

1 **Macroscopic digestive anatomy of ring-tailed lemurs (*Lemur catta*), including a**
2 **comparison of frozen and formalin-stored specimens**

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24

25 **Abstract**

26 Digestive tract measurements are often considered species-specific, but little information exists
27 on the degree to which they change during ontogeny within species. Additionally, access to
28 anatomical material from nondomestic species is often limited, with fixed tissues possibly
29 representing the only available source, though the degree at which this material is
30 representative in terms of dimensions and weight is debatable. In the present study, the
31 macroscopic digestive tract anatomy (length of intestinal portions, and tissue weights of
32 stomach and intestines) of $n=58$ *Lemur catta* (from neonates to 25 years of age) was quantified,
33 of which 27 had been stored frozen and 31 fixed in formalin. Particular attention was paid to
34 the caecum and the possible presence of an appendix. The intraspecific allometric scaling of
35 body mass (BM)^{0.46[0.40;0.51]} for total intestine length and BM^{0.48[0.41;0.54]} for small intestine
36 length was higher than the expected geometric scaling of BM^{0.33}, similar to literature results on
37 interspecific scaling. This difference in scaling is usually explained by the hypothesis that the
38 diameter of the intestinal tube cannot increase geometrically, to maintain optimal absorption.
39 Therefore, geometric volume gain of increasing body mass is accommodated by more-than-
40 geometric length scaling. Literature describes *L. catta* as being variable with respect to the
41 presence of an appendix. No appendix was found in specimens of the present study. The
42 proportions of length measurements did not change markedly during ontogeny, indicating that
43 proportions developed in the foetus are already representative for the adult animal. By contrast,
44 width and tissue-mass scaling of the caecum indicated a disproportionate growth of this organ
45 during ontogeny that was not reflected in its length. Compared to overall intraspecific variation,
46 the method of storage (frozen vs. formalin) had no relevant impact on length or weight
47 measurements.

48

49 *Key words* anatomy, allometry, digestive tract, primates, strepsirrhini

50 **Introduction**

51 Based on geometric considerations, volume measurements should scale isometrically (in other
52 words, linearly) with body mass, surface measurements should scale to body mass to the power
53 of 0.67, and length measurements – such as the length of intestinal tract sections – should scale
54 to body mass to the power of 0.33 (Calder 1996; Clauss and Hummel 2005). However, several
55 studies found a higher scaling exponent for interspecific scaling relationships of various
56 intestinal section lengths with body mass in mammals (Woodall and Skinner 1993; Lavin et al.
57 2008; McGrosky et al. 2016; McGrosky et al. 2019a; McGrosky et al. 2019b). The common
58 explanation for this observation, developed to our knowledge by Woodall and Skinner (1993),
59 is that on the one hand, both intestinal volume and surface area do indeed scale geometrically
60 with body mass, but the intestinal diameter scales to a lower exponent in order to maintain
61 short diffusion distances from the lumen to the secretive and absorptive surfaces. Therefore,
62 the length of the intestine must scale more-than-geometrically to accommodate geometric
63 volume and surface scaling. If this reasoning were correct, we would expect a similar scaling
64 at the intraspecific level across ontogeny, particularly because the transition from milk to any
65 other diet generally implies a decrease in diet digestibility, theoretically making short distances
66 between lumen and surface all the more relevant.

67 On a completely different level of consideration, anatomical material from nondomestic
68 species can be hard to come by. Given that hunting expeditions or culling operations are no
69 longer socially acceptable, the accretion of sample sizes typically depends on storage of
70 deceased individuals collected as single specimens from zoological collections, or during field
71 work. Typically, this storage occurs either as frozen material, or fixed in formalin. Formalin
72 often leads to tissue shrinkage compared to fresh material (Lentle et al. 1997), and comparisons
73 of intestine length measurements between frozen or formalin-fixed material on a limited
74 number of specimens indicated some degree of shortening during formalin storage (Hume et

