

1 **Title:** Fractal geometry of a complex plumage trait reveals bird's quality

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18 **Running head:** Fractal geometry and plumage ornaments

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24 **Abstract:**

25 Animal colouration is key in natural and sexual selection, playing significant roles in
26 intra- and inter-specific communication because of its linkage to individual behaviour,
27 genetics and physiology. Simple animal traits such as the area or colour intensity of
28 homogeneous patches have been profusely studied. More complex patterns are
29 widespread in nature, but they escape our understanding because their variation is
30 difficult to capture effectively by standard, simple measures. Here we used fractal
31 geometry to quantify inter-individual variation in the expression of a complex plumage
32 trait, the heterogeneous black bib of the red-legged partridge (*Alectoris rufa*). We show
33 that a higher bib fractal dimension predicted better individual body condition, as well as
34 immune responsiveness, which is condition-dependent in our study species. Moreover,
35 when food intake was experimentally reduced during moult as a means to reduce body
36 condition, the bib's fractal dimension significantly decreased. Fractal geometry
37 therefore provides new opportunities for the study of complex animal colour patterns
38 and their roles in animal communication.

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40 **Keywords:** communication; condition-dependence; fractals; honest signals;
41 immunocompetence; ornaments

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47 **1. INTRODUCTION**

48 Colourful scales, feathers, furs or skins are often used by animals for camouflage and
49 communication and play key roles in many natural and sexual selection processes [1-3].
50 To study these processes, we need to accurately measure trait variability, and study how
51 it relates to fitness. In many cases, the trait of interest is too complex to be easily and
52 accurately described by simple approaches. This is particularly true for patterns whose
53 variability lies not only in the colouration or size of the patches, but in the spatial
54 distribution and shape of colours across the body. Spotted, striped, and other
55 heterogeneous patterns are commonly found in the animal kingdom, showing different
56 shapes, sizes, colours and distribution of their constituent units. Several methods have
57 been developed to summarize and analyze trait colour characteristics, even considering
58 the particularities of the observer visual system [4, 5]. However, only recently some
59 techniques have been developed to describe spatial arrangement and patterning of
60 complex colour patches [6-9] (table 1). Here we propose that fractal geometry provides
61 a simpler method that can be easily applied to many animal colour patterns, providing
62 an integrative measure that captures the complexity of a whole pattern when explored at
63 different scales, which would be of great help to study their variability and
64 functionality.

65 Fractal dimension (FD) was developed to describe self-similar mathematical
66 objects, or fractals, whose shape is too complex to be described by Euclidean geometry
67 [10]. FD is a highly integrative parameter whose value is influenced by properties such
68 as number, length, tortuosity and connectivity of elements within a given object.
69 Interestingly, many structures that we find in nature can be considered “statistical
70 fractals” and their shape has often been successfully described by their FD [10-12]. In
71 ecology and evolutionary biology, FD has proven useful for describing habitat structure

72 [13, 14], evolution and extinction rates [15, 16] and the spatial ecology of individuals
73 [17-19]. Here we propose that fractal geometry could be extremely useful to study the
74 complex forms and colour patterns displayed by animals. Many of these complex colour
75 patterns are fitness-related traits whose production likely requires coordinating
76 processes at different scales to produce a coherent colouration pattern. Thus, fractal
77 geometry might help to unravel information on the quality of the individual conveyed
78 by these characters that could otherwise be difficult to assess with other methods.

79 We tested this idea using the red-legged partridge (*Alectoris rufa*) as a model
80 species. Both sexes of this medium-sized bird display a conspicuous black bib, which is
81 eumelanin-based and characterized by a complex pattern of black arrow-like patches
82 against a white plumage backdrop [20, 21] (figure 1). This kind of melanin-based
83 plumage trait is very common in birds and often used as a social signal [3]. Although
84 the area covered by melanin is easy to quantify by digital photography [21], there is
85 great variability in pattern and shape (figure 1b), which is much more difficult to
86 capture. Because of the heterogeneous nature of the partridge's black bib, we
87 hypothesized that inter-individual variability could be well described by fractal
88 geometry, and that FD could reveal hidden biological information conveyed by the trait
89 expression.

