An arms race between producers and scroungers can drive the evolution of social cognition

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4 The 'social intelligence hypothesis' states that the need to cope with complexities of 5 social life has driven the evolution of advanced cognitive abilities. It is usually invoked in 6 the context of challenges arising from complex intragroup structures, hierarchies and 7 alliances. However, a fundamental aspect of group living remains unexplored as a driving 8 force in cognitive evolution: the competition between individuals searching for resources 9 (producers) and conspecifics that parasitize their findings (scroungers). In populations of 10 social foragers, abilities that enable scroungers to steal by outsmarting producers, and 11 those allowing producers to prevent theft by outsmarting scroungers, are likely to be 12 beneficial and may fuel a cognitive arms race. Using analytical theory and agent-based 13 simulations we present a general model for such a race that is driven by the producer-14 scrounger game, showing that the race's plausibility is dramatically affected by the nature 15 of the evolving abilities. If scrounging and scrounging-avoidance rely on separate, 16 strategy-specific cognitive abilities, arms races are short-lived and have a limited effect 17 on cognition. However, general cognitive abilities that facilitate both scrounging and 18 scrounging-avoidance undergo stable, long-lasting arms races. Thus, ubiquitous foraging 19 interactions may lead to the evolution of general cognitive abilities in social animals, 20 without the requirement of complex intragroup structures.

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Keywords: game theory; social foraging; social intelligence hypothesis; intraspecific
arms race

24 INTRODUCTION

25 Recent decades have seen great interest in social cognition and its evolution, due largely 26 to the non-trivial nature of such abilities (e.g., putting one's self in others' shoes), as well 27 as the idea that coping with social challenges may underlie the evolution of general 28 intelligence (Shettleworth 2010). Indeed the latter suggestion, known as the 'social 29 intelligence hypothesis' (Jolly 1966; Humphrey 1976; Byrne and Whiten 1988), relies 30 heavily on the finding that species exhibiting advanced cognitive abilities often maintain 31 elaborate social structures. While this hypothesis initially referred to humans and other 32 primates, it has also been related to advanced cognition in other species, including 33 corvids (Emery and Clayton 2004), hyenas (Holekamp 2007), and cetaceans (Marino 34 2002). However, regardless of such elaborate social structures, group-living animals face 35 a more fundamental challenge which is often ignored in this context: social foraging 36 (Giraldeau and Caraco 2000).

37

Foraging together for resources is a ubiquitous feature of group living, observed across taxa from insects to humans; it is perhaps one of the most common forms of social interaction, as it spans fundamental aspects of life such as food and shelter. Social foraging interactions have been framed in terms of the producer-scrounger (PS) game, in which individuals have the option either to produce (i.e. independently search for) resources, or scrounge them from producers (Barnard and Sibly 1981; Barnard 1984; Giraldeau and Caraco 2000; Giraldeau and Dubois 2008).

45

46 While scrounging saves the time and energy that must be invested in order to produce 47 resources, it requires a sufficiently high frequency of producers in the population to be 48 beneficial. The negative, frequency-dependent selection operating on these two strategies 49 results in a mixed evolutionarily stable strategy (ESS) (Barnard and Sibly 1981; Barnard 50 1984; Giraldeau and Caraco 2000; Giraldeau and Dubois 2008). In such populations, 51 selection can be strong enough to give rise to a suite of scrounging-avoidance tactics by 52 producers, and consequent counter-tactics by scroungers (Barnard 1984; Coussi-Korbel 53 1994; Emery and Clayton 2001; Flynn and Giraldeau 2001; Bugnyar and Kotrschal 2002; 54 Held et al. 2002; Bugnyar and Heinrich 2006; Shaw and Clayton 2013). Thus, selection 55 on social foragers to outsmart each other can lead to an intraspecific evolutionary arms 56 race (Dawkins and Krebs 1979) that results in increased cognitive abilities (Barnard 57 1984; Bugnyar and Kotrschal 2002; Grodzinski and Clayton 2010).

58

59 In many species of social foragers, the PS game may have selected for cognitive 60 adaptations that involve plastic responses to the presence of others (an 'audience effect') 61 (Barnard 1984; Byrne and Whiten 1988; Coussi-Korbel 1994; Norris and Freeman 2000; 62 Emery and Clayton 2001; Flynn and Giraldeau 2001; Bugnyar and Kotrschal 2002; Held 63 et al. 2002; Bugnyar and Heinrich 2006; Shaw and Clayton 2013). For example, in spice 64 finches, as well as pigs and gorillas, producers keep their distance from potential 65 scroungers (Byrne and Whiten 1988; Flynn and Giraldeau 2001; Held et al. 2002); in 66 mangabeys and chimpanzees, producers lead scroungers away from food (Byrne and 67 Whiten 1988; Coussi-Korbel 1994); scrub jays return to re-cache, in private, food items 68 they have been observed by conspecifics to have been hiding (Emery and Clayton 2001);

69 Eurasian jays attempt to prevent auditory information of their caching activities from 70 reaching potential scroungers (Shaw and Clayton 2013); scrounging ravens watch 71 caching from a distance and delay their approach until the cacher (producer) has left 72 (Bugnyar and Heinrich 2006), and scrounging chimpanzees may hide to watch 73 conspecifics recover food, and emerge from hiding to steal it (Byrne and Whiten 1988). 74 While success in the PS game may be influenced by a number of traits, from body size to 75 dominance ranking (Giraldeau and Beauchamp 1999), these observations suggest that 76 potential targets for adaptation are likely to include data-processing and decision-making 77 abilities. However, the cognition underlying such abilities is likely to entail a cost, which 78 may be developmental, physiological and/or derived from prolonged data processing (e.g. 79 Burger et al. 2008).

80

81 Here, we examine the conditions under which mutations in the cognitive apparatus that 82 increase performance in the PS game provide sufficient benefit to outweigh such costs, 83 and analyze the consequences of evolving general versus strategy-specific cognitive 84 abilities. As the nature of the cognitive abilities involved in the aforementioned examples 85 is far from clear, it is impossible to model them in any detail without restricting the 86 generality of the model. To avoid this, we model these cognitive abilities simply as traits 87 affecting the performance of producers and scroungers competing against each other (as 88 detailed below). Consequently, our model is in fact much more general, and concerns any 89 such traits.

90

92 MODEL AND RESULTS

We model a population of social foragers playing the PS game. We consider both the case of individuals playing pure social foraging strategies, and the more realistic case of mixed strategies. For simplicity we describe the pure strategy model first, and then extend it to include mixed strategies.