75 al. 1993). Most recently, a comparative study in humans in which intestine length was
76 measured during abdominal surgery in live patients and at dissection in formalin-fixed
77 cadavers, indicated significantly shorter length measured in the fixed specimens; the results
78 also indicated that the length measures in the fixed specimens were shorter than those reported
79 for freshly dissected cadavers in the literature (Zhou et al. 2020). Evidently, these results leave
80 room for shrinkage to be a consequence of time after death itself, irrespective of the method.
81 For example, studies on skin samples indicated that tissue shrinkage occurred as an effect of
82 excision and was not exacerbated by formalin storage (Dauendorffer et al. 2009), and fishes
83 shrank shortly after killing, irrespective of the preservation method, without additional effects
84 of longer storage (Parker 1963). For intestines, both the effects of relaxation-elongation and of
85 contraction-shortening after death have been reported literature (Zhou et al. 2020). An older
86 comprehensive study in dogs documented intestinal shortening of fresh material occurred
87 within the first few hours after death (Nickel 1933). This shortening sometimes persisted, but
88 that it was more often followed by a relaxation that exceeded the shortening within 48 hours,
89 leading to longer-than-life measurements at this timepoint that are considered to represent the
90 relaxation of the natural tonus of the smooth intestinal musculature (Nickel 1933). These
91 findings add to the overall uncertainty of measuring intestinal lengths, and effects of storage
92 and fixation will depend on the state of the material at the moment of applying fixatives or
93 freezing. There are most likely many other factors, such as whether material is frozen or fixed
94 with or without the mesenteries, the temperature at dissection, or the forces involved in laying
95 out an intestinal section into a straight line for measuring (Underhill 1955), that could all
96 influence the final outcome.

97 In the present study, we used the opportunity of access to three different collections of
98 gastrointestinal tracts of ring-tailed lemurs (*Lemur catta*), either preserved frozen attached to
99 the mesenteries, or preserved in formalin after dissection of the mesenteries. The main aims of

100 the study were to test whether intraspecific allometries of intestinal lengths resembled those
101 reported for interspecific comparisons in other mammals, and whether a systematic difference
102 between the two preservation methods could be detected. In addition, we aimed to investigate
103 whether the prominence of the caecum, the site of microbial fermentation of complex
104 carbohydrates deriving from plant fibre (Campbell et al. 2000), changed across ontogeny from
105 milk-dependent neonates to mature individuals. Ring-tailed lemurs have been described as a
106 species in which a caecal appendix may occur variably (Smith et al. 2013, 2017), macroscopic
107 description of the caecum did not indicate the presence of an appendix (Campbell et al. 2000;
108 McGrosky et al. 2019b). Therefore, special attention was given to the appearance of the apex
109 of the caecum.

110

111 **Methods**

112 Three different specimen collections of ring-tailed lemurs (*Lemur catta*) were available for the
113 study, with a total of $n=58$. One consisted of 12 specimens (from neonates to 24 years old,
114 body mass 0.07-3.48 kg, 7 females and 5 males) from various zoological collections, stored
115 frozen as whole carcasses for varying amounts of time (3-20 years), and thawed and dissected
116 for the present study. The second set consisted of 15 specimens (0.1-16 years of age, 0.57-2.67
117 kg, 6 females and 9 males) of a large family group originating from a single zoological facility,
118 whose gastrointestinal tract had been excised immediately after death, including all
119 mesenteries, and stored frozen until dissection (for 12 months). The third consisted of 31
120 specimens (known ages 0.33-25 years, 0.73-2.85 kg, 19 females and 12 males) from a single
121 zoological collection, where the gastrointestinal tract had been dissected from freshly deceased
122 specimens, freed of mesenteries, partially opened (along their lengths), and stored in formalin
123 for varying amounts of time (1-60 years). In total, 18 animals surpassed the mean body mass
124 range for free-living ring-tailed lemurs of 2-2.5 kg (Sussman 1991; Drea and Weil 2008), yet

125 our age-body mass graph (Fig. 1) largely resembled that given by Koyama et al. (2008), and
126 only two animals appeared to be of excessive weight for their age, being distinctively above
127 maximum weights recorded in the natural habitat of 2.6 kg by Simmen et al. (2010). These
128 findings suggested that obesity was not a major factor in the study populations. These two
129 animals were excluded from all analyses. No animals of unknown age exceeded 2.60 kg.

130 All gastrointestinal tracts were freed from mesenteries and adhering adipose tissue and
131 photographed (Fig. 2). For photography and measurements, thawed intestines were laid out
132 without deliberate stretching beyond that countered by the friction of the intestine on the metal
133 dissection table. Intestines preserved in formalin were gently pulled to a straight form for length
134 measurements. Length measurements included the small intestine, caecum, and the
135 combination of colon and rectum. In thawed (unopened), but not in formalin-preserved (and
136 generally opened) caeca, the width at the base was measured as well. Subsequently, the
137 stomach, small intestine, caecum and the joined colon-rectum were cleared of contents, blotted
138 dry with paper towels, and weighed.