90

91 **2. MATERIAL AND METHODS**

92 **(a) Correlational study**

93 42 six-month-old male red-legged partridges hatched and reared in communal outdoor
94 pens were isolated in individual cages with water and food provided *ad libitum* [22, 23].
95 At the time of individual isolation all birds were weighted with a Pesola spring balance

96 (± 5 g) and their tarsus length measured with a digital calliper (± 0.01 mm). For 24 of
97 these males, we used the phytohaemagglutinin skin test [24] to measure immune
98 responsiveness. 0.5 mg of phytohaemagglutinin (Sigma-Aldrich, ref. L-8754)
99 suspended in 0.1mL of phosphate buffer solution were injected in the patagium of the
100 wing. The thickness of the patagium was measured three times before injection and 24
101 hours later with a digital spessimeter (Mitutoyo Absolute 547-315) to the nearest
102 0.01mm. Both initial ($r=0.99$, $F_{23,48}=510.3$, $p<0.001$) and final wing web thickness
103 measurements ($r=0.99$, $F_{23,48}=336.2$, $p<0.001$) were highly repeatable [25]. The
104 difference between average initial and final measurements was used as index of cellular
105 immune responsiveness [24]. We took digital photographs (2272 \times 1704 pixels; Nikon
106 Coolpix 4500 camera) of the breast of each bird under standard light conditions and bird
107 position (the neck totally extended [21]), and keeping the bird-camera distance constant
108 (40cm). For each photo, the same standard grey reference and scale (Kodak Gray Scale,
109 Kodak, New York, USA) was placed next to the bird's neck.

110

111 **(b) Experimental study**

112 68 one-year-old birds (34 males and 34 females) were housed as for the correlative
113 study during the moulting period, i.e. late June to mid November [20]. Before the moult
114 (10th June), all birds were weighed and their bibs photographed as described above.
115 Before the food restriction experiment (10th June), control and experimental birds did
116 not differ in body weight ($F_{1,64}=0.17$, $p=0.68$), bib size ($F_{1,64}=1.87$, $p=0.17$) or bib FD
117 ($F_{1,64}=0.0$, $p=0.89$), irrespective of their sex (non-significant sex \times treatment interactions
118 for all variables; all $p>0.37$). Cover feathers of the flange and breast were painted with
119 permanent markers to later confirm that all birds completely moulted these plumage
120 areas. For 20 males and 13 females, food provisioning was restricted during the

121 moulting period, so that their body mass was ca. 13% lower than controls (14 males and
122 21 females that were fed *ad libitum*) (see electronic supplementary material, figure A1).
123 The amount of food provided to food-restricted birds was continuously adjusted
124 according to our monitoring of bird's body weight to create significant but reasonable
125 (i.e. within the range found in our captive population) differences between control and
126 experimental birds [22]. Body mass of all birds was recorded on 31st July, 21st August,
127 23rd September and 30th October (electronic supplementary material, figure A1). For
128 logistical reasons, only a subsample of 31 birds was weighed on 31st July. Our food
129 restriction protocol created the expected differences in body mass between control and
130 experimental birds throughout the moulting period (treatment×date effect on body mass:
131 $F_{1,279}=6.27$, $p=0.013$; electronic supplementary material, figure A1) and similarly
132 affected males and females (non-significant treatment×date×sex interaction: $F_{1,279}=0.21$,
133 $p=0.65$). Birds in poor condition exhibit narrower breasts due to reduced pectoral
134 muscle thickness [21], which could potentially affect our measures of bib size. To avoid
135 this potential methodological artefact, digital photographs of the bib after moult
136 completion were taken for each individual once both groups reached similar weights
137 (10th January). This was achieved by feeding all birds *ad libitum* after the moult
138 (treatment effect vanished at 10th January: $F_{1,41}=2.90$, $p=0.10$).

139

140 **(c) Photograph analysis**

141 RGB values of all photographs were adjusted relative to those of the grey reference
142 placed next to the bird by using Adobe® Photoshop® CS3 (version 10.0.1). To do so,
143 RGB values of all pictures were equalized according to those of the grey reference
144 ($R=G=B=160$). Although linearization of RGB values was not performed here [26], this
145 is unlikely to affect our results because pictures were subsequently thresholded (i.e.

