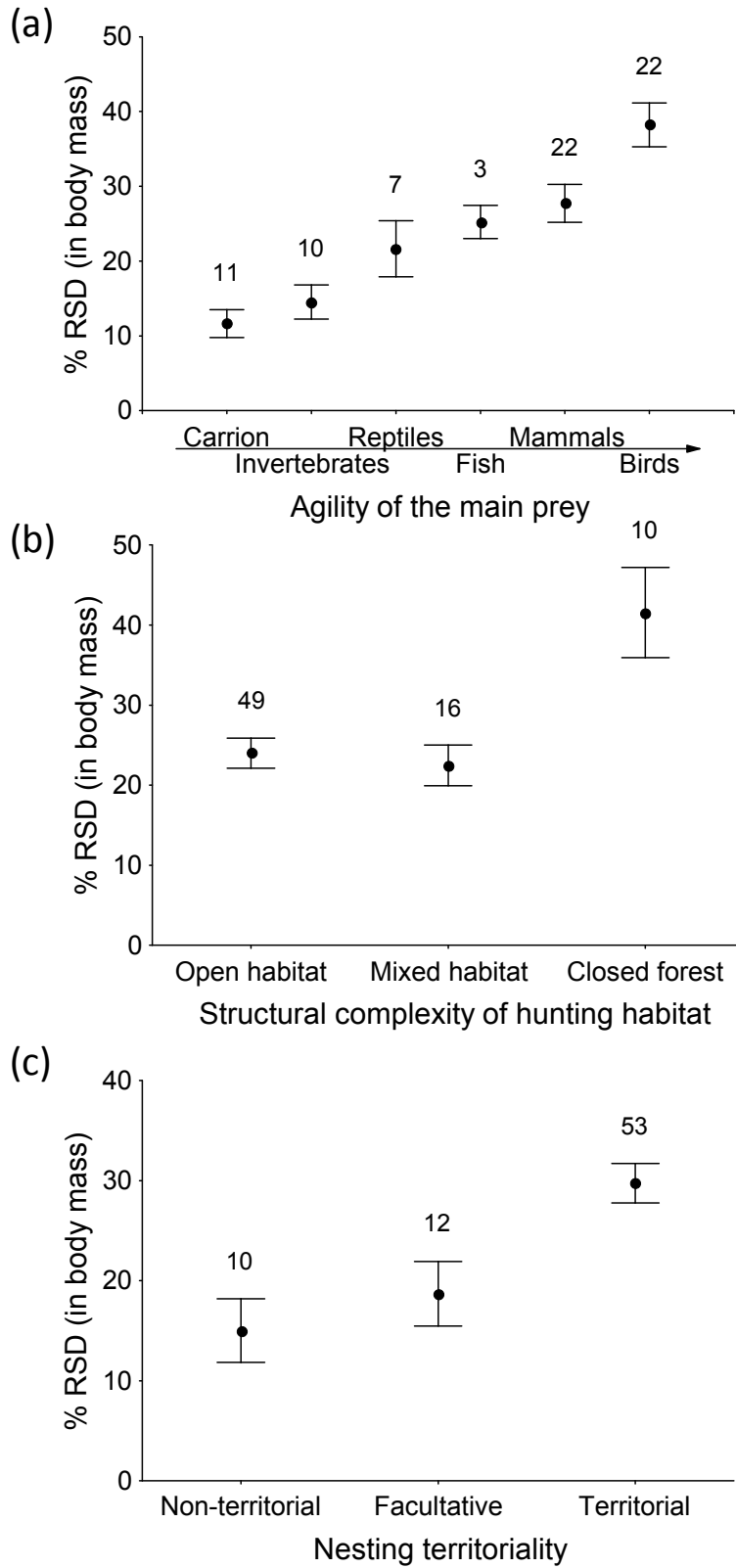
571 Figure 1. Relationship of RSD in New World and Western Palearctic raptors (based on body
572 mass) to (a) agility of the main prey; (b) hunting habitat in breeding season, scored on a scale
573 from open habitat to interior of closed forest; and (c) nesting territorial behaviour. Error bars
574 indicate 1 S.E and number above bars the number of raptor species. Statistical significance as
575 measured by a phylogenetic ANOVA (Garland et al. 1993) was found for agility of the main
576 prey ($F= 11.564$; $p = 0.001$), hunting habitat ($F= 7.987$; $p = 0.038$) and, nesting territoriality
577 ($F= 7.239$; $p = 0.015$). For the equivalent figure showing RSD based on cubed wing length,
578 see Supplementary material Appendix 3, Fig. A1.