139 Statistical evaluations were performed in R (R Core Team 2017). Linear models based
140 on log-transformed data were used. First, we tested the allometric relationships of all intestine
141 lengths, caecum width and weights with body mass. Additionally, the effect of body mass on
142 organ measurements expressed as % of either total intestinal length or total gastrointestinal
143 tract (GIT) tissue weight were assessed in the same manner, to test whether changes in the
144 prominence of organs occurred across maturation. The results are given to facilitate
145 comparison with other allometries, even though residuals of the models were mostly not
146 normally distributed. Then, the models were repeated, including information about sex and
147 preservation method (frozen or fixed), where applicable, including the interaction using ranked
148 data for quantitative measures, and including body mass. Whether body mass was a significant
149 covariable in these secondary models or not was identical to whether the scaling exponent was

150 significant in the primary models, and is therefore not indicated separately. The significance
151 level was set to 0.05.

152

153 **Results**

154 The macroscopic appearance of the ring-tailed lemurs' digestive tracts in the present study
155 resembled that shown previously by Campbell et al. (2000) and McGrosky et al. (2019b) (Fig.
156 2). Although in some individuals, the visual impression of a caecal appendix appeared possible
157 (e.g., Fig. 2C), when opened, the apex of the caecum never visually indicated a different section
158 and did not visually resemble a lymphatic organ (Fig. 3).

159 The measurements taken in the present study were of a range that included those of an
160 individual published by Campbell et al. (2000) (Fig. 4) except for the caecum, for which these
161 authors reported a greater length. The allometric scaling of length measures of all intestinal
162 sections yielded exponents whose 95% confidence intervals were above the 0.33 scaling
163 exponent expected from geometry (Table 1). The scaling exponent of caecum width was
164 particularly high at 0.57. The relative length of the intestinal sections did not change with body
165 mass, suggesting that their proportions (small intestine 59%, caecum 8%, colon & rectum 32%
166 of total intestinal length) remain stable during ontogeny (Table 1; Fig. 5A). Preservation
167 method only had an effect on the length of the colon & rectum, where specimens preserved in
168 formalin had higher values, but the results also indicated an interaction with sex, suggesting
169 that preservation method affected the sexes differently in the dataset (Table 1; Fig. 4C).
170 Therefore, samples fixed in formalin had a slightly longer relative colon & rectum length (34
171 $\pm 4\%$ vs. $30 \pm 4\%$) and a shorter relative small intestine length ($57 \pm 4\%$ vs. $62 \pm 5\%$) (Table
172 1).

173 The body-mass scaling exponents for organ masses exceeded a linear scaling in their
174 95% confidence interval, except for the stomach (Table 2). Of the intestine sections, the small

175 intestine showed the least distinct deviation (exponent confidence interval: 1.01;1.28), and the
176 caecum (1.21;1.54) the most distinct deviation from linearity. As for length measures,
177 preservation status had an effect on caecum and colon & rectum tissue mass (Table 2).
178 Therefore, total intestinal mass and total GIT mass were slightly higher in formalin-fixed
179 specimens (Table 2). Considering the entire GIT, the relative mass of the small intestine and
180 colon & rectum did not vary with body mass; by contrast, the relative mass of the stomach
181 declined, and that of the caecum increased, with body mass (Table 2; Fig. 5B). Considering
182 only the intestinal tract, relative caecum mass increased with body mass (Table 2). Relative
183 tissue mass of the colon and rectum of the total GIT was higher in formalin-fixed specimens
184 (frozen: 27 ± 7 %; fixed 35 ± 6 % of total GIT mass) (Table 2).

185

186 **Discussion**

187 The present study has relevance for both methodological and biological aspects of digestive
188 tract anatomy. The data indicate substantial intraspecific variation in intestinal measurements
189 within mature specimens. For example, Fig. 4D indicates that at 2 kg of body mass, the length
190 of the intestinal tract in ring-tailed lemurs may vary by a metre. In humans, at evidently higher
191 body masses, the documented variation in small intestine length can be more than four metres
192 (reviewed in Zhou et al. 2020). A large body of literature exists that documents intraspecific
193 variation in intestinal length in rodents due to diet and/or energetic constraints, and intraspecific
194 intestinal length flexibility has been linked to the number of different habitats small rodent
195 species can occupy (Naya et al. 2008). However, for large mammals no corresponding
196 compilations exist. To date, variation such as described in humans or in the lemurs of the
197 present study remains largely unexplained. In the lemurs, effects of diet or different husbandry
198 conditions appear unlikely. Thus, the variation remains unexplained. While such variation may
199 not be a systematic problem for large-scale comparisons of intestinal length (Woodall and

200 Skinner 1993; Lavin et al. 2008; Lovegrove 2010), studies exploring quantitative differences
201 between only a few specimens of a few species need to take this variation into account and
202 should include a sufficient number of individuals.

