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## **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  $\beta$ . 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  $\beta$ ,  
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  $\beta$ . 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  $\beta$  is a fixed exponent characterizing the environment, being the main parameter in  
125 the model. If  $\beta$  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  $\beta$  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  $\beta$  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  $\beta$   
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  $\beta$  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  $\beta$  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  $\beta$  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  $\beta$  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  $\beta$  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  $\beta$  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  $\beta$  upon the size of  
291 formed subgroups. Particularly for values of  $\beta$  between 2 and 4, the size of formed  
292 subgroups is sensibly larger than for the other values of  $\beta$ . 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  $\beta$  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  $\beta$  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  $\beta$ , 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  $\beta$ , 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  $\beta$  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  $\beta$ . 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  $\beta$  and for both knowledge situations. As  $\beta$  increased, associations were of shorter  
321 duration, although there was an intermediate range of values of  $\beta$  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  $\beta$  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  $\beta$  upon the tendency to form  
338 preferential associations. However, the fact that foragers formed larger subgroups at  
339 particular values of  $\beta$ , 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  $\beta$ .

342

343 Figure 4a shows the relative affinities expected randomly and those observed in the model,  
344 for different values of  $\beta$ , when foragers had full knowledge. At all values of  $\beta$ , 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  $\beta$ . 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  $\beta$ .

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  $\beta$ . 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  $\beta$ , particularly for  $\beta = 2.5$  and 3, when the largest subgroups were  
361 formed (see Figure 2). Similarly, there was a clear effect of  $\beta$  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  $\beta$  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  $\beta$ , for

371 both knowledge situations. At low values of  $\beta$ , social networks had a high clustering  
372 coefficient in both the full and partial knowledge situations. However, as  $\beta$  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  $\beta$ . 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  $\beta$ , 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  $\beta$ . The clusters of strong bonds are smaller in size and  
400 no clear percolation property is observed at any value of  $\beta$ . 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  $\beta$ , 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,  $\beta$ . 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  $\beta$ , 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  $\beta$ , 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  $\beta$  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  $\beta$ , 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  $\beta$ . 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  $\beta$  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  $\beta$  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  $\beta$  that we considered in our model and with empirical measurements of  $\beta$  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  $\beta$ . 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  $\beta$ ) or when most are small (large  $\beta$ ), 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  $\beta$  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  $\beta$ : 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  $\beta$  is small, foragers stay in the  
527 very common large trees, while at higher values of  $\beta$ , 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  $\beta$ , 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  $\beta$ . The description of the  
558 foraging patterns can explain this: at low values of  $\beta$ , 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  $\beta$ , associations last only short periods of time as they always  
563 occur in small trees. At intermediate values of  $\beta$ , 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  $\beta$ , 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  $\beta$ , 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  $0.21 \pm 0.07$  S.D. Another group, with 23 adults, had an average value  
579 of  $0.59 \pm 0.14$  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  $\beta$ , 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  $\beta$ , 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