97

98 Basic model and the scrounging success probability function

99 Each generation consists of multiple rounds of foraging, and in each round some fraction 100 of producers finds food and receives a payoff. A producer that finds food experiences 101 scrounging attempts with probability f, which, if scrounging is successful, causes the 102 payoff to be evenly split between the scrounger and the producer. The probability that a 103 scrounging attempt is successful, σ , is determined by the difference d in cognitive 104 abilities between the scrounger and the producer: scroungers with relatively advanced 105 cognitive abilities are more often successful at obtaining food, whereas producers with 106 relatively advanced abilities are more often successful at avoiding loss of food to 107 scroungers. It is then reasonable that σ should increase monotonically with the cognitive 108 difference d. We model this effect by assuming that σ is a logistic function of d: $\sigma(d) = a + (1 - a)/(1 + e^{-sd})$. The parameter 0 < a < 1 determines the size of the effect that 109 110 cognition has on scrounging success: it represents the lowest possible scrounging success 111 rate, which occurs when a producer has an infinitely higher cognitive level than a scrounger (*i.e.* $d \rightarrow -\infty$). In other words, if a is large the influence of cognition should be 112 113 weak, as scrounging is then likely to succeed regardless of the exact difference in 114 cognitive abilities. We assume that the probability of successful scrounging is not

115	determined solely by cognitive abilities, but that these abilities are still significant in
116	determining scrounging success (<i>i.e.</i> $0 < a < 1$). The parameter <i>s</i> determines the size of
117	the effect that a single cognitive mutation has on the probability of successful scrounging:
118	each mutation changes σ by $\sim s$ until it saturates at some maximum or minimum value for
119	sd >> 1. The effects of these assumptions can be seen in Figure 1, which shows
120	scrounging success probability as a function of <i>d</i> for different values of <i>a</i> and <i>s</i> .
121	
122	Effect of cognitive mutations on fitness
123	Given the probability of scrounging success σ , the relative fitness advantage $\alpha_{\scriptscriptstyle P}$ of a
124	mutation that changes producers' cognitive ability by δ is given by
125	$\alpha_P(\delta) = e^{-\delta\gamma} \left[1 - f\sigma(d-\delta)/2\right] / \left[1 - f\sigma(d)/2\right] - 1$, where γ scales the cost of increasing
126	cognitive ability. The advantage α_s of a mutation that changes scroungers' cognitive
127	ability by δ is given by $\alpha_s(\delta) = e^{-\delta \gamma} \sigma(d+\delta) / \sigma(d) - 1$.
128	
129	To be advantageous, the potential benefits of cognition-increasing mutations in relation to
130	the PS game must outweigh their cost (corresponding roughly to $s > \gamma$), which we will
131	assume in what follows. However, this does not guarantee that increasing cognition is
132	always favored, because the advantage of a mutation that increases cognitive ability in a
133	producer (scrounger) depends on its current cognitive level relative to scroungers
134	(producers) (Fig.2). When scroungers are slightly smarter than producers (i.e. d is small
135	and positive), producers are selected to increase their cognitive level. When producers are
136	slightly smarter than scroungers (d is small and negative) scroungers are selected to

137 increase their cognitive level. Thus, small differences in cognitive level support an

138 evolutionary arms race between social foraging strategies (Fig. 2). On the other hand,

139 cognitive differences that are too large have remarkably different consequences. If the

140 producers are substantially smarter than the scroungers (*d* is large and negative), or vice

141 versa (*d* is large and positive), the probability of successful scrounging, σ , is only slightly

142 affected by further mutations, because it is close to either of its asymptotic values (a or 1,

143 respectively). Since the benefit of an increased cognitive level is low in such cases, it is

144 outweighed by the cost, and selection will favor decreased cognitive levels (Fig. 2).

145

146 Effect of specialized vs. generalized cognition on the race

147 We consider two possibilities for the influence of cognition on the PS game. In the

148 generalized cognition model (GCM), a single cognitive trait, 'C', determines both the

ability to successfully scrounge and the ability to avoid being scrounged when producing.

150 In the specialized cognition model (SCM), one trait, '*Cs*', determines scrounging ability,

151 while another, '*Cp*', determines the ability of producers to avoid being scrounged.

152 Comparing both types of models analytically and using agent-based simulations, we

153 show that the SCM is unable to support a consistent arms race and results either in

154 scroungers' extinction or in a race to decrease cognitive level (a 'backwards race'). The

155 GCM, in contrast, exhibits persistent arms races, a result independent of the specific

156 conditions.

157

158 We use agent-based computer simulations to demonstrate the population dynamics of this

159 competition. Here, fitness is determined through explicitly-modeled repeated PS

160 interactions rather than through the abovementioned fitness functions α_p and α_s . A

161	population commences at some baseline cognitive level, labeled 'level 0' for
162	convenience. A generation consists of T repeated foraging interactions as described
163	above, and at each interaction scroungers are randomly assigned to successful producers
164	(one scrounger per producer); the probability of successful scrounging at each interaction
165	is determined by the relative cognition of the specific producer and scrounger involved,
166	using the aforementioned function $\sigma(d)$. Mutations increasing (+1) or decreasing (-1)
167	cognitive level, as well as mutations in social foraging strategy (transforming a producer
168	into a scrounger or vice versa) occur randomly at a low rate, μ , at each generation. The
169	number of offspring per individual is set probabilistically, based on the relative payoff
170	accumulated through its lifetime (see SI section 2 for full details of the simulations).
171	
172	In a population initially made up of individuals with equal cognitive abilities, the
173	scroungers' relevant cognitive ability (C in the GCM, Cs in the SCM) typically increases
174	in either type of model (Fig. 3). This increases the probability that scrounging is
175	successful, intensifying the selective pressure on producers to avoid being scrounged and
176	leading producers' relevant cognitive ability (C in the GCM, Cp in the SCM) to rise.
177	Improved producer cognitive ability, in turn, puts pressure on scroungers to re-adapt, and
178	the consequent positive feedback loop leads to a continuous evolution of increased
179	cognitive abilities in both producer and scrounger populations (Fig. 3). The rate of this
180	increase depends on the rate and magnitude of cognitive mutations: higher mutation rates
181	and higher values of s result in faster-evolving races (see SI). In the SCM, the escalation
182	in relevant cognitive abilities is accompanied by a decrease in the unused cognitive
183	abilities (Cs for producers, Cp for scroungers), due to their cost.

