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The version of record:

Martínez-Hestekamp, S. et al., 2018. Territoriality in diurnal raptors: relative roles of recent evolution, diet and nest site. *Biological Journal of the Linnean Society*, 124(1), pp.126–137.

Available at <http://dx.doi.org/10.1093/biolinnean/bly020>

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(Article begins on next page)



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Territoriality in diurnal raptors: relative roles of recent evolution, diet and nest site

Journal:	<i>Biological Journal of the Linnean Society</i>
Manuscript ID	Draft
Manuscript Type:	Original article
Date Submitted by the Author:	n/a
Complete List of Authors:	Martínez-Hestekamp, Sara; University of Alcala, Department of Life Sciences Rebollo, Salvador; University of Alcala, Department of Life Sciences Kennedy, Patricia; Oregon State University, Eastern Oregon Agriculture & Natural Resource Program & Department of Fisheries and Wildlife Pérez-Camacho, Lorenzo; University of Alcala, Department of Life Sciences García-Salgado, Gonzalo; University of Alcala, Department of Life Sciences Morales-Castilla, Ignacio; University of Alcala, Department of Life Sciences
Keywords:	body size, phylogeny, prey agility, prey size, territory size

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3 1 **Territoriality in diurnal raptors: relative roles of recent evolution, diet and nest**
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39 14 **Running title: Territoriality in diurnal raptors**
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3 15 **Abstract**
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5 16 Animal territoriality, defined here as defense of well delimited breeding areas to
6
7 17 exclude competitors, has been widely studied. However, the phylogenetic and
8
9 18 ecological characteristics influencing the variation in the expression of this behavior are
10
11 19 poorly understood. We evaluated the effect phylogeny and key ecological factors have
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13 20 on territorial behavior and territory size in diurnal raptors from the western Palearctic
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15 21 and New World. To our knowledge, our work is the first comparative analysis of raptor
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17 22 territorial behavior and territory size that accounts for phylogenetic relationships. One
18
19 23 important finding is that territorial behavior has not been strongly conserved across
20
21 24 evolutionary time, but differences in territoriality of diurnal raptors have been
22
23 25 influenced by recent evolution, which led to variations of this behavior in response to
24
25 26 climate and habitat changes. Raptor current ecology is also associated with the
26
27 27 expression of these traits. Species that capture more agile prey and nest in more
28
29 28 protected sites were most likely territorial. Additionally, territorial species that are
30
31 29 bigger and capture more agile and bigger prey defended larger territories than species
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33 30 feeding on more vulnerable and smaller prey. We discuss potential mechanisms for
34
35 31 these patterns and the implications of our findings for future research on avian
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37 32 territoriality.
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42 33 *Key-words:* body size; phylogeny; prey agility; prey size; territory size
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34 INTRODUCTION

35 Animal territoriality, defined here as defense of well delimited breeding areas to
36 exclude competitors from use of limiting resources, has puzzled researchers since the
37 early twentieth century, when Howard (1920) described this behavior in birds.
38 Individuals holding a territory have advantages over conspecifics by ensuring exclusive
39 use of limited resources, provided those resources are defensible in terms of cost-benefit
40 balances (Brown 1964; 1969; Davies 1980; Maher & Lott 1995). At least twenty
41 ecological variables have been suggested to relate to territoriality within vertebrate
42 species (for a review see Maher & Lott 2000). Despite the large volume of information
43 on the topic, it is not clear what species-specific characteristics and ecological factors
44 ultimately determine whether or not a species is territorial.

45 Previous studies on territorial behavior and territory size focused mostly on a single
46 species (Nice 1941; Hinde 1956; Stamps 1994). However, because this pattern is so
47 widespread, we wanted to elucidate general patterns on factors influencing variation in
48 territoriality by means of an interspecific comparison (Rolland, Danchin & de Fraipont
49 1998). In comparative analyses, species may not be statistically independent of each
50 other, because closely related species tend to be more similar due to a common lineage
51 (e.g. Freckleton, Harvey & Pagel 2002; Blomberg, Garland & Ives 2003; Rezende &
52 Diniz-Filho 2012). Testing for the presence of phylogenetic signal, i.e., the tendency of
53 closely related species to resemble each other, also can be used to study how phenotypic
54 (e.g., territorial behavior) variation is distributed across species and how it changed over
55 evolutionary time (Blomberg, Garland & Ives 2003; Rezende & Diniz-Filho 2012).

56 Phenotypic differences or similarities among species could be the result of shared genes
57 from a common ancestor or reflect recent evolutionary adaptations to contrasting
58 environmental conditions (Rezende and Diniz-Filho 2012). To date, these phylogenetic

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3 59 relationships have not been analyzed to study the variability of territorial behavior
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5 60 among raptors.
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8 61 Studies of territoriality analyze food most commonly as the limiting resource (Stamps
9
10 62 1994). Intermediate amounts, moderately clumped, and predictable food resources
11
12 63 promote territorial behavior (Brown 1964; Newton 1979; Maher & Lott 2000);
13
14 64 therefore, food types whose attributes reduce their availability or increase their
15
16 65 predictability are more likely to be associated with territorial behavior (Maher & Lott
17
18 66 2000). In territorial species, food availability also induces changes in territory size
19
20 67 (Schoener 1968, Patterson 1980), which affects individuals' fitness (Adams 2001).

21
22
23 68 Territory size increases with low densities of food (Schoener 1968; Verner 1977; Both
24
25 69 & Visser 2003) and with higher proportions of meat in the diet (Schoener 1968).

26
27 70 Species that capture large prey might defend larger territories, because large prey are
28
29 71 usually less abundant than small ones (Newton 1979; 1980; Krüger 2000). Raptor body
30
31 72 mass, which is positively correlated with territory size (Schoener 1968; Newton 1979;
32
33 73 Palmqvist et al. 1996), also influences territory size. These two variables are in fact
34
35 74 closely related, as prey size incrementally increases with raptor body size (Newton
36
37 75 1979). Additionally, in avian predators such as raptors, the agility of their food is
38
39 76 hypothesized to influence territory spacing and size. Species that capture more evasive
40
41 77 prey (e.g., birds and large mammals) tend to have larger territories that are spaced in
42
43 78 more regular patterns, than do species that feed on less agile prey (e.g., reptiles and
44
45 79 amphibians; Nilsson, Nilsson & Sylvén 1982).

