

The importance of protein in leaf selection of folivorous primates

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Abstract

Protein limitation has been considered a key factor in hypotheses on the evolution of life history and animal communities, suggesting that animals should prioritize protein in their food choice. This contrasts with the limited support that food selection studies have provided for such a priority in nonhuman primates, particularly for folivores. Here, we suggest that this discrepancy can be reconciled if folivores only need to select for high protein leaves when average protein concentration in the habitat is low. To test the prediction, we analyzed published and unpublished results of food selection and protein concentrations from 47 studies of folivorous primates. To counter potential methodological flaws, we differentiated between methods analyzing nitrogen and soluble protein concentrations. We found that leaves containing either high concentrations of total nitrogen or high soluble protein were selected more in low protein forests. There was no relationship (either negative or positive) between the concentration of protein and fiber in the food. Overall our study suggests that protein is limiting only in protein-poor environments, explaining the sometimes contradictory results in previous studies on protein selection.

58

Key words: primates, food chemistry, food selection, leaf-eating, nutrient requirements, protein availability

61

INTRODUCTION

Protein has been considered a major limiting factor involved in the evolution of animal communities and life history traits [e.g., White, 1993]. The need to satisfy protein requirements plays a central role in hypotheses on the evolution of morphological, physiological and behavioral life history traits (such as gut specialization, reduced metabolism in folivores, social systems linked to the

68 distribution of different types of food, and community composition; e.g., White, 1993).
69 The essentials of this idea have been developed for primates by Kay [1984] and
70 illustrated by Terborgh [1992]. Specifically, while most primates eat fruit to satisfy
71 their energy requirements, fruits typically do not provide enough available protein for
72 survival and reproduction, though this may not always be the case [reviewed by
73 Klaasen and Nolet 2008; Ganzhorn *et al.*, 2009; Schwitzer *et al.* 2009]. Therefore,
74 smaller-bodied species feed on insects and fruit to support their protein needs.
75 Larger species are unable to obtain enough protein from insects because the capture
76 rate of insects is independent of body mass [Hladik, 1978; Rothman *et al.*, 2014].
77 Consequently they eat leaves, which usually contain more protein than fruit and can
78 be found in sufficient quantities to satisfy the protein needs of a larger species.
79 According to this scenario, within the broad constraints of body mass, protein
80 represents the ultimate factor that determines whether a species is insectivorous or
81 folivorous. The idea that protein is limiting has received support from the studies of
82 Milton [1979], Oates *et al.*, [1990] and Davies and Oates [1994 and their
83 contributors]. Milton [1979] postulated that the densities and biomass of folivorous
84 howler monkeys are closely related to the average leaf quality of a forest expressed
85 as the ratio of protein to fiber (most commonly measured as acid detergent fiber –
86 ADF) concentrations. Oates and collaborators (1990) tested and found support for
87 this idea through a wide comparison of colobine monkeys. ADF concentrations were
88 included because ADF should represent the refractory fraction of the cell wall
89 (cellulose + lignin) and increasing ADF concentrations are also likely to reflect greater
90 amounts of indigestible protein [Rothman *et al.*, 2008]. The concept of protein to fiber
91 ratios was extended to additional populations of colobines [e.g., Chapman *et al.*,
92 2002, 2004; Wasserman & Chapman, 2003; Fashing *et al.*, 2007] and supported with
93 independent datasets on lemurs [Ganzhorn, 1992; Simmen *et al.*, 2012] and howler

94 monkeys [Peres, 1997]. The biological relevance of this ratio has been questioned
95 based on biochemical considerations, statistical issues around the use of ratios
96 [Wallis *et al.*, 2012], and empirical grounds [Gogarten *et al.*, 2012; Chapman *et al.*,
97 2014] but it seems to retain some predictive capacity.

