

A complex social structure with fission-fusion properties can emerge from a simple foraging model

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1 **ABSTRACT**

2 Precisely how ecological factors influence animal social structure is far from clear. We
3 explore this question using an agent-based model inspired by the fission-fusion society of
4 spider monkeys (*Ateles* spp). Our model introduces a realistic, complex foraging
5 environment composed of many resource patches with size varying as an inverse power-
6 law frequency distribution with exponent β . Foragers do not interact among them and start
7 from random initial locations. They have either a complete or a partial knowledge of the
8 environment and maximize the ratio between the size of the next visited patch and the
9 distance traveled to it, ignoring previously visited patches. At intermediate values of β ,
10 when large patches are neither too scarce nor too abundant, foragers form groups (coincide
11 at the same patch) with a similar size frequency distribution as the spider monkey's
12 subgroups. Fission-fusion events create a network of associations that contains weak bonds
13 among foragers that meet only rarely and strong bonds among those that repeat associations
14 more frequently than would be expected by chance. The latter form sub-networks with the
15 highest number of bonds and a high clustering coefficient at intermediate values of β . The
16 weak bonds enable the whole social network to percolate. Some of our results are similar to
17 those found in long-term field studies of spider monkeys and other fission-fusion species.
18 We conclude that hypotheses about the ecological causes of fission-fusion and the origin of
19 complex social structures should consider the heterogeneity and complexity of the
20 environment in which social animals live.

21

22 **Keywords:** fission-fusion, spider monkeys, chimpanzees, agent-based models

23 **INTRODUCTION**

24

25 Competition for food and predation risk are the most widely cited influences on the size
26 and structure of animal groups (Alexander 1974; Bradbury and Vehrencamp 1976; Pulliam
27 and Caraco 1984; van Schaik 1989). In primate societies, protection from alien male attacks
28 (Wrangham, 1979), defense of group resources (Wrangham, 1980) and prevention of
29 infanticide (Hrdy, 1977; rev. in van Schaik and Janson, 2000) also have been shown to be
30 important determinants of group size and structure. However, when confronted with the
31 wide variation in social structure existing among different taxa and even among populations
32 of the same species, socioecological theory remains limited in its explanatory power
33 (Janson 2000; DiFiore et al. in preparation).

34

35 Species with so called “fission-fusion” societies, such as chimpanzees (Goodall 1968),
36 spider monkeys (Symington 1990) and dolphins (Connor et al. 2000), present both
37 opportunities and challenges for socioecological theory. On the one hand, group size in
38 these species changes over short temporal and spatial scales, such that large amounts of
39 data can be gathered on a single population on the variation in group size and how it
40 correlates with food abundance (e.g. Symington 1988; White and Wrangham 1988). On the
41 other hand, the flexible nature of grouping patterns in fission-fusion societies creates
42 methodological difficulties in defining, measuring and analyzing group size variation
43 (Chapman et al. 1993), while the complexity of their foraging environments imposes
44 difficulties in measuring resource abundance and distribution (Chapman et al. 1992).

45

46 In the studies carried out so far on fission-fusion primate species, no clear-cut pattern has
47 emerged on the relationship between subgroup size and food availability. In a study on the
48 interacting effects of the size, density and distribution of food patches upon the grouping
49 behavior of spider monkeys and chimpanzees, Chapman et al. (1995) developed a simple,
50 general model of how these three ecological variables should affect group size. They
51 assumed that food patches could be found in one of three different configurations, each one
52 leading to small or large subgroups: depleting and uniformly distributed, depleting and
53 clumped and non-depleting patches. In their analysis, the authors found that only half or
54 less of the variance in subgroup size in both spider monkeys and chimpanzees could be
55 explained by habitat-wide measures of food abundance or variation in food patch size.
56 Similarly, Newton-Fisher et al. (2000) found no correlation between subgroup size and
57 habitat wide measures of food abundance; also, Anderson et al. (2002) found that party size
58 in chimpanzees does not increase with food aggregation. Symington (1988) reported
59 somewhat higher linear correlation indices for the average party size of spider monkeys and
60 the size of feeding trees, although parties were larger at intermediate food patch densities
61 than at low or high densities.

62

63 One reason for the lack of empirical support for socioecological explanations is that the
64 development of testable, *a priori* predictions has lagged behind the accumulation of data
65 and the formulation of *posthoc* explanations of why there is a correlation between, say,
66 group size and the average size of feeding patches. This is especially true when considering
67 that the real distribution and abundance of feeding patches found by forest-dwelling
68 primates is far from being captured by idealized dichotomies such as clumped vs. uniform
69 or large vs. small. Even when feeding for several days on only one species of fruit, it is

70 likely that fruit-bearing trees of widely different size will be found, simply because of the
71 age structure of the tree population. Recent studies (Enquist et al. 1999; Enquist and Niklas
72 2001) have found that tree size can be best described by an inverse power law frequency
73 distribution, with similar exponent values across different forests throughout the world. In
74 other words, small trees tend to be found in much higher numbers than large trees, but very
75 large trees can sometimes be found. The importance of these “fat tails” in the size
76 frequency distribution of feeding sources may be underestimated by averaging their size
77 accross seasons or areas. The same argument applies to the size of animal groups, which
78 has been found to vary, within a single species, according to power laws with “fat tails”
79 (Bonabeau et al. 1999; Sjöberg et al. 2000; Lusseau et al. 2004).

80

81 What is required is a null model of social grouping that predicts the way in which subgroup
82 size will vary when confronted with a realistic foraging environment. In such a model,
83 agents would not interact through any social rules; rather, various agents may coincide at
84 the same food patch, forming a group until they split as a consequence of the individual
85 foraging trajectories. In a recent workshop on fission-fusion societies (Aureli et al. in
86 preparation), DiFiore et al. (in preparation) proposed the use of agent-based models in
87 which simple foragers and their emerging grouping patterns could be analyzed as a function
88 of realistic environmental variation. This approach could allow behavioral ecologists to
89 determine what would be the minimum conditions leading to variable grouping patterns and
90 even non-random association patterns, simply as a consequence of the way in which
91 animals forage in variable environments (DiFiore et al. in preparation).

92

93 In a spatially explicit model we developed recently (Boyer et al. in press), we showed that
94 the complex foraging trajectories described by spider monkeys (Ramos-Fernández et al.
95 2004) could be the result of the distribution and abundance of food patches of varying size.
96 In the model, a parameter defines the decay of the tree size frequency distribution and a
97 single forager visits trees according to a least effort rule (minimizing the distance traveled
98 and maximizing the size of the next patch). We found that complex foraging trajectories,
99 similar in many aspects to those described by spider monkeys in the wild, emerged only at
100 intermediate values of this parameter, that is, when large trees are neither too scarce nor too
101 abundant (Boyer et al. in press). In the present paper we build on the same model,
102 introducing several foragers into the same environment. We measure the tendency of these
103 foragers to form groups and analyze their association patterns. Our purpose is not to test
104 predictions of socioecological theory, but rather to develop a null model of the grouping
105 and association patterns that should be expected to occur in a realistic foraging
106 environment. We take advantage of the fact that this kind of model allows the manipulation
107 of environmental variables, such as the relative abundance of feeding patches of different
108 size, using only one parameter. We compare the results of the model with field data from
109 spider monkeys.

110

111 **METHODS**

112

113 **Model**

114 We modelled the foraging environment as a two-dimensional square domain of area set to
115 unity for convenience, and uniformly filled with 50,000 points (or targets) randomly
116 distributed in space. These represent fruit-bearing trees. To each target i we assigned a

117 random integer $k_i \geq 1$ representing its fruit content. All targets did not have the same fruit
118 content a priori. At the beginning of the simulations, we set the fruit content of each tree to
119 a random initial value $k_i^{(0)} \geq 1$, drawn from a normalized, inverse power-law probability
120 distribution

121

$$122 \quad p(k) = Ck^{-\beta}, \quad C = 1 / \sum_{k=1}^{\infty} k^{-\beta} \quad (1)$$

123

124 where β is a fixed exponent characterizing the environment, being the main parameter in
125 the model. If β is close to 1, the range of sizes among the population is very broad, with
126 targets of essentially all sizes. In contrast, when $\beta \gg 1$, practically all targets have the same
127 fruit content and the probability to find richer ones ($k_i^{(0)} = 2, 3 \dots$) is negligible.

128

129 This environment can be assumed to accurately represent a typical spider monkey habitat,
130 where fruit content is known to be linearly dependent upon tree size (Chapman et al. 1992;
131 Stevenson et al. 1998), which in turn has been shown to vary according to an inverse
132 power-law of the type of Eq. (1) in different tropical forests (Enquist et al. 1999). Exponent
133 values measured in most forest types are in the range $1.5 < \beta < 4$ (Enquist and Niklas 2001,
134 Niklas et al. 2003), while a typical spider monkey habitat in the Yucatan peninsula,
135 Mexico, had a value of 2.6 (Boyer et al. in press). The number of trees was set according to
136 the fruit tree densities in a typical spider monkey habitat (Ramos-Fernández and Ayala-
137 Orozco 2003), which, depending on the species, lie between 3 and 300 trees per hectare
138 (i.e. between 600 and 60,000 trees in a 200 hectare home range). The highest end of the
139 range for the number of trees in a typical spider monkey habitat was chosen in order to

140 obtain a wide range of variation in fruit content, similar to what monkeys would face when
141 feeding on several species on a single day (Stevenson et al. 1998).
142
143 In this environment, we placed 100 foragers at different locations. These foragers represent
144 spider monkeys or chimpanzees that forage for fruits among the existing trees. We chose
145 100 as it is close to what has been reported for spider monkey and chimpanzee community
146 size (Goodall 1968; Symington 1990). Each forager was initially located at a randomly
147 chosen target and moved according to the following rules: (a) the forager located at the tree
148 number i next moved to a tree j such that the quantity $l_{ij} / k_j^{(0)}$ was minimal among all
149 available tree $j \neq i$, where l_{ij} is the distance separating the two trees and $k_j^{(0)}$ is the
150 initial fruit content of tree j ; (b) the forager did not choose a tree that it had already visited
151 in the past. Thus, valuable trees (large k) could be chosen even if they were not the nearest
152 to the foragers' position, as schematically illustrated in Fig. 1a. The ratio l / k roughly
153 represents a cost/gain ratio. Rule (b) was set according to the typical foraging trajectories of
154 spider monkeys and other primates, who seldom retrace their own steps but rather visit a
155 large number of distinct feeding sources before returning to a previously visited one
156 (Milton 2000; Ramos-Fernández et al. 2004). In the model, time is discrete: during one
157 time iteration (from t to $t+1$), a forager ate one unit of fruit of the tree it was located at. As
158 several foragers could coincide at a given tree, at each iteration, the fruit content k_i of a tree
159 i decreased by 1 for each forager present on that tree. When the fruit content of the
160 occupied tree reached zero, the forager(s) moved in one time unit to the next tree according
161 to rules (a) and (b) above.
162

163 We used two different assumptions about the degree of knowledge that foragers had about
164 the location and initial fruit content of trees. In the complete knowledge situation, foragers
165 had perfect knowledge of the location of all trees and their initial fruit content, such that
166 their choice, at every new move, was to visit the tree at which the ratio $l/k^{(0)}$ was minimum
167 among all possible trees. In the partial knowledge situation, foragers only knew a random
168 half of all possible trees (each forager knowing a different subset of trees). Thus, in the
169 latter situation a forager could move in such a way that the ratio $l/k^{(0)}$ was not minimal
170 among all the possible trees in the environment. Also, in both the complete and partial
171 knowledge situations, due to the fact that a given forager only knew the initial size of
172 targets not yet visited, it could visit targets that had already been depleted by other foragers
173 (with a lower k than expected). As explained above, when reaching an empty tree, the
174 forager abandoned the tree in the next iteration. More details about the numerical
175 procedures used to implement this model are presented in Boyer (2006).

176

177 Since each forager was unaware of the sequence of trees visited by others, a consequence of
178 rule (b) above is that two foragers (A and B) meeting at a tree could split later on. This
179 happened, for instance, when B had previously visited a target that A had not yet visited,
180 but which A considered to be the next best target (Fig. 1b).

181

182 For each value of β and degree of forager knowledge, we ran a total of 50 different
183 simulations in which trees and forager starting locations were randomly distributed in
184 space. Each run consisted of 100 time iterations in which foragers either made a move to
185 another tree or decreased the value k of their current tree by 1.