185	Such arms races occur in both the GCM and the SCM, and are temporarily stable as long
186	as cognitive differences between foraging types are small, consistent with our analysis
187	above showing that small d values support an evolutionary arms race. However, the arms
188	race is interrupted when either foraging type acquires a large cognitive advantage over
189	the other ($ sd >> 1$); such an advantage emerges stochastically due to the random
190	processes in the simulation and finite population size. If producers have a sufficiently
191	large advantage, the (unsuccessful) scroungers cannot obtain resources and are driven to
192	extinction. Once this happens, they can only reappear through mutation that converts a
193	producer into a scrounger. In the SCM, such mutants will have the high Cp and low Cs
194	values typical of producers, but since this makes them unfit as scroungers, scroungers
195	cannot recover from extinction (Fig. 3a). In the GCM, however, a mutant's high
196	cognitive ability C, inherited from its producer parent, will make it a good scrounger.
197	This enables scroungers to re-invade the population, reestablishing the cognitive arms
198	race from the current cognitive level of the population (Fig. 3b).
199	
200	A large cognitive advantage for scroungers, in contrast, will not lead producers to

200 A large cognitive advantage for scroungers, in contrast, will not lead producers to
201 extinction, due to the frequency-dependence of the PS game. Instead, mutations that
202 decrease producers' cognitive level will be favored because the benefits in reducing
203 cognitive costs will outweigh their effect on scrounging-avoidance success (which is
204 minimal under these conditions since scroungers are much smarter). Once producers'
205 cognitive levels are reduced, selection will act on the scroungers to follow suit for similar
206 cost-saving reasons, resulting in a 'backwards' race. This 'backwards' race scenario is

207	likely to occur and escalate in SCM populations (Fig. 3c), but in GCM populations a
208	large cognitive advantage for scroungers will quickly be reduced by scroungers mutating
209	into producers while retaining their high C levels, thus reestablishing the race.
210	
211	Mixed strategies
212	So far we have considered pure producers and pure scroungers. In nature, however, the
213	PS trait is usually manifested as a mixed strategy, and individuals have been observed to
214	employ both strategies to varying degrees based on their previous experience and on
215	social and environmental conditions (Mottley and Giraldeau 2000; Katsnelson et al.
216	2008; Morand-Ferron and Giraldeau 2010; Katsnelson et al. 2011). In simulations of both
217	of our models, inclusion of mixed strategies yields qualitatively similar results to those
218	described above: GCM races persist, while SCM races are bound to collapse. As in the
219	pure-strategy case of the SCM, gaps between Cp and Cs arise stochastically. If Cs
220	becomes much larger than Cp, the latter decreases (as in the pure case) to avoid cognitive
221	costs, resulting in a 'backwards race' (Fig. 3d). If Cp becomes much larger than Cs,
222	selection favors foraging strategies that produce as often as possible, and scrounging
223	disappears from the population (Fig. 3e), as in the pure case. This disappearance of
224	scrounging from the population as its adaptive value decreases is plausible given that in
225	nature, social foraging strategies can be adjusted to provide better solutions for changing
226	environmental conditions (Mottley and Giraldeau 2000).
227	
228	

230 Ending the race

231 As shown above, arms races involving general cognitive abilities are not limited by the 232 instability and short-life typical of those involving specialized cognition. However, it 233 does not follow that these arms races will continue forever. For example, when cognition-234 costs become too high compared to their benefits the population may go extinct. As costs 235 become too high the population may also become prone to invasion by migrants with 236 baseline cognitive levels; such an invasion is possible because these migrants, despite 237 their poor cognitive abilities, do relatively well altogether as they do not suffer such high 238 cognitive costs. In this case, a cyclic pattern of escalation and collapse may emerge, as 239 the population repeatedly regresses to the cognitive baseline and then restarts the arms 240 race (Fig 3f). Alternatively, a general cognitive ability may co-evolve with other traits 241 (such as foraging efficiency or diet, in our case), changing the very parameters 242 considered here that govern the evolution of social cognition. Interestingly, increased 243 general cognition resulting from the race may have pleiotropic benefits, such as enabling 244 the exploitation of new food sources or habitats, which could themselves outweigh the 245 costs of cognition. Conversely, if producers become better at exploiting food sources, 246 producing may become much more profitable than scrounging. The consequent low 247 frequency of scroungers will make the PS game less important, slowing down the 248 cognitive arms race or drawing it to an end.

249

250 **DISCUSSION**

251 Our results suggest that a cognitive arms race improving performance of players in the 252 producer-scrounger game can persist and escalate, but only if it involves a general

253 cognitive ability competing against itself. Arms races between two separate abilities may 254 escalate temporarily, but are bound to collapse. In the present formulation, the increased 255 stability of arms races, when they involve generalized rather than specialized cognitive 256 abilities, is independent of the specific details of our model. Indeed, arms races involving 257 a single trait should generally be more stable than those between two (or more) traits that 258 mutate and evolve separately, since destabilizing asymmetries will arise less frequently in 259 the former. That intra-species arms races should tend to persist for longer than inter-260 species ones is one possible implication.

261

262 Intraspecific evolutionary arms races are often mentioned in the context of sexual 263 selection (Dawkins and Krebs 1979), sexual conflicts (Chapman et al. 2003), brood 264 parasitism (Petrie and Møller 1991) and parent-offspring conflict (Kilner and Hinde 265 2008). Social foraging adds a further, rather general framework within which multiple, 266 unrelated traits may each evolve by racing "against itself". While the model we present 267 here was designed with cognition in mind, it is, as stated above, certainly not limited to 268 cognitive abilities. It appears that the producer-scrounger game can facilitate the 269 evolution of many traits that improve scrounging and scrounging-avoidance: body-size, 270 aggressiveness, motivation, and more.

271

That our model applies to a range of traits affecting interactions among foragers may
indeed suggest that improved cognition is not the only possible consequence of social
living. However, we believe that cognition might be especially affected, for two reasons.
First, as mentioned in the introduction, there is strong evidence that cognitive abilities

276 such as information processing, learning, and decision-making have strong effects on 277 scrounging and scrounging-avoidance. Second, many other relevant traits, such as body 278 size, are likely to be under strong stabilizing selection as the cost of increasing them 279 becomes too high. For example, developing and maintaining a large body size requires 280 high energy intake and may entail a higher risk of predation (e.g. Blanckenhorn 2000; 281 Quinn, Hendry, and Buck 2001; Rotella, Clark, and Afton 2003; Bonduriansky and 282 Brassil 2005; Herczeg, Gonda, and Merilä 2009); an escalation of aggressive behavior is 283 likely to result in high rates of injury and death, and is evolutionarily unstable (Maynard 284 Smith and Price 1973). Improved cognitive abilities are likely to involve a fitness cost as 285 well, as demonstrated in some species of insects (Burger et al. 2008; Snell-Rood, 286 Davidowitz, and Papaj 2011). Seemingly complex abilities can be achieved through 287 surprisingly simple neural structures (Chittka et al. 2012), but it is quite possible that 288 brain size evolution is constrained by the energetic costs of maintenance (Isler and van 289 Schaik 2006). However, maintaining a large body to an extent that will make a difference 290 in success in the game most probably requires greater energy than maintaining a 291 cognitive tweak that will achieve the same difference. In other words, it seems likely that 292 cognitive mutations that improve foragers performance in the PS game will tend to cost 293 less than an increase in body size or aggressive behavior that could provide the same 294 improvement. Thus, while our model describes a scenario applicable to many traits, 295 cognition may be one of the few for which the benefit and cost parameters fall in the 296 region supporting an arms race.