203 Given the magnitude of this general intraspecific variation, the variation introduced by
204 the use of formalin-fixed material appeared to be of a negligible magnitude in the present study.
205 The material that was compared was either frozen at unknown times (but most likely within 24
206 hours) after death, then thawed and dissected from the mesenteries, or dissected at unknown
207 times after death and subsequently placed in formalin. Of the two processes, freezing and
208 thawing could be assumed to counteract any potential effect of post-mortem contraction. By
209 contrast, formalin fixation could theoretically have occurred at any stage of post-mortem
210 contraction or relaxation, and therefore, on average shorter dimensions could have been
211 expected for this method. However, if at all, the opposite was the case, with formalin-fixed
212 specimens showing somewhat longer large intestines (Table 1). One theoretical explanation
213 could be the effect of opening the intestines lengthwise, with no effect on the length of the
214 smooth-walled small intestine, but with an effect on the haustrated large intestine: if opened,
215 the haustra might not constrain the length of the organ as much as in a closed state.
216 Unfortunately, this finding only became evident after the frozen/thawed material had been
217 disposed, otherwise a comparison of the length of the same material with a closed and an
218 opened intestine could have been performed. However, the formalin-fixed large intestines were
219 also heavier – and longitudinal cuts should not affect mass measurements – suggesting that this
220 difference between the preservation methods for the large intestine might simply have been
221 due to chance.

222 Regardless of the large variation in intestinal measures in mature specimens, the
223 intraspecific allometry, including neonates and juveniles, yielded scaling relationships
224 comparable to those previously reported in the literature in interspecific studies (see

225 Introduction), in the range of a 0.4-0.5 scaling exponent. A similar, more-than-geometric
226 intraspecific scaling of the small and the large intestine across ontogeny was demonstrated in
227 rats (Toloza and Diamond 1992) and mice (Wołczuk et al. 2011). As in the ring-tailed lemurs,
228 the scaling effect was mostly found in the neonate and juvenile stages, and was not evident
229 within the mature specimens. The more-than-geometric scaling of intestinal lengths, as
230 explained in the introduction, appears to be a general feature of mammalian macroanatomy.

231 In ruminants and possibly other foregut fermenters, the change in proportions of the
232 different GIT sections when going from milk-feeding to weaning, are very distinct. Indeed the
233 fermentation compartments increase disproportionately in tissue weight (e.g., Wardrop and
234 Coombe 1960; Godfrey 1961) and, by inference, in volume. In horses, the length proportion of
235 the caecum and proximal colon – which represent the fermentation chambers – similarly
236 increase with age until maturity (Smyth 1988). For the ring-tailed lemurs, a similar ontogenetic
237 change in GIT proportions linked to the change in diet was not evident in length measurements.

238 The scaling of organ tissue masses surprisingly appeared more-than-linear, with 95%
239 confidence intervals of the scaling exponent consistently above 1.00 (Table 2). To our
240 knowledge, no recent comprehensive interspecific treatise for gastrointestinal tissue mass
241 exists. Calder (1996) cites the scaling in 41 mammal species established by Brody (1945) with
242 an exponent of 0.94; using the standard error for the exponent given in the original by Brody
243 (1945), the 95% confidence interval of that exponent includes linearity at 0.85-1.03 (and is
244 nearly identical for the exponent found for birds in that study). In the original data from
245 Navarrete et al. (2011) for 100 mammal species, a similar scaling exponent with a confidence
246 interval of 0.88-0.94 can be calculated, and Prothero (2015) found a scaling exponent of 0.93
247 in mammals that also excluded linearity in the confidence interval. Why mammalian and avian
248 GIT scaling should be slightly less-than-linear has not been explained so far, and we also do
249 not offer an explanation. We hypothesize that the more-than-linear scaling found in our data is