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49 80 Availability and distribution of suitable nest sites also influences degree of spacing and
50
51 81 territoriality in birds (Hinde 1956; Stamps 1994; Both & Visser 2003). When
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53 82 availability of potential nest sites is too low or has a clumped distribution, number of
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55 83 competitors might increase up to a threshold where nests are no longer economically
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3 84 defensible (Newton 1979). Availability of high quality nest sites might also be reduced
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5 85 by presence of predators, which decreases suitability of those sites for breeding;
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7 86 therefore, nest predation risk also might influence territoriality. Territorial species tend
8
9 87 to breed in more concealed nest sites than colonial breeders do, probably because the
10
11 88 former can use the protection conferred by those sites to hide from predators attracted
12
13 89 by territorial display and signaling (Crook 1965; Brown & Orians 1970). Furthermore,
14
15 90 territorial species could reduce the frequency with which predators can locate nests by
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17 91 defending a large exclusive area that separates them from neighbor's nests (Crook 1965;
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20 92 Brown & Orians 1970).

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22
23 93 Our aim was to evaluate phylogenetic and the aforementioned ecological factors
24
25 94 associated with territorial behavior in diurnal raptors. We chose diurnal raptors for this
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27 95 investigation because territoriality is well studied in this group and species-level data on
28
29 96 factors influencing territoriality is available for a large number of species. Additionally,
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31 97 for territorial species only, we explored which factors were more strongly associated
32
33 98 with their territory size. Using western Palearctic and New World diurnal raptors (the
34
35 99 most well-studied group of raptors), we analyzed the phylogenetic signal of both
36
37 100 territorial behavior and mean territory size. Given that the common ancestor of birds
38
39 101 was likely territorial (Rolland et al. 1998; Varela et al. 2007) and that territoriality is
40
41 102 widely represented among raptors (Newton 1979), we hypothesized that the
42
43 103 phylogenetic signal for territorial behavior would be high in this group. On the other
44
45 104 hand, because mean territory size varies intra- and interspecifically among raptors, we
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47 105 expected a low phylogenetic signal for this variable. In addition, we analyzed the role
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49 106 played by current ecological factors in determining territoriality using comparative
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51 107 analyses of diurnal raptors. We chose diet and nest site as explanatory variables because
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53 108 previous literature suggests these are the primary factors related to territorial behavior
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3 109 (e.g., Nice 1941; Hinde 1956; Stamps 1994; Both & Visser 2003). However, these
4
5 110 hypotheses are yet to be tested in comparative analysis. Based on the existing literature,
6
7 111 we predict that probability of showing territorial behavior and larger mean territory
8
9 112 sizes will occur in raptor species that 1) capture more agile prey; 2) are bigger and feed
10
11 113 upon larger prey, and 3) nest in protected sites (i.e., concealed and/or inaccessible sites).

14 114 **METHODS**

16 115 **Data collection**

18 116 We collated data for western Palearctic and New World species of diurnal raptors
19
20 117 because those species have been extensively studied. The majority of the data were
21
22 118 collected from avian and raptor compendia (Cramp 1998; del Hoyo, Elliott & Sargatal
23
24 119 1994; Ferguson-Lees & Christie 2001), but for several species, data were completed
25
26 120 using other sources (see lists 1 and 2 in Appendix S1, Supporting Information). We
27
28 121 focus on the study of large breeding territories, which contain more than the nest area,
29
30 122 where mating, nesting and at least some food-seeking occur (Nice 1941, Hinde 1956).
31
32 123 Using this literature, we used a binary response variable that classified species'
33
34 124 territorial behavior into one of two categories: 0 = non territorial, i.e., a species that
35
36 125 breeds in colonies or loose colonies; and 1 = always territorial, i.e., solitary species that
37
38 126 consistently defend an area containing more than just the nest.

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43 127 To find data on mean territory size, we conducted a bibliographical review of the mean
44
45 128 nearest neighbor distance during the breeding season for each species, since this is the
46
47 129 most commonly used metric to measure degree of territoriality in raptors (i.e., Newton
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49 130 1979; Nilsson, Nilsson & Sylvén 1982; Rebollo et al. 2017, see list 3 in Appendix S1
50
51 131 for more examples). We performed searches in Web of Science, Zoological Record and
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53 132 Wildlife and Ecology Studies Worldwide using the following search terms: *nest*
54
55 133 *distance* or *distribution* or *spacing* or *dispersion* or *territory*, *spatial pattern*, *nearest*

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3 134 *neighbor*, and *raptor* or the name of one raptor group (e.g., vulture, eagle, hawk). We
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5 135 scanned over 850 papers looking for mean inter-nest distances between conspecifics. Of
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7 136 these 850 papers, 123 publications (see list 3 in Appendix S1, Supporting Information)
8
9 137 contained mean between-nest distance data for territorial species. Mean distances were
10
11 138 log transformed to obtain a normal distribution of errors.

139 We obtained information on diet and nest site from the same sources used to
140 categorically describe territorial behavior. For the prey agility variable, we classified
141 each species by the agility of its main prey, defining this as the most preferred prey
142 taxon according to the species general diet description in different compendia (del
143 Hoyo, Elliott & Sargatal 1994; Cramp 1998; Ferguson-Lees & Christie 2001; see
144 similar approach in Newton 1979, Temeles 1985 and Krüger 2005): 1 = carrion
145 (including eggs, nestlings and injured prey), 2 = invertebrates, 3 = reptiles and
146 amphibians, 4 = fish, 5 = mammals, and 6 = birds. The prey size variable was based
147 also on the diet descriptions, taking into account preferences for different prey items.
148 We assigned each prey item to one of the following categories, and calculated prey size
149 as the weighted mean value for all items included in the diet description: 1 = 0-10 g
150 (e.g., insects, small molluscs, larvae), 2 = 10-100 g (e.g., large molluscs, small lizards,
151 mammals and birds), 3 = 100-1500 g (e.g., fish, large lizards, snakes, medium-sized
152 birds and mammals), and 4 = >1500 g (e.g., large birds and mammals). Raptor body
153 mass was calculated as the mean of male and female adult mid-range weight for each
154 species. The nest protection variable followed a scale of increasing inaccessibility or
155 concealment of the nest site (area immediately surrounding the nest; see similar
156 approach in Rolland et al. 1998): 1 = ground (in open or semi-open habitat, i.e.,
157 grassland, steppe, savannas, wetlands), 2 = isolated tree (in open or semi-open habitat),
158 3 = facultative (nest site category varies between populations of the same species), 4 =