297

298 We have seen that the arms race in a trait is only stable if the trait contributes to both 299 scrounging and scrounging-avoidance; what general cognitive abilities, then, might serve 300 both of these tactics? The requirement that the ability must be useful for such distinct 301 behaviors strongly suggests some form of social cognition. An example consistent with 302 our model is the strategies used by some corvid species to protect food-caches from being 303 scrounged and to successfully pilfer others' caches. It has been suggested that these 304 strategies involve a general cognitive ability, and perhaps even some form of Theory of 305 Mind (Bugnyar and Kotrschal 2002; Dally, Clayton, and Emery 2006; Grodzinski and 306 Clayton 2010). Indeed, the finding that some cache-protection strategies require previous 307 experience in pilfering (Emery and Clayton 2001) lends some support to this notion 308 (Bugnyar and Kotrschal 2002; Dally, Clayton, and Emery 2006; Grodzinski and Clayton 309 2010). Our analysis shows that from an evolutionary perspective, evidence for advanced 310 cognitive abilities makes it more likely that they are general rather than due to cognitive 311 mechanisms that serve caching and pilfering separately, or else they would probably not 312 have evolved.

313

Decades ago, an arms race of cognitive abilities ('runaway intellect') was proposed within the context of the social intelligence hypothesis (Humphrey 1976). It was also suggested that Theory of Mind itself is likely to involve increasing degrees of complexity (Premack 1988). We show that the fundamental and ubiquitous interactions between social foragers can give rise to an arms race of general cognitive abilities. This raises the question of whether traits such as attribution of knowledge and intentions to others have

evolved in a much wider range of taxa than currently suggested and, if not, what hasinhibited them.

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- 413

415 FIGURE LEGENDS

416 Fig. 1. Successful scrounging probability, σ , for different values of cognition effect size

417 *a*, and cognitive mutation effect size *s*. Dashed black line: a = 0.7, s = 1.5; solid gray line:

418 a = 0.5, s = 0.5; solid black line: a = 0.5, s = 1.5; Dashed gray line: a = 0, s = 1.5.

419

420 **Fig. 2**. The selective advantage α_p to producers (solid line) and α_s to scroungers (dashed 421 line) accorded by a (+1) cognitive mutation, as a function of *d*, the cognitive difference 422 in favour of scroungers. The proportion of each foraging strategy is fixed at the 423 proportion found to evolve in computer simulations (0.7 producing, 0.3 scrounging). 424 Parameters values used: s = 1.5, a = 0.5, $\gamma = 0.05$.

425

426 Fig. 3. Examples of GCM and SCM population dynamics in agent-based simulations, 427 under various conditions. Black and white panels show producer frequency over time; 428 color panels show mean cognitive level over time: GCM (b, f) - two lines representing 429 mean C levels for producers (red) and scroungers (teal); SCM (a, c-e) – four lines 430 representing mean level of specialized cognitive ability for producing, Cp, in producers 431 (red) and scroungers (blue) and mean level of specialized cognitive ability for 432 scrounging, Cs, for producing, Cp, in producers (orange) and scroungers (teal). In 433 mixed-strategy simulations (d-e), 0-50% producing is included under 'scroungers', 60-434 100% producing is included under 'producers'. Where red line is not visible it is hidden 435 by the teal or blue lines. In all simulations population size n = 100; cognitive cost is a fractional deduction of size $\gamma = C/100$ in GCM, $\gamma = (Cp + Cs)/100$ in SCM; scrounging 436

- 437 success baseline probability a = 0.5; mutation rate $\mu = 1/n$ for all genes; mutations in
- 438 C/Cp/Cs increase or decrease cognitive ability by 1. Note that the y axis scales in colored
- 439 panels vary. (a) SCM, pure producing/scrounging (PS), s = 1.5. (b) GCM, pure PS,
- 440 s = 1.5. (c) SCM, pure PS, s = 0.5. (d) SCM, mixed PS, s = 1.5. (e) SCM, mixed PS,
- 441 s = 1.5. (f) GCM, pure PS, random inwards migration of individuals with baseline
- 442 cognitive level (*C*=0).



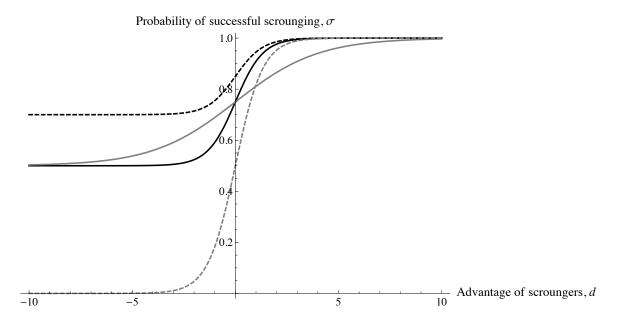
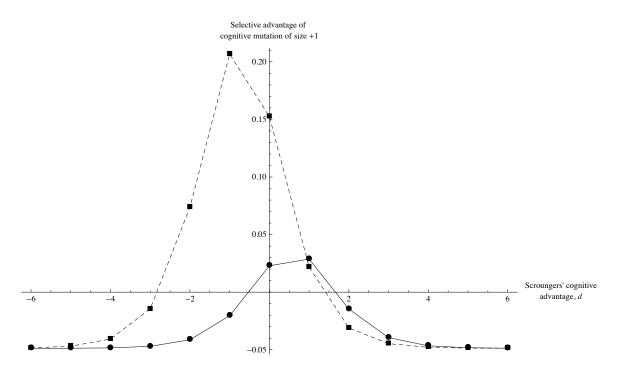
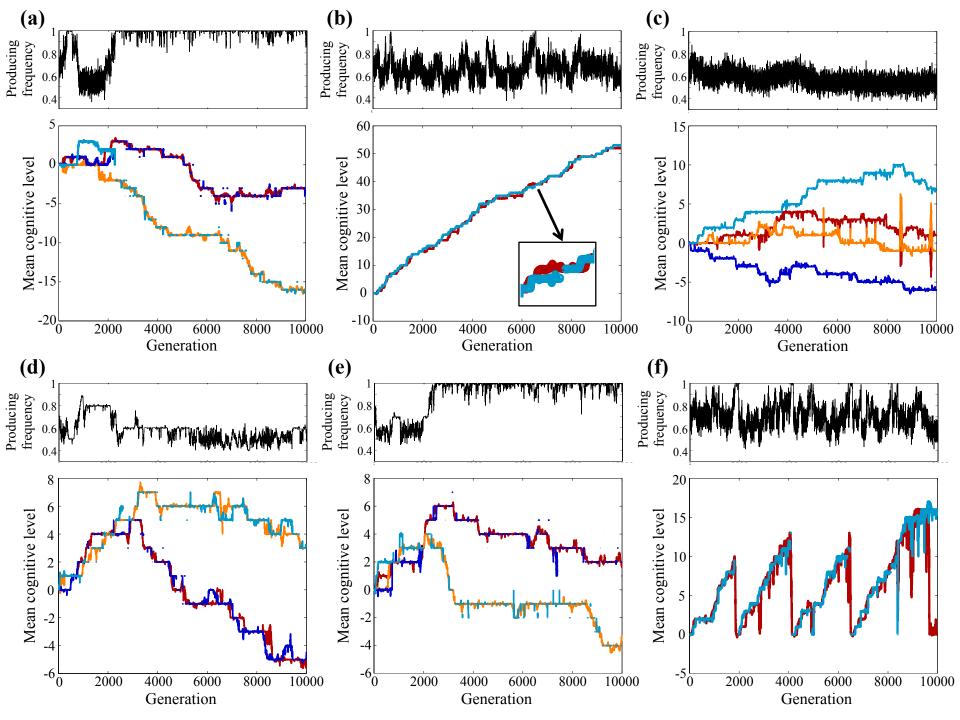