98 Restricting the considerations to protein alone, several studies have shown
99 that protein can be limiting with lasting effects on development and lifetime fitness
100 [e.g., Fleagle *et al.*, 1975; Elias & Samonds, 1977; Altmann, 1991, 1998; Degabriel *et*
101 *al.*, 2009]. However, the evidence that folivorous primates actually select leaves with
102 high protein content is ambiguous. Considering protein alone, some studies found
103 positive selection by primates for high protein leaves [e.g., *New World howler*
104 *monkeys*: Milton, 1979, 1998; Glander, 1981; *Old World non-colobine monkeys*:
105 Beeson, 1989; Barton & Whiten, 1994; *Old World colobines*: Davies *et al.*, 1988;
106 Waterman *et al.*, 1988; Mowry *et al.*, 1996; Koenig *et al.*, 1998; Yeager *et al.*, 1997;
107 *Apes*: Calvert, 1985; *Lemurs*: Ganzhorn, 1988, 1992, 2002; Mutschler, 1999] but
108 others failed to do so [e.g., *New World howler monkeys*: Gaulin & Gaulin, 1982;
109 Estrada & Coates-Estrada, 1986; *Old World colobines*: Oates *et al.*, 1980; McKey *et*
110 *al.*, 1981; Waterman *et al.*, 1988; Kool, 1992; Dasilva, 1994; Chapman *et al.*, 2002;
111 *Apes*: Conklin-Brittain *et al.*, 1998; Rothman *et al.*, 2011; *Lemurs*: Ganzhorn, 1988;
112 Ganzhorn *et al.*, 2004; Simmen *et al.*, 2014]. Thus, we are left with the conundrum
113 that protein is hypothesized to be an important component in primate food selection
114 while only about half of the studies on food selection criteria demonstrate that
115 primates actively select high protein leaves. This discrepancy can be due to
116 methodological, ecological, or species-specific reasons, or the hypothesis may
117 simply be wrong.

118 On the methodological side, different studies have applied different methods to
119 measure “protein”. While the conventional method of measuring crude protein uses

120 total nitrogen concentrations multiplied by 6.25 (or a species specific factor [Milton &
121 Dintzis, 1981]) as a surrogate for protein, this measure does not actually distinguish
122 between protein and non-protein nitrogen [e.g. N in cyanogenic glycosides, non-
123 protein amino acids, nitrates or alkaloids], or between available protein and protein
124 bound to other components and thus unavailable for digestion [DeGabriel *et al.*,
125 2008; Rothman *et al.*, 2008]. To overcome this shortcoming, some studies have
126 analyzed total amino acids [e.g., Glander, 1981; Simmen & Sabatier, 1996;
127 Mutschler, 1999; Curtis, 2004] or soluble protein [e.g., Ganzhorn, 1988; Koenig *et al.*,
128 1998; Conklin-Brittain *et al.*, 1999; for methodological considerations see Ortmann *et al.*
129 *et al.*, 2006; Rothman *et al.*, 2012]. Although the selection for high protein items was
130 more consistent in studies that analyzed soluble protein than in studies based on
131 crude protein, none of these methods accounts for differences in protein quality
132 (defined by essential amino acids), or digestibility [Robbins, 1983; NRC, 2003; Wallis
133 *et al.*, 2012; DeGabriel *et al.*, 2014].

134 From an ecological perspective, the lack of positive selection for high protein
135 items could also be explained by the assumption that primates are able to satisfy
136 their protein requirements with a diet containing about 6.4 – 8% crude protein [NRC,
137 2003]. The crude protein concentration of leaves and the average concentration of
138 protein in primate foods are around or well above these requirements [e.g., Hladik,
139 1977; Oftedal, 1991; Conklin-Brittain *et al.*, 1998; Ganzhorn *et al.*, 2009]. Thus,
140 primates might not need to select high protein items but could simply feed according
141 to the average availability of protein in the environment provided that the digestibility
142 of protein from the food was not hindered by other components such as fiber or
143 tannins [Mowry *et al.*, 1996; Yeager *et al.*, 1997; Simmen *et al.*, 2014].

144 Deviations from selecting high protein leaves may also be caused by species-
145 specific adaptation of gut morphology and digestive physiology [Chivers *et al.*, 1984;

146 Cork & Foley 1991; Hughes, 1993; Langer & Chivers, 1994; Van Soest, 1994;
147 Lambert, 1998; Milton, 1998, 1999; Campbell et al., 1999, 2004; Edwards & Ullrey,
148 1999a,b; Godfrey et al., 2004]. The effect of gut physiology may be more important
149 than the effect of body mass on dietary characteristics in primates as hindgut-
150 fermenters process food differently than foregut fermenters and both deviate from
151 species with unspecialized digestive tracts, regardless of size. For example,
152 Campbell et al. [2004] found that different adaptations of the digestive tract result in
153 food passage times largely independent of body mass [see also Clauss et al., 2008],
154 such as larger primate species with foregut fermentation (colobines) or hindgut
155 fermentation (gorillas), and small primates with hindgut fermentation and caecotropy
156 (e.g., *Lepilemur* spp.) [Charles-Dominique & Hladik 1971], or enlargement of the
157 small intestine (Indriidae). This supports the conclusion that body mass is not a
158 useful surrogate to understand primate feeding and digestion, including protein
159 requirements [Lambert, 1998].