146 converted to black and white), and the black pattern of interest showed very high
147 contrast with pale grey background colouration in the original images (figure 1). Bib
148 size (i.e. the absolute surface area covered by melanin, in mm²) was measured by
149 quantifying the area covered by black pigmentation using the “magic wand” tool of the
150 same program. The processed images were subsequently used for calculating the FD
151 using the box-counting method [10, 27] with the FracTop v0.3b software
152 (<http://seit.unsw.adfa.edu.au/staff/sites/dcorth//Fractop/>). Figure 2 illustrates how
153 the box counting method quantifies bib’s FD. Repeatabilities, estimated from a subset
154 individuals photographed on two consecutive days, were high (bib size: F_{1,10}=30.2,
155 p<0.001, r=0.94; bib FD: F_{1,10}=8.9, p<0.001, r=0.80).

156

157 **(d) Statistical analyses**

158 For correlations, we used General Linear Models implemented in SAS 8.01 [28], testing
159 whether bib size and FD predicted individual body condition or cellular immune
160 responsiveness. For body condition, the dependent variable was the log₁₀(body mass),
161 with log₁₀(tarsus length) as a fixed effect to control for structural size variation [29].
162 When entered as a fixed factor, body condition was estimated as the standard residuals
163 of the regression of log₁₀(body mass) against log₁₀(tarsus length). Bib size and FD were
164 entered as fixed effects. The bib’s FD positively correlated with total bib size
165 (r=0.53, p<0.001, n=42). Therefore, to avoid multicollinearity issues, we ran the models
166 either with bib size or FD as fixed effects and computed AICc differences between
167 models (Δ AICc) in order to compare how well different models predicted body
168 condition or cellular immune responsiveness [30]. If bib’s FD model performed better
169 than the one with bib size it would mean that despite both variables are correlated, bib’s
170 FD was better predictor of the dependent variable. For the experiment, we used General

171 Linear Mixed Models with individual identity included as random factor. Body mass,
172 bib size or bib FD were considered as dependent variables, whereas sex, sampling time
173 (before vs. after moult) and treatment (control vs. food-restricted) and all their
174 interactions were entered as fixed effects. Given the mentioned relationship between bib
175 size and FD, bib size was entered as covariate in the model for bib FD. Full models for
176 the effect of experimental manipulation on bib size and bib FD are given in table 1. All
177 tests are two-tailed and means or slopes are given \pm s.e.m. Data are deposited in the
178 Dryad repository (<http://dx.doi.org/10.5061/dryad.83873>).

179

180 **3. RESULTS**

181 **(a) Correlational study**

182 Bib FD predicted individual body condition ($F_{1,39}=13.7, p<0.001$,
183 slope \pm s.e.m. $=0.47\pm0.13$, whole model adjusted $R^2=0.36$). Bib size also predicted body
184 condition ($F_{1,39}=5.36, p=0.02$, slope $=0.32\pm0.14$, adjusted $R^2=0.24$), but the model was
185 worse than the one including FD as explanatory variable ($\Delta AICc=7.2$). Bib's FD also
186 predicted cell-mediated immune responsiveness ($F_{1,22}=17.4, p<0.001$, slope $=0.66\pm0.16$,
187 adjusted $R^2=0.42$), whereas bib size did not ($F_{1,22}=2.88, p=0.10$, slope $=0.34\pm0.20$,
188 adjusted $R^2=0.07$). Accordingly, bib's FD model performed better than bib size
189 model ($\Delta AICc=11.0$). Body condition and cell-mediated immunity were positively
190 associated ($F_{1,22}=25.5, p<0.001$, slope $=0.73\pm0.14$, adjusted $R^2=0.52$), and body
191 condition predicted cell-mediated immunity better than FD ($\Delta AICc=4.4$). Therefore,
192 the association between the bib's FD and immune responsiveness might be mediated by
193 condition. Indeed, when body condition was added as a covariate, the relationship
194 between bib FD and cell-mediated immunity became non-significant ($F_{1,20}=1.37$,

195 $p=0.25$). Irrespective of the mechanism involved, these results indicated that fractal
196 geometry provided a simple measure of the complex pattern that revealed biologically
197 meaningful information about the bearer's quality.