Figure 2





1	Supplementary Information
2	
3	We present below a mathematical analysis of the model for small parameter values,
4	complemented with computer simulations of evolving populations for a larger parameter
5	range.
6	
7	Symbols used throughout the paper and supplementary material are summarized in table
8	S1.
9	
10	1. Analytical model
11	We focus on a population of <i>n</i> individuals, a variable fraction φ of which are pure
12	scroungers, and $1-\varphi$ of which are pure producers. Each individual has a cognitive level
13	C that determines how good it is at scrounging (for scroungers) or avoiding being
14	scrounged (for producers). Each generation comprises many foraging steps. In one such
15	step, a fraction ρ of the producers each finds one unit of food. Each scrounger is then
16	randomly assigned to one of the producers that found food and attempts to scrounge. If
17	multiple scroungers are assigned to the same producer, only one (chosen randomly) is
18	allowed to attempt to scrounge. With probability σ (given above), the scrounging attempt
19	is successful and the producer and scrounger split the food evenly. Once all the foraging
20	steps are completed, the next generation is produced according to a Wright-Fisher
21	process, with each individual's fitness proportional to the total amount of food it acquired,
22	multiplied by a factor $e^{-\delta \gamma}$ to account for the cost of additional cognition. In this
23	analytical section, we will focus on parameter values ρ , $s << 1$ and $a = 0$; we examine

24 larger values ($\rho = 0.25$, $s \sim 1$, a = 0.5) in the simulation section below.

25

26 <u>1.1. Frequency of scroungers</u>

27 In the following analysis, we will assume that mutations are sufficiently rare ($n\mu \ll 1$) 28 that there is a separation of timescales. Each foraging type is usually fixed for a single 29 cognitive level, and producers and scroungers are present in the population at the 30 equilibrium frequency determined by the difference in cognitive levels. Occasionally, a 31 mutation occurs that changes either an individual's cognitive ability (by one level) or its 32 foraging type. If the mutation initially confers a selective advantage α , it has a chance to 33 escape drift and increase in frequency in the population. We assume that if it does so, it 34 fixes and the frequency of scroungers relaxes to its new equilibrium value before the next 35 mutation occurs. We now find the equilibrium frequency of scroungers (note that this is 36 always complemented by the frequency of producers).

37

We assume that each scrounger independently chooses a producer with food from which it attempts to scrounge, but that if multiple scroungers choose the same producer, only one can actually make a scrounging attempt. (This is the same model as in the simulation section 2.1.2 below.) Since there are $n\varphi$ scroungers and $n\rho(1-\varphi)$ producers with food, the probability *f* that a producer that finds food will face a scrounging attempt is

43
$$f = 1 - \left[1 - \frac{1}{n\rho(1-\varphi)}\right]^{n\varphi}$$
, and the probability that, in a given foraging step, a scrounger

will find a producer with food that is also available to be scrounged from is fρ(1-φ)/φ.
Assuming that *n* is large enough that many producers find food every foraging step

46 $(n\rho(1-\varphi) >> 1), f$ is approximately

47
$$f = 1 - \exp\left[-\frac{\varphi}{\rho(1-\varphi)}\right]$$
. (2)

48 The two foraging types then have relative fitnesses (up to an overall normalizing 49 constant) w_P and w_S given by their expected payoffs, adjusted for the cost of cognition:

50

51
$$w_p = \rho \left[1 - \frac{\sigma(d)}{2} f \right]$$
 (3)

52
$$w_s = e^{-\gamma d} \frac{\sigma(d)}{2} \frac{f\rho(1-\varphi)}{\varphi}.$$
 (4)

53 The equilibrium frequency of scroungers, $\dot{\varphi}$, is the value of φ at which $w_p = w_s$; 54 scroungers go extinct if $w_p(\varphi = 0) > w_s(\varphi = 0)$.

55

56 In order to find a simple approximate expression for $\hat{\varphi}$, note that for scroungers to be 57 maintained in the population, it must not be too easy for producers to find food, *i.e.*, ρ 58 must be small. Assuming that $\rho \ll \varphi$, we have $f \approx 1$, and therefore from (3) and (4)

59
$$\hat{\varphi} \approx \frac{\sigma e^{-\gamma d}}{2 - \sigma (1 - e^{-\gamma d})}.$$
 (5)

Further assuming that the cognitive gap is not likely to grow to levels such that it imposes an enormous selective disadvantage, we have $|\gamma d| << 1$, and we can further approximate

62
$$\hat{\varphi} \approx \frac{\sigma}{2} \left[1 - \gamma d \left(1 - \frac{\sigma}{2} \right) \right].$$
 (6)

63 Figure S1 shows the accuracy of this approximation.

65 <u>1.2. Selective coefficients of mutations</u>

As stated in the main text, the selective advantage of a mutation increasing cognitive abilities by δ is $\alpha_P(\delta)$ for producers and $\alpha_S(\delta)$ for scroungers, where α_P and α_S are given by:

69
$$\alpha_{p}(\delta) = e^{-\gamma\delta} \frac{1 - f\sigma(d - \delta)/2}{1 - f\sigma(d)/2} - 1$$
 (7)

70
$$\alpha_s(\delta) = e^{-\gamma\delta} \frac{\sigma(d+\delta)}{\sigma(d)} - 1.$$
 (8)

71 We assume that scroungers are at a frequency $\hat{\varphi} >> \rho$, so that $f \approx 1$ in the above

equations. Further assuming that each mutation has only a small effect on scrounging

- 73 probability or cognitive cost ($|s\delta| << 1$ and $|\gamma\delta| << 1$), the right-hand sides of (7) and (8)
- 74 are approximately given by the first-order Taylor expansions in δ :

75
$$\alpha_{P}(\delta) = \delta \left[\frac{s\sigma(d)(1 - \sigma(d))}{2 - \sigma(d)} - \gamma \right] + O(\delta^{2})$$
(9)

76
$$\alpha_s(\delta) = \delta[s(1 - \sigma(d)) - \gamma] + O(\delta^2).$$
 (10)

(Recall that we assume that a=0.) The behaviors of $\alpha_P(1)$ and $\alpha_S(1)$ as functions of *d* are shown is figure S2.