250 an intraspecific effect of ontogeny, reflecting the shift from milk feeding to solid food. In the
251 case of the ring-tailed lemur, the natural diet comprises fruits, leaves and other plant parts (e.g.,
252 Rasamimanana and Rafidinarivo 1993; Simmen et al. 2006). On the one hand, an increasing
253 tissue mass with age could derive from a disproportionately increased muscle mass as an effect
254 of processing solid material. On the other hand, it could derive in particular from absorptive
255 mucosa development in those compartments (caecum, colon) where fermentative digestion
256 intensifies after the switch to solid food. The enhancing effect of short-chain fatty acids, the
257 main products of microbial fermentation, on gut mucosa development - and hence tissue mass
258 - is well-known (e.g., Kripke et al. 1989). Fermentative microbial digestion has been suggested
259 for ring-tailed lemurs (Campbell et al. 2000) and was demonstrated by the measurement of
260 short-chain fatty acids in the faeces of captive specimens (McKenney et al. 2018).
261 Correspondingly, the scaling exponent of tissue mass was highest for the caecum, followed by
262 the colon and rectum, whereas the small intestine only scaled slightly higher than linearly, and
263 the stomach scaling was linear (Table 2). A shift in the faecal microbiome from milk-feeding
264 to weaning has been demonstrated in lemurs, including ring-tailed lemurs (McKenney et al.
265 2018), which would be expected to parallel the increased tissue mass.

266 The present study did not find evidence for the presence of a caecal appendix in ring-
267 tailed lemurs. The review of the primate appendix by Fisher (2000) did not include ring-tailed
268 lemurs as either a species with or without an appendix, and neither Campbell et al. (2000) nor
269 McGrosky et al. (2019b) reported evidence for an appendix in ring-tailed lemurs. The external
270 appearance of the caeca of some individuals included an apparent narrowing of the caecal apex
271 that created the impression of an appendix (Fig. 2), but neither thickening of the mucosa nor
272 macroscopic appearance of lymphatic tissue were evident (Fig. 3). A recent description of the
273 gastrointestinal anatomy of another lemur species, *Eulemur coronatus*, also did not suggest the
274 presence of an appendix (Schwitzer 2009), although the species is among those for which an

275 appendix is assumed in the literature (Fisher 2000; Smith et al. 2013, 2017). A more detailed
276 histological study of the putative appendices of lemur species might be interesting.

277

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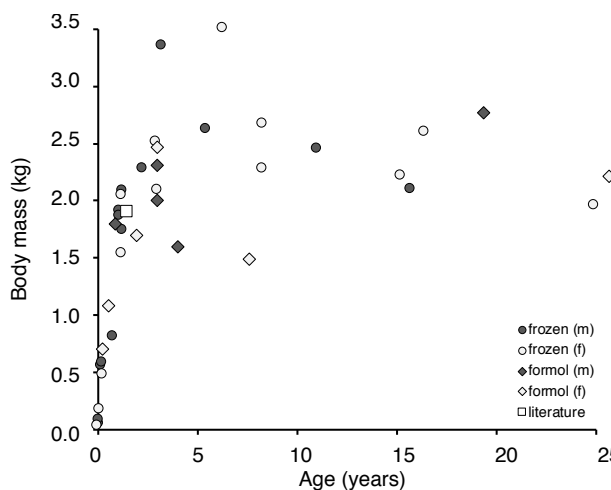
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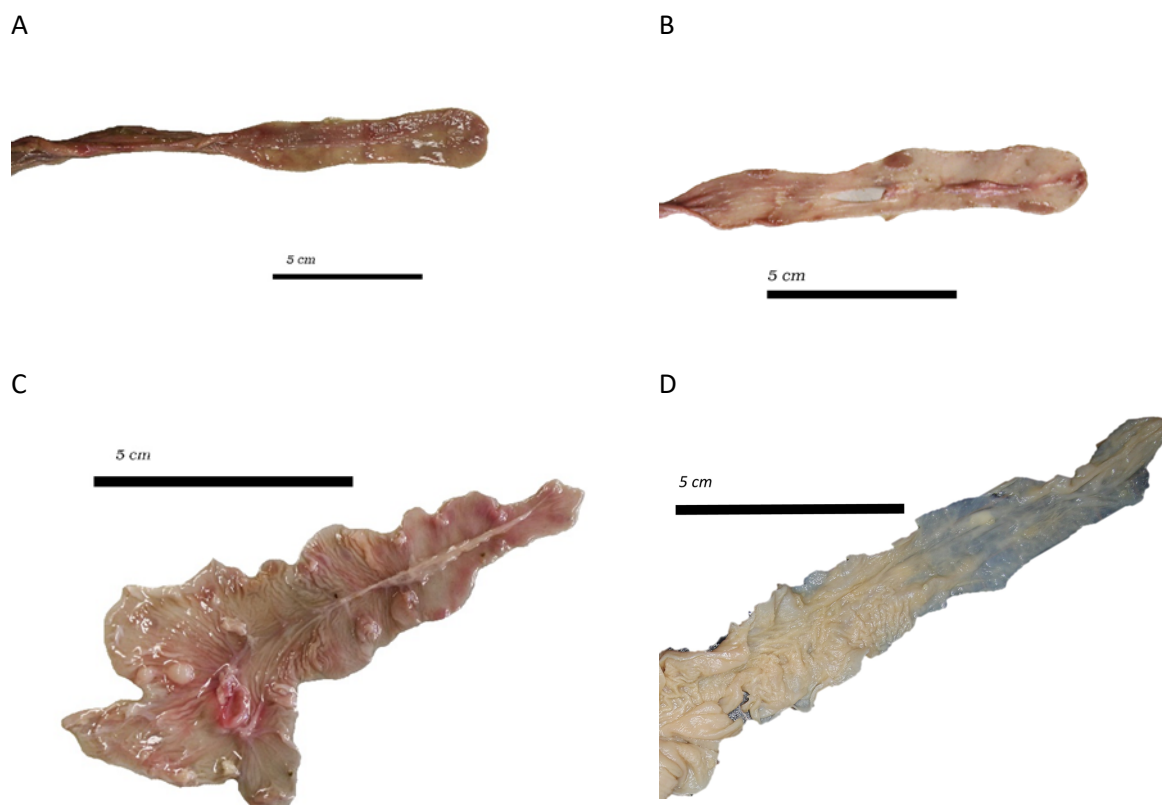