160 Thus, in order to investigate protein selection in folivorous primates, we
161 consider the availability of protein in the environment and test the hypothesis that
162 protein is a limiting component and therefore primates should search for high protein
163 and/or low fiber leaves. According to this hypothesis, selection for high protein items
164 would not be necessary if animals could obtain enough protein from their overall diet.
165 However, if protein concentrations in the environment are low, folivorous primates
166 should seek high protein leaves. Therefore, we predict that selectivity for high protein
167 leaves declines with increasing average protein content in leaves encountered by the
168 animals in their home range. We could expect there to be an inverse relationship
169 between concentrations of protein and fiber in foliage reflecting a maturation of the
170 leaf ontogenetically and temporally. We also tested for this relationship and

171 separately tested whether fiber in the food selected differed from that of a general
172 sample.

173

174 **METHODS**

175 **Database**

176 The analyses presented here are based on published data from all primate
177 radiations (except for apes; see below), supplemented by new data of folivorous
178 primates from Madagascar, the New World and Nepal (Table 1). Analyses were
179 restricted to forest dwelling species that have been classified as “folivores” because
180 the majority of their food items were from photosynthetic material [Kappeler &
181 Heymann, 1996]. As more studies are conducted, it appears that the classification of
182 species into specific feeding guilds does not reflect the species-specific variability of
183 diet [Hemingway & Bynum, 2005; Garber *et al.*, 2015]. Thus, we call those species
184 “folivores” that are supposed to derive their protein from leaves and not insects
185 according to Kay’s [1984] hypothesis.

186 Species that feed primarily on the leaves of grasses, bamboo (*Hapalemur*
187 *spp.*, *Prolemur simus*) and herbs (*Gorilla spp.*) were not included, as grass and herbs
188 have different physico-chemical properties than leaves from trees, such as different
189 lignin, a general lack of tannins and incorporation of silica in grasses [Robbins, 1983].
190 However, *Hapalemur meridionalis* from Mandena (south-eastern Madagascar) was
191 included as these animals live in an area without bamboo and feed on grass and
192 other leaves [Eppley *et al.*, 2011]. For the current analysis we removed all grasses
193 that were used as food and restricted the analysis to the proportion of their diet that
194 consists of leaves from trees. We also included body mass in the database provided
195 in Table I. Data for primate body mass were taken from Smith and Jungers [1997]
196 and Mittermeier *et al.* [2010] and averaged between sexes.

197

198 **Food Types and Nutritional Analyses**

199 Foods included in the present analysis were leaves or flower buds from trees,
200 shrubs or vines. We further restricted the analysis to concentrations of nitrogen
201 (measured by the Kjeldahl method), or by a combustion procedure with subsequent
202 analysis of elementary nitrogen (the Dumas method), or based on near infrared
203 reflectance spectroscopy (NIRS) (calibrated against the Kjeldahl or Dumas method),
204 soluble protein and acid detergent fiber (ADF). Data presented as “crude protein” (i.e.
205 total nitrogen multiplied by 6.25) was re-transformed to total nitrogen concentration
206 as the biological significance of the conversion factor is presently debated and its
207 biological meaning is unclear (Milton & Dintzis, 1981; NRC, 2003; for methodological
208 reviews see Ortmann *et al.*, 2006; Rothman *et al.*, 2012). The Kjeldahl and Dumas
209 methods yield almost identical results (regression between nitrogen measured by
210 Kjeldahl [y] and by the Dumas method [x] forced through the origin: $y = 0.94x$; $R^2 =$
211 0.99 ; $n = 90$; Supplementary Material [Terboven, 2014]). Near infrared reflectance
212 spectroscopy also provides accurate estimates for nitrogen concentrations when
213 models were tested with truly independent data (Kjeldahl: $y = 1.06x$, $R^2 = 0.97$, $N =$
214 18 ; combustion: $y = 0.97x$, $R^2 = 0.97$; $N = 18$; Supplementary Material).