79

80 <u>1.3. Speed of the cognitive arms race</u>

81 In populations experiencing a stable cognitive arms race, the gap between the cognitive 82 levels of the two foraging types settles down to a roughly steady value \hat{d} at which both 83 types increase in cognitive level at the same rate. In the rare-mutation regime we are 84 considering, this rate is given by the mutation supply times the probability that mutants

- 85 with a cognitive ability increased by one unit ($\delta = +1$) will fix. Assuming that $\alpha_p(1)$ and
- 86 $\alpha_s(1)$ are small compared to one, the probability of fixation is only 2α (Ewens 2004).
- 87 The two foraging types therefore evolve higher cognition at the same rate when

88
$$n\left(1-\hat{\varphi}\right)\mu\left(2\alpha_{p}(1)\right)=n\hat{\varphi}\mu\left(2\alpha_{s}(1)\right), i.e., \text{ when}$$

89
$$\left(1-\hat{\varphi}\right)\alpha_{P}(1)=\hat{\varphi}\alpha_{S}(1).$$
 (11)

90 Inserting the above expression (6) for $\hat{\varphi}$, and (9) and (10) for α_p and α_s , and assuming 91 that food is hard to find ($\rho \ll 1$), this reduces to

92
$$(1-\sigma)\left(1-\frac{sd\sigma}{2}\right) \approx \gamma d\sigma \left(1-\frac{\sigma}{2}\right).$$
 (12)

93 When the cost of cognition is low ($\gamma \ll s$), the expression simplifies further to $d \approx 2/s\sigma$, 94 and we find that the rates of advance balance at a cognitive gap of

95
$$\hat{d} \approx \frac{2}{s}$$
, (13)

96 corresponding to a probability of scrounging success $\sigma \approx 0.9$. This is illustrated in Figure 97 S3, where the blue and purple curves intersect at $d \approx 2/s$. At this value of *d*, both 98 producers and scroungers accumulate cognitive mutations at a rate of approximately 99

$$100 \qquad n\left(1-\hat{\varphi}\right)\mu\left(2\alpha_{P}(1)\right) \approx n\,\hat{\varphi}\,\mu\left(2\alpha_{S}(1)\right) \approx \frac{n\mu s}{10}\left(1-\frac{10\gamma}{s}\right). \tag{14}$$

101 Note that if the cost of cognition is too large $(\gamma > \frac{s}{10})$, a stable race is impossible; either 102 cognition is too costly to ever evolve, or else it quickly becomes too costly for producers 103 to keep up with scroungers, leading to the collapse of the race.

104

105

106 <u>1.4. Mixed strategies and sexual reproduction</u>

107 Above, we have focused on asexual populations of individuals following pure producing 108 or scrounging strategies. We now consider the opposite limit, in which nearly all 109 individuals follow a single mixed foraging strategy, scrounging with probability φ and 110 producing with probability $1-\varphi$. Equivalently, we can consider a sexual population of 111 individuals following pure strategies with frequent recombination between the foraging 112 locus and the cognition locus or loci. In both cases, producer-scrounger interactions will 113 typically occur between individuals with the same cognitive genotype, and cognitive 114 mutations will, on average, be present in an individual acting as a scrounger with 115 frequency φ , and in an individual acting as a producer with frequency $1 - \varphi$. We will 116 continue to assume that the dynamics of the foraging strategy locus are fast, so that the 117 scrounging frequency can be approximated by its equilibrium value given the current cognitive genotype of the population, $\varphi = \dot{\varphi}$ (for the mixed strategy case, this means that 118 119 we assume that the population is at the evolutionarily stable foraging strategy). 120

121 In this case, the selective coefficients on cognitive mutations of size δ are

122
$$\alpha_{P}(\delta) = e^{-\gamma\delta} \left[\hat{\varphi} + \left(1 - \hat{\varphi}\right) \frac{\left(1 - f\sigma(d - \delta)\right)/2}{\left(1 - f\sigma(d)\right)/2} \right] - 1$$
(14)

123
$$\alpha_{s}(\delta) = e^{-\gamma\delta} \left[1 - \hat{\varphi} + \hat{\varphi} \frac{\sigma(d+\delta)}{\sigma(d)} \right] - 1.$$
(15)

124 When food is hard to find ($\rho \ll 1$) and mutations are small ($|s\delta|, |\gamma\delta| \ll 1$), these are both

126
$$\alpha(\delta) \approx \delta \left[\frac{s\sigma(1-\sigma)}{2} - \gamma \right].$$
 (16)

127 Since mutations increasing the producing and scrounging cognitive levels both appear in 128 the population at rate $n\mu$, the rate of increase of cognition (assuming $\delta = 1$ for all 129 mutations) is

130
$$n\mu\alpha(1) \approx n\mu\left(\frac{s}{8} - \gamma\right)$$
 (17)

131 as long as cognitive levels remain roughly balanced (|sd| << 1, so that $\sigma \approx \frac{1}{2}$).

132

133 2. Agent-based simulations

134 <u>2.1. General properties</u>

135 *2.1.1. The population*

136 We simulated a population of n = 100 haploid social foragers. Foragers' PS behavior was

- 137 determined by their genotype in the F gene, which was their probability to play the
- 138 producer strategy. A pure producer carries the *F* genotype of 1, a pure scrounger carries
- 139 0; an agent with an *F* genotype of, for example, 0.7, played producer with probability 0.7
- 140 on any given foraging step, and scrounger with probability 0.3. In pure-strategy
- simulations, the only possible *F* alleles were 0 and 1, and in mixed-strategy simulations

142	there were 11 possible alleles: 0, 0.1, 0.2 1. Alleles included in the simulation were
143	assigned at equal probabilities in the population's first generation.

145 Cognitive ability was determined by the C gene in the General Cognition Model (GCM)

146 and by the *Cp* and *Cs* genes in the Specialized Cognition Model (SCM). In both models,

147 foragers' cognitive level in the first generation was set to zero, *i.e.* in the GCM all

148 foragers had the 0 allele in the *C* gene, and in the SCM all foragers carried the 0 allele in

149 both the *Cp* and *Cs* gene.