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3 159 cliff, crags or rocky area, and 5 = tree within a forest. We transformed our predictor
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5 160 variables into discrete ordered categories following Gelman & Hill (2007; pp. 66-67),
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7 161 except prey size, which was a continuous variable. See Table S1 (Supporting
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9 162 Information) for information on the data used for each species.
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12 163 We acknowledge there are exceptions within the categories used in this study. For
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14 164 example, the evasiveness of prey can vary largely (e.g., within insects there are flying
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16 165 and non-flying prey species). These categories do not reflect all variation among prey
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18 166 but were designed to reflect general patterns and as other investigators have
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20 167 demonstrated (e.g., Newton 1979; Krüger 2005), are a good conceptual construct to test
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22 168 our hypotheses and examine general patterns.
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26 169 **Phylogenetic analyses**

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28 170 For the families Cathartidae, Pandionidae and Accipitridae (73% of analyzed species)
29
30 171 we used the avian phylogeny by Jetz et al. (2012). We sampled 1000 phylogenies for
31
32 172 our raptor species from <http://www.birdtree.org> and built a consensus ultrametric tree
33
34 173 using the Mesquite software (Maddison & Maddison 2011). We chose the Jetz et al.'s
35
36 174 phylogeny because: (1) it is the most comprehensive avian phylogeny published to date,
37
38 175 (2) it allows calculating result uncertainty given that it provides the Bayesian posterior
39
40 176 distribution of possible phylogenetic trees and, (3) it is widely utilized in studies of
41
42 177 avian phylogenetic trends (>950 citations since publication). For the Falconidae family
43
44 178 we used the recent phylogeny by Fuchs, Johnson and Mindell (2015), as this family
45
46 179 contains a high proportion of polytomies in the Jetz' phylogeny. We combined both
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48 180 phylogenies in one ultrametric tree for the analysis. Because we sampled sequenced
49
50 181 phylogenies—which lacked data for some species—from the initial 140 species found
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52 182 in the western Palearctic and New World we retained for the analyses 74 species, for
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54 183 which both sequence and territorial behavior data were available (Fig. 1). Within this
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3 184 subset, we found data on territory size for 38 species.
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6 185 We calculated the phylogenetic signal in both response variables (territorial behavior
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8 186 and territory size) using two metrics: Pagel's (1999) λ , which varies from 0 (no
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10 187 phylogenetic signal; traits are less similar among species than expected from their
11
12 188 phylogenetic relationships) to 1 (phylogenetic signal indicates an evolution compatible
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14 189 with a Brownian Motion [BM] model or random walk, which results in a linear
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16 190 association between divergence times and expected phenotypic variance); and Pagel's δ ,
17
18 191 which informs about the tempo of evolution, i.e., increasing or decreasing rates of trait
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20 192 change through time. Values of $\delta < 1$ suggest traits changed rapidly at early stages of
21
22 193 evolution and remained stable afterwards (trait is conserved across evolution). Values of
23
24 194 $\delta > 1$ indicate traits changed proportionally more in later branches (recent evolution
25
26 195 influenced traits more than earlier events). We used likelihood ratios to test whether λ
27
28 196 was significantly different from 0 and 1, and δ was significantly different from 1
29
30 197 (Cooper, Jetz & Freckleton 2010). To calculate p-values we ran likelihood ratio tests
31
32 198 comparing the likelihood values of the λ and δ parameters fitted by maximum-
33
34 199 likelihood against those resulting from transforming the branches of the phylogeny with
35
36 200 λ fixed to 0 and 1, respectively, and δ fixed to 1. For both traits, we expected a λ value
37
38 201 different from zero, suggesting the existence of some phylogenetic signal. For territorial
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40 202 behavior we expected a δ value < 1 , whereas a δ value > 1 for territory size, suggesting
41
42 203 that the former was conserved across evolution and the latter was not conserved, as
43
44 204 territory size varies intra- and interspecifically among raptors and may be more affected
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46 205 by ontogenetic factors.
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51 206 **Statistical analyses**

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54 207 We used a logistic regression model (LRM) to study the relationship of territorial
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56 208 behavior with predictor variables, and an ordinary least squares (OLS) model to analyze
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3 209 associations of mean territory size with predictor variables. To test the effect of the
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5 210 phylogeny in those associations, we compared the results of the LRM and OLS with
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7 211 models that take into account the phylogenetic dependence between species: a
8
9 212 phylogenetic logistic regression model (Phylo-LRM; Ives & Garland 2010) for
10
11 213 territorial behavior, and a phylogenetic generalized least squares model (PGLS; Martins
12
13 214 & Hansen 1997) for territory size. For the OLS and PGLS we used 36 species of the
14
15 215 initial 38, after removing two outliers (Egyptian vulture (*Neophron percnopterus*) and
16
17 216 Bearded vulture (*Gypaetus barbatus*) detected in a preliminary analysis of binary
18
19 217 correlations between territory size and each predictor variable.
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21
22

23 218 To avoid collinearity between predictor variables, we employed the method of variable
24
25 219 reduction proposed by Green (1979) where pairs of intercorrelated variables ($r > 0.6$)
26
27 220 are considered as estimates of a single underlying factor. Only prey size and raptor body
28
29 221 mass were correlated ($r = 0.65$). We compared two models that included all the
30
31 222 predictors but only one of these two variables, and retained for analysis raptor body
32
33 223 mass, since this variable fitted the data better according to the relative ranking of
34
35 224 Akaike's Information Criterion modified for small sample sizes ($AIC_c = 64.2$ for the
36
37 225 model including prey size and $AIC_c = 53.7$ for raptor body mass). Since our goal was
38
39 226 not to build accurate predictive models but rather to understand the relationships
40
41 227 between response and predictor variables, we used saturated models (i.e., including all
42
43 228 non-correlated predictors—prey agility, raptor body mass, and nest protection) in all
44
45 229 territorial behavior and territory size models. All phylogenetic and statistical analyses
46
47 230 were performed in R 3.3.3 (R Development Core Team, 2017) using the packages
48
49 231 'phylolm' (Ho & Ane 2014), 'geiger' (Harmon et al. 2008), 'ape' (Paradis, Claude &
50
51 232 Strimmer 2004) and 'caper' (Orme et al. 2013).
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56 233 **RESULTS**

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234 **Evolution of territorial behavior and territory size in raptors**

235 Among the 74 species used in this study (Fig. 1), 53 were territorial (71.6%) and 21
236 were non territorial (28.4%) Although the majority of species were territorial, it was
237 difficult to visually detect a clear pattern of territorial behavior across the raptor
238 phylogeny studied. In some genera such as *Aquila* or *Accipiter* all species were
239 territorial, whereas within the *Falco* genus, congeneric species differed notably in their
240 territorial behavior.