215 Studies that published soluble protein concentrations (measured by the
216 method outlined by Bradford, [1976]) but without estimates of crude protein were
217 included in the analysis, when available. However, these two datasets were analyzed
218 separately. “Available protein” would be a more biologically appropriate measure of
219 protein than crude protein [DeGabriel *et al.*, 2008, 2014; Wallis *et al.*, 2012] and
220 probably also than soluble protein as soluble protein concentrations are correlated
221 with available protein in some studies but not in others [Ganzhorn, unpubl.]. To date,
222 too few data exist for available protein to allow for comparative analyses.

223 In primate studies, fiber concentrations are most commonly reported as acid
224 detergent fiber (ADF). However, not all studies report exact details of the procedures
225 (e.g. whether ADF is analyzed sequentially following isolation of neutral detergent
226 fiber (NDF)). In addition, most studies do not specify whether ADF is reported on an
227 ash-free basis or corrections are made for residual dry matter. Furthermore, there is
228 little appreciation in primate literature that fiber residues can be contaminated with
229 tannin-protein complexes [Wallis *et al.*, 2012]. All these factors can contribute to
230 unknown errors in the reported ADF concentrations, but how significant they are in
231 different studies is hard to gauge and it is not possible to apply a consistent
232 correction factor to compensate for methodological differences. We emphasize the
233 need for rigorous analysis to avoid these uncertainties [Rothman *et al.*, 2012]. As a
234 result, the accuracy of the “ADF” data is likely to be low and conclusions derived from
235 fiber concentrations should be considered with these limitations in mind

236 All as yet unpublished chemical analyses were carried out in the laboratory of
237 the University of Hamburg [Donati *et al.*, 2007] (Table I). All results are expressed as
238 % of dry matter.

239

240 Insert Table I here

241

242 **Quality of Leaves Available in Different Forests (“representative samples”)**

243 Most measures of the availability of protein and leaf quality in different forests
244 (here termed “representative samples”) are based on mature tree leaves. Leaves
245 were collected opportunistically or from the most abundant tree species and were
246 assumed to represent a proxy for year-round leaf quality [e.g., Oates *et al.*, 1990;
247 Ganzhorn, 1992; Chapman *et al.*, 2002, 2004; Wasserman & Chapman, 2003;
248 Simmen *et al.*, 2014]. The representative samples for *Semnopithecus schistaceus* in

249 Ramnagar (Nepal) are based on mature leaves of the 25 most abundant tree species
250 [Chalise 1995; Chalise & Koenig, unpubl.] and for *Propithecus edwardsi* in
251 Ranomafana (Madagascar) on 14 tree species sampled haphazardly [Wright &
252 Daniels, unpubl.].

253 Some studies collected separate representative samples for young and
254 mature leaves [Mowry et al., 1996; Liu et al., 2013] or separate samples for the wet
255 and the dry season [Ganzhorn, 2002]. These samples were considered as
256 independent data points and were entered in the analyses as independent units. Our
257 rationale is that we wanted to have some measure of leaf nutritional quality in
258 samples of leaves that we could use for the analyses of selection of leaves
259 consumed as food against this representative sample (see “Selection Criteria for
260 Consumed Leaves” below).

261

262 **Selection Criteria for Consumed Leaves**

263 Determination of the significance of selection for specific chemical
264 components was restricted to photosynthetic parts (leaves, sometimes differentiated
265 in different parts of leaves). Analyses of selection were always restricted to the same
266 types of plant parts because we wanted to know when selection occurs with respect
267 to the representative sample. For example; if the representative sample consisted of
268 mature leaves, then only food items consisting of mature leaves were considered. If
269 the representative sample consisted of young leaves, then only young leaf food items
270 were considered. If the representative sample consisted of mature leaves and the
271 animals were feeding only on young leaves, no comparison was calculated.

272 The data for *Propithecus coronatus* are based on the early dry season.

273 During this time of the year, the diet consisted of 85-90% leaves. The chemical

274 analyses were based on a reconstructed diet, made by mixing aliquot proportions of
275 each food species consumed according to its dietary proportion [Pichon, 2012].