579

580 Figure 2. Relationship of RSD in New World and Western Palearctic raptors (based on body
581 mass) to territory size index. This index was calculated as the average nearest-neighbour
582 inter-nest distance in the population/ \log_{10} (mean male body mass). For the equivalent figure
583 showing RSD based on cubed wing length, see Supplementary material Appendix 3, Fig. A2.

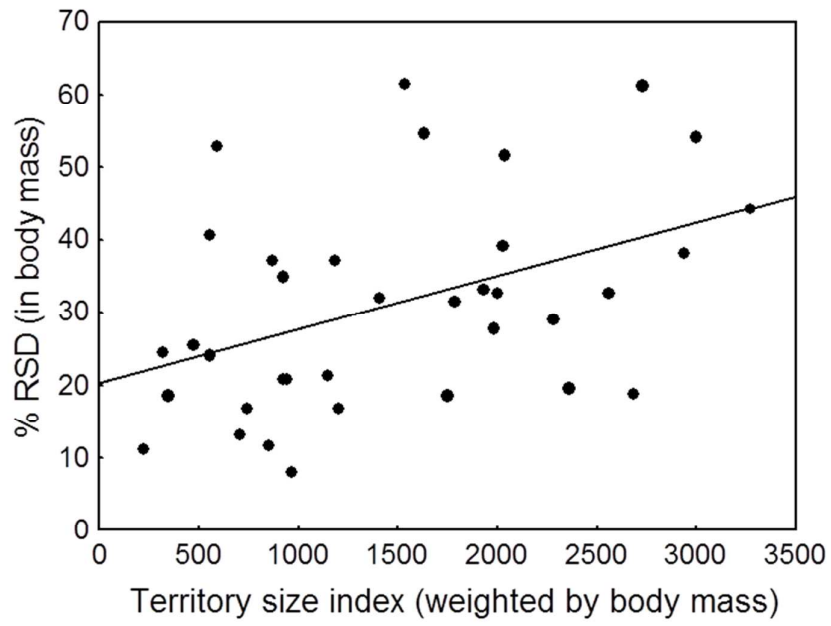
584

585 Figure 3. Euler diagrams of 3-way partial regressions illustrating shared and independent
586 relationships among prey agility (blue), habitat structure (green) and territoriality or territory
587 size (purple) for explaining different amounts of variation in RSD across raptor species in
588 New World and Western Palearctic raptors for (a) all species ($n = 75$) and (b) the subset of
589 territorial species ($n = 36$). Ellipse size is proportional to the amount of variation in RSD
590 explained by each predictor. Note that in panel (b), the grey-shaded area indicates a negative
591 value resulting from interactions among predictor variables. See Supplementary material
592 Appendix 3, Table A1 for details on partial regression results.



593

594 Figure 1



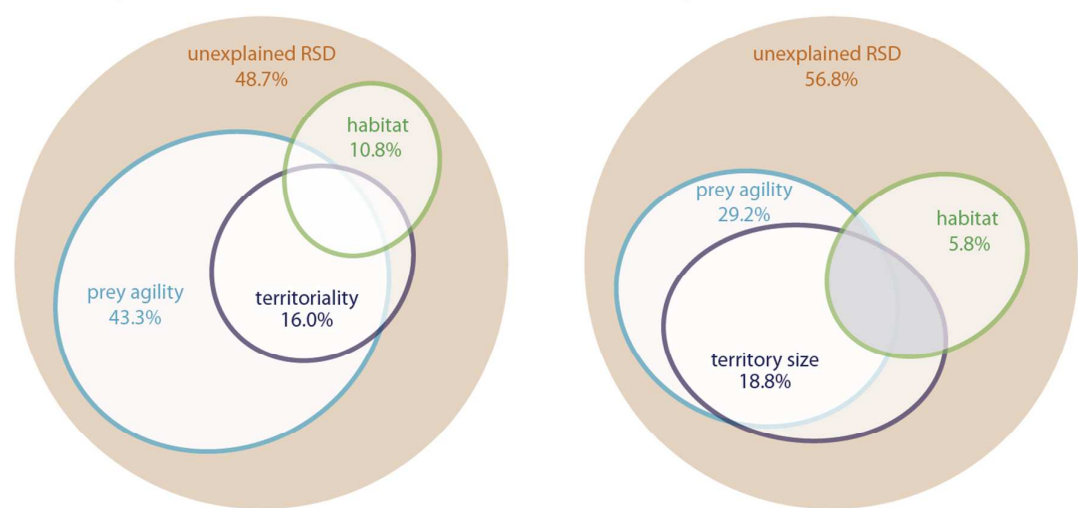
595

596 Figure 2

Review Only

A) 75 species

B) 36 species



597

598 Figure 3

For Review Only

Supplementary material for “Structural complexity of hunting habitat and territoriality increase the reversed sexual dimorphism in diurnal raptors”.