241 As predicted, both response variables (territorial behavior and territory size) showed
242 phylogenetic signal significantly different from zero (Table 1). However, the signal for
243 territorial behavior ($\lambda = 0.892$) was significantly < 1 , which indicated that related
244 species resembled each other differently than expected under a Brownian Motion [BM]
245 model. This result together with Pagel's δ statistic, which was significantly > 1 ($\delta =$
246 11.257), indicated territorial behavior changed proportionally more in later branches. In
247 the case of mean territory size, the λ statistic ($\lambda = 0.822$) was also lower than expected
248 under BM, and Pagel's δ was significantly > 1 ($\delta = 10.949$) as predicted (Table 1).
249 These results suggest that neither territorial behavior nor mean territory size have been
250 strongly conserved across evolutionary time, but rather might be the product of recent
251 evolution in raptors.

252 **Ecological predictors of territorial behavior and territory size in raptors**

253 Both LRM and Phylo-LRM models for territorial behavior explained a moderate
254 proportion of the overall variability of this factor (Nagelkerke $R^2 = 0.35$ and $R^2 = 0.29$,
255 respectively). Model coefficients and their significance were qualitatively similar in
256 both models (Table 2), which indicates that taking phylogeny into account did not
257 change results. Territorial behavior was related to prey agility and nest site protection.
258 The probability of a species showing territorial behavior was mostly associated with an

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3 259 increase in the agility of the main prey; species that captured more agile prey (e.g.,
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5 260 birds), were likely territorial, whereas species that captured less agile prey tended to be
6
7 261 non-territorial. This probability was also associated with nest site protection; raptors
8
9 262 breeding in forests were more likely to be territorial than raptors nesting on the ground.
10
11 263 Raptor body mass was not significantly associated with the degree of territorial
12
13 264 behavior (Table 2).

15
16 265 In the case of mean territory size, both OLS and PGLS models also explained a similar
17
18 266 proportion of the overall variability ($R^2 = 0.65$ and $R^2 = 0.54$, respectively), and model
19
20 267 coefficients and their significance were also qualitatively similar (Table 3). In both OLS
21
22 268 and PGLS mean territory size showed a significant positive relationship with raptor
23
24 269 body mass and main prey agility, which suggests the defended area would be larger in
25
26 270 territorial species that are bigger and feed upon more agile prey. Finally, nest site
27
28 271 protection was not significantly associated with territory size (Table 3).

31 32 272 **DISCUSSION**

33
34 273 Our results suggest differences in degree of territorial behavior and territory size in
35
36 274 diurnal raptors were mostly influenced by recent evolution, which has led to variations
37
38 275 of these traits in response to recent environmental and ecological changes. We detected
39
40 276 a general pattern for territorial behavior and territory size based on aspects of raptors'
41
42 277 current ecology. Probability of being territorial was related to main prey agility and nest
43
44 278 site protection, whereas mean territory size was related to main prey agility and body
45
46 279 mass of the raptor species.

49 50 280 **Evolution of territorial behavior and territory size in raptors**

51
52 281 Contrary to our initial hypothesis, extant, closely related raptor species do not resemble
53
54 282 each other in their territorial behavior as a Brownian motion model of evolution would

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3 283 predict, suggesting that territorial behavior has not been strongly conserved across
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5 284 evolutionary time. Although most current raptor species show territorial behavior
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7 285 (Newton 1979), the phylogenetic signal in both territorial metrics (territorial behavior
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9 286 and territory size) was different from the BM expectation. This result, along with high
10
11 287 values of δ , suggest changes and reversals between non territorial and territorial states,
12
13 288 as well as changes in mean territory size, occurred frequently during recent evolution.
14
15 289 Most modern orders and families of birds appeared after the Cretaceous-Paleogene mass
16
17 290 extinction event about 66 million years ago (Jarvis et al. 2014). The earliest fossil
18
19 291 records of most traditional orders and families occurred during the Paleogene (65–23
20
21 292 Mya; James 2005), when a gradual global change from sub-tropical forested
22
23 293 environments to cooler climates was taking place (Blondel & Mourer-Chauviré 1998;
24
25 294 Hawkins et al. 2007). Most modern genera arose from 23 million years ago, when
26
27 295 avifauna colonized new types of habitat (i.e., temperate forests, grasslands and steppes)
28
29 296 favored by those climatic changes (Blondel & Mourer-Chauviré 1998; James 2005). In
30
31 297 this context of change, and given that the common ancestor of birds was likely
32
33 298 territorial (Rolland et al. 1998; Varela et al. 2007), the ancestral raptor would have lived
34
35 299 in forested environments defending territories, and when new open habitats appeared,
36
37 300 certain descendants would have adapted to breeding in aggregations. This process of
38
39 301 global change continued until the late Pliocene and Pleistocene (3.6–0.8 Mya), when
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41 302 differentiation of most of the extant species occurred, and coincided with a series of
42
43 303 strong, short-term, wet-dry and cool-warm climatic fluctuations (Blondel & Mourer-
44
45 304 Chauviré 1998; James 2005). A plausible explanation for the recent departure from
46
47 305 ancestral territorial behavior could be related to those epochs of climate and habitat
48
49 306 upheaval, justifying a stronger influence of current ecological conditions in shaping the
50
51 307 current pattern of territorial behavior than past evolutionary relationships. However,
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3 308 more comprehensive and detailed studies on the ancestral state and evolution of these
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5 309 traits should be performed to assess this hypothesis in more detail.
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8 310 **Ecological predictors of territorial behavior and territory size in raptors**