198

199 **(b) Experimental study**

200 In order to confirm our correlative results, we restricted food access throughout
201 moulting period to a group of 43 partridges so that their body condition was
202 significantly lower than that of a control group ($n=35$) that was fed *ad libitum*. Bib size
203 increased after moult in all birds, and similarly in control and treated birds (figure 3a
204 and table 2). In contrast, experimental reduction of body mass reduced bib's FD in both
205 sexes (significant time×treatment interaction, but not significant sex×time×treatment
206 interaction; figure 3b and table 2): in controls, the bib's FD did not change significantly
207 ($F_{1,33.1}=0.18, p=0.68$) whereas the bib's FD was significantly reduced in birds that
208 experienced food restriction during moult ($F_{1,35.7}=18.2, p<0.001$; figure 3b). We
209 therefore confirmed a causal relationship between body condition and FD, evidencing
210 that fractal geometry captures quality-related information codified in an animal colour
211 pattern that would remain unnoticed otherwise.

212

213 **4. DISCUSSION**

214 By combining correlational and experimental evidence, we have shown that fractal
215 geometry can reveal biologically meaningful information encoded in a complex
216 plumage trait, the black spotted bib of the red-legged partridge. Our correlative results
217 indicate that both better condition and greater immune responsiveness can be predicted
218 from bibs with higher FD. Given that individuals in better condition had greater

219 immune responsiveness to PHA, a mediating effect of condition in the relationship
220 between bib FD and immune responsiveness is likely. Both immunocompetence and
221 body condition are indicative of individual quality, and were better predicted by bib FD
222 than by bib size alone. In addition, the condition-dependence of bib FD was supported
223 by experimental evidence: when individual body condition was experimentally
224 worsened during moult, new bibs showed a lower FD than bibs previously displayed by
225 the same birds, while control (*ad libitum* fed) individuals moulted bibs with a similar
226 FD. Therefore, the fractal properties of the plumage trait were dynamically updated
227 according to bird body condition during moult, thus potentially being an honest signal
228 in communication scenarios.

229 The FD provided a simple measure (one variable) of the complex trait's pattern
230 that was more informative about condition or immune responsiveness of the individual
231 than the total bib area alone. But, what does FD tell us about bib morphology? Natural
232 fractal objects are heterogeneous objects that behave (statistically at least) similarly at
233 different scales [10]. That is, they do not show sharp transitions when one gradually
234 zooms in and out of the object. The black bib of the red-legged partridge is composed
235 by an upper solid black area that turns into a series of spots that spread through the chest
236 of the bird (figure 1). For the partridges' bib, the FD may accurately describe the
237 smoothness of the transition between the plain and spotted areas of the bib (figure 1a).
238 Accordingly, once taking into account the total pigmented area, those bibs with
239 relatively higher FD are those characterized by a smooth transition between the uniform
240 black throat patch and the lower spots (figure 1b). In contrast, those bibs with relatively
241 smaller FD (for a given bib size) showed a sharp discontinuity between the solid black
242 collar and the spotted lower part of the bib (figure 1b). What makes measuring FD
243 particularly interesting for bird colour patches or other complex animal patterns is that

244 FD not only captures the traditional way of quantifying these traits (e.g. total size or
245 surface area, figure 1), but also improves the quality of the information by adding a
246 measure about the internal structure of the colour patch. However, the specific
247 information conveyed by FD should be explored in each case, as we have done for our
248 study pattern. Note that even negative correlations between FD and a fitness trait may
249 also be expected; e.g. if a simpler colouration pattern such a well-defined striped patch
250 is more difficult and costly to produce than a more noisy and complex pattern.