150

151 *2.1.2. The producer-scrounger game*

152 The lifetime of one generation included a series of 50 PS interactions, or steps, which 153 were independent of each other and their order unimportant. This number of steps was 154 chosen in order to allow foragers to interact with a large sample of the population. At the 155 beginning of each step, all foragers draw a PS strategy according to their F genotype, and 156 those who play producer receive a set payoff (e.g. 4, although the value does not matter) 157 at a probability of 0.25. This probability was set to introduce a cost to the producer 158 strategy and to allow an effective PS game. Foragers who play scrounger are then 159 assigned randomly and independently to producers who found food. We assume only one 160 scrounger can join each successful producer, and therefore if two or more scroungers are 161 assigned to the same producer, only one of them will be able to attempt scrounging. The 162 difference *d* between the (relevant) cognitive levels of the scrounger and producer 163 involved was calculated as d = [scrounger's C] - [producer's C] in the GCM and as d = [scrounger's C] - [producer's C]164 [scrounger's Cs] – [producer's Cp] in the SCM. In the case of successful scrounging, the

165	scrounger receives half of the producer's food finding. It should be noted that when
166	setting scrounging success probability to 1, such populations evolve a PS ratio fluctuating
167	around $0.5:0.5$. Scrounging success baseline probability, <i>a</i> , used to calculate the
168	probability of successful scrounging $\sigma(d)$, was set to 0.5 in all simulations, to allow for a
169	stable producer-scrounger game under simulation conditions on one hand, and for
170	cognition to play a significant role in determining the probability of successful
171	scrounging on the other. Increasing the value of <i>a</i> will result in lower collapse rates in the
172	SCM; however, this contributes little to how cognitive abilities affect scrounging success
173	and we therefore ignore it here.
174	
175	2.1.3. Selection and reproduction
176	After completing 50 interactions, the foragers reproduce asexually, in proportion to their
177	relative lifetime accumulated payoff, and immediately die (population size remains
178	constant). Offspring are genetically identical to their parent, but for mutations, which
179	occur in all genes at a rate of $\mu = n^{-10}$. Mutations in the <i>F</i> gene change it within the
180	simulation's defined allele pool. In the cognition genes, a mutation changes the mutated
181	allele by one level, either increasing (+1) or decreasing it (-1). We allow the population to
182	evolve for 10,000 generations; under each parameter set, we repeated the simulation 100
183	times.
184	
185	

188 2.2. Factors affecting race speed and collapse rate

189 2.2.1. Cognitive mutation effect size (s)

190 We simulated populations under three possible values of s (mutation effect size): 0.25, 191 0.5 and 1.5. In both GCM and SCM populations, a larger s resulted in faster races; in 192 SCM populations, it also resulted in a higher collapse rate (Figure S4). When s is large, a 193 single mutation increasing cognitive level of a scrounger (producer) when the cognitive 194 difference between producers and scroungers is small or zero, entails a significant increase in the probability of successful scrounging (successful scrounging avoidance). 195 196 Such a mutant has a relatively large advantage over other individuals and the mutation is 197 therefore likely to spread rapidly. This spread, in turn, provides a background on which a 198 counter-mutation will have a large advantage, in the same manner. In GCM population 199 with pure strategies, this will be a mutation increasing the producer's or scrounger's 200 cognitive level C; in SCM populations, this will be a mutation increasing the cognitive 201 level relevant to the foraging allele (*i.e.* Cp for producers and Cs for scroungers). 202 Stochastic events, resulting from the probabilistic nature of the payoff distribution, 203 scrounger-to-producer assignment, selection, reproduction, and finite population size may 204 lead one side to accumulate more mutations and increase its cognitive level before the 205 other side responds, thus increasing the absolute value of d. When the cognitive 206 advantage of either side is large enough (e.g. d = -3 when s = 1.5), a single cognitive 207 mutation of ± 1 has a negligible effect on the scrounging or scrounging avoidance success 208 of its carrier, and its spread rate is very low. As we explain in the main text, if such a 209 large cognitive difference is to the advantage of producers, scroungers are likely to go 210 extinct before they can increase their cognitive level; if the difference is in favor of

211 scroungers, producers may begin decreasing their cognitive level because a lower 212 cognitive cost outweighs the slight reduction in scrounging-avoidance abilities. In GCM 213 populations a large cognitive difference is transient, as F gene mutations transfer 214 cognitive abilities between strategies, and the race resumes at roughly the same point 215 where it stopped. In SCM populations the race collapses or escalates "backwards" under 216 these conditions, because mutations in F uselessly transfer low Cs levels from producers 217 (who had no use for high Cs levels) to scroungers and low Cp levels from scroungers to 218 producers. How large the cognitive difference d must be to cause such effects depends on 219 s. When s, the effect size of cognitive mutations is large, relatively small values of d will 220 be sufficient for the race to collapse, leading to higher collapse rates for large s, as does 221 the generally faster race associated with large s values.

222

223 2.2.2. The effect of cognitive cost

224 We assume that a higher cognitive level incurs a cost, which may be developmental, 225 physiological or derive from the possibly longer processing times associated with high 226 cognitive levels. We use a cost proportional to the agent's cognitive level, which is a 227 fractional deduction from the final accumulated payoff. For example, maintaining 228 cognitive level 10 resulted in deductions of 10% of payoff, regardless of PS strategy. 229 Unsurprisingly, setting the cost to 0 (Figure S4a) resulted in faster races (compare to 230 Figure S4b). In SCM populations, it also caused the cognition genes which were 231 irrelevant to the foraging strategy (Cs for producers and Cp for scroungers) to drift rather 232 than decrease, as there was no selection acting on them in either direction. Additionally,

fewer race collapses occurred in such populations, but this was the case only for lower *s*values (see table S2).

235

236 <u>2.3. Evolution in the *F* gene</u>

237 In simulations where the F gene was free to evolve, the frequency of producers and 238 scroungers fluctuated; the F gene inevitably co-evolves with the genes determining 239 cognitive level, but the interaction is complex due to the negative frequency-dependence 240 defining the PS game. To examine the effect of these fluctuations on the arms race, and to 241 explore the nature of arms races in SCM populations where scroungers cannot become 242 extinct, we ran a set of simulations with no fluctuations by holding the frequencies of 243 producers and scroungers constant, at 0.7 and 0.3, respectively. This ratio was based on 244 the frequencies observed in populations where the cognitive level was held at 0 with no 245 cognitive mutations, while the F gene was allowed to evolve (producer frequency for the 246 last 100 of 10,000 generations was 0.697 ± 0.009 mean \pm SD; Population size n = 100, s =247 1.5; 100 simulation repeats). To still allow transfer of cognitive abilities between 248 producers and scroungers (a key feature of the GCM) while keeping PS frequencies fixed, we allowed F gene mutations (at a rate of $\mu = n^{-10}$) which changed one producer into a 249 250 scroungers and one scrounger into a producer (retaining their cognitive levels). 251 Incidentally, the effective mutation rate was thus doubled. 252 253 The arms race in GCM populations was faster under constant PS frequencies (Figure 254 S4d), which can be expected given the higher mutation rate. This result does, however,

255 indicate that the fluctuations in PS frequencies that are typical of the PS game are not the

256	driving force behind the arms race, as might be hypothesized. Interestingly, the fact that
257	scroungers could not go extinct did not promote consistent arms races in SCM
258	populations. Instead of extinction, once a large gap formed in cognitive abilities between
259	producers and scroungers, scroungers decreased their cognitive level and the race did not
260	progress (Figure S4d).
261	
262	References
263	Ewens, W. J. 2004. Mathematical Population Genetics. P. 25. Springer, New York.
264	