9
10 311 Raptor species that hunt the most agile prey and nest in protected (concealed or
11
12 312 inaccessible) sites were those with the highest probability of expressing territorial
13
14 313 behavior. At least two nonexclusive hypotheses can explain the effect of agile prey on
15
16 314 territorial behavior. First, raptors that nest in more dispersed and regularly spaced sites
17
18 315 can lower the possibility of interference with conspecifics when hunting agile prey
19
20 316 (Crook 1965; Nilsson, Nilsson & Sylvén 1982). Reducing this interference is important
21
22 317 because the presence of non-cooperative individuals during hunting could alert the prey
23
24 318 and thus, increase their chances of escaping (Nilsson, Nilsson & Sylvén 1982; Selas &
25
26 319 Rafoss 1999). Moreover, this evasiveness effect could be magnified in structurally
27
28 320 complex habitats (i.e., forests), where prey detectability is lower because there are more
29
30 321 places to hide (Ontiveros, Pleguezuelos & Caro 2005), and consequently, prey
31
32 322 availability is also reduced. Second, we propose that raptors whose main diet is birds
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34 323 (including nestlings and fledglings) might have a higher probability of preying upon
35
36 324 their neighbor's offspring than raptors that do not eat birds. Although the risk of
37
38 325 predation by conspecifics might be low, it has been well documented (Newton 1979;
39
40 326 1986; Squires & Kennedy 2006; Gangoso et al. 2015). Predation risk is probably higher
41
42 327 within colonial species, where predation is more frequent in dense colonies, and always
43
44 328 occurred between nearby nests (Gangoso et al. 2015). Therefore, territorial species
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46 329 might benefit from defending territories that separate them from conspecifics, to avoid
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48 330 not only competitors but also potential conspecific predators.
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54 331 Furthermore, the two least evasive categories of prey (carrion and invertebrates) are
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56 332 temporally and/or spatially unpredictable sources of food relative to the other food
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3 333 categories (Newton 1979). Raptors that prey on these less evasive prey are predicted to
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5 334 be non-territorial, because this resource is not economically defensible (Brown 1964;
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7 335 Newton 1979; Goldberg, Grant & Lefebvre 2001; Overington, Dubois & Lefebvre
8
9 336 2008). Thus, difficulty in locating food would have favored breeding in colonies
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11 337 because individuals can share information about food location (Danchin & Wagner
12
13 338 1997). On the other hand, we believe that difficulty capturing agile but more predictable
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15 339 prey could have favored solitary breeding because territory owners have immediate
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17 340 access to exclusive hunting areas during the breeding period, which is a period of high
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19 341 energy demand.

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23 342 Our results also supported our predictions about nest site protection and territorial
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25 343 behavior. According to some authors, species that mark territories by vocalizations and
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27 344 displays might attract more predators, but they could use the protection conferred by
28
29 345 their nest sites to avoid predation (Crook 1965; Brown & Orians 1970). In this context,
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31 346 territorial raptors dwelling in forests might benefit from exclusive use of an area with
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33 347 high cover where their fledglings find protection, especially if parents spend some time
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35 348 away hunting or patrolling the territory, compromising nest defense (Dewey & Kennedy
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37 349 2001). Our results support previous studies which documented nest exposure to
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39 350 predators was related to evolution of coloniality in birds (Rolland et al. 1998; Varela et
40
41 351 al. 2007). Colonies are more conspicuous than solitary nests, and therefore, they could
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43 352 attract more predators to the nest site than do territorial species (Varela et al. 2007).
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45 353 Morrison et al. (2006) found that North American raptors nesting in open cover types
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47 354 were more aggressive (i.e., regularly physically attack nest predators), suggesting they
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49 355 were subjected to higher predation risk compared to birds nesting in more closed
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51 356 habitats. Thus, colonial birds also experience predation pressure, but unlike territorial
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53 357 species, they could have balanced the costs of breeding in exposed nests by using social
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3 358 anti-predator behaviors such as the dilution effect, group vigilance or collective defense
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5 359 (Brown & Orians 1970). We found that in raptors, colonial behavior is more probable
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7 360 when a species breeds in more exposed nest sites and when they prey upon less agile
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9 361 and less predictable prey. Thus, current non-territorial behavior in raptors may represent
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11 362 a trade-off between costs of predation risk and benefits of finding unpredictable food
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13 363 sources.

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16 364 Among territorial raptor species, the bigger species and those that hunt the most agile
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18 365 prey, defended the larger territories. Difficulty with capturing more agile and evasive
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20 366 prey can reduce the effective availability of that prey in the area, and hence, raptors
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22 367 need to defend larger areas when feeding upon more agile prey (Nilsson, Nilsson &
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24 368 Sylvén 1982; Peery 2000). However, some raptor species feed on several prey
25
26 369 categories, and thus selective pressures associated with agility of their main prey would
27
28 370 be lower than for specialist species. Thus, in a preliminary analysis, we tested two
29
30 371 variables related to specialism: dietary breadth (in the sense of Nagy, Végvári & Varga
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32 372 2017), i.e., number of different groups of prey consumed, and a second variable where
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34 373 we categorized the species as “Very specialized” (feeds upon only one type of prey),
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36 374 “Specialist” (2 different groups of prey), and “Generalist” (3 or more). Neither of these
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38 375 variables have a significant impact on the models (p -value = 0.5927 and p -value =
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40 376 0.3902, respectively), and were eliminated from the final analysis. Moreover, we
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42 377 believe our results showed a pattern that supports our initial hypotheses, i.e., raptors
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44 378 show territorial behavior and defend larger territories when their main prey is more
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46 379 agile. This outcome is also supported by similar results from studies that used actual
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48 380 proportions of different food types in the diet, but lacked a phylogenetic context
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50 381 (Schoener 1968, Nilsson, Nilsson & Sylvén 1982).

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53 382 Finally, the bigger raptors defended the larger territories. In our model, raptor body
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3 383 mass was positively correlated with prey size, as expected from large raptors usually
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5 384 feeding upon larger prey species (Newton 1979; 1980). Given that population density
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7 385 decreases with increasing body mass (Newton 1979; Krüger 2000; Peery 2000), our
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9 386 results support the prediction that large raptors defend larger territories to compensate
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11 387 for lower food availability (large prey is less abundant), and thereby, territory size
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13 388 would be adjusted to the individual energetic requirements of raptors (Palmqvist et al.
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15 389 1996).

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18 390 The three ecological factors we evaluated explained 35% of the variation of territorial
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20 391 behavior in this sample of raptor species. This suggests that there are unmeasured
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22 392 factors that likely influence territoriality and might explain the exceptions found in the
23
24 393 general pattern. Therefore, future comparative analyses should include other resources
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26 394 and functions potentially related to territoriality (i.e., distribution of mates, roosting
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28 395 sites, intraspecific kleptoparasitism, familiarity with the environment, or epidemics and
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30 396 diseases; i.e., Hinde 1956; Maher & Lott 2000). For example, the Egyptian vulture
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32 397 (*Neophron percnopterus*) and the related bearded vulture (*Gypaetus barbatus*) are
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34 398 territorial but exploit unpredictable food resources (but see López-López, García-
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36 399 Ripollés & Urios 2014 or Gil et al. 2014, where it is shown that both species exploit
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38 400 predictable food sources). Other species, e.g., Eleonora's falcon (*Falco eleonora*), prey
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40 401 upon birds but nest in colonies. However, this species also preys upon insects (Mellone
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42 402 et al. 2013), and the birds captured are mainly fledglings, which probably have little
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44 403 ability to react evasively (Nilsson, Nilsson & Sylvén 1982).