276 Selection criteria were taken from the original paper, or leaves that were
277 consumed were compared with representative samples from the forest, or
278 concentrations of chemical components were correlated with the frequency of
279 consumption (assumed to represent the amount of leaf material ingested). Thus, p-
280 values listed in Table I and Figure 1 are based on t-tests between samples of
281 material consumed versus the representative sample or on correlations between the
282 frequency of consumption and the concentration of the chemical component in
283 question.

284

285 **Statistical Analyses**

286 Published data are based on the analysis of a single individual per plant
287 species or averages based on several different individuals of the same plant species
288 or on averages weighted by the frequency of abundance or the frequency of
289 consumption. When possible, we base our analyses on unweighted means of plant
290 species. Surprisingly, and despite the known temporal and inter-individual variation
291 within plant species [Ganzhorn & Wright 1994; Chapman et al., 2003], the variation
292 between weighted and unweighted samples seems to average out in large samples
293 (Table II). Statistical tests were made with SPSS 21.0.

294

295 Insert Table II

296

297 **RESULTS**

298 **Selection of Leaves in Relation to the Average Concentrations of Nitrogen,**
299 **Soluble Protein or ADF in a Given Forest**

300 Measures of nitrogen, soluble protein and ADF in representative samples of
301 plant leaves were found for 19, 18 and 33 studies, respectively (Table I).
302 Concentrations of the same components in food plants were found for 35, 22 and 41
303 studies. The data for soluble protein were unevenly distributed in the dataset, and
304 were mainly available for foods of lemurs. Studies of the same species in different
305 areas or during different times of the year were treated as independent units since
306 the concentrations of chemical components vary significantly between sites and
307 seasons.

308 Selectivity for leaves containing high concentrations of nitrogen increased
309 significantly with declining nitrogen concentrations in forests ($r_s = 0.62$, $P = 0.008$, N
310 $= 17$; Figure 1; Table I). Restricting the correlation to the Colobinae does not alter the
311 principal result but removes significance ($r_s = 0.51$, $P = 0.075$, $N = 13$).

312 For soluble protein data, selection of high protein leaves was stronger in
313 forests with low concentrations of soluble protein in representative samples of leaves
314 than in forests with high concentrations ($r_s = 0.66$, $P = 0.004$, $N = 17$). Removing
315 *Semnopithecus schistaceus* from the correlation (the only species for which soluble
316 protein data are available for representative samples of leaves outside Madagascar;
317 thus restricting it to lemurs) does not change the result ($r_s = 0.66$, $P = 0.005$, $N = 16$).

318 Combining the data for the two measures of protein and including the type of
319 protein analysis as a random categorical variable in a GLMM results in a highly
320 significant effect of the concentrations of protein in representative samples of leaves
321 on the strength (significance) of selection ($F = 21.58$; $P < 0.001$).

322 There was no relationship between concentrations of nitrogen or soluble
323 protein and fiber in the data set. There were no significant correlations between the
324 selection (or rather discrimination) against ADF and the ADF in representative

325 samples, either over all the data ($r_s = 0.12$, $P = 0.534$, $N = 31$), or when considering
326 various primate radiations separately.

327

328 Insert Figure 1

329

330 **DISCUSSION**

331 The present analysis sought to better understand the discrepancy between the
332 findings of some studies that identify protein as a limiting resource, including those
333 that focus on non-human primates [Kay 1984] and others that find no evidence for
334 this phenomenon. Primates (and animals in general) need to satisfy their protein
335 needs by selecting protein-rich food, but we found that many primatological studies
336 failed to demonstrate such a selection for high protein food (Table I). A number of
337 studies have pointed out that selection of high protein food would only be required if
338 the food items in the environment have average protein concentrations below the
339 required needs [e.g., Mowry et al., 1996; Yeager et al., 1997; Ganzhorn et al., 2009;
340 Simmen et al., 2014] and that, once protein concentrations are above requirements,
341 selection could be based on other components and criteria, such as the availability
342 within the environment [e.g., Oftedal, 1991; Fashing et al., 2007] or secondary plant
343 chemicals [Moore & Foley 2005] or minerals such as sodium [Rothman et al 2006].
344 While this idea has been around for some time, it has rarely been tested [Marsh et
345 al., 2014; Jensen et al., 2015]. Studies started to focus instead on long-term nutrient
346 budgets and nutrient balancing using the conceptual approach of geometric
347 frameworks [e.g., Felton et al., 2009; Rothman et al., 2011; Johnson et al., 2013;
348 DeGabriel et al., 2014; Irwin et al., 2014], on new methods on how to measure
349 protein that is actually available [DeGabriel et al., 2008], or on an understanding of
350 other confounding variables [Wallis et al., 2012], Our results illustrate that primates