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841 **FIGURE LEGENDS**

842

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

851

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

860

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

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

866

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

874

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

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

890

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

898

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

903

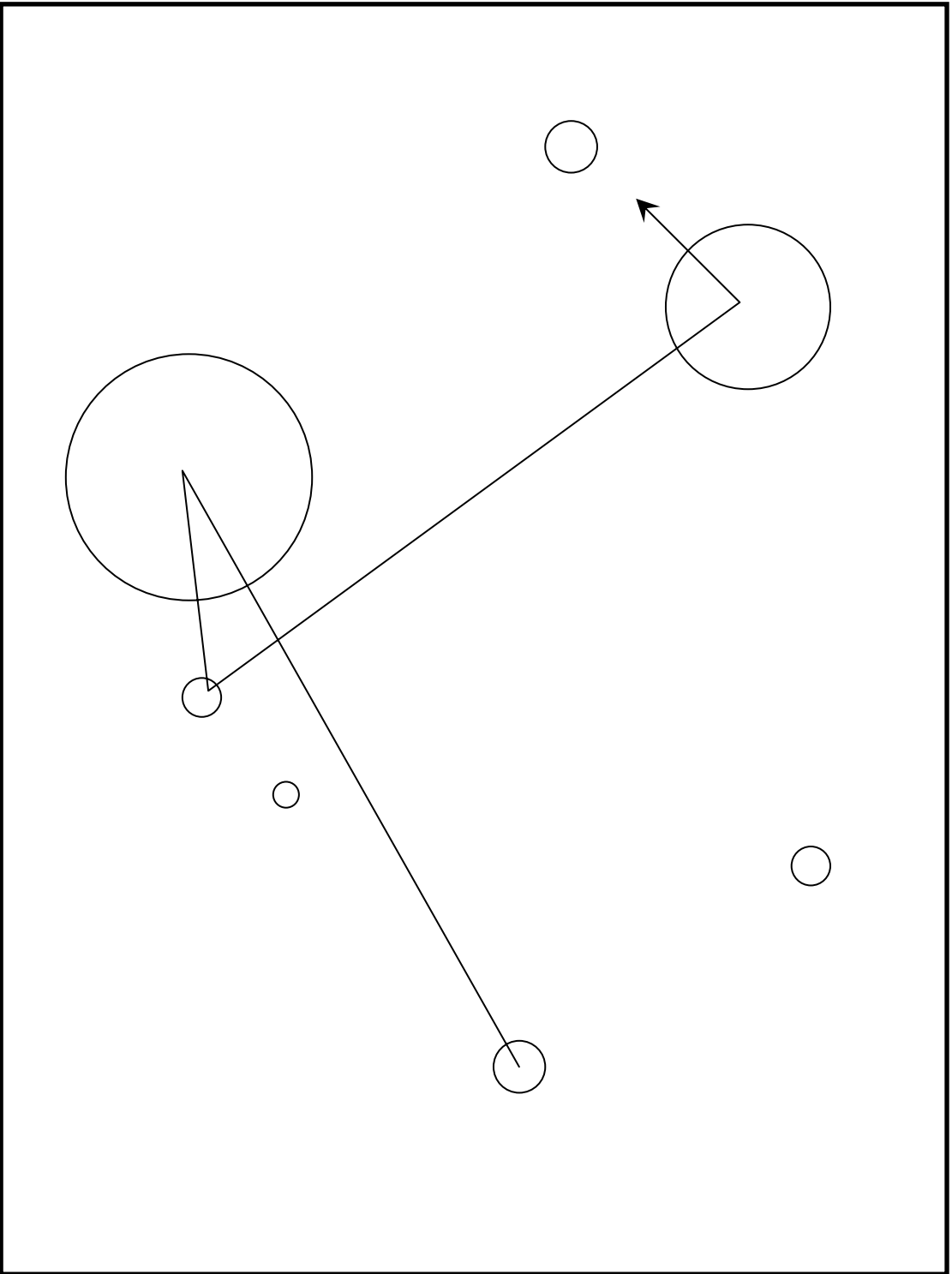


Figure 1a



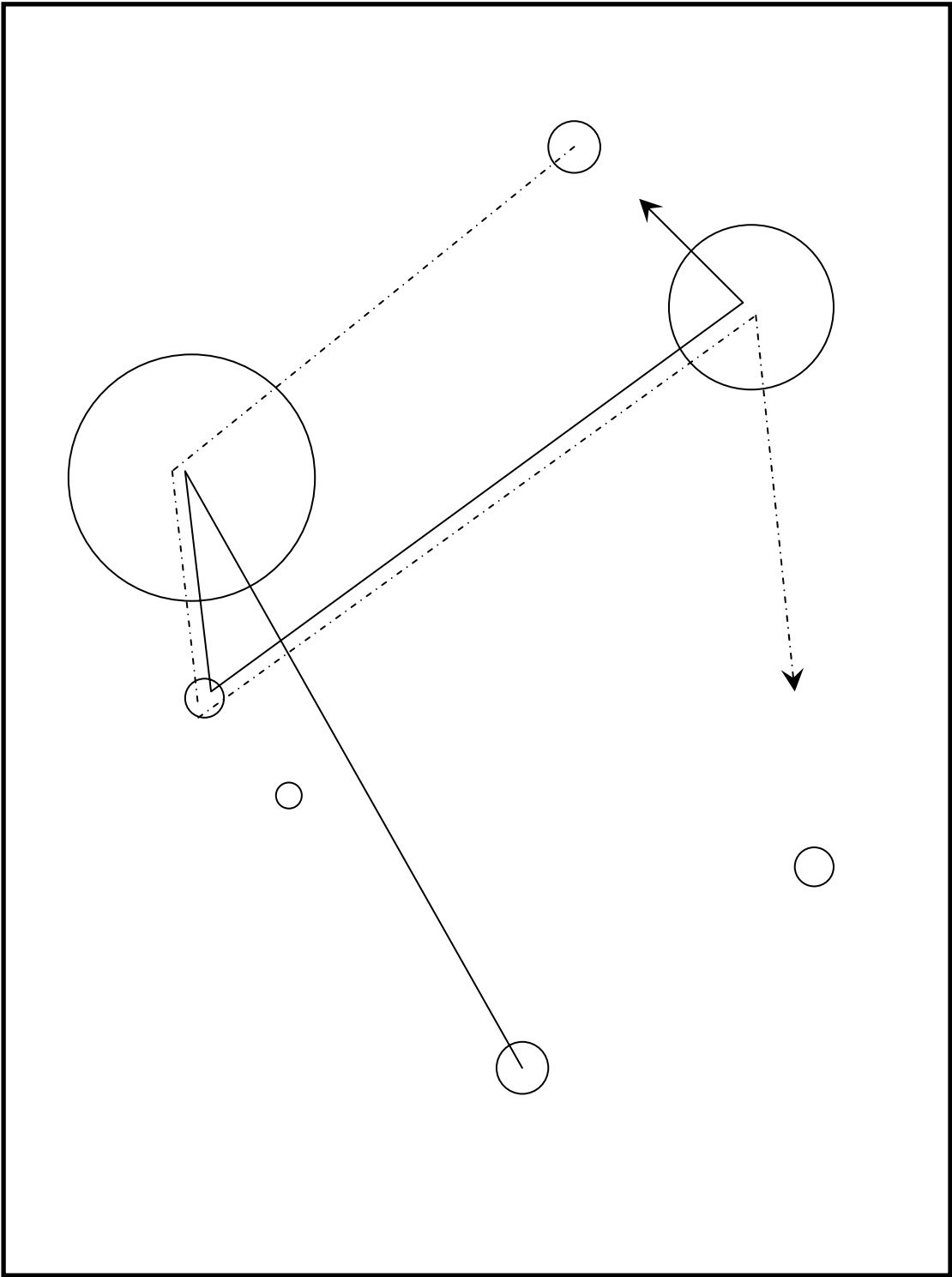


Figure 1b

Figure 2a

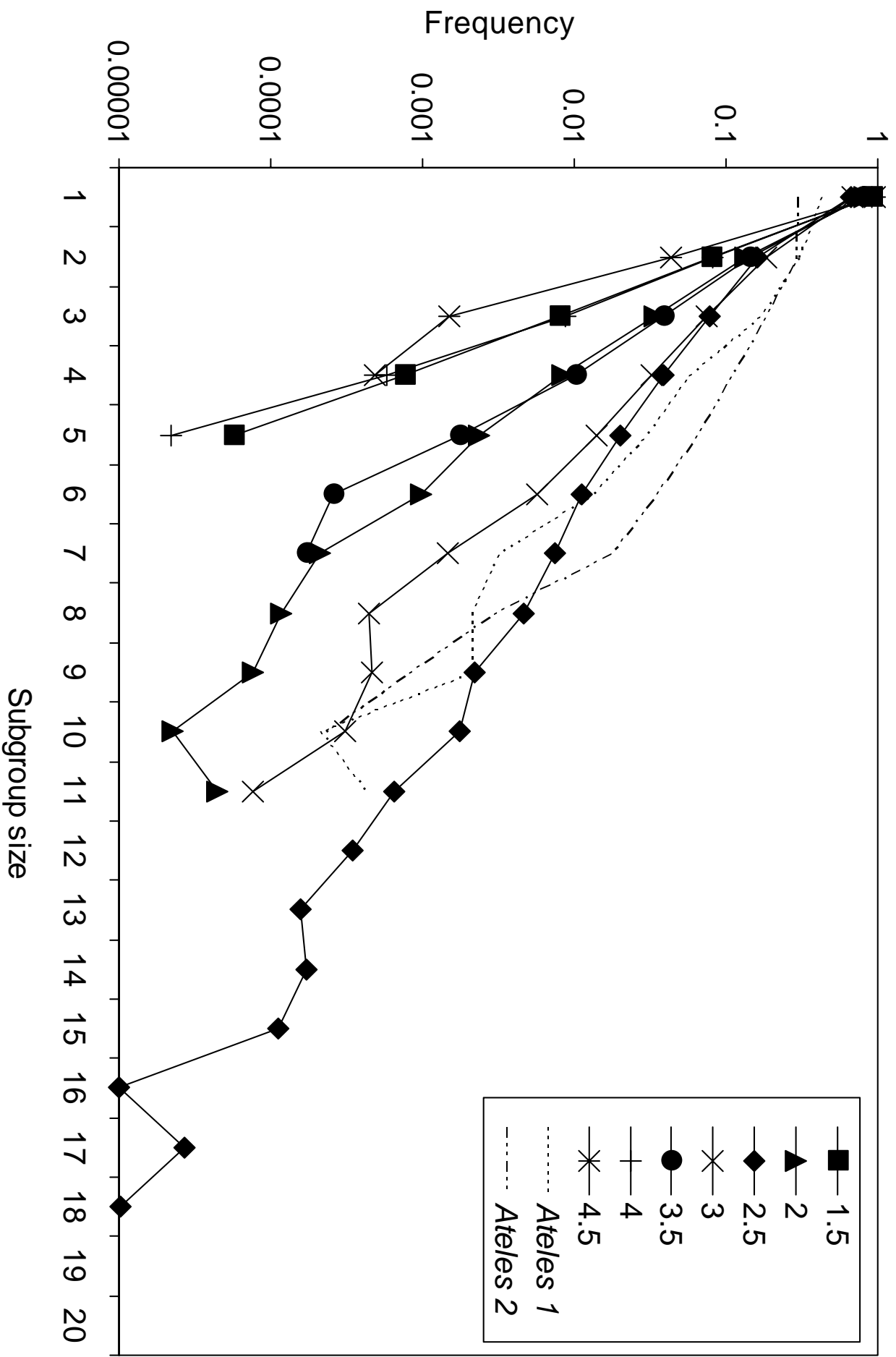




Figure 2c