Appendix 1. Complete data set (Table A1) and lists of data sources used in this work.

Table A1. Complete data set of the respond and predictor variables for the 75 species of diurnal raptors used in this work. Territory size index was calculated only for territorial species for which we had data on distances to nearest neighbour nests (n=36). Reversed sexual dimorphism was calculated using body mass and cubed wing length ($RSD = 100 \times [(female\ body\ measure - male\ body\ measure) / (0.5 \times (female\ measure + male\ measure))]$). Hunting habitat: 1 = open habitat; 2 = semi-open habitat; 3 = closed habitat. Prey agility (i.e. species' main prey): 1 = carrion; 2 = invertebrates; 3 = reptiles and amphibians; 4 = fish; 5 = mammals; 6 = birds. Territorial behaviour: 0 = non-territorial; 1 = facultative; 2 = territorial. Territory size index = mean inter-nest distance / \log_{10} (mid-range of male body mass). ND = Not Determined.

Family	Species	RSD (body mass)	RSD (cubed wing length)	Hunting habitat	Prey agility	Territorial behavior	Territory size index
Falconidae	<i>Micrastur semitorquatus</i>	33.6	14.2	3	5	0	-
Falconidae	<i>Herpetotheres cachinnans</i>	12.9	1.1	2	3	2	ND
Falconidae	<i>Caracara plancus</i>	13.3	4.1	1	1	2	ND
Falconidae	<i>Ibycter americanus</i>	20.7	6.1	3	2	2	ND
Falconidae	<i>Milvago chimango</i>	3.7	15.2	1	1	0	-
Falconidae	<i>Phalcoboenus australis</i>	10.5	8.5	1	1	1	-
Falconidae	<i>Falco deiroleucus</i>	54.3	40.0	1	6	2	2994.7
Falconidae	<i>Falco rufigularis</i>	48.3	49.6	1	6	2	ND
Falconidae	<i>Falco vespertinus</i>	7.0	10.5	1	2	1	-
Falconidae	<i>Falco columbarius</i>	20.9	27.1	1	6	2	936.1
Falconidae	<i>Falco sparverius</i>	11.0	9.9	1	2	1	-
Falconidae	<i>Falco eleonora</i>	10.3	18.7	1	6	0	-
Falconidae	<i>Falco subbuteo</i>	28.0	12.0	1	6	2	1982.8
Falconidae	<i>Falco tinnunculus</i>	18.7	15.3	1	5	1	-
Falconidae	<i>Falco naumanni</i>	27.6	5.0	1	2	0	-
Falconidae	<i>Falco mexicanus</i>	37.2	32.4	1	5	2	865.3
Falconidae	<i>Falco pelegrinoides</i>	54.8	37.1	1	6	2	1630.0
Falconidae	<i>Falco peregrinus</i>	44.3	38.2	1	6	2	3264.3
Falconidae	<i>Falco rusticolus</i>	38.3	19.4	1	6	2	2932.9
Falconidae	<i>Falco cherrug</i>	32.8	35.1	1	5	2	1995.8
Falconidae	<i>Falco biarmicus</i>	37.0	31.9	1	6	2	ND