251 The study of pattern components has been neglected compared to analyses of
252 patch colouration. Apart of attempts to quantify the entire colour pattern of animals
253 considering the relationships among the colours of an individual [5], methods to
254 quantify the shape and geometry of these colour patterns have been explored only
255 recently. These methods are briefly described in table 1. FD can potentially be applied
256 to any kind of pattern (spotted, barred or irregular shapes) and provides a synthetic
257 description of a patch's appearance. Another interesting feature of FD analysis is its
258 simplicity of calculation: FD can be easily computed from digital images, requires
259 minor image processing and can be obtained from a variety of freely downloadable
260 softwares easy to use (e.g. Fractop, HarFa, ImageJ). However, one potential limitation
261 is that FD may sometimes be difficult to interpret. Given that it results from a
262 combination of several independent features (i.e. proportion of area pigmented, size,
263 shape, location or connectivity of colour markings), identifying what aspect/s of the
264 pattern is/are actually producing the results may require further exploration, as we have
265 done here (figure 1b). In any case, whether FD relates (and if so, to what extent) to the
266 indices provided by methods listed in table 1 could be explored in the future. This will
267 help to determine the most appropriate combination of indices to better describe a given
268 colour pattern.

269 Our results open up a new research window for the study of complex animal
270 traits or to unravel new aspects of simpler ones. Colour patterns are the result of a tight
271 control over the expression of multiple mechanisms that must be synchronized at very
272 different scales (from pigment synthesis and deposition into a single feather, scale or
273 hair, to the coordinated growth and distribution of these units along the entire body).
274 Factors affecting developmental stability [31] may alter this machinery, resulting in
275 changes in the FD of the trait. FD has precisely the virtue of measuring the continuity of
276 a pattern through scales. This property makes FD an interesting tool to capture the
277 variability in shape and structure resulting from the above mentioned multi-scaled
278 construction of many animal traits, which is particularly relevant for the study of honest
279 (costly to produce) animal signals. Also, other possible applications of FD may not
280 imply an intrinsic positive or negative fitness value of this variable, which may in turn
281 be used as a neutral descriptor to capture and summarize the appearance variability
282 between individuals, morphs, populations or taxa [32, 33]. There are multiple potential
283 applications of fractal geometry to extract meaningful information from complex animal
284 patterns, and future studies should further explore the usefulness as well as the possible
285 shortcomings of this promising tool.

286 But, apart from the methodological insights, our work claims for further studies
287 on fractal perception in animals, depending on their visual processing abilities. The only
288 requirement for FD to convey information available to the receiver is that differences in
289 pattern appearance captured by FD are actually detectable by a specific animal visual
290 system. Studies in animals addressing this issue are currently lacking. In humans,
291 however, studies have shown that the FD of artworks unconsciously influences our
292 perceived beauty and preferences, be they purely abstract designs or realistic
293 representations [34-36]. Non-human animals may similarly prefer traits with higher (or

294 lower) fractal dimensions, particularly if these advertise a better individual quality, as
295 we report here. We therefore suggest that considering FD should shed new lights onto
296 the evolution and maintenance of complex animal patterns.

297

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395

396

397 Table 1. Summary of the main capabilities and limitations of the available methods to quantify pattern appearance, including the use of fractal
398 dimension proposed here.

Method	Information provided	Limitations
Regularity of barred patterns [6]	Measures the regularity of a striped plumage patch. An index of within-pattern luminance contrast can also be obtained.	Only applicable to barred patterns.
Granularity analysis [7, 8]	A granularity spectrum is obtained for each pattern, allowing obtaining independent descriptors of marking size distribution and degree of contrast between markings and background.	Requires programming skills and complex image processing. It does not provide information about the shape of the markings or their connectivity.
Colour adjacency [9]	Allows calculating independent indicators of relative colour frequency, pattern regularity (i.e. transition density) and pattern elongation (i.e. aspect ratio).	Requires programming skills and complex image processing.
Fractal dimension (FD) [this study]	A single index (FD) captures variability in trait appearance integrating different aspects of pattern shape across scales.	The specific aspect/s of the pattern appearance contributing to FD must be explored case by case.