186

187 **Analysis**

188 Given that our purpose was to evaluate subgroup formation by foragers and to compare this
189 situation with what happens in real animals, we analyzed the resulting data sets in the same
190 way as we would analyze field observations, particularly with regard to the following
191 aspects:

192

193 *Subgroup size* was quantified by counting the number of times a forager was seen either
194 alone or with different numbers of other foragers. The frequency distribution of subgroup
195 size was obtained for different values of the resource parameter β and different degrees of
196 forager knowledge, averaging over 50 independent runs and over all foragers. The average
197 subgroup size refers to the average number of foragers with whom all 100 foragers were
198 observed.

199

200 *Subgroup duration* was quantified by the average number of iterations that subgroups of a
201 particular size lasted, averaged over 50 independent runs under various combinations of β
202 and degree of forager knowledge.

203

204 *Relative affinity* was evaluated as the variance in the time each forager spent with each of
205 the other foragers in the group. A high relative affinity implies that foragers were selective
206 in their associations, limiting them mostly to a subset among all individuals they met, while
207 a small relative affinity implies that all possible associations were more or less likely. For
208 each forager x , we determined who it met (i.e. coincided at least once at the same tree) and
209 for how long during the run. For all possible pairs, we computed an affinity $A_{x,y}$, defined as

210 the amount of time units (not necessarily consecutive) that foragers x and y were together.
211 For each forager x , we averaged $A_{x,y}$ and computed its variance over all the distinct y 's met
212 by forager x . Dividing the variance of $A_{x,y}$ over its average, we obtained a non-dimensional
213 number, lower than unity, that refers to the relative affinity of forager x with others: if close
214 to 0, then x was "democratic" (i.e. it spent exactly the same amount of time with all
215 foragers it met). If close to 1, forager x was "selective": it spent a lot of time with a few
216 others, and a short time with most of the others it met. We then averaged this quantity over
217 all independent runs and over all foragers, for a given combination of β and degree of
218 forager knowledge. In order to compare this average relative affinity with what would be
219 expected if encounters were at random, we obtained the same quantity for a randomized
220 data set in which each forager x met the same number of distinct individuals y , and where
221 the same total number of encounters made by x was distributed randomly among these y 's
222 (for details on this randomization technique, see Whitehead 1999).

223

224 *Total bonds* refer to the number of distinct foragers met by a forager during a run. We
225 obtained the average of this number, over all foragers and all independent runs, for various
226 combinations of β and degree of forager knowledge.

227

228 *Strong bonds* refer to that subset of the total bonds that are more frequent than what would
229 be expected from random and independent encounters. Therefore, it represents the number
230 of "close associates" a forager had (Whitehead 1999). We determined, for a forager x , who
231 it met during the run (foragers $y_1, y_2\dots$), and for how long ($A_{x,y_1}, A_{x,y_2}\dots$). Then we calculated
232 L_x , the total number of meetings for forager x (the sum over all A_{x,y_1}, A_{x,y_2}). In parallel, we

233 calculated the probability $P(w)$ that, among the total number L_x of meetings, forager x had
234 w meetings with the same individual if associations were at random. This was done
235 analytically as follows: a number L_x of bonds was drawn sequentially, from forager x
236 toward a randomly chosen forager included in its total bonds. Since L_x and the total number
237 of bonds are known from the simulation, we could compute $P(w)$ for these values. From
238 this probability distribution we found the value w_c such that $P(w > w_c) < 0.05$. The values w
239 $> w_c$ are therefore very unlikely for random and independent meeting events. Strong bonds
240 from forager x to others were defined as those in which $A_{x,y} > w_c$. We obtained the average
241 number of strong bonds over all independent runs, for various combinations of β and
242 degree of forager knowledge.

243

244 *Weak bonds* refer to the total bonds that are not strong bonds.

245

246 *Clustering coefficients* for the networks formed by strongly bonded individuals refer to the
247 probability that, if forager A has a strong bond with B and C, the latter are also strongly
248 bonded among them (Newman 2000). Clustering measures the degree of transitivity in the
249 social bonds of a network (or its degree of "cliquishness"). Let r_x denote the number of
250 strong bonds that forager x has. Given the way in which we defined the strong bonds
251 among foragers, the resulting network is not reciprocal *a priori*, but directed: a link going
252 from x to y , or out of x , does not imply that there is a link from y to x ; in other words, y may
253 be important for x , but x may not be for y . The clustering coefficient C_x is the ratio between
254 the number of connections linking neighbors of x to each other and the maximum value,
255 $r_x*(r_x-1)$, that this number can take (Newman 2000). Thus, a C_x value of 0 means that any
256 pair of foragers with which forager x is strongly bonded are themselves not strongly

257 bonded. Conversely, a C_x value of 1 means that all the foragers strongly bonded to x are
258 also strongly bonded with each other. The clustering coefficient C of the network was
259 obtained by averaging C_x over all foragers that had more than one strong bond and over the
260 social networks obtained in the 50 independent runs, for each value of β and degree of
261 forager knowledge.

262

263 *Relative size of the largest cluster* of a network refers to the number of individual foragers
264 belonging to the largest cluster of the network divided by the total number of foragers. This
265 is a measure of the cohesion of a network (Newman et al. 2002). A cluster is defined as an
266 isolated part of the network, i.e. with no connections to other parts, that is itself not
267 composed of various smaller isolated parts. Thus, any pair of nodes belonging to a cluster
268 can be joined by at least one succession of bonds running through the cluster. Similarly, we
269 define the *average cluster size* of a network as the number of individuals that do not belong
270 to the largest cluster, divided by the number of clusters in the network (not counting the
271 largest one). Both the relative size of the largest cluster and that of the average cluster were
272 averaged for the 50 networks obtained in the independent runs, for each value of β and
273 degree of forager knowledge. A network is said to *percolate* if the largest cluster contains a
274 substantial fraction of the total number of nodes (see Newman et al. [2002] for a discussion
275 in the context of social networks). When a network percolates, the size of the largest cluster
276 (also called the giant cluster) is much larger than the average cluster size. We have
277 performed the cluster analysis separately for the networks formed by the two types of
278 bonds: i) total bonds, ii) strong bonds (see above).

279

280 It is important to note that, due to the high number of independent runs over which
281 averages were calculated in each of the above analyses, standard errors were small (2-10%
282 of the average value). Therefore, for clarity, results are shown without error bars.

283

284 **RESULTS**

285

286 **Subgroup size**

287 Figure 2a shows the normalized frequency distribution of subgroup size obtained in the
288 model for various values of β and, for comparison, the values observed in a long-term study
289 of two groups of spider monkeys (Ramos-Fernández and Ayala-Orozco 2003). Even though
290 the majority of time foragers were alone, there is a clear effect of varying β upon the size of
291 formed subgroups. Particularly for values of β between 2 and 4, the size of formed
292 subgroups is sensibly larger than for the other values of β . When $\beta = 2.5$ and $\beta = 3$, the
293 decay rate of the frequency distribution for subgroups in the model became
294 indistinguishable from that of the real spider monkeys. Here, foragers could form
295 subgroups of up to 17 individuals, although at a very low frequency. These values of β are
296 close to the observed values in different forest types (Enquist and Niklas 2001), including
297 one close to the study site where the data in Figure 2a come from, where a value of 2.6 was
298 found (Boyer et al. in press).

299

300 Figure 2b shows the same data for the situation in which foragers had a partial knowledge
301 of the location of feeding sites. As it can be seen, foragers formed smaller subgroups and

302 the effect of varying β upon the size frequency distribution was less marked than in the
303 situation with perfect knowledge.

304

305 The above can be seen more clearly when examining the way in which the average size of
306 subgroups varied as a function of β , with full or partial knowledge of the location of
307 feeding sites (Figure 2c). As can be observed, only in the full knowledge situation was
308 there an increase in subgroup size at intermediate values of β , particularly at 2.5 and 3. That
309 is, when foragers knew the location of all feeding sites, they formed the largest subgroups
310 in an environment where large patches of food were neither too scarce nor too abundant
311 compared to small patches.

312

313 **Subgroup duration**

314 Another way to analyze subgroup formation is by noting the time (in number of iterations)
315 that associations lasted. As shown in Figure 3a, larger subgroups lasted less than smaller
316 ones. For clarity, the graph shows subgroup size variation for only three values of β and the
317 full knowledge situation. Subgroups of up to 3 foragers tend to last longer for $\beta=2$ than for
318 other values of β . Focusing only on the most frequent type of association, Figure 3b shows
319 the duration of subgroups of size 2 only, averaged over 50 independent runs as a function
320 of β and for both knowledge situations. As β increased, associations were of shorter
321 duration, although there was an intermediate range of values of β that had little effect on
322 the average duration of pairs, particularly in the full knowledge situation. When foragers
323 had only a partial knowledge of the location of feeding trees, pairs tended to last a shorter
324 time, although this effect was more pronounced for values of β higher than 2. At $\beta=2$, large

325 trees were relatively common and foragers stayed there for times that approximated half of
326 the duration of the run, regardless of whether they had full or partial knowledge.
327 Conversely, at $\beta= 4.5$, when there was a very small proportion of large feeding sites,
328 foragers stayed a short amount of time at each one and visited a large number of different
329 sites. In this situation, associations were of shorter duration.

330

331 **Preferential association**

332 In order to explore whether subgroups in the model were being formed by foragers at
333 random, we calculated the relative affinity among foragers as the variance in the time they
334 spent with different individuals. A high relative affinity implies that foragers were selective
335 in their associations, limiting them mostly to a subset of all the individuals they met,
336 whereas a small relative affinity implies that all the observed associations were more or less
337 likely. We were interested in observing the effect of varying β upon the tendency to form
338 preferential associations. However, the fact that foragers formed larger subgroups at
339 particular values of β , implied that preferential associations could arise simply by chance.
340 Thus, we calculated the expected relative affinities if associations occurred by chance, for
341 each value of β .

342

343 Figure 4a shows the relative affinities expected randomly and those observed in the model,
344 for different values of β , when foragers had full knowledge. At all values of β , relative
345 affinities were higher than what would be expected if associations occurred by chance. The
346 largest departures from random expectation occurred at intermediate values of β . Figure 4b
347 shows the same data for the situation in which foragers had only partial knowledge of

348 feeding sites. As before, relative affinities were higher than it would be expected by chance,
349 but the difference is not so large as in the situation with perfect knowledge, particularly at
350 high values of β .

351

352 **Network properties**

353 The relative affinities described above imply that, of all associations formed by a forager,
354 some are more likely than would be expected by chance. In order to explore this skew in
355 relative affinity in more detail, we calculated the total number of individuals met by each
356 forager and, among these, determined who were the individuals that the forager met more
357 often than would be expected purely by chance (strong bonds). Figure 5a shows the average
358 number of bonds per forager as a function of β . As mentioned above, there was a clear
359 effect of subgroup size upon the total number of bonds: there were more associations at
360 intermediate values of β , particularly for $\beta = 2.5$ and 3, when the largest subgroups were
361 formed (see Figure 2). Similarly, there was a clear effect of β upon the number of strong
362 bonds, with the maximum number of strong bonds observed at $\beta = 2.5$. Figure 5b shows the
363 same data for the partial knowledge situation. The effect of varying β was the same, upon
364 the total number as well as the number of strong bonds.

365

366 Once we identified the strong bonds, it was possible to analyze the resulting social network
367 and calculate the probability that if forager A had a strong bond with B and C, B and C also
368 formed a strong bond between them (i.e. that there is transitivity in triadic relationships).
369 This is the clustering coefficient of the social network (Newman 2000) and it varies from 0
370 to 1. Figure 5c shows the average clustering coefficients in the model as a function of β , for

371 both knowledge situations. At low values of β , social networks had a high clustering
372 coefficient in both the full and partial knowledge situations. However, as β increased, the
373 clustering coefficients in the partial knowledge case fell sharply, while they remained high
374 in the full knowledge case, up to $\beta = 4.5$, when they also decreased sharply.