Table A1. Continuation

Family	Species	RSD (body mass)	RSD (cubed wing length)	Hunting habitat	Prey agility	Territorial behavior	Territory size index
Cathartidae	<i>Coragyps atratus</i>	8.8	0.1	1	1	0	-
Cathartidae	<i>Cathartes aura</i>	13.5	5.0	1	1	0	-
Pandionidae	<i>Pandion haliaetus</i>	25.0	13.5	1	4	1	-
Accipitridae	<i>Elanus leucurus</i>	11.8	4.4	1	5	1	-
Accipitridae	<i>Elanus caeruleus</i>	17.0	7.7	1	5	2	1200.1
Accipitridae	<i>Pernis apivorus</i>	8.0	2.9	2	2	2	963.6
Accipitridae	<i>Elanoides forficatus</i>	7.6	10.9	2	2	0	-
Accipitridae	<i>Gypaetus barbatus</i>	6.7	1.0	1	1	2	ND
Accipitridae	<i>Neophron percnopterus</i>	15.4	11.8	1	1	2	ND
Accipitridae	<i>Circaetus gallicus</i>	11.8	7.1	1	3	2	842.7
Accipitridae	<i>Aegyptius monachus</i>	7.8	16.3	1	1	1	-
Accipitridae	<i>Gyps fulvus</i>	6.4	13.3	1	1	0	-
Accipitridae	<i>Harpia harpyja</i>	61.4	22.0	3	5	2	2726.4
Accipitridae	<i>Spizaetus ornatus</i>	36.7	22.6	3	6	2	ND
Accipitridae	<i>Aquila pomarina</i>	37.3	9.5	1	5	2	1177.1
Accipitridae	<i>Aquila clanga</i>	17.7	16.1	1	5	2	ND
Accipitridae	<i>Hieraetus pennatus</i>	31.6	27.8	1	6	2	1780.0
Accipitridae	<i>Aquila chrysaetos</i>	32.8	23.0	1	5	2	2555.5
Accipitridae	<i>Aquila fasciatus</i>	19.0	11.2	1	6	2	2679.1
Accipitridae	<i>Aquila nipalensis</i>	18.8	23.8	1	5	2	1745.4
Accipitridae	<i>Aquila adalberti</i>	19.7	20.0	2	5	2	2353.7
Accipitridae	<i>Aquila heliaca</i>	39.2	16.0	1	5	2	2024.6
Accipitridae	<i>Accipiter striatus</i>	51.9	55.8	3	6	2	2034.8
Accipitridae	<i>Accipiter nisus</i>	53.1	48.7	3	6	2	587.0
Accipitridae	<i>Accipiter gentilis</i>	32.0	31.1	2	6	2	1404.8
Accipitridae	<i>Accipiter cooperii</i>	61.6	44.2	3	6	2	1525.7
Accipitridae	<i>Accipiter bicolor</i>	57.4	55.7	3	6	2	ND
Accipitridae	<i>Circus aeruginosus</i>	22.2	14.6	1	6	1	-
Accipitridae	<i>Circus cinereus</i>	38.1	32.4	1	6	1	-
Accipitridae	<i>Circus cyaneus</i>	40.9	27.0	1	5	1	-
Accipitridae	<i>Harpagus bidentatus</i>	13.4	16.6	3	2	2	700.8
Accipitridae	<i>Milvus milvus</i>	25.7	9.9	1	1	2	472.3
Accipitridae	<i>Milvus migrans</i>	16.3	10.1	1	1	1	-
Accipitridae	<i>Haliaeetus albicilla</i>	29.2	28.2	1	4	2	2277.9
Accipitridae	<i>Haliaeetus leucocephalus</i>	21.5	23.6	1	4	2	1144.6
Accipitridae	<i>Rostrhamus sociabilis</i>	14.5	2.9	1	2	0	-
Accipitridae	<i>Ictinia mississippiensis</i>	24.0	11.9	2	2	0	-
Accipitridae	<i>Ictinia plumbea</i>	11.4	6.1	2	2	2	212.0

Table A1. Continuation

Family	Species	RSD (body mass)	RSD (cubed wing length)	Hunting habitat	Prey agility	Territorial behavior	Territory size index
Accipitridae	<i>Buteogallus anthracinus</i>	40.8	14.3	2	3	2	551.9
Accipitridae	<i>Parabuteo unicinctus</i>	25.9	22.5	1	5	2	ND
Accipitridae	<i>Buteo magnirostris</i>	18.8	11.7	2	3	2	340.9
Accipitridae	<i>Buteo nitidus</i>	17.5	15.2	2	3	2	ND
Accipitridae	<i>Buteo lineatus</i>	24.1	8.8	2	3	2	551.1
Accipitridae	<i>Buteo ridgwayi</i>	25.8	28.1	3	3	2	ND
Accipitridae	<i>Buteo platypterus</i>	24.8	22.1	2	5	2	316.4
Accipitridae	<i>Buteo jamaicensis</i>	17.0	20.2	2	5	2	741.1
Accipitridae	<i>Buteo solitarius</i>	31.5	28.3	2	6	2	ND
Accipitridae	<i>Buteo galapagoensis</i>	36.3	31.5	2	6	2	ND
Accipitridae	<i>Buteo swainsoni</i>	34.9	13.0	1	5	2	916.4
Accipitridae	<i>Buteo albonotatus</i>	33.2	30.9	2	6	2	1925.7
Accipitridae	<i>Buteo regalis</i>	15.8	5.5	1	5	2	ND
Accipitridae	<i>Buteo lagopus</i>	21.0	18.0	1	5	2	914.7
Accipitridae	<i>Buteo rufinus</i>	36.5	19.3	1	5	2	ND
Accipitridae	<i>Buteo buteo</i>	15.2	12.5	1	5	1	-