404 **Final remarks**

405 It is noteworthy that, since early previous reviews about territorial behavior (e.g., Nice
406 1941; Hinde 1956; Brown 1969; Stamps 1994; Maher & Lott 1995), there has not been
407 further comprehensive research on the topic. To our knowledge, the present work is the

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3 408 first to analyze the phylogenetic relationships of raptor territorial behavior and territory
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5 409 size, and the first to study possible ecological determinants of both variables applying
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7 410 comparative methods. Our results confirm several hypotheses posed in the classical
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9 411 reviews, and confirm the results previously reported in other studies conducted with
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11 412 only one or a few species. Even after accounting for phylogenetic relatedness, major
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13 413 associations among the response variable and the predictors, hold. Applying a
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15 414 comparative approach is important, because several factors may influence territoriality
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17 415 simultaneously and the functions of territoriality could be different for each species
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19 416 (Hinde 1956). Nonetheless, with only three ecological predictors, our models rejected a
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21 417 strong influence of deep evolutionary events as an explanation of current raptor's
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23 418 territoriality and identified a general inter-specific pattern that explains a relatively high
24
25 419 amount of the variation of this behavior in raptors. Those ecological characteristics were
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27 420 related to limiting and defensible resources, which are known to be key factors
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29 421 determining territoriality at population levels, but had not been previously tested as
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31 422 explanatory factors in a broader inter-specific context. Thus, this work contributes to
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33 423 our understanding of territorial behavior and territory size in raptors and can be used to
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35 424 develop testable hypotheses in future research on territoriality in this group or in other
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37 425 avian taxa with similar ecology.
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426 **ACKNOWLEDGMENTS**

427 We thank Paloma Ruiz-Benito for help with the data base management. We are very
428 grateful to Travis Rosenberry from The Peregrine Fund library for providing copies of
429 several publications during the review process. We are also grateful to Pascual López-
430 López and the anonymous reviewers who helped to improve this manuscript with their
431 valuable comments. This work was supported by funds from CICYT projects of the
432 Spanish Ministerio de Educación y Ciencia (CGL2007-60533/BOS, CGL2010-

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3 433 18312/BOS and CGL2014–53308–P), and the REMEDINAL network (S-
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5 434 0505/AMB/0335, S2009 AMB-1783 and S2013/MAE–2719). SMH and GGS were
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7 435 supported by FPI and FPU fellowships from the Ministerio de Educación y Ciencia
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9 436 (BES-2008-006630 and AP2006-00891, respectively).

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3 583 **SUPPORTING INFORMATION**

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5 584 **Table S1.** Complete data set of the respond and predictor variables for the 74 species of diurnal
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7 585 raptors used in this work.

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9 586 **Appendix S1.** Lists of data sources used in this work.

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3 588 **Fig. 1** Representation of territorial behavior in the phylogeny of 74 diurnal raptors
4 589 species used in this study. The ultrametric tree is a result of the combination of a
5 590 consensus tree obtained from the avian phylogeny by Jetz et al. (2012; Cathartidae,
6 591 Pandionidae and Accipitridae families) with the recent phylogeny by Fuchs, Johnson
7 592 and Mindell (2015, Falconidae family).
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593 **Table 1** Phylogenetic signal metrics for territorial behavior of 74 diurnal raptor species,
 594 and log-transformed mean territory size of 38 raptor species. Pagel's λ informs about the
 595 degree of similarity between closely related species, and Pagel's δ informs about the
 596 tempo of evolution, i.e., increasing or decreasing rates of trait change through time.

<i>Variable</i>	<i>Pagel's λ</i>	<i>$p (\lambda=0)$</i>	<i>LR λ</i>	<i>$p (\lambda=1)$</i>	<i>Pagel's δ</i>	<i>LR δ</i>	<i>$p (\delta=1)$</i>
Territorial Behavior	0.892	0.004	45.048	< 0.001	11.257	44.071	< 0.001
Territory Size	0.822	0.004	15.968	< 0.001	10.949	13.259	< 0.001

Note: Significance (p value) evaluated with likelihood ratios (LR) to test whether λ was different from zero and one, and δ different from one.

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599 **Table 2** Comparison of the logistic regression model (LRM) and the phylogenetic logistic regression model (Phylo-LRM) results for territorial
 600 behavior among the 74 raptor species studied.

Model	Intercept				Prey Agility				Raptor Body Mass				Nest Protection				<i>Nagelkerke</i> <i>R</i> ²
	α	<i>SE</i>	<i>z</i> <i>value</i>	<i>p</i> \leq	β_1	<i>SE</i>	<i>z</i> <i>value</i>	<i>p</i> \leq	β_2	<i>SE</i>	<i>z</i> <i>value</i>	<i>p</i> \leq	β_3	<i>SE</i>	<i>z</i> <i>value</i>	<i>p</i> \leq	
LRM	-4.168	1.357	-3.072	0.002	0.597	0.183	3.266	0.001	0.025	0.153	0.166	0.868	0.845	0.280	3.017	0.002	0.35
Phylo-LRM	-3.546	1.183	-2.997	0.003	0.360	0.160	2.246	0.025	0.145	0.154	0.942	0.346	0.539	0.195	2.769	0.006	0.29

602 **Table 3** Comparison of the ordinary least squares (OLS) and phylogenetic generalized least squares (PGLS) models results for log-transformed
 603 mean territory size among the 36 territorial raptor species studied.