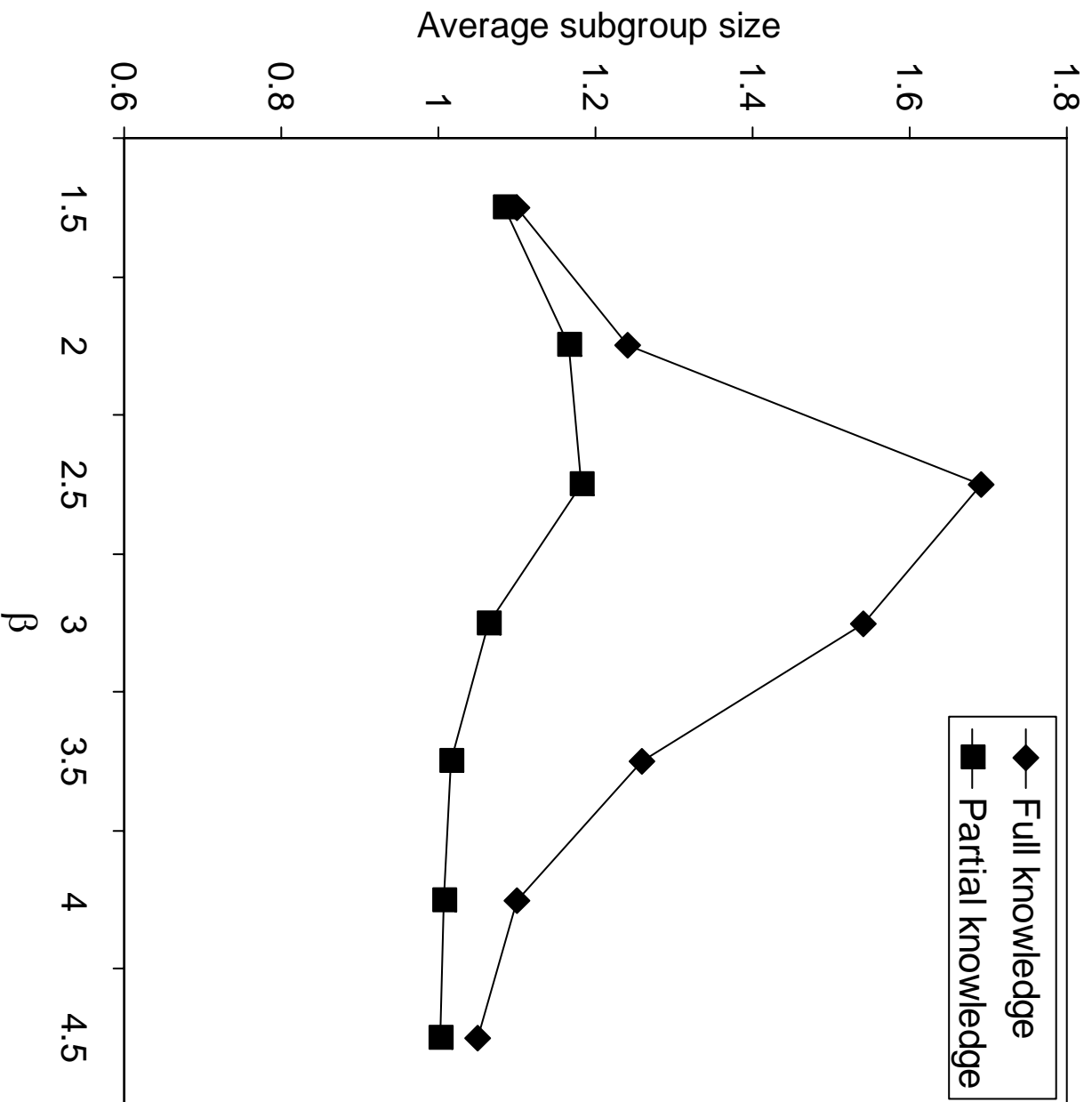


Figure 3a

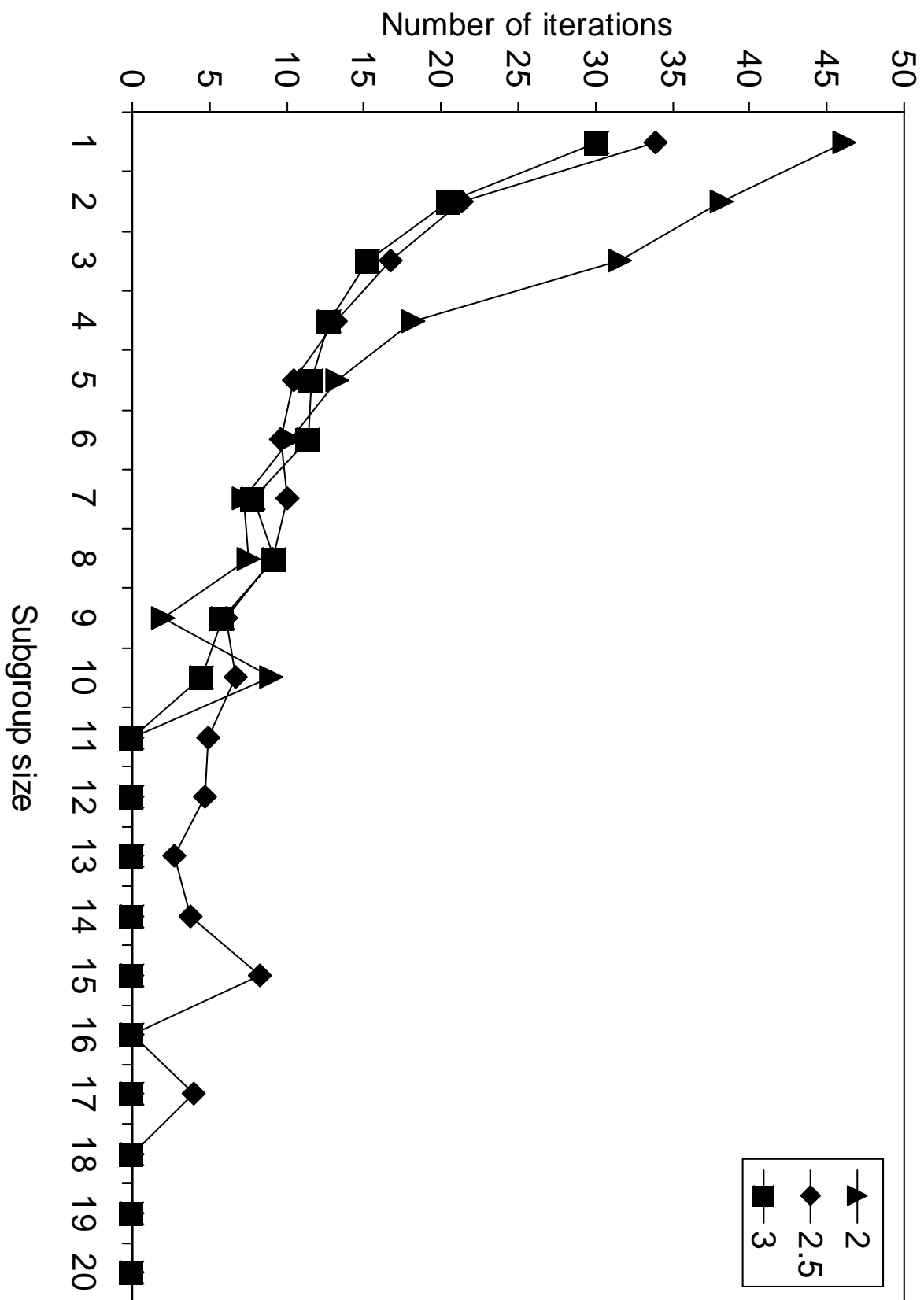


Figure 3b

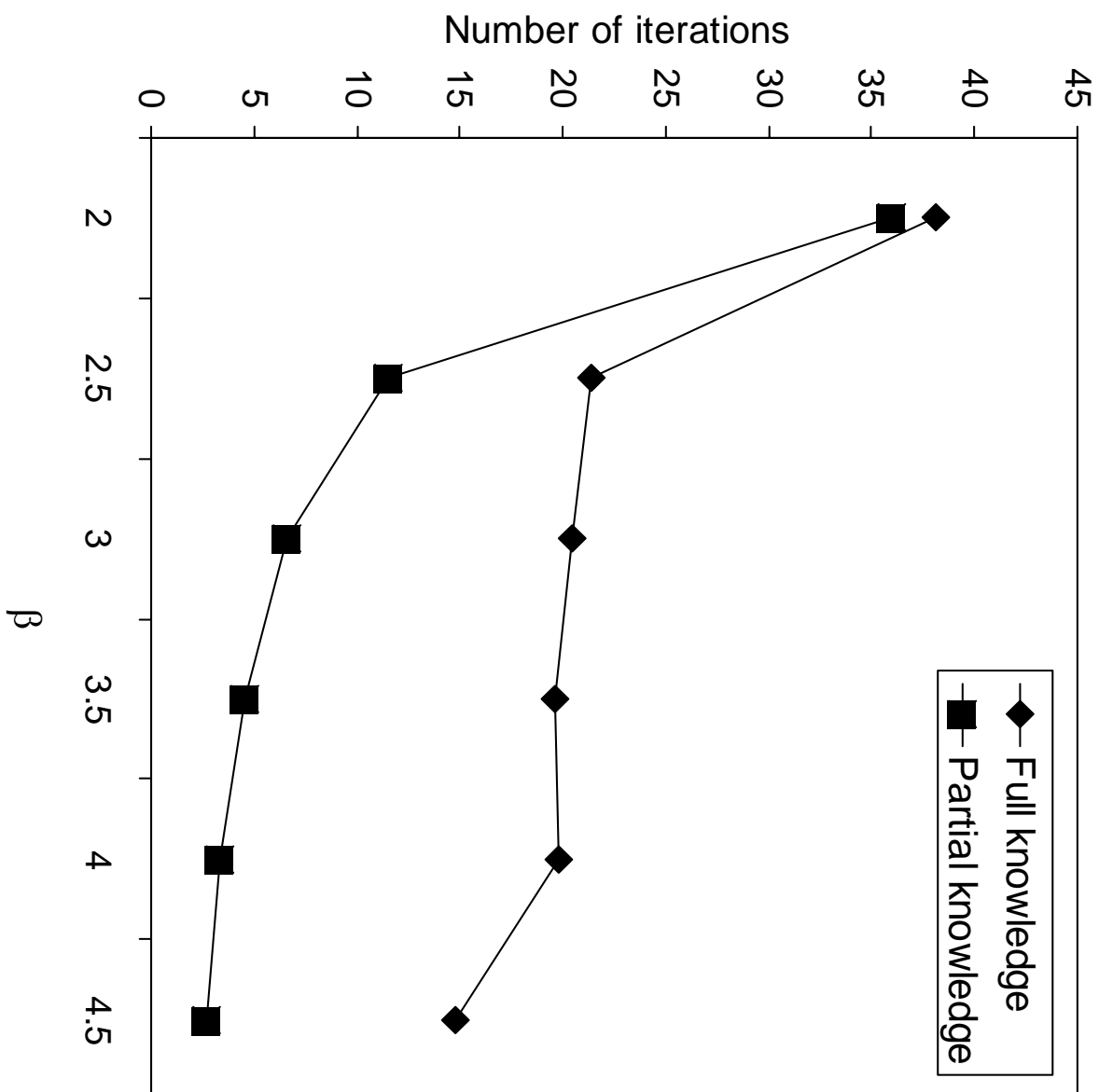


Figure 4a

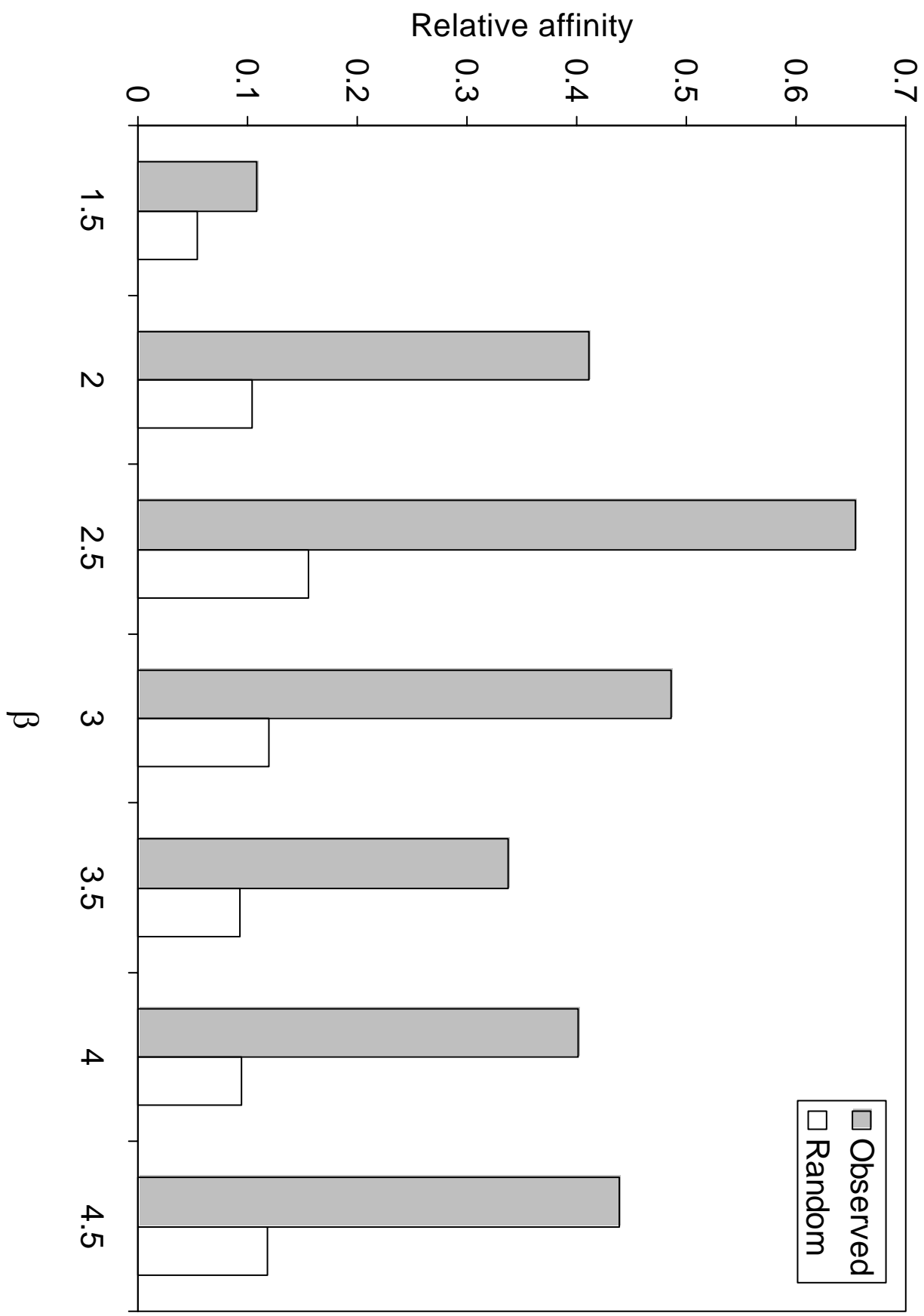