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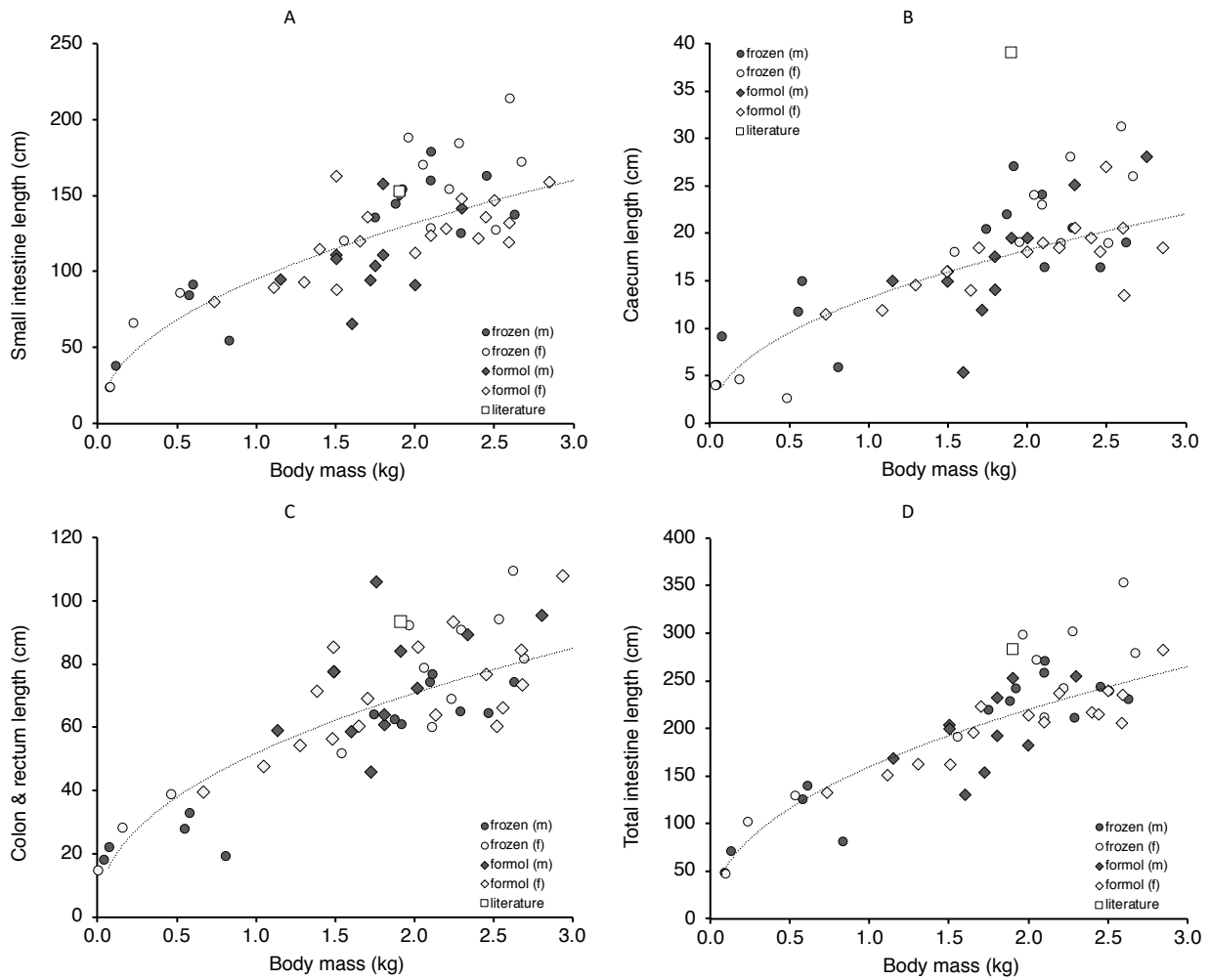
381 **Figure 1** Relationship of body mass and age in the male (m) and female (f) ring-tailed lemurs
382 (*Lemur catta*) for which age was known in the present study, separated by whether their
383 intestine was stored frozen or in formalin. Note two particularly heavy animals at body mass
384 > 3 kg, which were excluded from subsequent analyses.