Model	Intercept				Prey Agility				Raptor Body Mass				Nest Protection				<i>Nagelkerke</i> R^2
	α	<i>SE</i>	<i>t</i>	$P \leq$	β_1	<i>SE</i>	<i>t</i>	$P \leq$	β_2	<i>SE</i>	<i>t</i>	$P \leq$	β_3	<i>SE</i>	<i>t</i>	$P \leq$	
OLS	6.634	0.401	16.534	0.001	0.304	0.057	5.368	0.001	0.268	0.052	5.138	0.001	-0.085	0.066	-1.305	0.201	0.65
PGLS	6.805	0.555	12.265	0.001	0.260	0.070	3.734	0.001	0.278	0.065	4.299	0.001	-0.046	0.065	-0.710	0.483	0.54

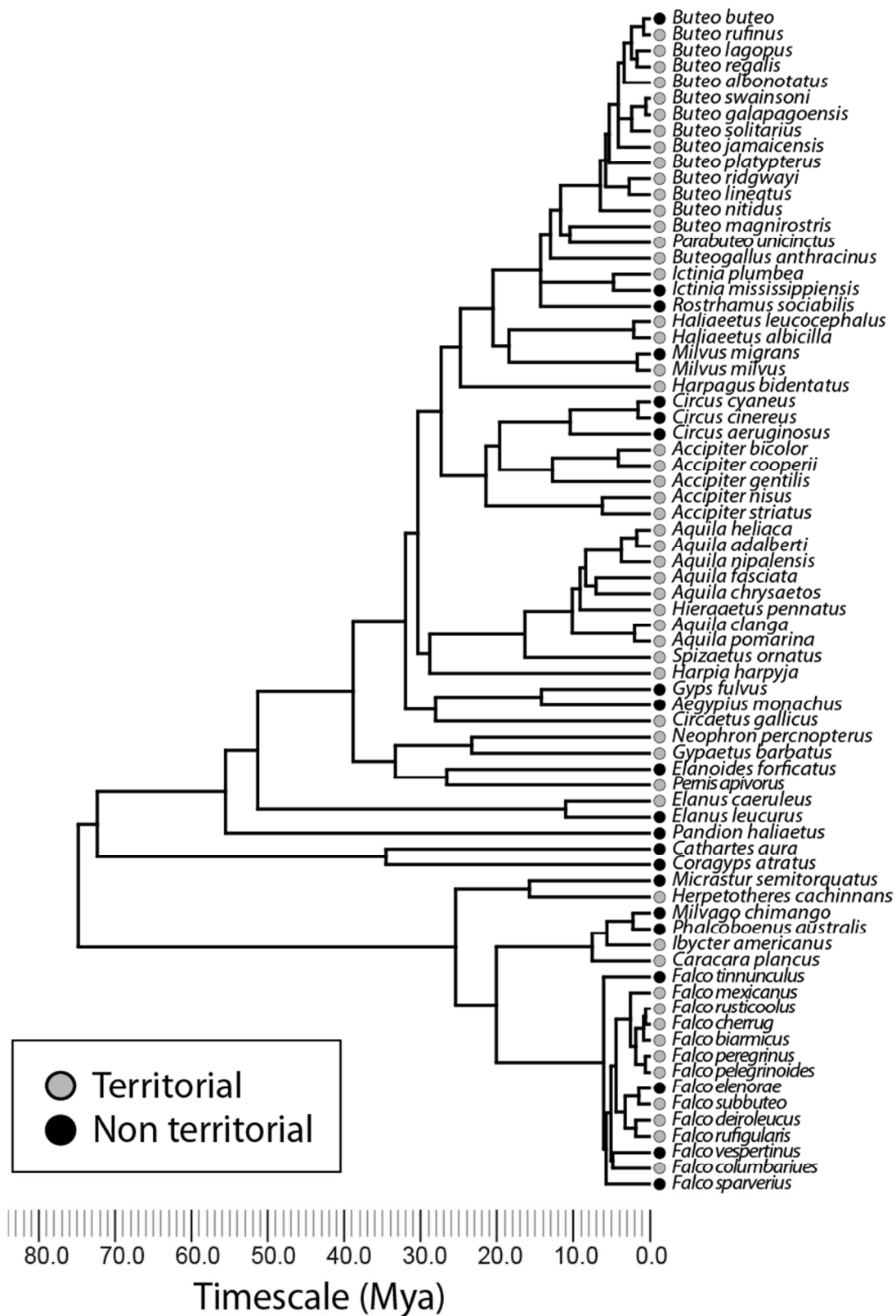


Figure 1

Supporting Information

Territoriality in diurnal raptors: relative roles of recent evolution, diet and nest site

Table S1. Complete data set of the respond and predictor variables for the 74 species of diurnal raptors used in this work. Territorial behavior: 0 = Non territorial; 1 = territorial. Territory size: mean nearest neighbor distance during the breeding season. Prey agility (i.e. species' main prey): 1 = carrion; 2 = invertebrates; 3 = reptiles and amphibians; 4 = fish; 5 = mammals; 6 = birds. Prey size: weighted mean value for all items included in the diet description, each item was assigned to one of the following categories; 1 = 0-10 g (e.g., insects, small snails, larvae); 2 = 10-100 g (e.g., big molluscs, small lizards, mammals and birds,); 3 = 100-1500 g (e.g., fish, large lizards, snakes, medium-sized birds and mammals); 4 = >1500 g (e.g., large birds and mammals). Nest site concealment/inaccessibility: 1 = ground (in open or semi-open habitat); 2 = isolated tree (in open or semi-open habitat); 3 = facultative (nest site category varies between populations of the same species); 4 = cliff, crags or rocky area; 5 = tree within a forest.

Family	Species	Territorial behavior	Territory size ^b (m)	Prey agility	Prey size	Raptor body mass (kg)	Nest concealment
Falconidae	<i>Micrastur semitorquatus</i>	0		5	3.0	0.702	5
Falconidae	<i>Herpetotheres cachinnans</i>	1	ND	3	3.0	0.670	3
Falconidae	<i>Caracara plancus</i>	1	ND	1	3.5	0.894	3
Falconidae	<i>Ibycter americanus</i>	1	ND	2	1.0	0.603	5
Falconidae	<i>Milvago chimango</i>	0		1	2.0	0.295	3
Falconidae	<i>Phalcooenus australis</i> ^a	0		1	3.5	1.588	4
Falconidae	<i>Falco deiroleucus</i> ^a	1	2840.8	6	3.0	0.474	3
Falconidae	<i>Falco rufigularis</i>	1	ND	6	2.0	0.169	3
Falconidae	<i>Falco vespertinus</i>	0		2	1.5	0.158	3
Falconidae	<i>Falco columbarius</i>	1	916.6	6	2.0	0.201	3
Falconidae	<i>Falco sparverius</i>	0		2	1.5	0.118	3
Falconidae	<i>Falco eleonorae</i>	0		6	2.0	0.369	3
Falconidae	<i>Falco subbuteo</i>	1	1927.0	6	1.5	0.211	2
Falconidae	<i>Falco tinnunculus</i>	0		5	2.0	0.214	3
Falconidae	<i>Falco mexicanus</i>	1	838.2	5	3.0	0.706	4
Falconidae	<i>Falco pelegrinoides</i>	1	1546.0	6	2.7	0.502	3
Falconidae	<i>Falco peregrinus</i>	1	3142.8	6	3.0	0.835	4
Falconidae	<i>Falco rusticolus</i>	1	2847.0	6	3.0	1.411	4
Falconidae	<i>Falco cherrug</i>	1	1943.8	5	2.7	0.975	3
Falconidae	<i>Falco biarmicus</i>	1	ND	6	2.7	0.675	3
Cathartidae	<i>Coragyps atratus</i>	0		1	3.5	2.081	3