375

376 **Percolation of the network**

377 Another structural aspect of the social networks that emerge in our model is the size of the
378 largest cluster of linked foragers. If this cluster is much larger than the average cluster size
379 (i.e. there is a “giant cluster”), a network is said to percolate. In a percolating social
380 network, there is a high probability that any two individuals can be linked through other
381 individuals that are themselves linked. The opposite of a percolating network is a
382 fragmented one, in which there are many isolated clusters of individuals that never meet
383 except amongst each other. Figure 5d shows the relative average size of the largest cluster
384 formed by individuals who met at least once during the run (total bonds) or by only those
385 individuals who met more often than expected by chance (strong bonds). A giant cluster is
386 formed by the network of the total bonds at intermediate values of β . In the case of full
387 knowledge and $\beta = 2.5$, the giant cluster contains about 20% of the foragers. The fact that
388 these clusters are indeed the “giant clusters” is shown by the fact that the average size of
389 the other clusters in the same network (data not shown) is much smaller, about 3.4
390 individuals. At both low and large values of β , no such percolation phenomenon is
391 observed: the largest cluster size and the average cluster size are similar (2.8 and 1.1,
392 respectively, for $\beta = 4.5$; 5.9 and 1.4 for $\beta = 2.0$). For the partial knowledge situation,
393 despite the fact that it generates a smaller number of bonds per individual (Figure 5b), a

394 giant cluster appears which is much larger: at $\beta=2.5$ it rises to 57% of the foragers. This
395 suggests that the total bonds are formed in a more random way when the knowledge is
396 limited, enabling easier connections between different parts of the network.

397

398 The network of the strong bonds exhibits fairly different properties than the network of
399 total bonds at intermediate values of β . The clusters of strong bonds are smaller in size and
400 no clear percolation property is observed at any value of β . The size of the largest cluster
401 contains at most 7% of the foragers ($\beta=2.5$), a value not much larger than the average size
402 of the other clusters in the same network (1.9 foragers). These values do not vary much
403 with the degree of forager knowledge. These results indicate that individuals linked by
404 strong bonds always form rather isolated structures. This property is consistent with the
405 high values of the corresponding clustering coefficients (Figure 5c). If the total bonds are
406 considered (which means adding all those bonds that are not strong, i.e. the weak bonds),
407 the resulting network percolates at intermediate values of β , with clusters of strong bonds
408 connected to each other via weak bonds. This situation is evident in Figure 6, which shows
409 one of the networks that resulted at $\beta=2.5$ in a simulation with full knowledge. The weak
410 bonds thus play an important role in the cohesion of the network when it is percolating.

411

412 **DISCUSSION**

413

414 We have developed a simple foraging model that contains no algorithm specifying how
415 foragers should interact. Our model focuses on the heterogeneity and structural complexity
416 of the environment, summarized by the main parameter in the model, β . Despite its
417 simplicity, the behavior generated by our model is quite rich (summarized in Table 1):

418 subgroups that vary their size in time are formed by foragers in response to the distribution
419 and size of feeding targets; their size frequency distribution varies in response to β , being
420 larger and more variable at intermediate values of this parameter, that is, when variation in
421 tree size is intermediate, large targets being neither too scarce nor too abundant compared
422 to small targets. Pairwise associations among foragers last longer at low values of β , when
423 large targets are very common, but in these conditions the average size of subgroups is not
424 the largest. In addition, there is little preferential association and few pairwise bonds that
425 are more likely than random. It is at intermediate values of β that we observe the largest
426 subgroups and where preferential associations arise. Foragers in these condition show many
427 strong bonds and the social network formed by these strong bonds has a high clustering
428 coefficient, a measure of the transitivity in the social bonds of the network (or the tendency
429 of of foragers to form “clusters” or “cliques”). The weak bonds in that same network, on
430 the other hand, connect different parts of the network, enabling it to percolate. At high
431 values of β , when most targets are small, foragers group in smaller units with a short
432 duration and their association patterns do not show as much preference as with other values
433 of β . The social network in that situation does not percolate. Still, the foragers show a few
434 strong bonds and the social network is moderately clustered at the local level.

435

436 Networks with properties similar to the ones described above have also been obtained in a
437 model of mobile agents following stochastic trajectories and colliding with each other
438 (González et al. 2006). In this study, though, the network structure does not arise from the
439 complexity of the medium, which is uniform, but from particular kinetic rules for the
440 agents.

441

442 In our model, foragers are able to decide which target to visit among several thousands of
443 possible targets, representing the trees in a tropical forest that contain fruit at any given
444 time. Even though a mental map of sorts can safely be assumed to exist in primate species
445 (Janson 1998; Garber 2000), a full knowledge on the location and size of all possible
446 targets is a strong assumption of our model. For this reason, we ran simulations in which
447 foragers only knew a random half of the targets in the environment. The net effect of this
448 “error” in the selection of the best target is that foragers form smaller subgroups, with less
449 strong bonds and, consequently, a social network that is less clustered. However, even in
450 the partial knowledge situation, there is a strong effect of intermediate values of β upon the
451 tendency of foragers to be in subgroups and to associate preferentially with others.

452

453 As stated in the Introduction, our purpose in developing this model was not to test existing
454 hypotheses about how resources affect subgroup formation in fission-fusion societies, but
455 to develop new predictions using numerical simulations, which can represent a complex
456 environment better than simple conceptual models. The prevailing model on subgroup size
457 and food resources in both chimpanzees and spider monkeys proposes that subgroups result
458 from the interacting effects of the size and distribution of feeding patches (Symington
459 1988; Chapman et al. 1995). Large patches would feed more individuals than small patches,
460 and the overall density of food patches would provide more opportunities for either a)
461 traveling in large subgroups, as they would find food for all; b) dispersing in smaller
462 subgroups as there would be no need to concentrate on a single patch. Depending on the
463 assumptions made about predation pressure or other advantages of being in groups, the

464 prediction on the effect of food density can be posed in both ways: larger or smaller
465 subgroups in a high density of resources.

466

467 The study by Chapman et al. (1995) is an explicit test of these predictions. This study finds
468 that a portion of the variance in subgroup size in spider monkeys (50%) and chimpanzees
469 (30%) can indeed be explained by the overall density of food (the sum of the diameter at
470 breast height or DBH of all available trees per hectare) and the distribution of food patches
471 (variation in the number of fruiting trees per unit area). As density increases, subgroups
472 tend to be larger. Also, when patches are farther apart from each other, subgroups tend to
473 be smaller (Chapman et al. 1995). In another study, Newton-Fisher et al. (2000) found no
474 correlation between subgroup size and food abundance in a chimpanzee group with a
475 seemingly hyper abundant resource base. The authors of this study suggested that the
476 relationship between food abundance and subgroup size is not linear, but curvilinear, such
477 that “other factors” (Newton-Fisher et al. 2000, pp. 625) control the size of chimpanzee
478 subgroups at high levels of food. In both studies, the authors attribute the weak correlations
479 or the lack thereof to differences in how feeding competition affects age/sex classes
480 (Chapman et al. 1995; Newton-Fisher et al. 2000).

481

482 Instead of developing *post-hoc* explanations, which eventually prevent the integration of
483 social and ecological factors in the same model (Di Fiore et al. in preparation), it may be
484 necessary to review the initial prediction of how food should affect grouping patterns. It is
485 unlikely that, at any given time, spider monkeys or chimpanzees will find all patches to be
486 small or to be widely spaced from each other. Most tropical tree species show clumped
487 patterns in their distributions (Condit et al. 2000), and this pattern is highly dependent on

488 scale, appearing uniform at small scales, clumped at intermediate scales and random (or
489 Gaussian) at very large scales (Pélissier 1998). Also, the overall variation in tree size is best
490 described by an inverse power-law (Enquist and Niklas 2001) and not by a Gaussian
491 distribution. These important fluctuations imply that the mean may not be the best statistic
492 to describe tree size. Moreover, both chimpanzees and spider monkeys may feed on several
493 different species within a single day, let alone over periods of months or years (van
494 Roosmalen and Klein 1987; Wrangham et al. 1996). Finally, the phenology of tropical trees
495 is highly complex (Newstrom et al. 1994), with annual, sub-annual and supra-annual
496 patterns all being relatively common (Bawa et al. 2003). These conditions result in a highly
497 variable resource base, both temporally and spatially, which can hardly be captured by
498 average temporal tendencies or overall spatial indices (Di Fiore et al. in preparation).

499

500 In our model, we use the variation in tree size as the independent variable, that is, tree size
501 always varies but the parameter β specifies exactly how this variation occurs. This
502 parameter modifies the inverse power-law frequency distribution in Eq. (1). Tree-size
503 distributions based on measurements of DBH are commonly characterized by exponents
504 with values between 1.5 and 4 (Enquist and Niklas 2001), a range compatible with the
505 values of β that we considered in our model and with empirical measurements of β in a
506 typical spider monkey habitat (Boyer et al. in press).

507

508 In a previous version of our model (Boyer et al. in press), we explored the effect of tree size
509 variation upon the movement trajectories of a single forager. We found that the longest and
510 most variable movement trajectories, similar to those described by spider monkeys in the

511 wild (Ramos-Fernández et al. 2004), appear at intermediate values of β . This situation is
512 when the variance in the length of sojourns (or walks) given in the same direction is largest.
513 This results from the foraging rule that the model introduces: when large trees are
514 intermediate in their relative abundance, trajectories are composed of a series of short
515 sojourns to visit mostly small trees, but every so often a large tree that is far away is worth
516 the trip, so the forager takes a long sojourn to reach it. Conversely, when there are many
517 large trees (small β) or when most are small (large β), the forager performs more regular
518 trajectories composed of sojourns of similar length.

519

520 A similar pattern appears in the present version of the model in which the only change is
521 the introduction of many foragers that move according to the same rules. It is only at
522 intermediate values of β that foragers move in steps of variable size, often concentrating on
523 small trees within a subregion but also traveling to large trees that are far away (data not
524 shown). This explains why the largest subgroups are found at these values of β : foragers
525 tend to consider rare, large trees as valuable and so they tend to coincide in them and, due
526 to their size, to spend long periods of time in them. When β is small, foragers stay in the
527 very common large trees, while at higher values of β , there are too few large trees and so
528 foragers only spend small amounts of time in smaller trees that are close by. In both of
529 these situations, they meet others rarely.

530

531 It is possible that, rather than the overall amount of food in the habitat of chimpanzees and
532 spider monkeys, it is the relative importance of large trees when they neither too scarce nor
533 too common that creates the conditions for large feeding aggregations to appear. Symington

534 (1988) reported a nonlinear relationship (a second order polynomial) between patch density
535 and the size of spider monkey feeding parties, which were larger at intermediate food patch
536 densities. A similar result, but in another context, was obtained by Wilson and Richards
537 (2000), who modelled a resource-consumer interaction in a spatially explicit environment.
538 The authors found that, in the absence of rules by which consumers should interact,
539 intermediate consumer densities (with a constant resource base) led to the formation of
540 groups. The authors cite several other empirical examples where this occurs.

541

542 Our model simply presents the minimum conditions that could lead to a variable grouping
543 pattern in a complex environment. It is clear that in real animals with fission-fusion
544 societies, differences among age/sex classes in their reliance on food resources as well as
545 their social strategies must play an important role in determining grouping and association
546 patterns. However, upon close analysis of the composition of subgroups arising in the
547 model, we found that, even when our model does not introduce any rule for their interaction
548 or differences in their foraging strategies, foragers associate in nonrandom ways. For
549 particular values of β , with full and partial knowledge, we find that foragers associate
550 preferentially with certain others. This could simply be due to the fact that foragers are
551 limited to particular regions of the environment, meeting only with those with whom, by
552 chance, they share a common area. However, when taking only into account those
553 individuals with whom an individual met at least once, there is still preference for some
554 particular ones (Figures 4 and 5). Thus, we can conclude that this finding is not an artifact
555 of the use of certain areas.

556

557 Preferential associations arise especially at intermediate values of β . The description of the
558 foraging patterns can explain this: at low values of β , when there are many large trees,
559 foragers only associate with those with whom they coincide upon reaching their first,
560 common large tree. In a sense, this situation easily becomes “frozen,” as foragers spend a
561 large amount of time in each tree and there are many large trees in the environment.
562 Conversely, at high values of β , associations last only short periods of time as they always
563 occur in small trees. At intermediate values of β , when large trees are neither scarce nor
564 common, foragers coincide with, and spend more time with, a larger subset of the available
565 foragers. In addition, if this occurs at the beginning of the run, they may stay together for
566 the whole run, as they would stay together throughout their subsequent foraging choices. At
567 intermediate values of β , the fruit content of trees visited by a forager fluctuates widely
568 (Boyer et al. in press), a fact that may explain why the time spent by the forager with other
569 individuals (as measured by the affinity) also fluctuates so much. For these values of β , the
570 foragers are also the most mobile, moving further away from their starting point (Boyer et
571 al. in press). Therefore, it seems that the combination of two factors generates preferential
572 association in our model: on the one hand, some heterogeneity in patch size, and on the
573 other hand, relatively high forager mobility, allowing a large number of encounters.