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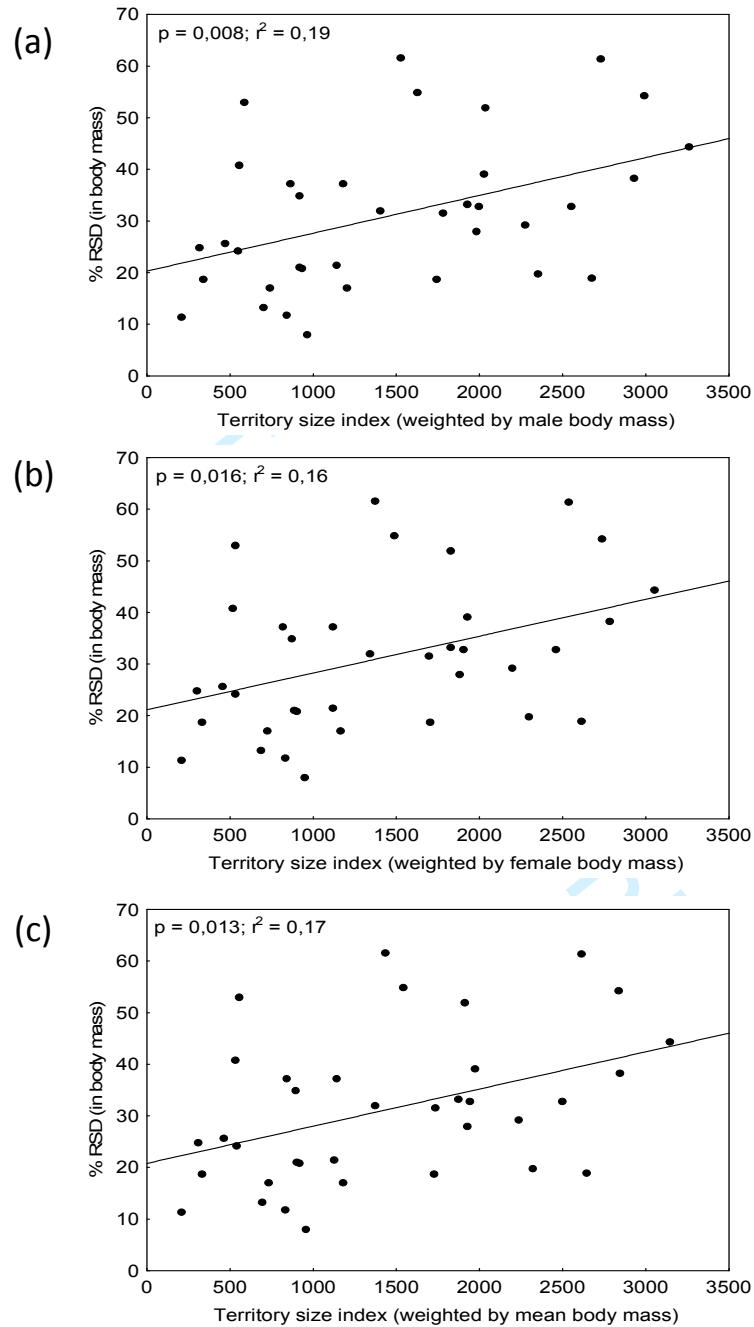
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Supplementary material for “Structural complexity of hunting habitat and territoriality increase the reversed sexual dimorphism in diurnal raptors”.



Appendix 2. Figure A1.

Figure A1. Relationship between RSD in New World and Western Palearctic raptors and territory size index (average nearest-neighbour inter-nest distance in the population/ $\log_{10}(\text{body mass})$) using body mass of: (a) male; (b) female; and (c) mean of both sexes.

For Review Only

Supplementary material for “Structural complexity of hunting habitat and territoriality increase the reversed sexual dimorphism in diurnal raptors”.

Appendix 3. Table A1 and Figures A1-A4.

Table A1. Proportions of RSD variation explained (R^2) individually and jointly by agility of the main prey, hunting habitat structure and territoriality or territory size. These data are summarised in Figure 3.