Figure 4b

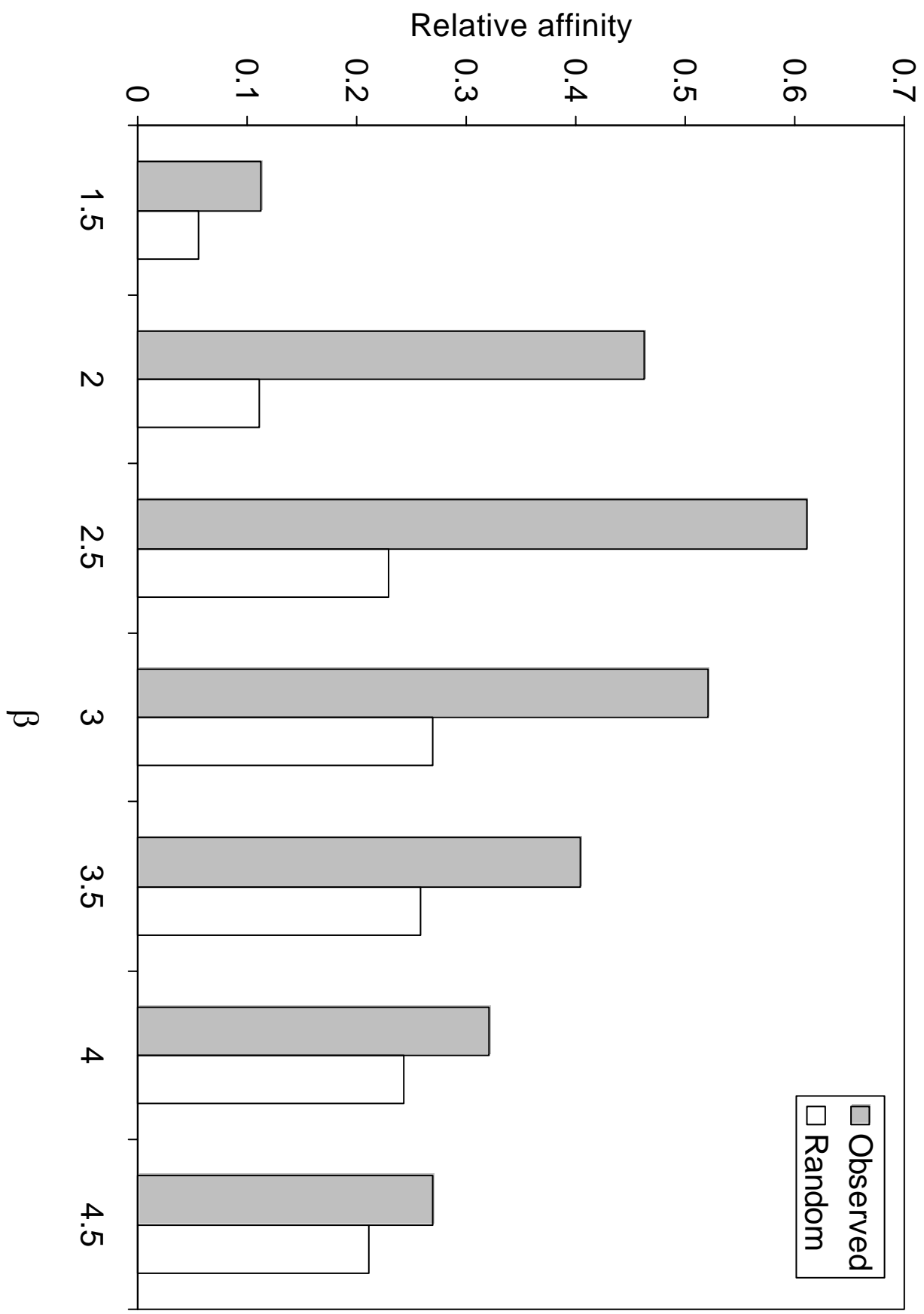




Figure 5a

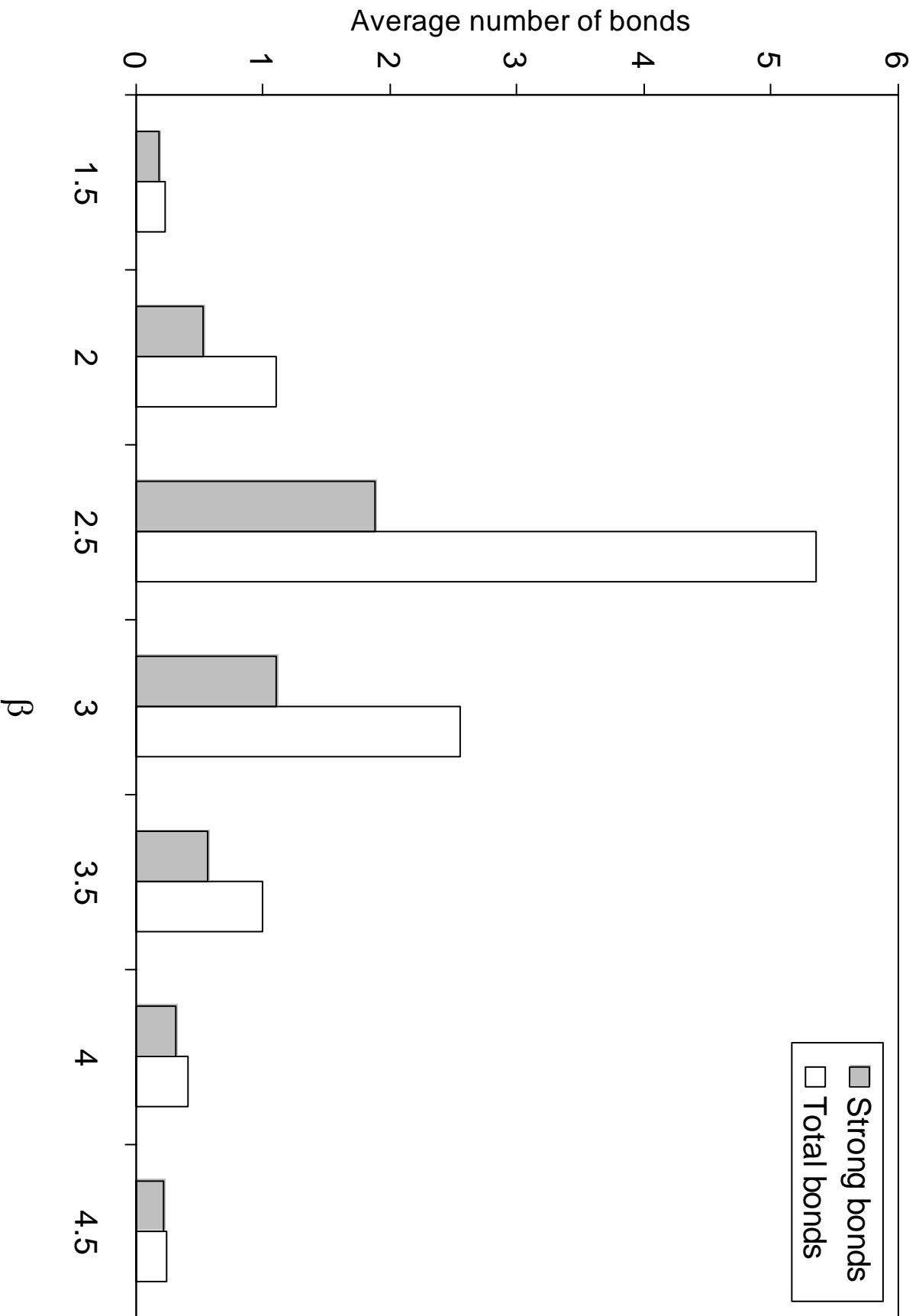


Figure 5b

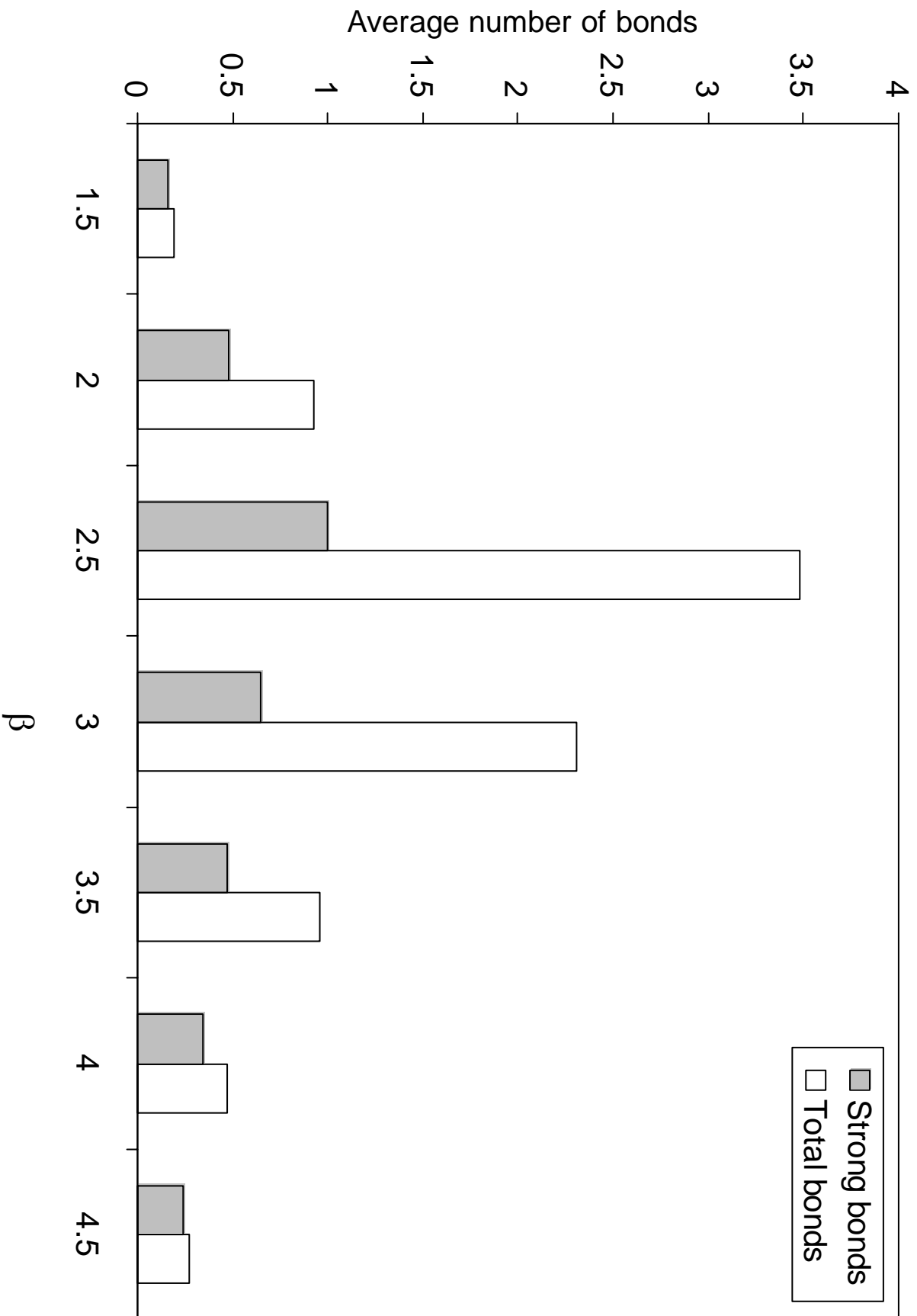


Figure 5c