574

575 The values of relative affinities we find in the model are comparable to those calculated
576 from association matrices of two groups of spider monkeys by Ramos-Fernández (2001),
577 using the same definition as in the present study. One group, with 9 adult individuals, had
578 an average value of 0.21 ± 0.07 S.D. Another group, with 23 adults, had an average value
579 of 0.59 ± 0.14 S.D. (Ramos-Fernández, unpublished data). Similarly, wild spider monkeys

580 associate at detectable rates with the majority of the adults in their group (equivalent to the
581 total bonds shown in Figure 5), but only 7-10 % of those associations are higher than it
582 would be expected by chance (equivalent to the strong bonds in Figure 5; Ramos-
583 Fernández 2001). Similar trends were found in chimpanzees by Pepper et al. (1999).

584

585 These results demonstrate that selective, nonrandom associations among animals (as
586 defined by proximity) can arise simply from the way in which they forage and not
587 necessarily as a result of their social relationships. We do not mean to imply that sex/age
588 classes or social relationships are not important determinants of grouping patterns in social
589 animals, but we find that nonrandom associations can emerge from the way in which
590 foragers move in a complex environment. After all, social relationships in gregarious
591 animals cannot have developed in an ecological vacuum: they must have developed within
592 the existing grouping patterns that ecological conditions imposed.

593

594 A final aspect we explored was the structure of the social network formed by those foragers
595 that were strongly bonded (i.e. those that associated more frequently than it would be
596 expected by chance among all pairs that actually formed). This type of analysis of social
597 networks has recently been applied to the social networks of dolphins, another species with
598 a fission-fusion society (Lusseau 2003). One of the properties that defines the structure of a
599 social network is its clustering coefficient, or the probability that if A is closely bonded
600 with individuals B and C, the latter two are closely bonded too. This measure of the
601 “cliquishness” of the social network formed by the foragers in our model is strikingly high.
602 Social networks in wild spider monkeys have clustering coefficients between 0.26 and 0.30
603 (Ramos-Fernández, unpublished data), while the dolphin social network studied by Lusseau

604 (2003) had a clustering coefficient of 0.303. In our model, the fact that clustering
605 coefficients are close to 1 for most values of β , only in the full knowledge situation, may be
606 a key to interpreting this result: when foragers coincide early in the run at a given tree, they
607 will remain together for the remain of the run, which produces a large degree of selectivity
608 and repeated associations among a few individuals. When foragers only know a random
609 subset of all available trees, it is practically impossible that they will remain together for the
610 whole run, as some trees will be known only by some but not all the foragers that may have
611 coincided in a large tree at the beginning of a run.

612

613 Another property that characterizes the structure of a network is percolation, i.e. the
614 possible existence of a “giant cluster” of individuals that can be linked through individuals
615 that are themselves linked. The opposite of a percolating network is a fragmented one, in
616 which there are many isolated clusters of individuals that never meet except amongst each
617 other. The percolating properties of social networks of animals have received recent
618 interest. The dolphin societies studied by Lusseau and Newman (2004) are formed of
619 clustered sub-communities that are linked to each other by a few “broker” individuals. Two
620 sub-communities were observed to interact very little while one of the brokers disappeared
621 temporarily during the study (Lusseau and Newman 2004). These individuals are located at
622 the periphery of the sub-communities but maintain the cohesion between them. Similarly, a
623 typical social network emerging from our model includes relatively small clusters of
624 strongly linked individuals. If the weak bonds are removed, the network formed by the
625 strong bonds does not percolate. The network of the total bonds, however, does percolate at
626 intermediate values of β , showing the importance of the weak bonds on its cohesion. In a
627 different context, this so-called “strength of weak ties”, has been long recognized to

628 mediate interactions between agents belonging to different communities in human social
629 networks (Granovetter 1973, 1983). In the case of animal fission-fusion societies, an
630 intriguing aspect has been the fact that social relationships can be maintained in such a
631 loose aggregation pattern (Kummer 1968; Smolker 2000; Ramos-Fernández 2005). While a
632 percolating property based on a combination of strong and weak bonds has only been
633 demonstrated in dolphins (Lusseau 2003), it remains to be determined whether the social
634 networks of other species with fission-fusion societies also contain these structural
635 properties. Our model points out at a mechanism by which these properties could emerge,
636 simply out of the way in which animals forage in a complex environment.

637

638 Our model contrasts with that of te Boekhorst and Hogeweg (1994), who developed an
639 agent-based model of a fission-fusion society in order to explain the differences in grouping
640 tendencies between males and females. Even though the authors do not specify how trees in
641 their model vary in size or how they are distributed in space, the model by te Boekhorst and
642 Hogeweg (1994) contains rules by which foragers interact, that follow from the different
643 behavioral strategies that both sexes should pursue, as proposed by Trivers (1972). As such,
644 this model is not informative of the minimum conditions required for a variable grouping
645 pattern to appear. Another modelling approach, aimed at understanding the emergence of
646 social structure, has been taken by Hemelrijk (2000). She has modelled the emergence of
647 dominance relationships as a consequence of the spatial distribution of individuals. Her
648 models also incorporate rules by which individuals form groups, interact and modify their
649 future social behavior according to these interactions. Both of the above examples of agent-
650 based models are aimed at understanding the emergence of particular social relationships
651 and structure. Thus, they incorporate differences among agents and rules by which they

652 interact. Our model, in turn, does not make any assumption about the tendency to form
653 groups or search each other. Rather, it is a spatially explicit depiction of agents foraging in
654 a complex environment, as a result of which they form subgroups. As such, the results of
655 our model should be used as a starting point to make more elaborated predictions about the
656 relationships we should find between subgroups and their environment in fission-fusion
657 societies.

658

659 Our results lead us to propose the following predictions for field studies of fission-fusion
660 social systems:

661

- 662 1) The relative abundances of small vs. large food patches should be better predictors of
663 subgroup size than average food patch size, average food density or degree of
664 clumpness.
- 665 2) Large patches may induce large subgroups that last for long periods of time, but due to
666 the relative importance of large patches, an intermediate level of variation in patch size
667 could induce the largest subgroups (albeit with a shorter duration). Therefore, we
668 should observe large subgroups forming at large and infrequent patches and not in large
669 and common ones.
- 670 3) Long trajectories could result from the relative importance of large patches. Therefore,
671 we should observe these types of trajectories more frequently when food is found in less
672 dense but very large patches. The resulting high mobility of foragers should enhance the
673 frequency of encounters.

674 4) The social networks of fission-fusion species should be composed of several clusters of
675 closely associated individuals that, in turn, are linked by looser relationships that
676 nevertheless allow most individuals to remain within a single social network.

677

678 In conclusion, we have explored the minimum conditions that could lead to complex
679 grouping and association patterns using an agent-based model that includes a spatially
680 explicit representation of environmental variation. An intermediate degree of variation in
681 the size of feeding patches can lead to larger feeding aggregations and more opportunities
682 for social interactions to develop among foragers. Studies on the evolution of animal social
683 relationships in complex environments must take these constraints into consideration.

684

685

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840 **FIGURE LEGENDS**

841

842 Figure 1. (a) Trajectory map for a single forager. The size of targets represents their k
843 value or fruit content. A forager starting at the target on the far right will go directly to the
844 largest target, ignoring other smaller targets that were at shorter distances. (b) Trajectory
845 map for several foragers. An additional forager to the one shown in Figure 1a (dotted lines),
846 which started at the target on the far left would meet the first forager at the largest target
847 (thus producing a fusion) and would stay with it, visiting the same targets until their history
848 of previous visits would split them apart: the first forager would visit the target where the
849 second forager departed, but the second would not visit this same target twice.

850

851 Figure 2. (a) Frequency distribution of subgroups of different size, for different values of β
852 and under the full knowledge situation. Each point corresponds to the average subgroup
853 size in which all 100 foragers were found, averaged over all 50 independent runs. (b) The
854 same as above, for the partial knowledge situation. For comparison, both (a) and (b) show
855 data from two groups of spider monkeys (Ramos-Fernández and Ayala-Orozco 2003). (c)
856 Average subgroup size as a function of β . The graph shows the average values for each of
857 the distributions shown in (a) and (b). Standard errors are below 10% of the average values
858 (not shown).

859

860 Figure 3. (a) Duration, in number of iterations, of subgroups of different size for three
861 different values of β and the full knowledge situation. (b) Subgroup duration as a function
862 of β and the degree of forager knowledge. In both figures, each point represents the average

863 number of iterations that all formed forager subgroups lasted in all 50 independent runs for
864 each condition. Standard errors are below 10% of the average values (not shown).

865

866 Figure 4. Relative affinity in associations among foragers in the model. A value close to 1
867 shows a high skew toward particular individuals among all possible foragers met, while a
868 value close to 0 implies an equal preference for all. Each value represents the average over
869 all 100 individuals and over all 50 independent runs for each value of β . Shown is the same
870 value of relative affinity for a randomized data set. See methods for the definitions. (a) Full
871 knowledge situation; (b) partial knowledge situation. Standard errors are below 10% of the
872 average values (not shown).

873

874 Figure 5. Average number of total bonds and number of bonds that can be considered as
875 strong, i.e. much more common than expected by chance. Shown is the average number of
876 bonds of each type over all 100 individuals and over all 50 independent runs in each
877 condition. See methods for the definition of strong bond. (a) Full knowledge situation; (b)
878 partial knowledge situation; (c) clustering coefficient calculated from the resulting social
879 networks as a function of β and degree of forager knowledge. The coefficient is a measure
880 of the “cliquishness” of the resulting networks, or the probability that if there is a strong
881 bond between a forager A and foragers B and C, then B and C are strongly bonded between
882 them too. Shown are the average coefficients for 50 independent social networks obtained
883 in each condition. (d) Average size of the largest cluster in the social network formed by
884 foragers who met at least once during the run (total bonds) or by foragers who met at higher
885 rates than random expectation (strong bonds), under conditions of full or limited

886 knowledge, as a function of β . Each point represents the average of 50 independent runs for
887 each value of β or knowledge condition. Standard errors are below 10% of the average
888 values (not shown).

889

890 Figure 6. Graphic depiction of one of the social networks that emerges in a situation with
891 complete knowledge and $\beta = 2.5$ (not all foragers are represented). Black arrows
892 correspond to strong bonds ($A \rightarrow B$ means that B is a strong associate for A), while grey
893 lines correspond to weak bonds (see Methods for definitions). The figure clearly shows that
894 the majority of foragers associate in clusters of strong bonds that are part of much larger
895 clusters held together by weak bonds. The graph was obtained using the Pajek software
896 (Batagelj and Mrvar 1998).

897

898 Table 1. Summary of main results. Subgroup size, duration of associations, relative affinity,
899 number of strong bonds, cliquishness (clustering coefficients) and percolation of the
900 network as a function of environmental heterogeneity (exponent β) and degree of forager
901 knowledge about the location and size of trees in the environment.