	All raptors (75 species)	Territorial raptors (36 species)
Total	0.513	0.398
Prey agility	0.433	0.292
Hunting habitat	0.108	0.058
Territoriality	0.160	
Territory size		0.188
Prey agility & Hunting habitat	0.035	-0.037
Prey agility & Territoriality	0.141	
Prey agility & Territory size		0.167
Hunting habitat & Territoriality	0.042	
Hunting habitat & Territory size		-0.064
Prey agility & Hunting habitat & Territoriality	0.032	
Prey agility & Hunting habitat & Territory size		-0.041

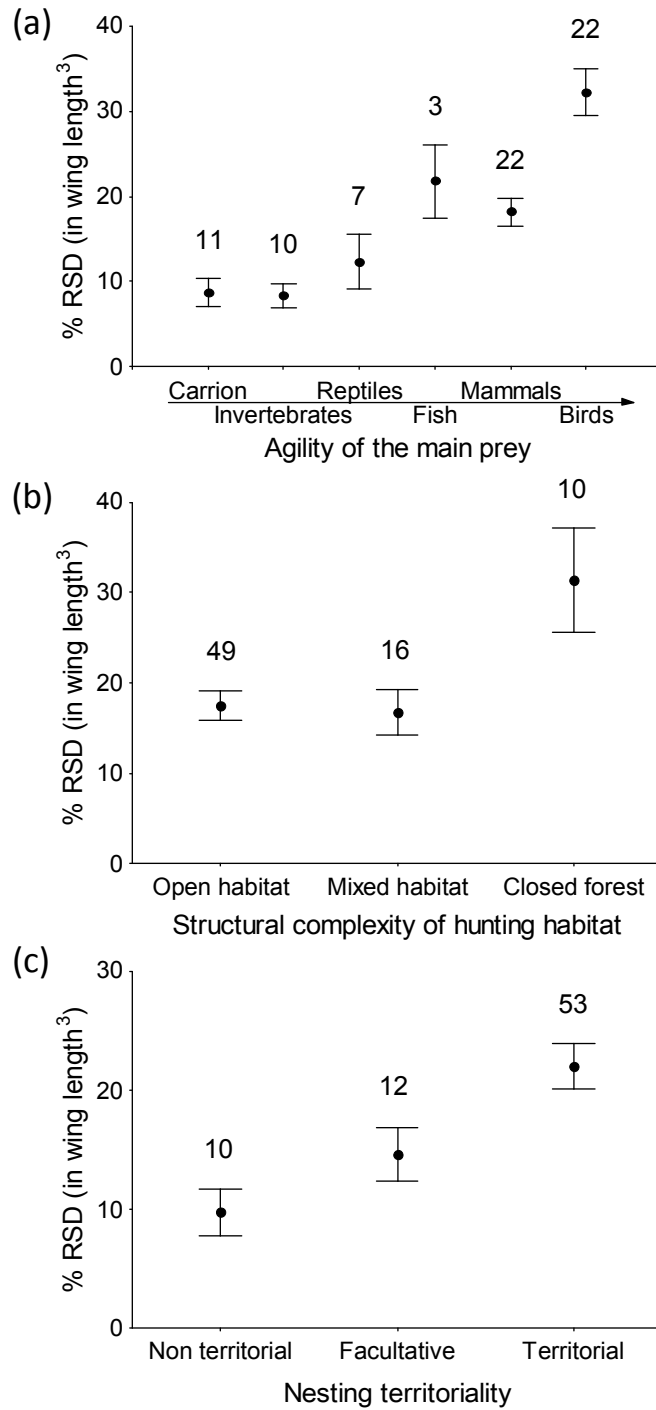


Figure A1. RSD of New World and Western Palearctic raptors was measured in terms of the cubed wing length and depicted as a function of: (a) agility of the main prey; (b) hunting habitat in breeding season; and (c) territorial nesting behaviour. Error bars indicate 1 S.E. and number above bars the number of raptor species.