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401 Table 2. Effect of the experimental reduction of body condition during moult on
402 partridges' bib size and fractal dimension. Significant effects are highlighted in bold.
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	Bib size			Bib fractal dimension		
	d.f.	F	p	d.f.	F	p
bib size	-	-	-	1, 113	102.2	<0.001
sex	1, 64	30.2	<0.001	1, 74.3	2.67	0.11
time	1, 64	11.5	0.001	1, 68.8	12.4	0.001
treatment	1, 64	0.34	0.56	1, 63.5	0.06	0.81
sex×time	1, 64	0.67	0.41	1, 64.2	0.35	0.56
sex×treatment	1, 64	0.2	0.65	1, 63.6	0.73	0.40
time×treatment	1, 64	2.93	0.092	1, 65.2	7.69	0.007
sex×time×treatment	1, 64	1.02	0.32	1, 64.3	2.12	0.15

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405 (Sex, time -“before” or “after” molt- and treatment -“control” or “food restricted”- were
406 entered as fixed factors in both General Linear Mixed Models, whereas bib size was
407 entered as a covariate in the first model. Individual was entered as a random term in
408 both models).

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416 Legends for figures

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418 Figure 1. (a) Male red-legged partridge displaying its black bib (photo credit: Hans
419 Hut). (b) Relationship between the fractal dimension (FD) and size (mm^2 of pigmented
420 area) of the black bib. Bibs of similar size but with high and low FDs (above and below,
421 respectively) are shown for a range of bib sizes. For a given bib size, bibs of higher FD
422 consistently show a smooth transition between the uniform black throat patch and the
423 lower spots whereas bibs with relatively smaller FD show a sharper discontinuity
424 between the solid and the spotted parts of the bib.

425

426 Figure 2. Example of calculation of bib fractal dimension (FD) using the box-counting
427 method. The black and white image of the bib (a) is overlaid by meshes of different cell
428 side lengths (e.g. $s=128$ pixels) and the number of cells occupied by at least one black
429 pixel is counted for each mesh size (e.g. $N=18$). This results in the dataset (b). Plotting
430 $\text{Log}(s)$ vs $\text{Log}(1/N)$, we estimate the FD of the bib as the slope of the fitted straight line,
431 e.g. $\text{FD}=1.794$ (c). Note that FD captures how the number of boxes containing the
432 plumage pattern changes when analysing the pattern at different scales (i.e. when
433 changing cell side length).

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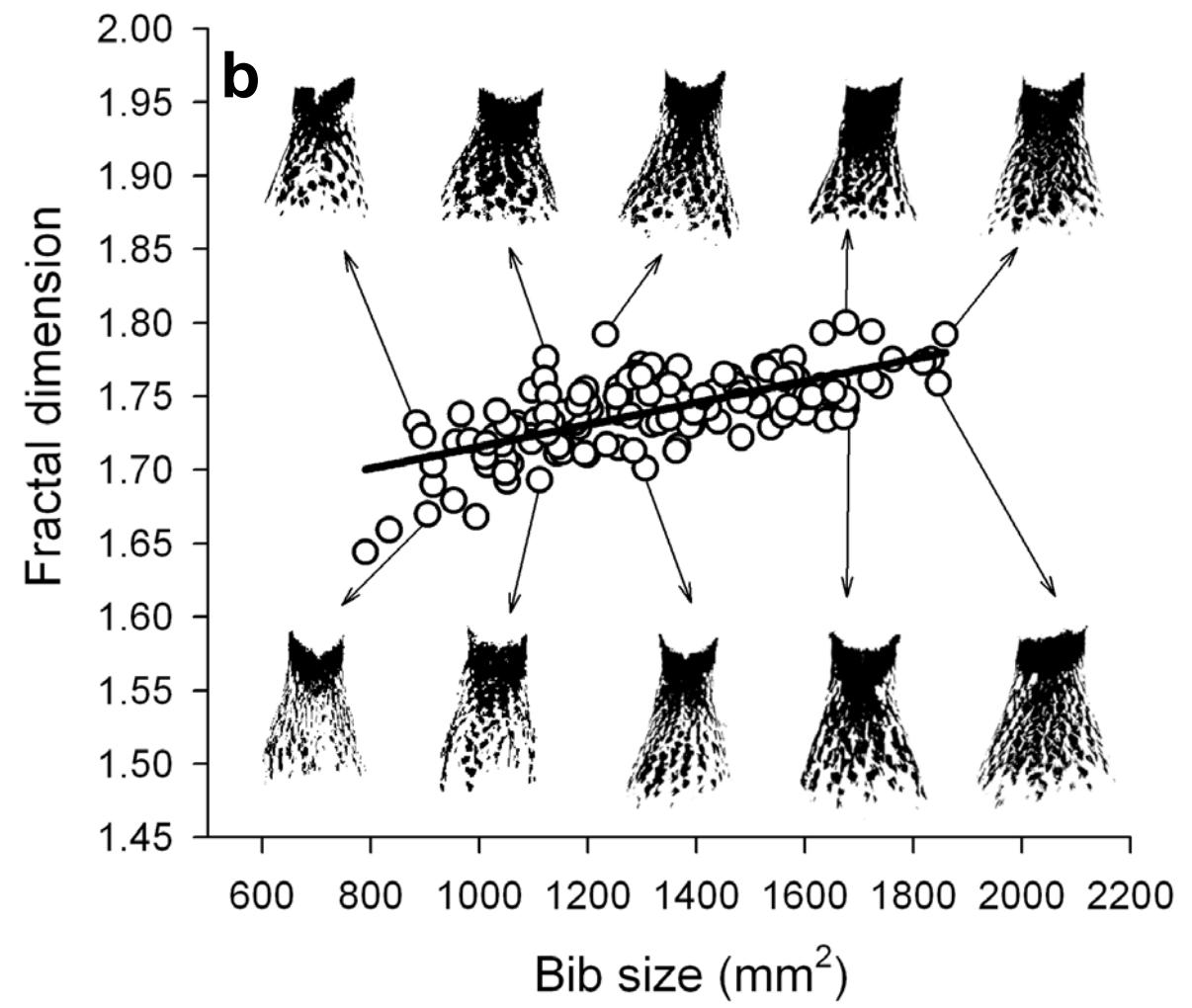
435 Figure 3. Changes in the mean ($\pm\text{s.e.m}$) (a) size and (b) fractal dimension (after
436 controlling for bib size) of the bib of red-legged partridges that were fed *ad libitum*
437 (control, $n=35$) or kept under food restriction ($n=33$) during moult.