902

Figure 1a

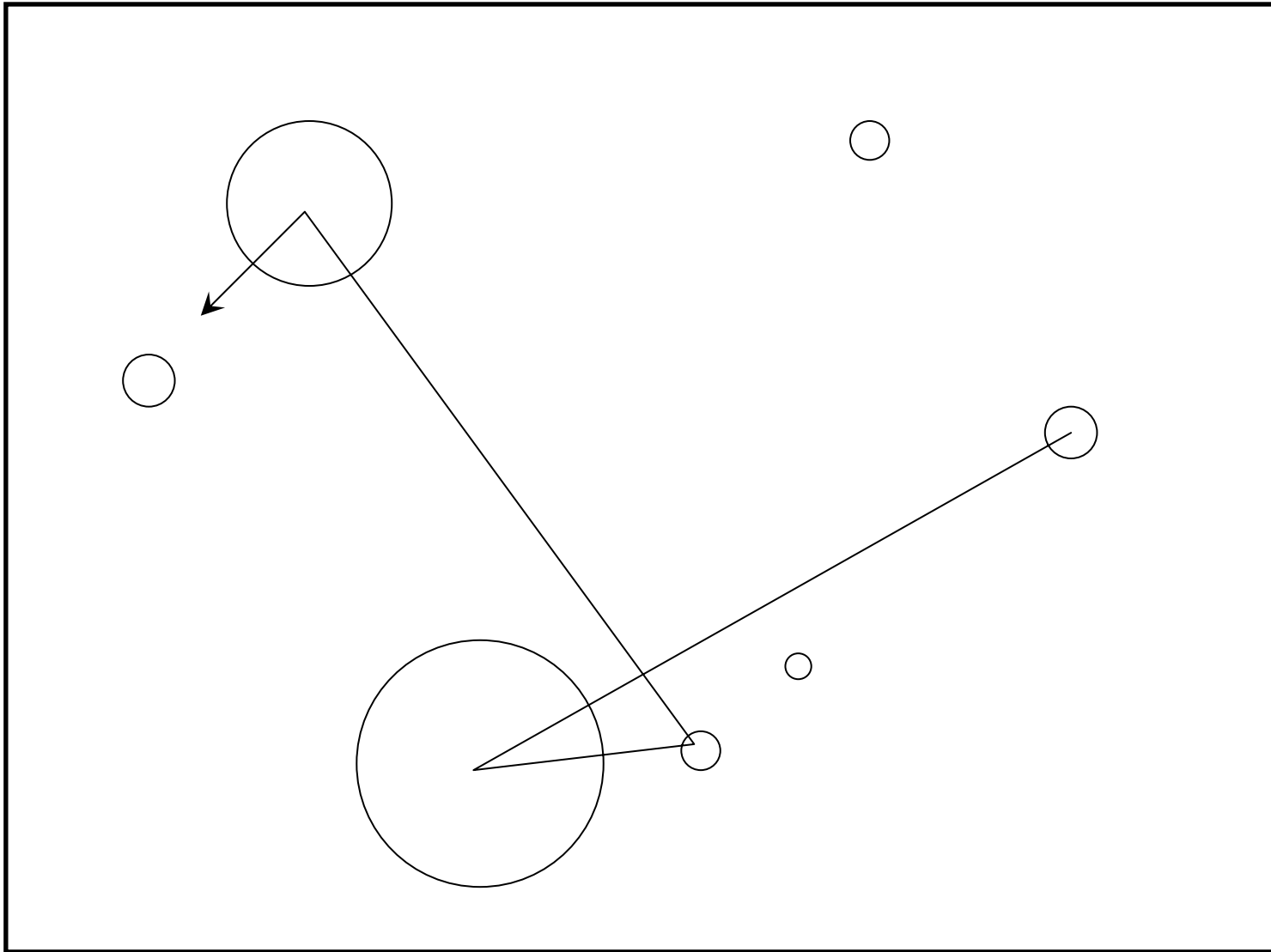


Figure 1b

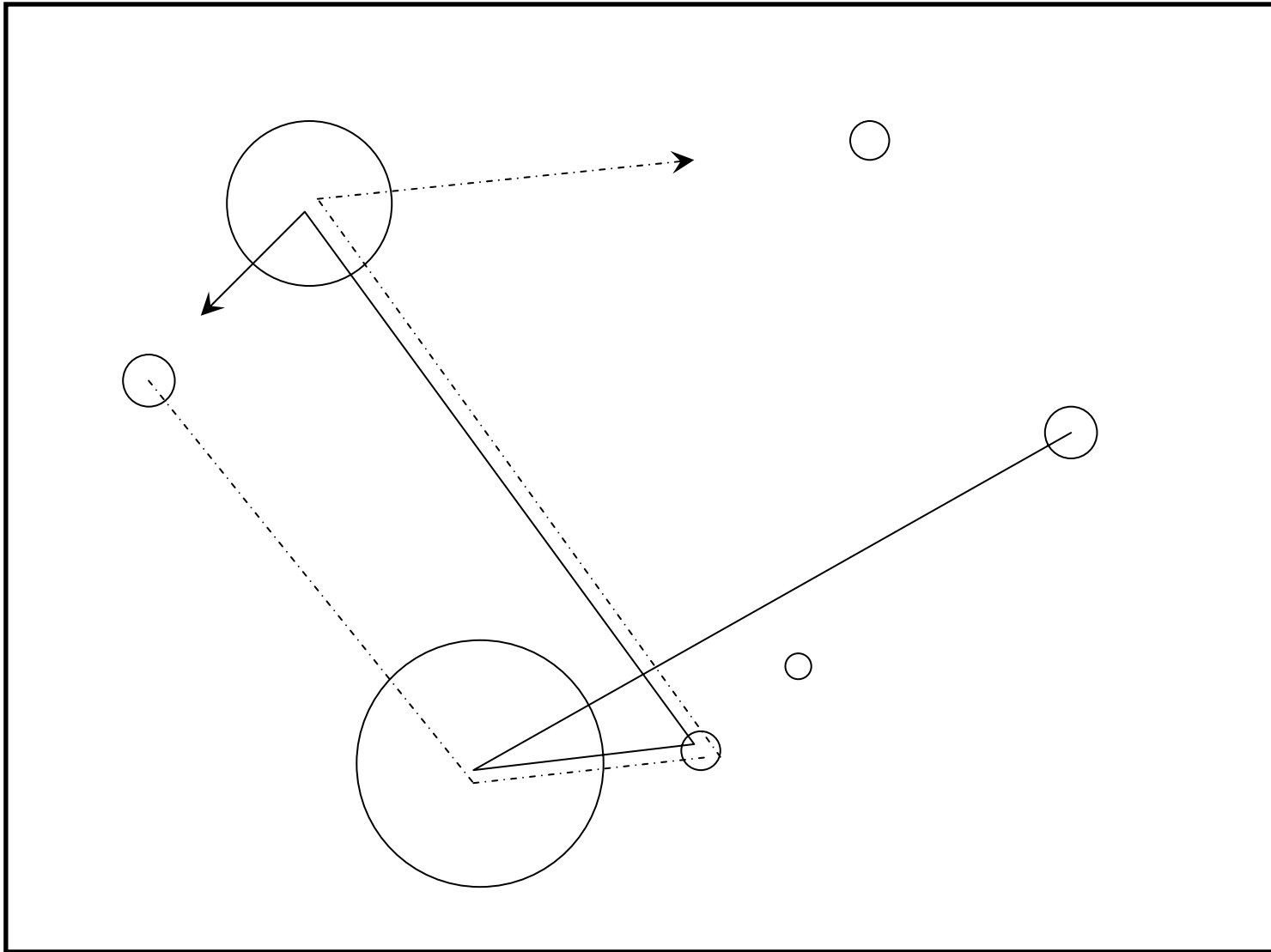


Figure 2a

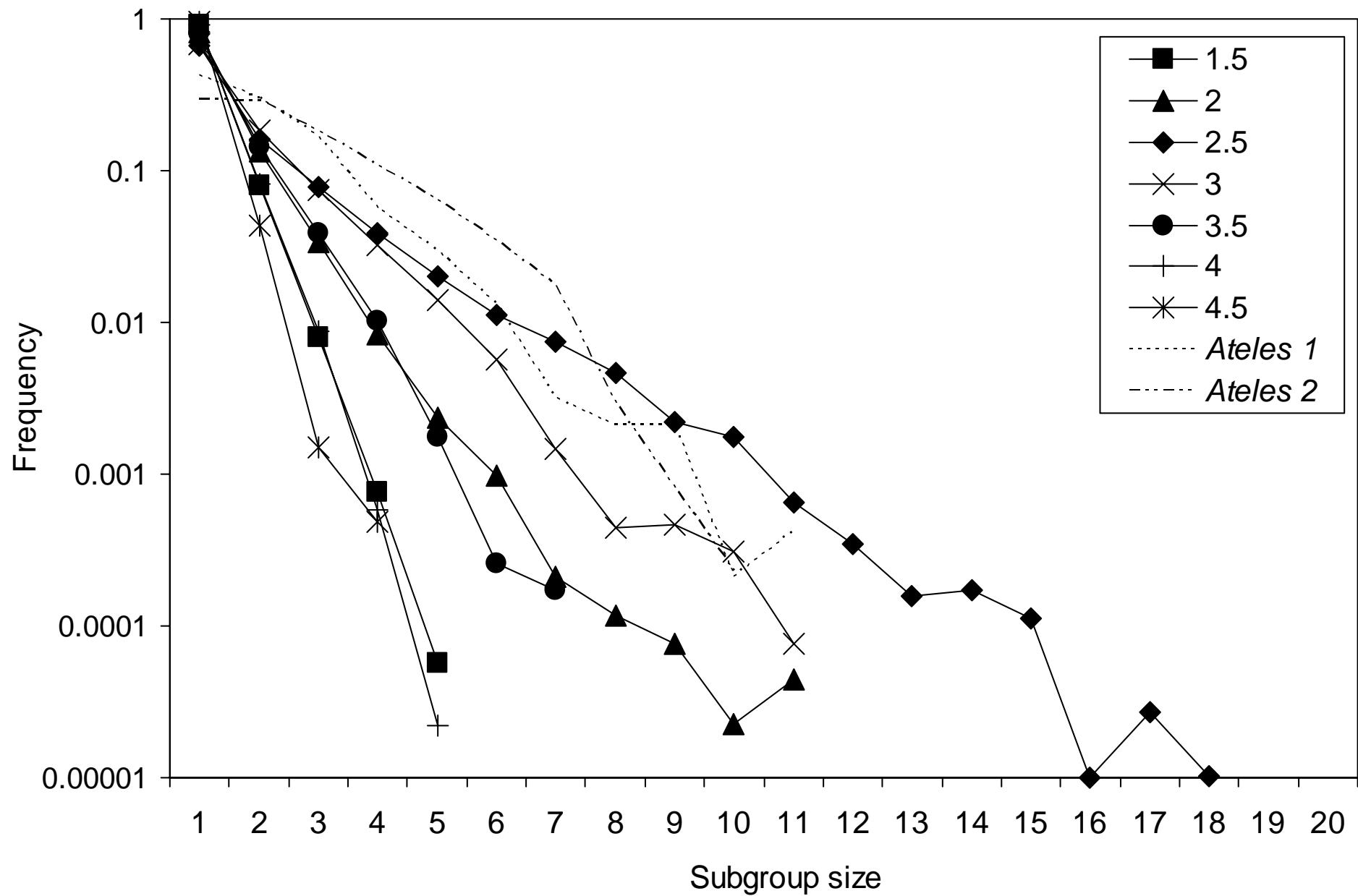


Figure 2b

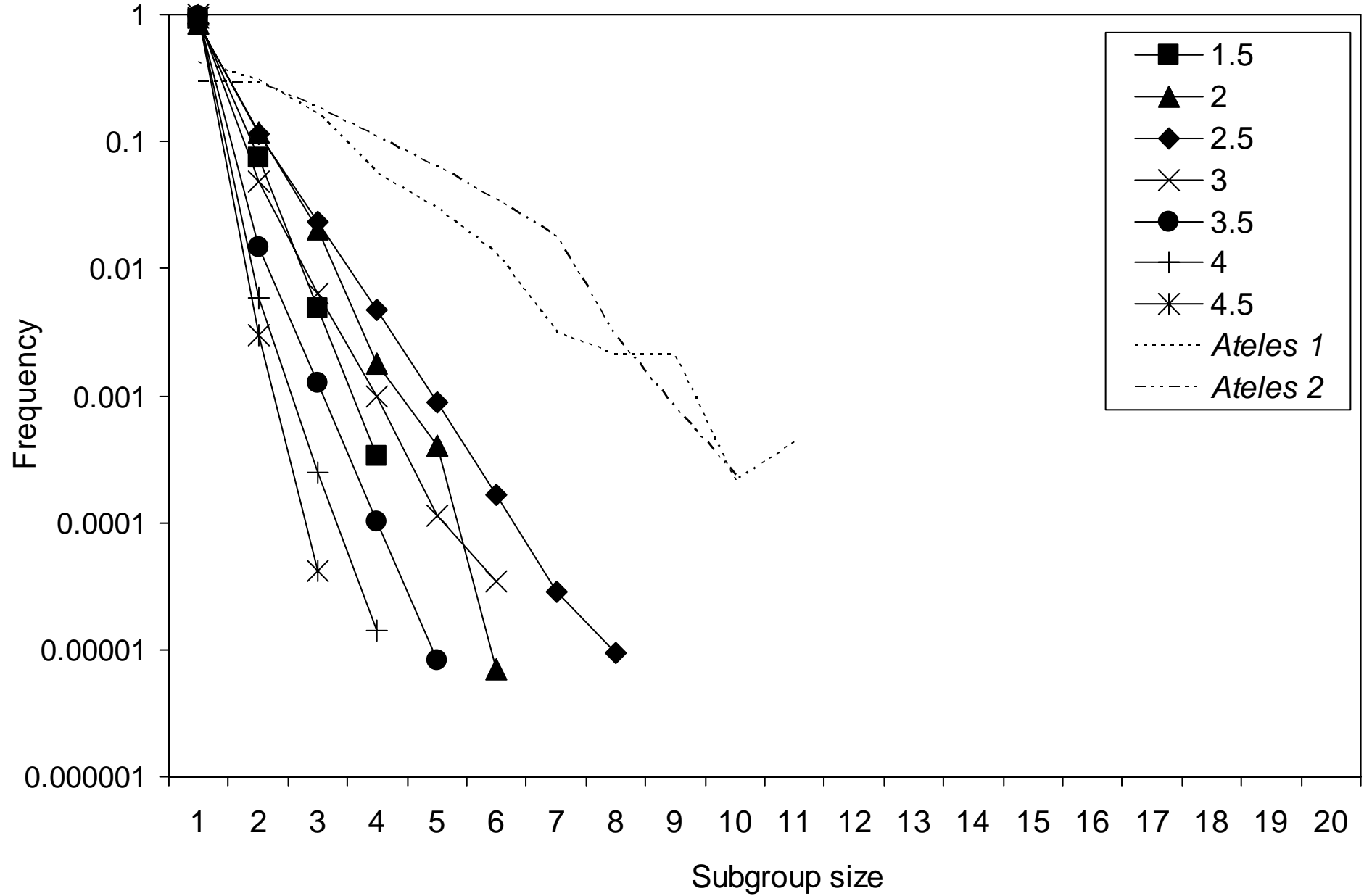


Figure 2c

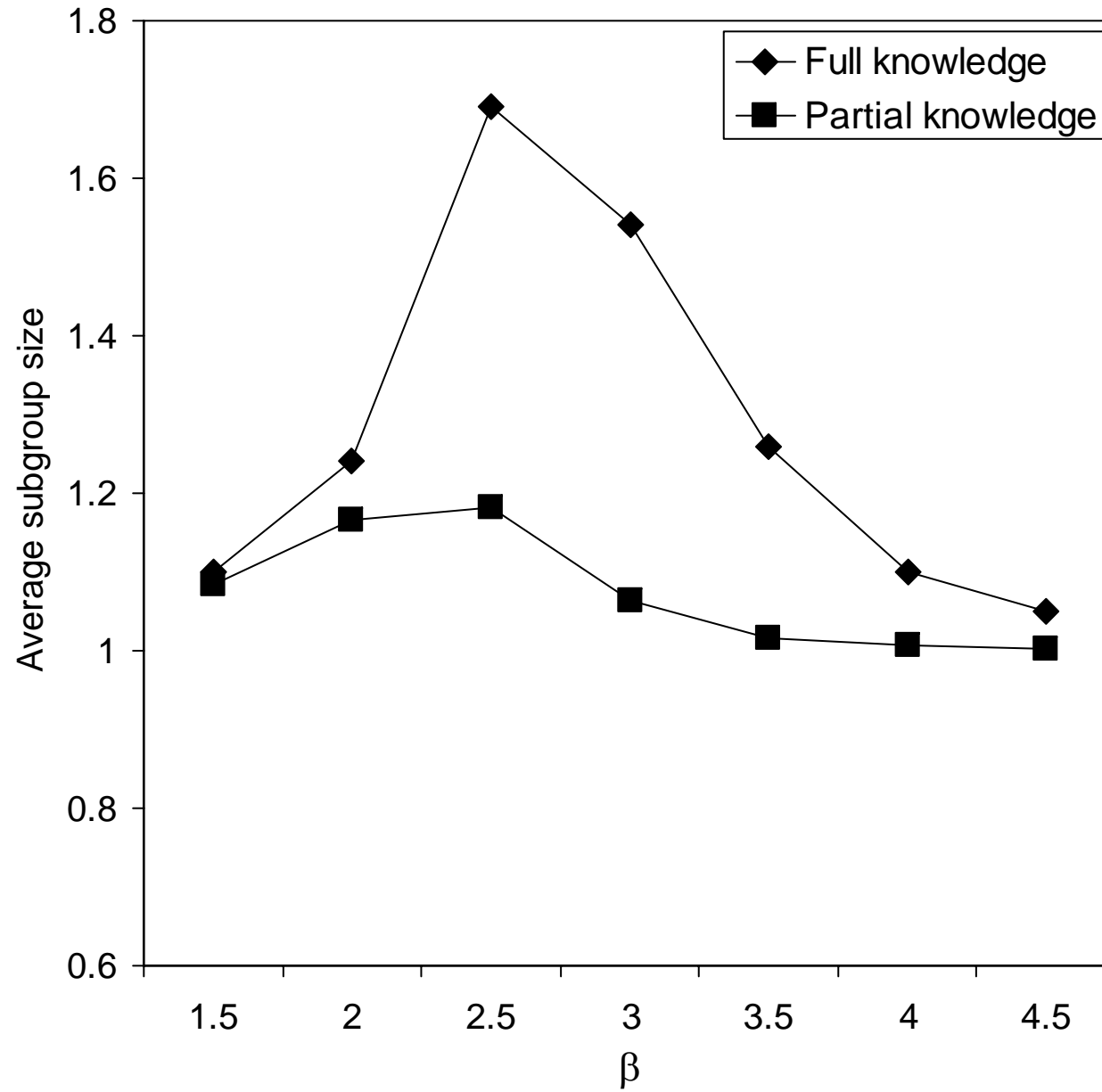


Figure 3a

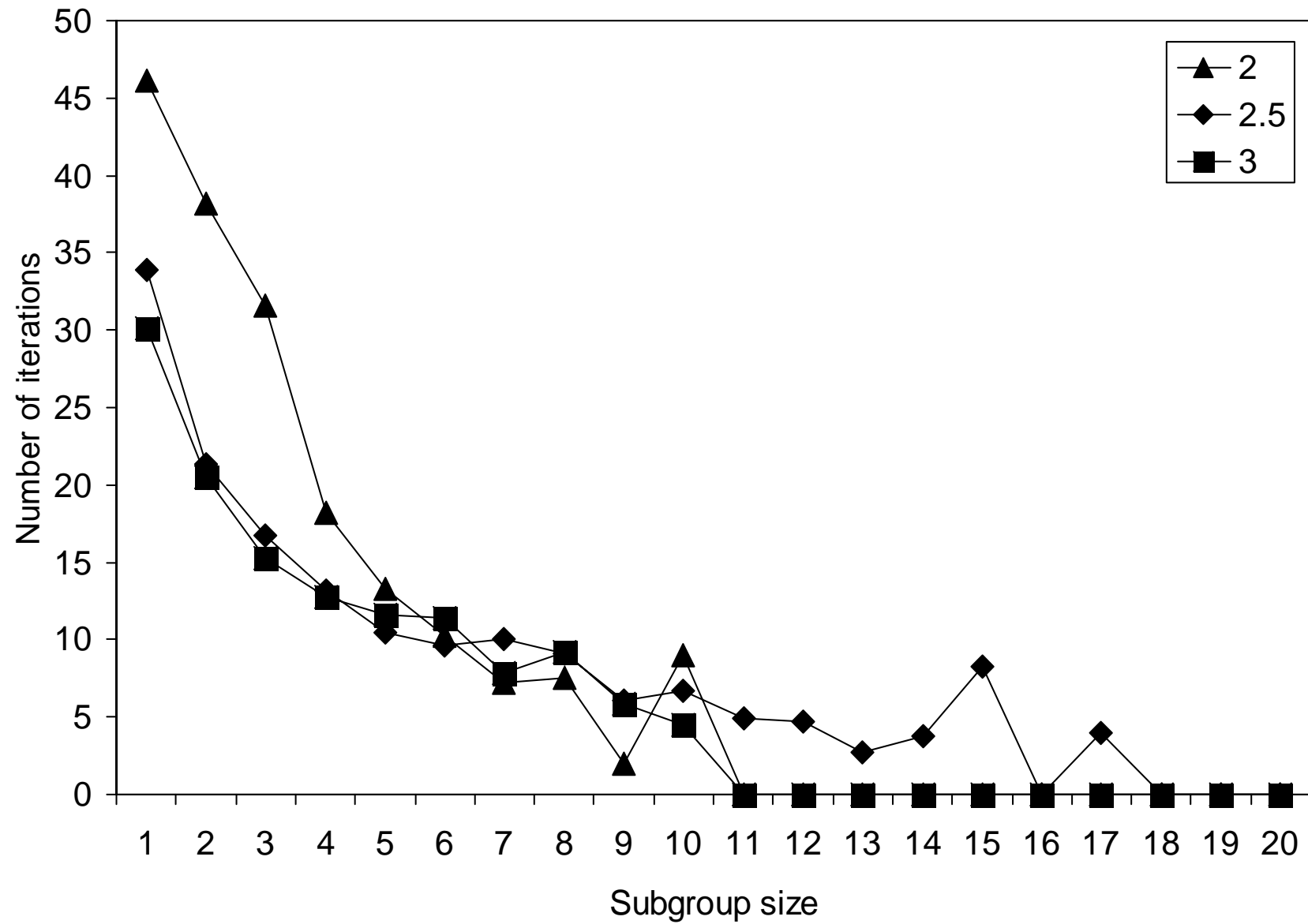


Figure 3b

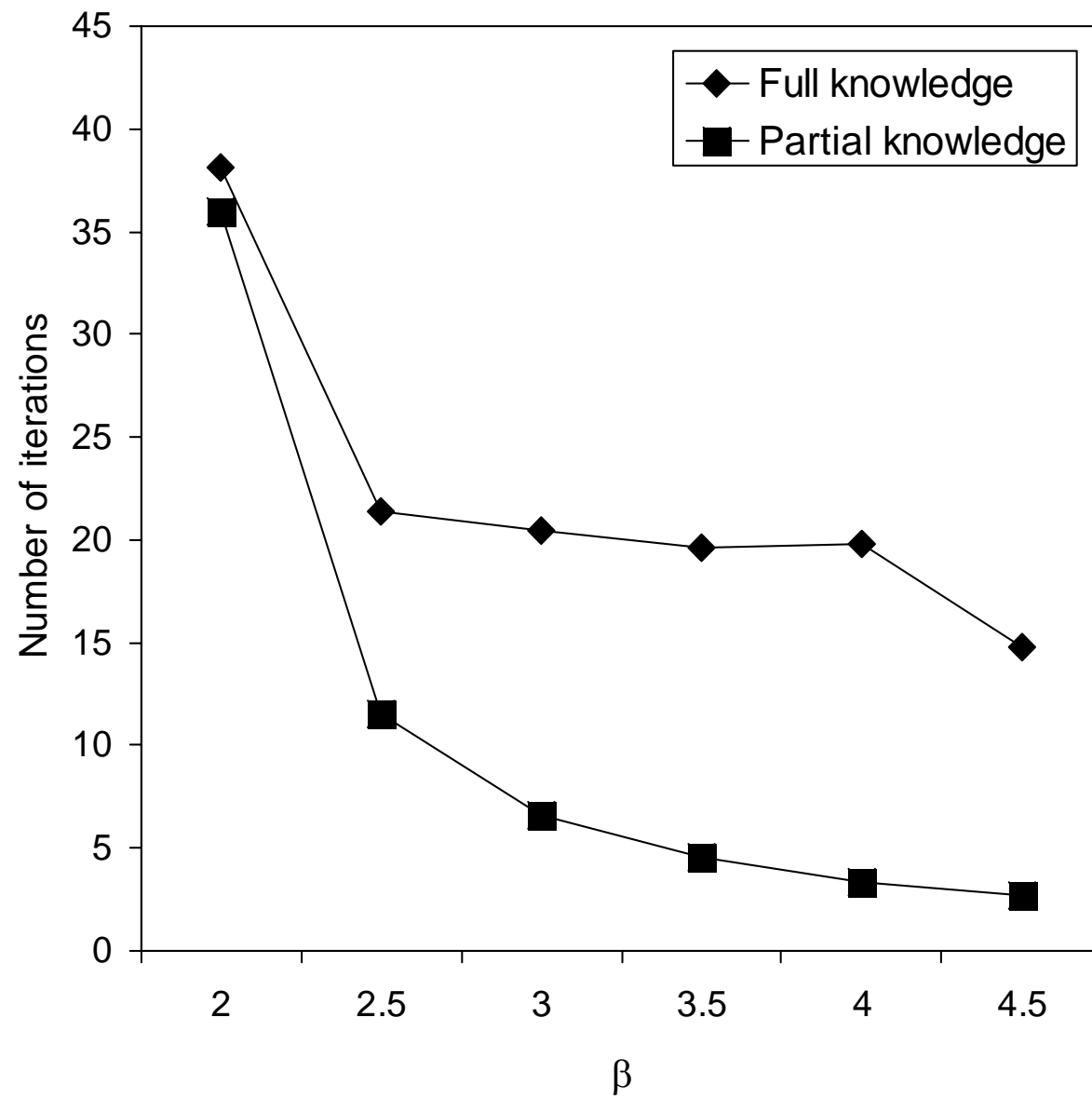


Figure 4a

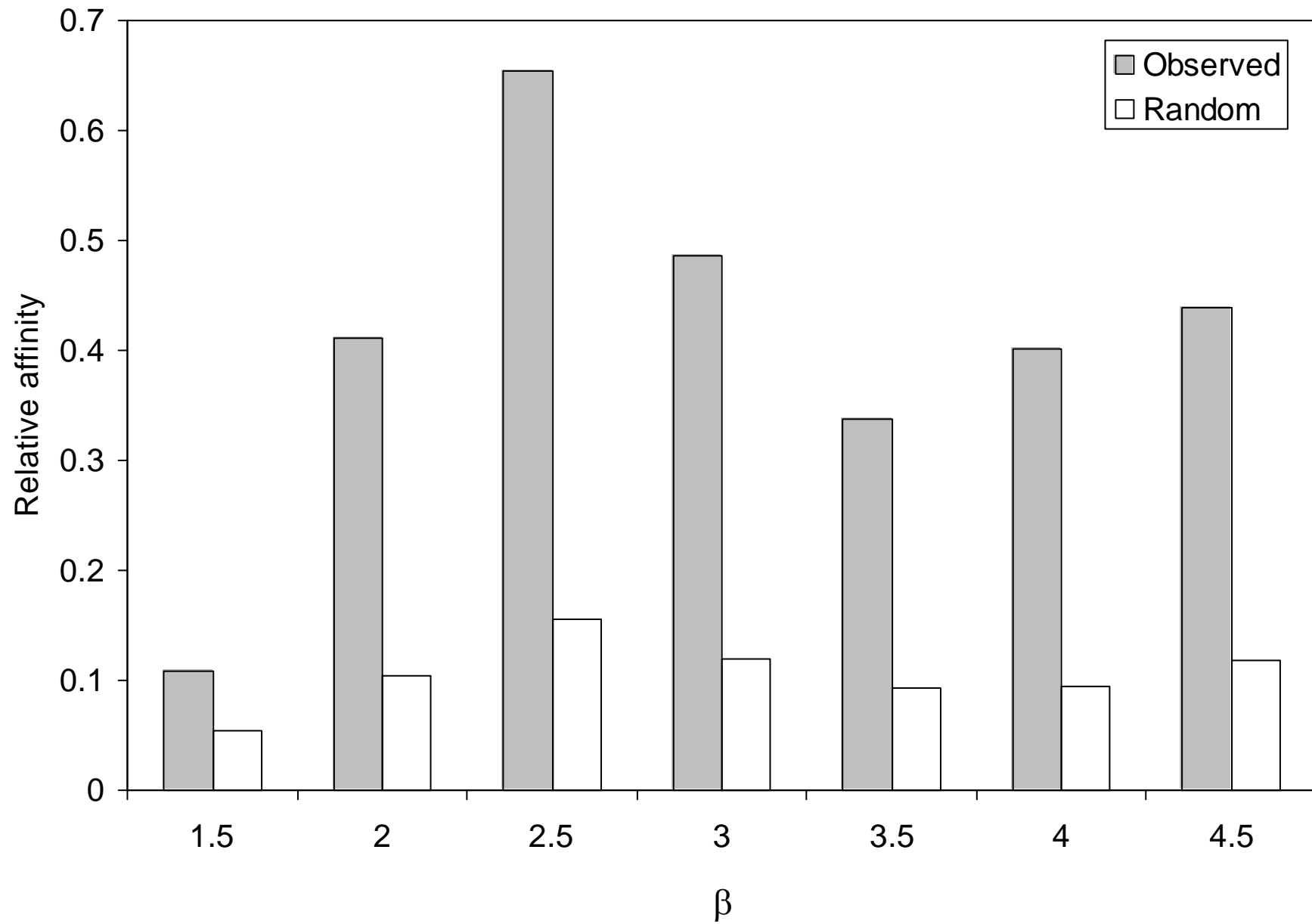


Figure 4b