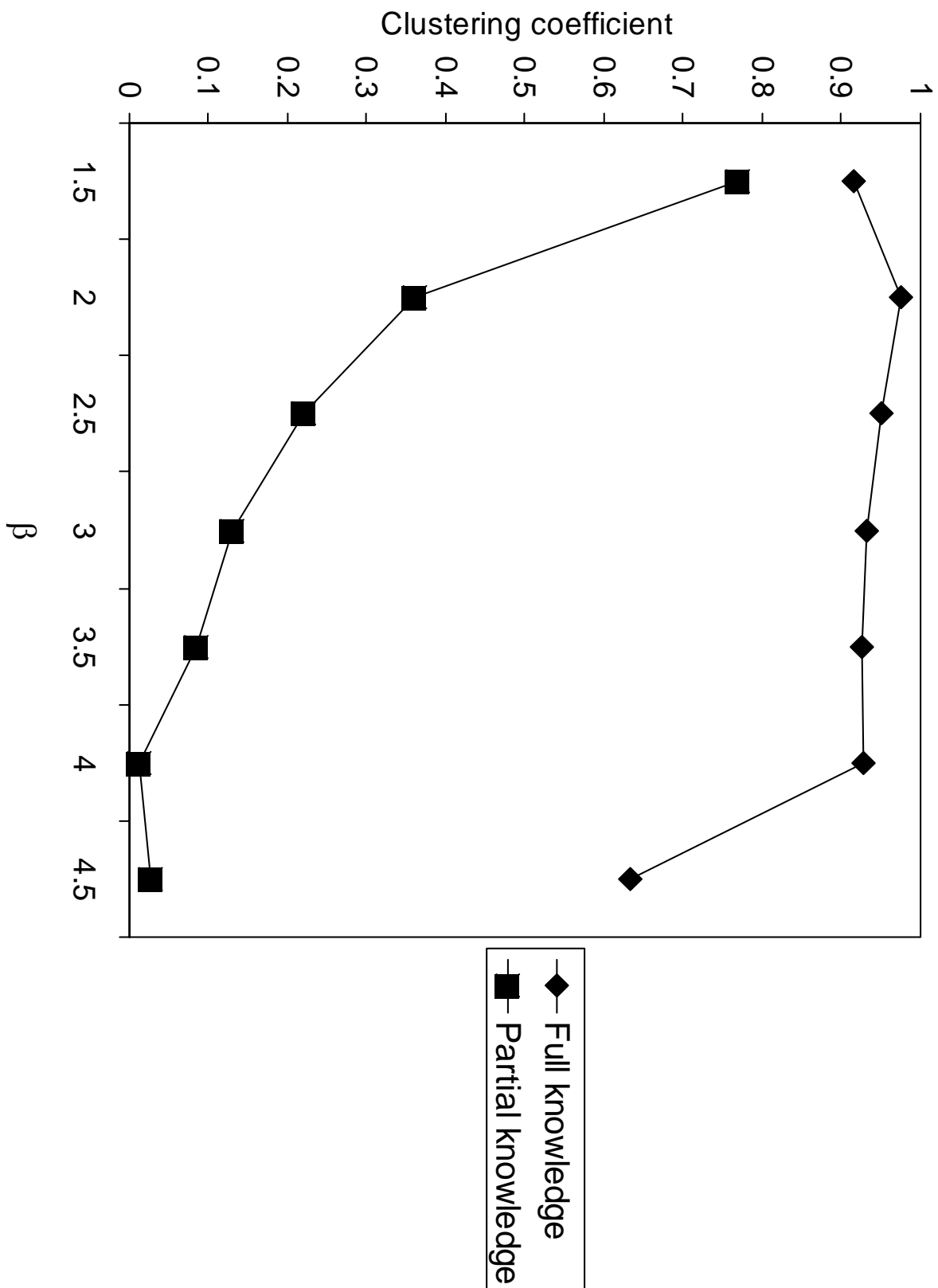


Figure 5d

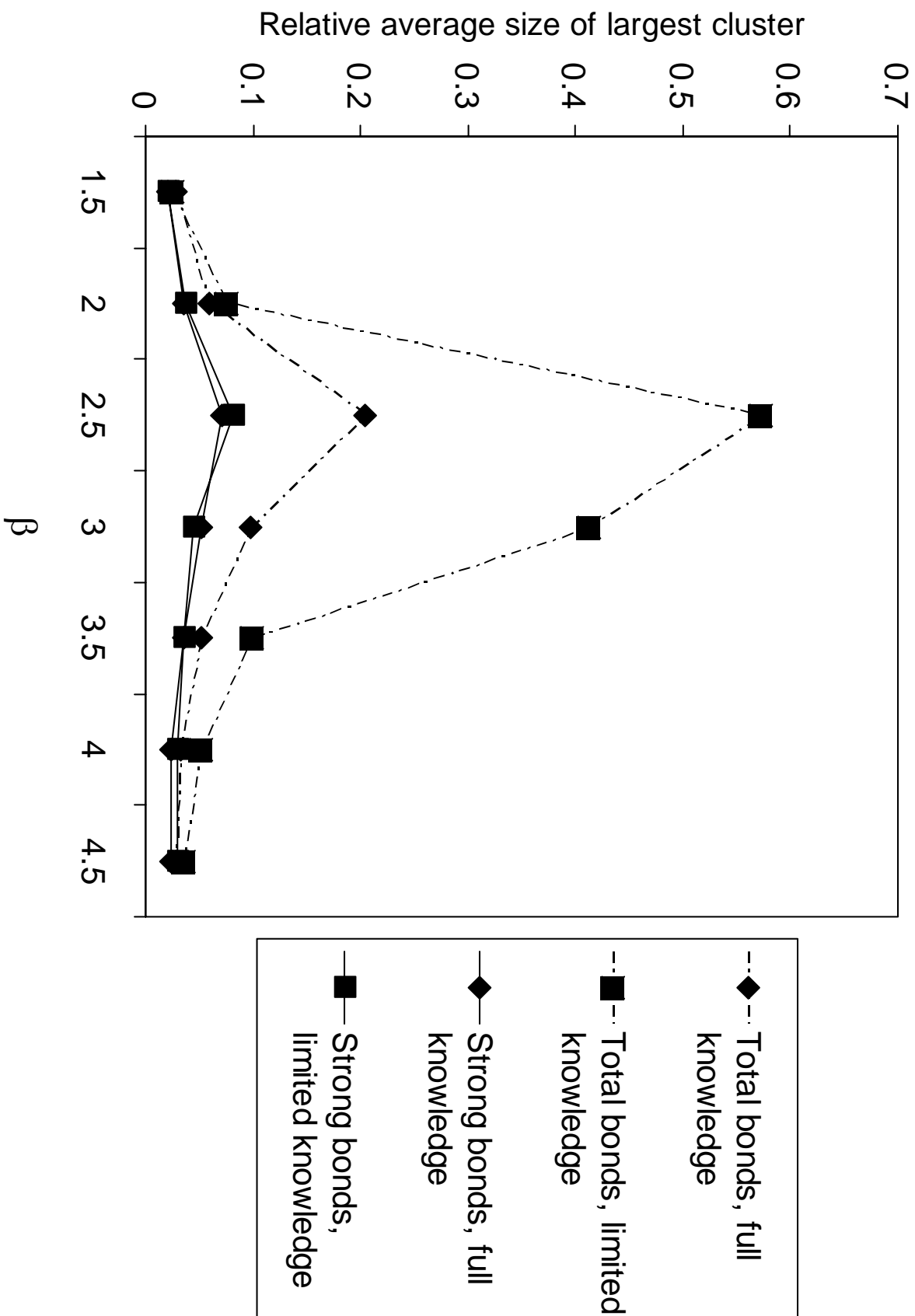


Figure 6

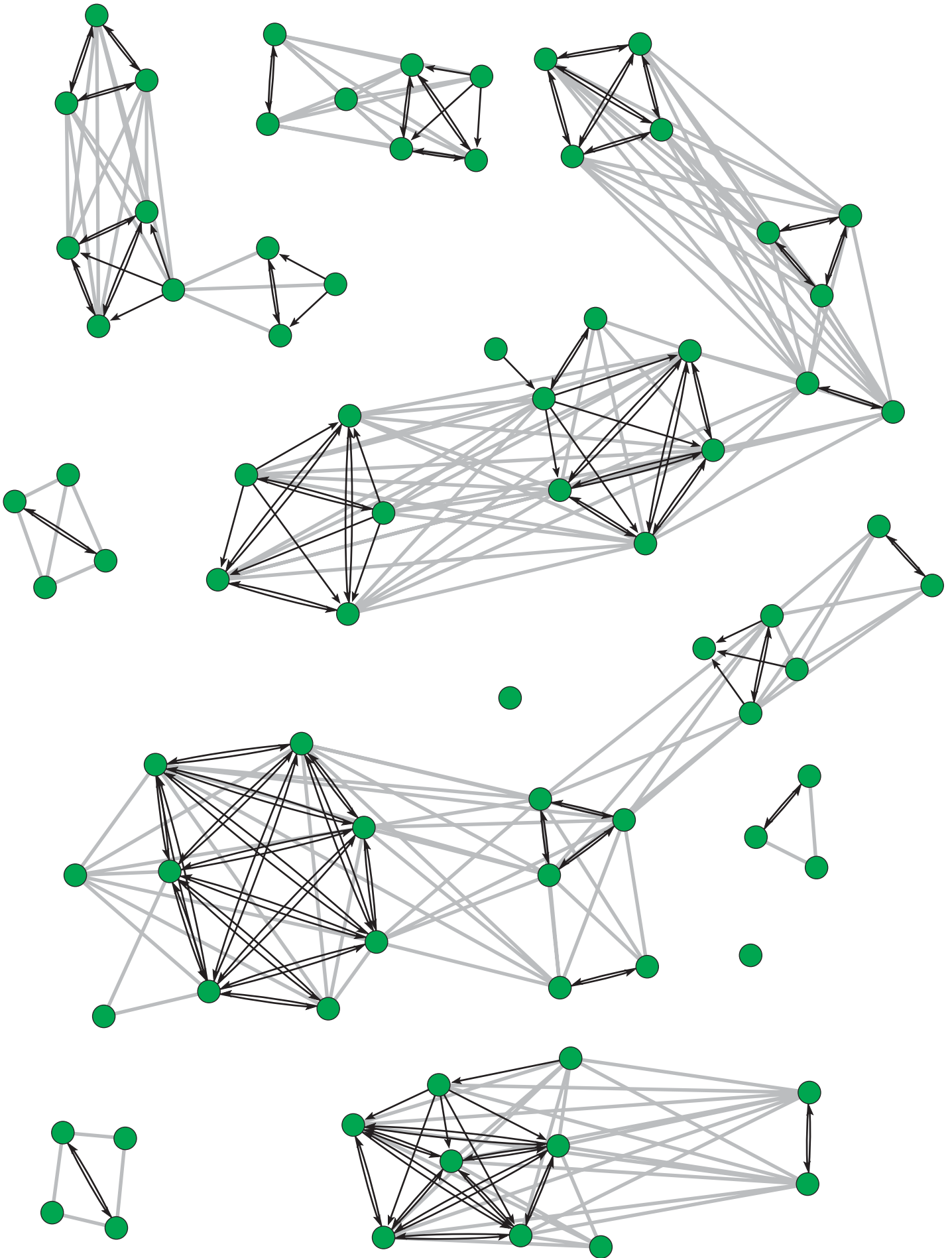


Table 1

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