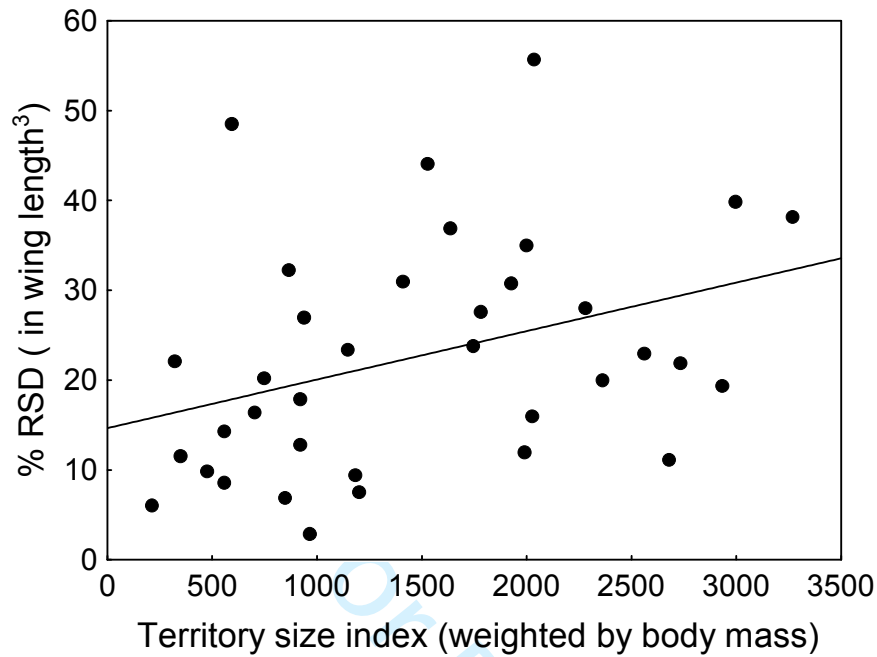


Figure A2. RSD of New World and Western Palearctic raptors was measured in terms of the cubed wing length and depicted as a function of territory size index: average nearest-neighbour inter-nest distance in the population/ $\log_{10}(\text{mean male body mass})$.

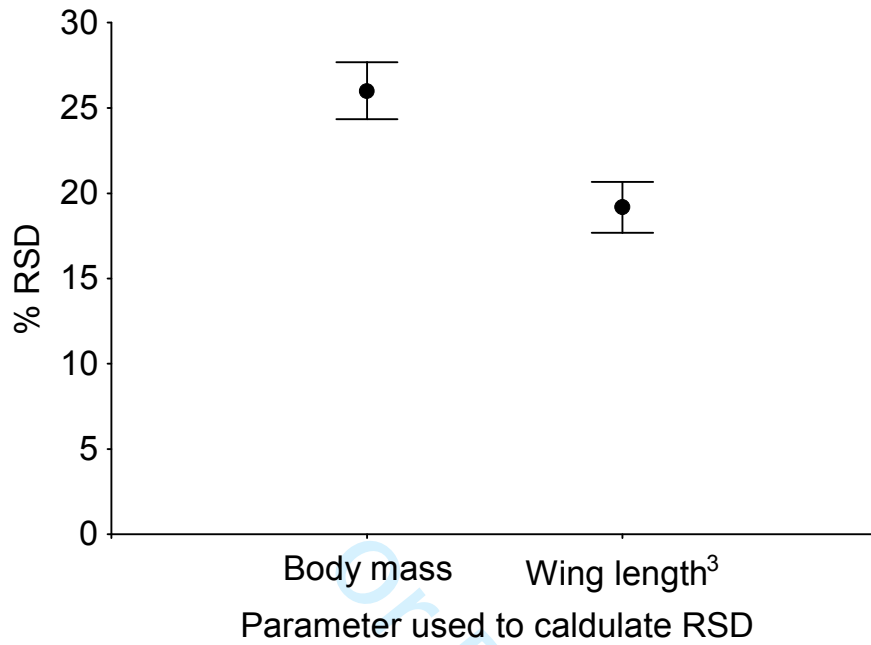


Figure A3. Comparison of RSD calculated based on body mass and RSD calculated based on cubic wing length for New World and Western Palearctic raptors. Error bars indicate 1 S.E.