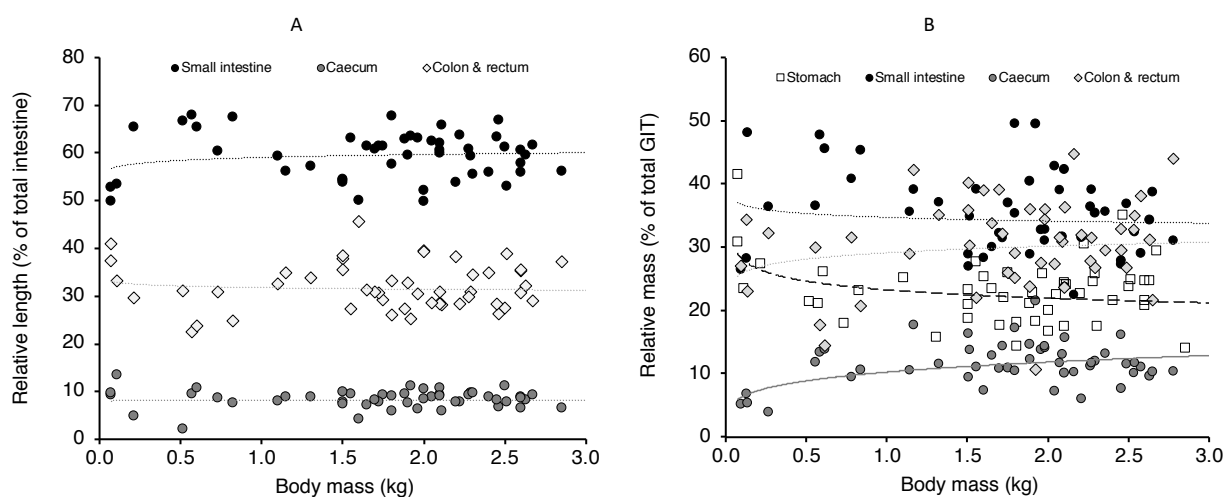
385 **Figure 2** Gastrointestinal tracts of ring-tailed lemurs (*Lemur catta*) stored frozen (A-C) or in
386 formalin (D): (A) a 16.2-year-old female of 2.6 kg, (B) an 8.2-year-old female of 2.3 kg, (C)
387 a 0.1-year-old male of 0.6 kg, (D) an adult female of 2.1 kg.



388 **Figure 3** The opened caecum in various ring-tailed lemurs (*Lemur catta*), with apex pointing
389 towards the right, suggesting an absence of a caecal appendix, stored frozen (A-C) or in
390 formalin (D): (A) a 16.2-year-old female of 2.6 kg, (see Fig. 2A), (B) a 3.2-year-old male of
391 3.4 kg, (C) a 0.1-year-old male *L. catta* of 0.6 kg, (see fig. 2C), (D) an adult female of 1.5 kg.



392 **Figure 4** Relationship between body mass (A) small intestine, (B) caecum, (C) colon and
393 rectum length and (D) total intestine length in ring-tailed lemurs (*Lemur catta*) of the present
394 study (males and females, preserved frozen or in formalin), compared to an individual from
395 Campbell et al. (2000). Statistics in Table 1.



396 **Figure 5** Relationship of body mass and (A) relative intestine lengths; (B) relative
397 gastrointestinal organ masses (both in % of total) in ring-tailed lemurs (*Lemur catta*) of the
398 present study. The only significant relationships are those for the relative mass of stomach
399 and caecum (cf. Table 2).