351 select for high protein leaves especially in situations where the average protein
352 content of leaves in a forest is low. No such correlation was found with respect to
353 fiber concentrations. Thus, it appears that protein is limiting for folivorous primates
354 under certain conditions, but clearly not in the majority of tropical forests studied. In
355 contrast, we found no evidence of either an expected inverse relationship between
356 protein and fiber concentrations in food or indeed any evidence that animals were
357 selecting against fiber. We cannot judge whether there is a significant effect of
358 methodology on this result but it is clear that fiber is analyzed inconsistently in
359 primatological studies with little regard to the effects of ash, tannins or other
360 interfering substances [Makkar & Singh 1995; Wallis et al., 2012]

361 Our comparative study also indicates a fundamental problem of field studies
362 on food selection. Animals are most frequently studied where they occur in high
363 densities. These are probably the best areas for survival and reproduction with high
364 quality food availability. Under these conditions, it is probably hard, if not impossible,
365 to identify factors that are actually limiting. Having enjoyed considerable time in
366 forests with plentiful animals, it may be an unfortunate conclusion, but in order to find
367 out what limits primates, researchers will likely need to turn their attention to regions
368 where animals are naturally scarce (e.g. Stalenberg 2015).

369

370 **Acknowledgements**

371 We thank Nicoletta Righini for her invitation to contribute to this special volume of the
372 American Journal of Primatology. Nicoletta Righini, Marcus Clauss and an
373 anonymous reviewer provided insightful comments on our manuscript, which we
374 greatly appreciate. Funding was provided to MKC and AK by the Alexander von
375 Humboldt-Foundation, the German Academic Exchange Service (DAAD), and the
376 German Research Council (DFG), to ID from DFG; to TE from the American Society

377 of Primatologists, Conservation International's Primate Action Fund, IDEAWILD,
378 Mohamed bin Zayed Species Conservation Fund, Primate Conservation Inc., and the
379 Primate Society of Great Britain/Knowsley Safari Park; to WJF from the DFG
380 Mercator Professorship and Alexander von Humboldt Award; to JUG from DFG; to
381 MTI from Margot Marsh Biodiversity Foundation, National Geographic Society CRE,
382 NSERC; to FK from DFG; to CM from the Emory University Graduate Division of
383 Biological and Biomedical Sciences; to MK from Fulbright; to EP from the Margot
384 Marsh Biodiversity Fund, Cornell University Department of Psychology, Silicon Valley
385 Community Foundation.

386 We confirm that the research adhered to the legal requirements of the country in
387 which the research was conducted and that this research adhered to the American
388 Society of Primatologists (ASP) Principles for the Ethical Treatment of Non-Human
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390

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703 **Tables**

704 TABLE I. Nitrogen, soluble protein and acid detergent fiber (ADF) concentrations in
705 leaves eaten by folivorous primates and in “representative samples” of leaves (RS) in
706 a given forest. “P” indicates significance of selection for high protein or low ADF
707 concentrations.

708

709 TABLE II. Comparison of the concentration of chemical components in leaves based
710 on measures of several individuals of the same plant species and on the mean per
711 plant species. Values are means \pm standard deviations; N = sample size. Data on
712 *Propithecus edwardsi* from Arrigo-Nelson (2006; unpubl.) based on mature leaves;
713 data on *P. candidus* from Patel [2012; unpubl.], restricted to leaves of species
714 identified unambiguously.

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717

718 **Figure captions**

719

720 Fig. 1. Significance values for the selection of leaves in relation to the average
721 concentrations of nitrogen (upper graph), soluble protein (middle graph) and ADF
722 (lower graph) in leaves available in different forests. Dots are lemurs, squares are
723 Old World Monkeys (Colobinae) and triangles are New World monkeys (*Alouatta*
724 spp.).

725