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441 Figure 1
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445 Figure 2

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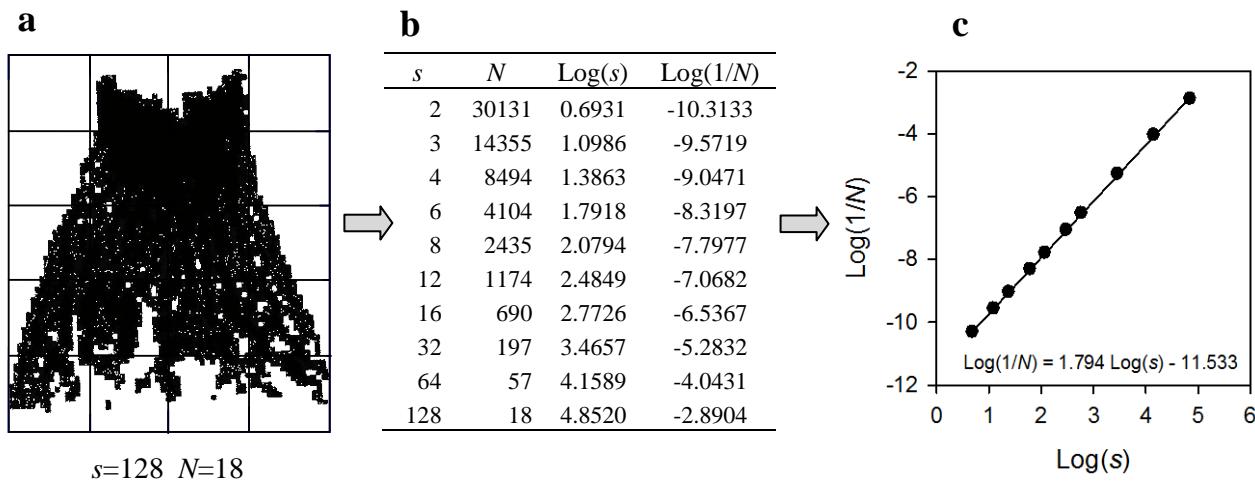
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464 Figure 3

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