400 **Table 1** Allometric regressions according to $y = a$ body mass^b including 95% confidence intervals for measures of intestinal lengths of ring-
 401 tailed lemurs (*Lemur catta*) of different sex and preservation method
 402

Dependent variable (y)	a [95% CI]	P	b [95% CI]	P	sex ¹	preservation ¹	interaction ¹
<i>Absolute length (cm)</i>							
Small intestine	95 [89;101]	<0.001	0.48 [0.41;0.54]	<0.001	n.s.	n.s.	n.s.
Caecum*	13 [12;14]	<0.001	0.47 [0.37;0.58]	<0.001	n.s.	n.s.	n.s.
Colon & rectum*	52 [49;55]	<0.001	0.45 [0.38;0.52]	<0.001	(+) 0.033	(+) 0.006	0.028
Total intestine*	160 [152;168]	<0.001	0.46 [0.40;0.51]	<0.001	n.s.	n.s.	n.s.
Caecum width	2.1 [1.9;2.4]	<0.001	0.57 [0.47;0.67]	<0.001	n.s.	-	-
<i>Relative length (% total intestinal length)</i>							
Small intestine	59 [58;61]	<0.001	0.01 [-0.01;0.04]	0.282	n.s.	n.s.	n.s.
Caecum*	8 [8;9]	<0.001	0.01 [-0.09;0.10]	0.913	n.s.	n.s.	n.s.
Colon & rectum	32 [30;33]	<0.001	-0.01 [-0.06;0.03]	0.568	n.s.	(+) 0.014	n.s.

403 body mass in kg; *indicates that residuals were not normally distributed
 404 ¹results of additional models testing for effects of sex and preservation using ranked data; (+) indicates higher values in females, or higher values in formalin-preserved tissues

405 **Table 2** Allometric regressions for weight measurements according to $y = a$ body mass^b including 95% confidence intervals for measures of
 406 tissue mass of gastrotintestinal tracts (GIT) of ring-tailed lemurs (*Lemur catta*) of different sex and preservation method
 407

Dependent variable (y)	a [95% CI]	P	b [95% CI]	P	sex ¹	preservation ¹	interaction ¹
<i>Absolute mass (g)</i>							
Stomach*	6.9 [6.2;7.8]	<0.001	1.08 [0.95;1.20]	<0.001	n.s.	n.s.	n.s.
Small intestine*	10.5 [9.3;11.9]	<0.001	1.14 [1.01;1.28]	<0.001	n.s.	n.s.	n.s.
Caecum*	3.0 [2.6;3.6]	<0.001	1.37 [1.21;1.54]	<0.001	n.s.	(+) 0.048	n.s.
Colon & rectum*	9.0 [7.7;10.6]	<0.001	1.22 [1.05;1.39]	<0.001	n.s.	(+) 0.002	n.s.
Total intestine*	22.8 [20.1;25.9]	<0.001	1.20 [1.06;1.33]	<0.001	n.s.	(+) 0.017	n.s.
Total GIT*	29.8 [26.4;33.7]	<0.001	1.17 [1.04;1.30]	<0.001	n.s.	(+) 0.027	n.s.
<i>Relative mass (% total GIT mass)</i>							
Stomach	23 [22;25]	<0.001	-0.08 [-0.15;-0.02]	0.014	n.s.	n.s.	n.s.
Small intestine	34 [33;37]	<0.001	-0.02 [-0.09;0.04]	0.458	n.s.	n.s.	n.s.
Caecum [#]	10 [9;11]	<0.001	0.21 [0.12;0.30]	<0.001	n.s.	n.s.	n.s.
Colon & rectum	29 [27;32]	<0.001	0.05 [-0.03;0.14]	0.244	n.s.	(+) 0.008	n.s.
<i>Relative mass (% total intestine mass)</i>							
Small intestine	46 [43;48]	<0.001	-0.05 [-0.11;0.00]	0.069	n.s.	(-) 0.019	n.s.
Caecum [#]	13 [12;15]	<0.001	0.18 [0.09;0.26]	<0.001	n.s.	n.s.	n.s.
Colon & rectum*	38 [35;41]	<0.001	0.02 [-0.07;0.11]	0.657	n.s.	n.s.	n.s.

408 body mass in kg; *indicates that residuals were not normally distributed; [#]in these cases, body mass was not significant in the ranked-data model

409 ¹results of additional models testing for effects of sex and preservation using ranked data; (+) indicates higher values in females, or higher values in formalin-preserved tissues

410