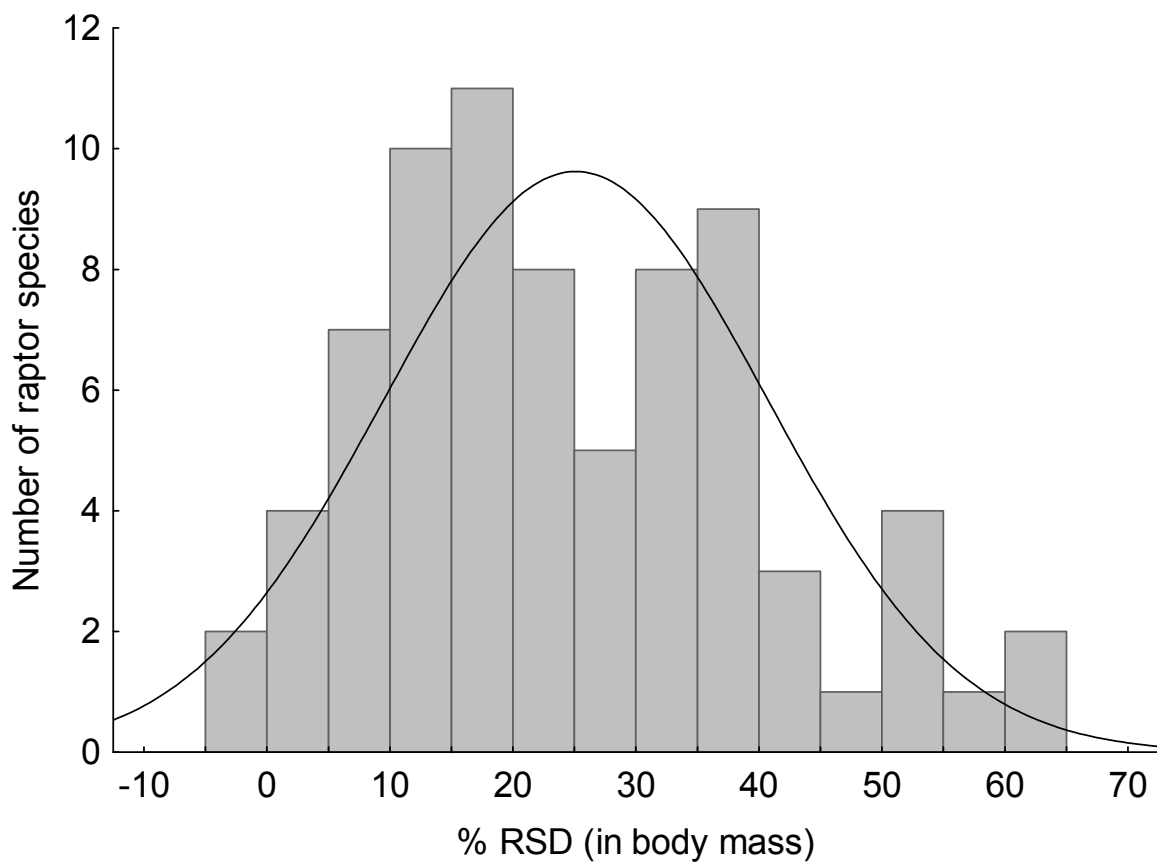


Figure A4. Histogram of the distribution of RSD in the studied raptor species. The line show the normal distribution.

Supplementary material for “Structural complexity of hunting habitat and territoriality increase the reversed sexual dimorphism in diurnal raptors”.

Appendix 4. Table A1.

Table A1. Generalized Linear Mixed Models (GLMM) with (i.e. GLMM.phylo) and without (i.e. GLMM) a random effect characterizing the phylogenetic relationships among species. Models are fitted within a Bayesian framework that uses Markov Chain Monte Carlo (MCMC) methods instead of adjusting maximum likelihood (Hadfield and Nakagawa 2010). Posterior means of coefficients together with their 95% Confidence Intervals are indicated for each predictor. Also, the Deviance Information Criterion (DIC) of each model is reported. Models were fit using a thinning interval of 10 a burn-in period of 3,000 iterations, and 17,000 iterations for models to converge. We report fixed effects to allow direct comparison against OLS and PGLS results. Results qualitatively coincide with those yielded by OLS and PGLS models in identifying prey agility and hunting habitat as significant predictors and, models accounting for phylogenetic relationships as showing better fits than non-phylogenetic models.

Model	Hunting habitat				Prey agility				Territoriality / Territory size				DIC
	posterior mean	low 95% CI	up 95% CI	<i>P</i>	posterior mean	low 95% CI	up 95% CI	<i>P</i>	posterior mean	low 95% CI	up 95% CI	<i>P</i>	
GLMM (75sp.)	5.113	1.701	8.451	0.003	4.586	3.184	5.884	0.001	2.108	-1.887	5.857	0.261	568.655
GLMM.phylo (75sp.)	5.114	1.575	8.727	0.006	4.347	2.780	5.725	0.001	2.679	-0.706	6.629	0.147	563.094
GLMM (36sp.)	6.923	1.775	12.522	0.011	4.411	1.135	7.941	0.007	0.005	-0.001	0.010	0.116	283.572
GLMM.phylo (36sp.)	6.989	1.892	13.240	0.020	4.356	0.772	7.362	0.011	0.004	-0.001	0.010	0.121	282.911