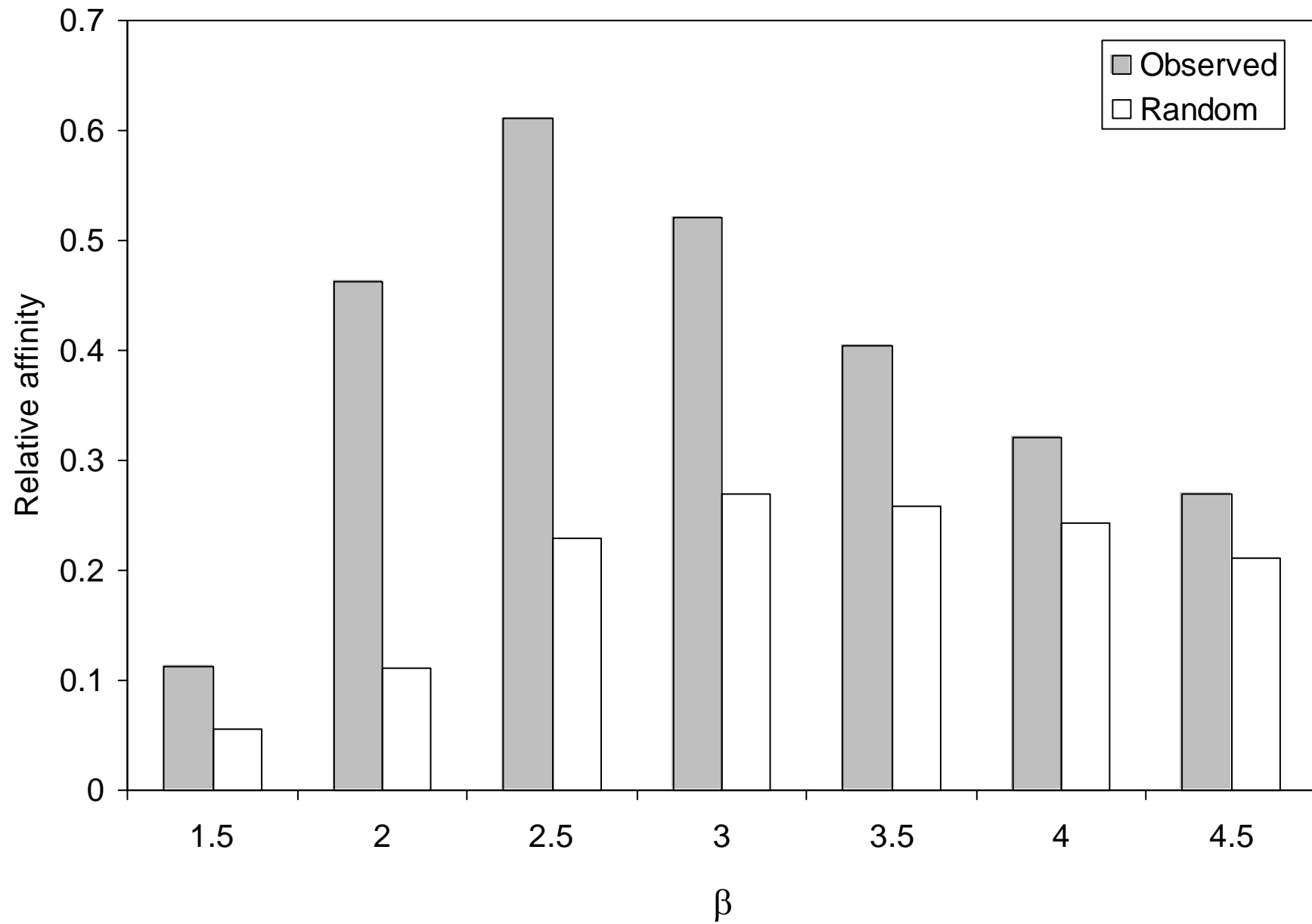


Figure 5a

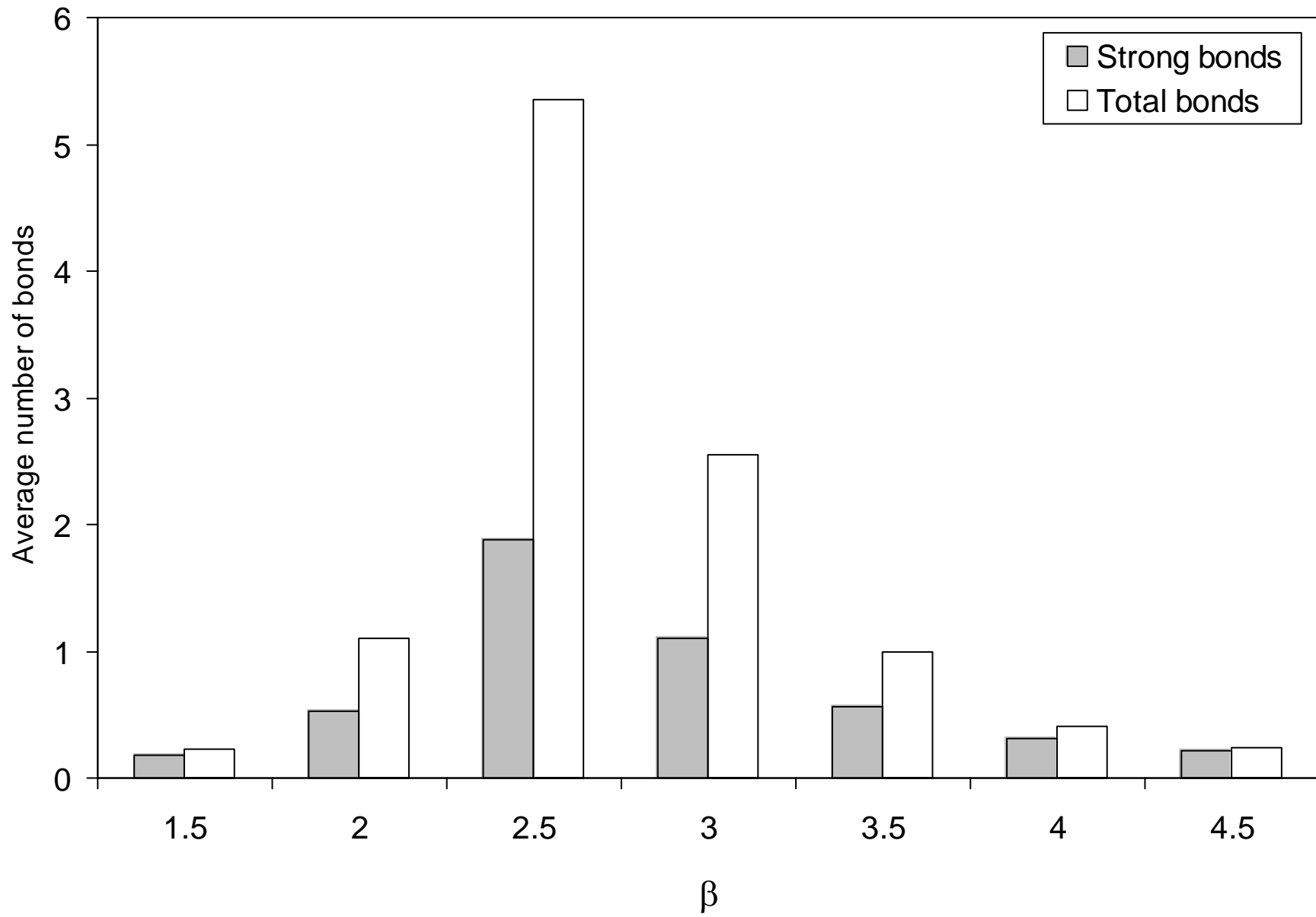


Figure 5b

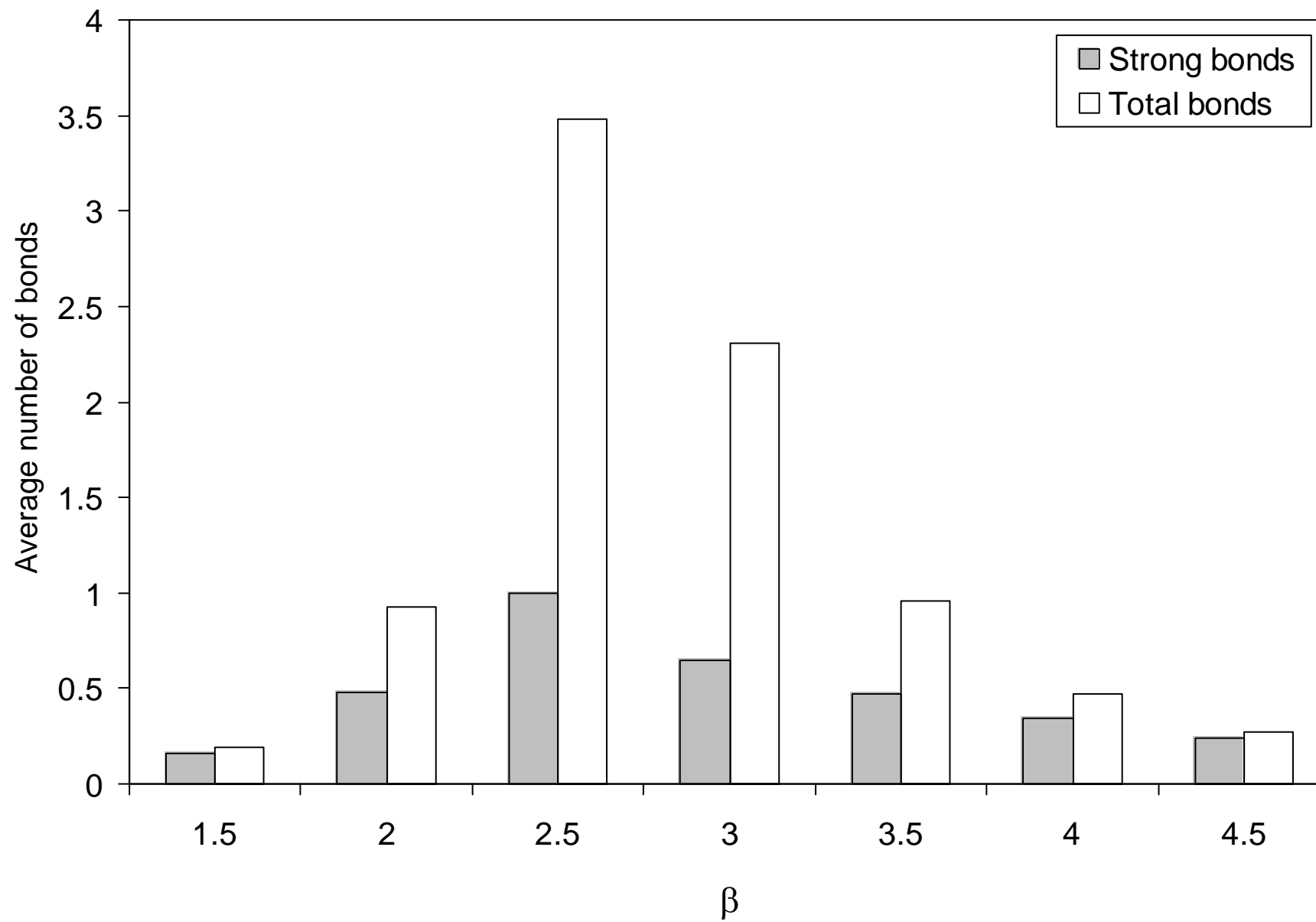


Figure 5c

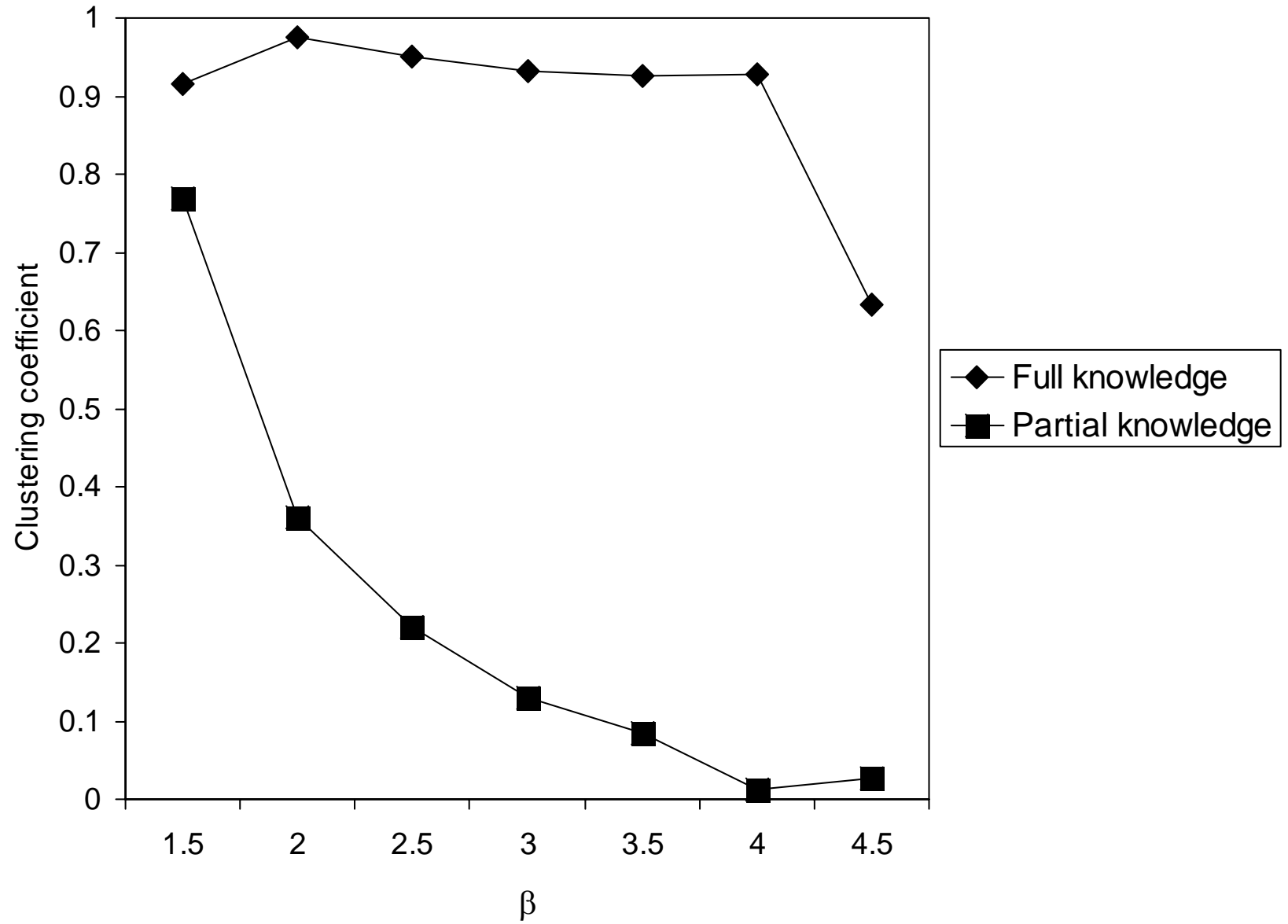


Figure 5d

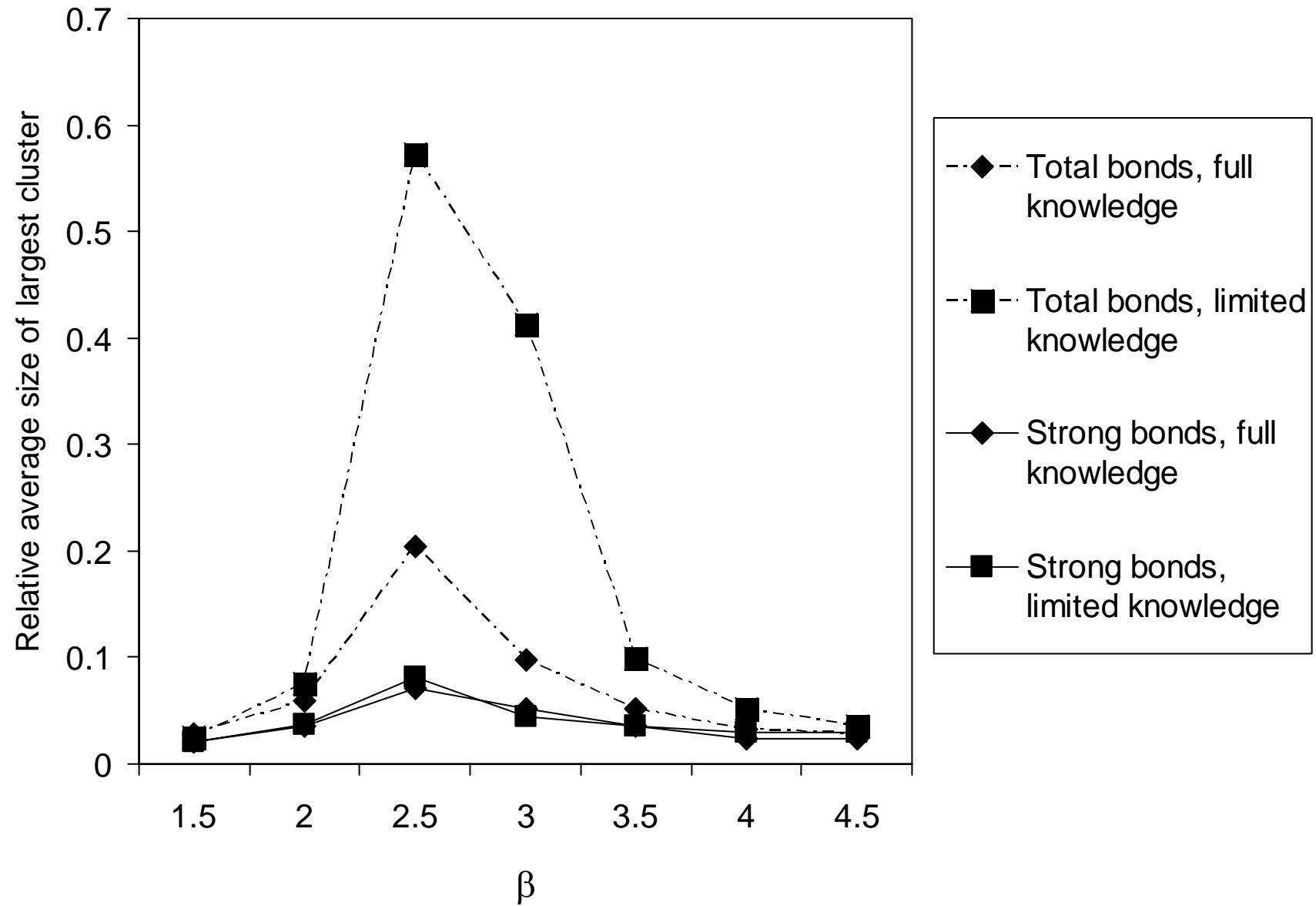


Table 1

Extent of knowledge	Variation in tree size		
	Large $\beta = 1.5 - 2$	Intermediate $\beta = 2.5 - 3$	Small $\beta = 3.5-4.5$
Full	<p>Small/medium subgroups</p> <p>Long lasting (“frozen”)</p> <p>Even relative affinity</p> <p>Few strong bonds</p> <p>Very cliquish</p> <p>Non-percolating network</p>	<p>Large subgroups</p> <p>Medium duration</p> <p>Skewed relative affinity</p> <p>Many strong bonds</p> <p>Very cliquish</p> <p>Percolating network</p>	<p>Small subgroups</p> <p>Medium-short duration</p> <p>Even relative affinity</p> <p>Few strong bonds</p> <p>Moderately cliquish</p> <p>Non-percolating network</p>
Partial	<p>Very small subgroups</p> <p>Long lasting (“frozen”)</p> <p>Even relative affinity</p> <p>Few strong bonds</p> <p>Cliquish</p> <p>Non-percolating network</p>	<p>Small subgroups</p> <p>Medium-short duration</p> <p>Skewed relative affinity</p> <p>Few strong bonds</p> <p>Moderately cliquish</p> <p>Percolating network</p>	<p>Very small subgroups</p> <p>Very short duration</p> <p>Even relative affinity</p> <p>Few strong bonds</p> <p>Not cliquish</p> <p>Non-percolating network</p>

Figure 6