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Cathartidae	<i>Cathartes aura</i>	0		1	3.5	2.009	3
Pandionidae	<i>Pandion haliaetus</i>	0		4	3.0	1.600	3
Accipitridae	<i>Elanus leucurus</i>	0		5	2.0	0.312	2
Accipitridae	<i>Elanus caeruleus</i>	1	1181.0	5	2.0	0.259	2
Accipitridae	<i>Pernis apivorus</i>	1	957.6	2	1.0	0.721	5
Accipitridae	<i>Elanoides forficatus</i>	0		2	1.5	0.375	5
Accipitridae	<i>Gypaetus barbatus</i>	1	3605.3	1	4.0	5.950	4
Accipitridae	<i>Neophron percnopterus</i>	1	4325.3	1	3.0	1.950	4
Accipitridae	<i>Circaetus gallicus</i>	1	835.8	3	3.0	1.700	2
Accipitridae	<i>Aegyptius monachus</i>	0		1	3.5	9.625	5
Accipitridae	<i>Gyps fulvus</i>	0		1	4.0	8.625	4
Accipitridae	<i>Harpia harpyja</i>	1	2612.1	5	4.0	6.350	5
Accipitridae	<i>Spizaetus ornatus</i>	1	ND	6	3.5	1.225	5
Accipitridae	<i>Hieraaetus pennatus</i>	1	1734.6	6	3.0	0.842	5
Accipitridae	<i>Aquila pomarina</i>	1	1143.8	5	2.3	1.475	5
Accipitridae	<i>Aquila clanga</i>	1	ND	5	3.0	1.975	5
Accipitridae	<i>Aquila chrysaetos</i>	1	2501.0	5	3.5	4.425	3
Accipitridae	<i>Aquila fasciata</i>	1	2644.1	6	3.0	2.055	4
Accipitridae	<i>Aquila nipalensis</i>	1	1724.0	5	2.5	3.063	1
Accipitridae	<i>Aquila adalberti</i>	1	2323.8	5	3.0	3.550	5
Accipitridae	<i>Aquila heliaca</i>	1	1969.9	5	3.0	3.215	2
Accipitridae	<i>Accipiter striatus</i>	1	1911.1	6	2.0	0.140	5
Accipitridae	<i>Accipiter nisus</i>	1	553.1	6	2.0	0.208	5
Accipitridae	<i>Accipiter gentilis</i>	1	1369.4	6	3.0	1.004	5
Accipitridae	<i>Accipiter cooperii</i>	1	1431.4	6	2.0	0.387	5
Accipitridae	<i>Accipiter bicolor</i>	1	ND	6	2.0	0.314	5
Accipitridae	<i>Circus aeruginosus</i>	0		6	2.5	0.603	1
Accipitridae	<i>Circus cinereus</i>	0		6	2.0	0.420	1
Accipitridae	<i>Circus cyaneus</i>	0		5	2.0	0.440	1
Accipitridae	<i>Harpagus bidentatus</i> ^a	1	691.6	2	1.0	0.193	5
Accipitridae	<i>Milvus milvus</i>	1	463.1	1	3.0	1.134	2
Accipitridae	<i>Milvus migrans</i>	0		1	2.5	0.711	3
Accipitridae	<i>Haliaeetus albicilla</i>	1	2235.5	4	3.0	4.800	3
Accipitridae	<i>Haliaeetus leucocephalus</i>	1	1129.2	4	3.0	4.740	3
Accipitridae	<i>Rostrhamus sociabilis</i>	0		2	1.0	0.372	2
Accipitridae	<i>Ictinia mississippiensis</i>	0		2	1.0	0.276	2

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Accipitridae	<i>Ictinia plumbea</i>	1	209.7	2	1.0	0.242	5
Accipitridae	<i>Buteogallus anthracinus</i>	1	533.6	3	2.0	0.996	5
Accipitridae	<i>Parabuteo unicinctus</i>	1	ND	5	3.0	0.833	3
Accipitridae	<i>Buteo magnirostris</i> ^a	1	334.9	3	2.0	0.277	5
Accipitridae	<i>Buteo nitidus</i>	1	ND	3	2.0	0.510	5
Accipitridae	<i>Buteo lineatus</i>	1	540.1	3	2.0	0.626	5
Accipitridae	<i>Buteo ridgwayi</i>	1	ND	3	2.3	0.357	5
Accipitridae	<i>Buteo platypterus</i> ^a	1	309.5	5	2.5	0.432	5
Accipitridae	<i>Buteo jamaicensis</i>	1	731.7	5	2.8	1.088	3
Accipitridae	<i>Buteo solitarius</i>	1	ND	6	2.0	0.524	2
Accipitridae	<i>Buteo galapagoensis</i>	1	ND	6	3.0	1.154	3
Accipitridae	<i>Buteo swainsoni</i>	1	890.8	5	2.5	0.981	2
Accipitridae	<i>Buteo albonotatus</i> ^a	1	1873.0	6	2.5	0.764	3
Accipitridae	<i>Buteo regalis</i>	1	ND	5	3.0	1.140	3
Accipitridae	<i>Buteo lagopus</i>	1	900.2	5	2.0	1.106	4
Accipitridae	<i>Buteo rufinus</i>	1	ND	5	2.5	1.144	3
Accipitridae	<i>Buteo buteo</i>	0		5	2.3	0.924	2

Note: ^a Territorial behavior for these species was collected from other sources different to the main encyclopedias used (see list No. 2 of references below). ^b Territory size data was collected only for territorial species from 123 publications by means of a bibliographical review of the mean nearest neighbor distance during the breeding season (see list No. 3 of references below). ND = Not Determined (i.e., data not available).

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