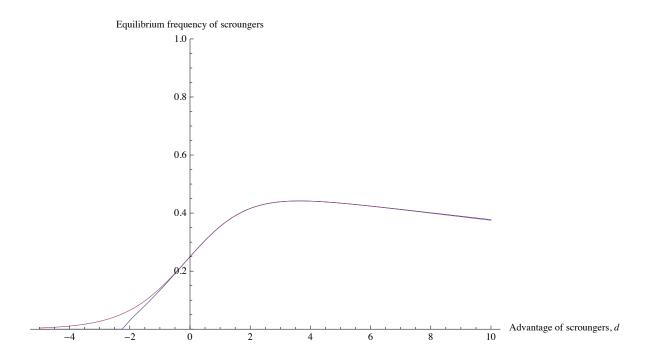


Figure S1. The equilibrium frequency of scroungers, $\hat{\phi}$, as a function of their cognitive advantage over producers, *d*. The blue curve shows the exact value obtained by solving Eqs. (3) and (4) for $w_p = w_s$, while the purple curve shows the approximate value given by Eq. (6). The other parameters are a = 0, s = 1, $\gamma = 0.05$, $\rho = 0.05$. As long as the probability of scrounging success, $\sigma(d)$, is larger than 2ρ , and the cost of cognition is not too high ($\gamma d \ll 1$), the frequency of scroungers is approximately $\hat{\phi} \sim \sigma/2$.

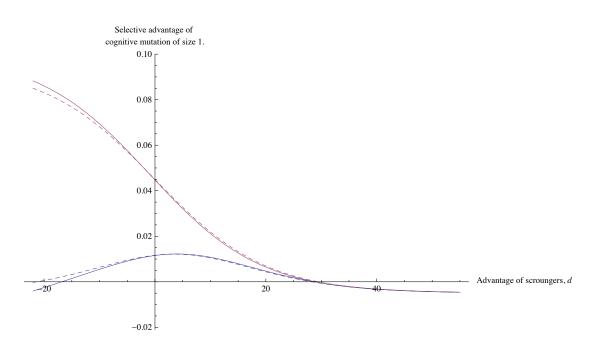


Figure S2. The selective advantage α for a mutation increasing the relevant cognitive ability by one unit in producers (blue) and scroungers (pink), as a function of the cognitive advantage of scroungers, *d*. The solid curves show the exact equations (7) and (8), while the dashed curves show the approximations (9) and (10). Negative values indicate that mutations reducing cognitive abilities are favored. The parameters are a = 0, s = 0.1, $\gamma = 0.005$, r = 0.05.

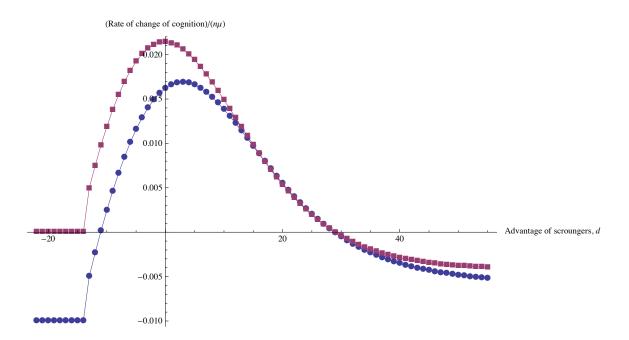
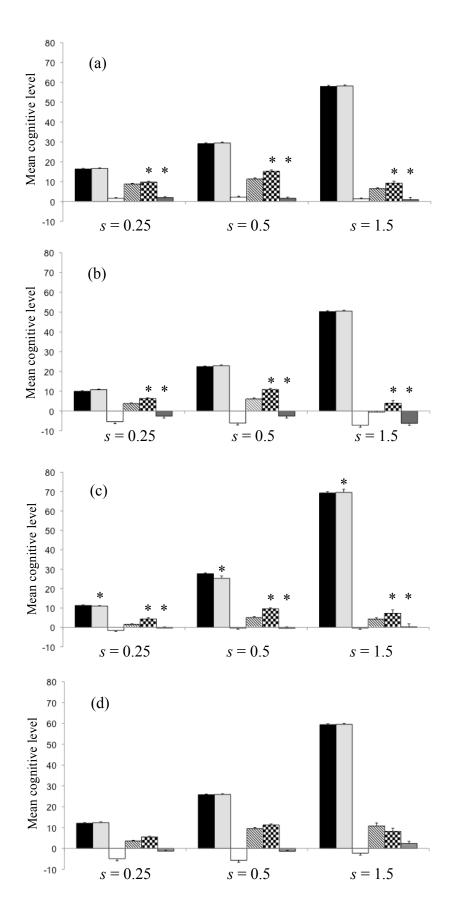


Figure S3. The rate at which mutations increasing cognitive ability are fixed, divided by $n\mu$, the number of mutations in the population per generation, as a function of the cognitive advantage of scroungers, *d*. The rate for producers is shown in blue, and for scroungers in pink. When the scroungers' rate is higher than that of the producers, the population will tend to move to higher values of *d*. Thus, the population will tend to move from d = 0 to $d \approx 20 = 2/s$ where the rates match. At very large values of *d*, producers tend to lose cognitive ability faster than scroungers, leading to a backwards race. At sufficiently negative values of *d*, scroungers are unable to get food and go extinct, removing the selection for cognitive abilities in producers. The parameters are a = 0, s = 0.1, $\gamma = 0.005$, r = 0.1.



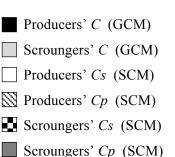


Figure S4. Mean and standard error of cognitive level among foraging strategies in agent-based-computer simulations of the GCM and SCM, under various assumptions. Each mean is calculated for generations 9,901-10,000, for 100 repeats of each simulation. Columns marked with (*) are means calculated for less than 90 repeats, i.e. at least 10 repeats did not have the marked genotype in at least one of the 100 generations considered (see table 2 for detailed account of valid data points). The three column groups in each subfigure corresponds to different values of s, slope coefficient of the scrounging success probability function. All simulations are for population size n = 100, T = 50 time steps, G = 10,000 generations, mutation rate $\mu =$ 0.01. (a) Pure social foraging strategies; cognitive level cost $\gamma = 0$. (b) Pure social foraging strategies; $\gamma = C/100$. (c) Mixed social foraging strategies (producing probability ≤ 0.5 alleles are grouped under "scrounger", producing probability > 0.5alleles are grouped under "producer"); $\gamma =$ C/100. (d) Pure social foraging strategies at fixed frequency of 0.3:0.7 scroungers to producers (i.e. no evolution in F gene); $\gamma =$ *C*/100.