Supplementary Information

We present below a mathematical analysis of the model for small parameter values.

Analytical model

We focus on a population of n individuals, a variable fraction φ of which are pure scroungers, and $1-\varphi$ of which are pure producers. Each individual has a cognitive level C that determines how good it is at scrounging (for scroungers) or avoiding being scrounged (for producers). Each generation comprises many foraging steps. In one such step, a fraction ρ of the producers each finds one unit of food. Each scrounger is then randomly assigned to one of the producers that found food and attempts to scrounge. If multiple scroungers are assigned to the same producer, only one (chosen randomly) is allowed to attempt to scrounge. With probability σ (given above), the scrounging attempt is successful and the producer and scrounger split the food, with the scrounger receiving a fraction u and the producer getting the rest. Once all the foraging steps are completed, the next generation is produced according to a Wright-Fisher process, with each individual's fitness proportional to the total amount of food it acquired, multiplied by a factor $e^{-\delta\gamma}$ to account for the cost of additional cognition. In this analytical section, we will focus on parameter values $\rho, s << 1$ and $a = 0$; we examine larger values ($\rho = 0.25$, $s \sim 1$, $a = 0.5$) in the simulation section below.

1. Frequency of scroungers

In the following analysis, we will assume that mutations are sufficiently rare ($n\mu << 1$)

that there is a separation of timescales. Each foraging type is usually fixed for a single cognitive level, and producers and scroungers are present in the population at the equilibrium frequency determined by the difference in cognitive levels. Occasionally, a mutation occurs that changes either an individual's cognitive ability (by one level) or its foraging type. If the mutation initially confers a selective advantage α, it has a chance to escape drift and increase in frequency in the population. We assume that if it does so, it fixes and the frequency of scroungers relaxes to its new equilibrium value before the next mutation occurs. We now find the equilibrium frequency of scroungers (note that this is always complemented by the frequency of producers).

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

$f = 1 - \left[1 - \frac{1}{n\rho(1-\varphi)}\right]^{n\varphi}$, 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 $f\rho(1-\varphi)/\varphi$. Assuming that n is large enough that many producers find food every foraging step ($n\rho(1-\varphi) >> 1$), f is approximately

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

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

$$w_P = \rho\left[1 - u\sigma(d)f\right] \quad (3)$$

$$w_S = e^{-\gamma d} u\sigma(d) \frac{f\rho(1-\varphi)}{\varphi}. \quad (4)$$

The equilibrium frequency of scroungers, $\hat{\varphi}$, is the value of φ at which $w_P = w_S$; scroungers go extinct if $w_P(\varphi = 0) > w_S(\varphi = 0)$.

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

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

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

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

Figure S1 shows the accuracy of this approximation.

2. Selective coefficients of mutations

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:

$$\alpha_P(\delta) = e^{-\gamma\delta}\frac{1 - fu\sigma(d-\delta)}{1 - fu\sigma(d)} - 1 \qquad (7)$$

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

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

$$\alpha_P(\delta) = \delta\left[\frac{us\sigma(d)(1-\sigma(d))}{1-u\sigma(d)} - \gamma\right] + O(\delta^2) \qquad (9)$$

$$\alpha_S(\delta) = \delta\left[s(1-\sigma(d)) - \gamma\right] + O(\delta^2). \qquad (10)$$

(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.

3. Speed of the cognitive arms race

In populations experiencing a stable cognitive arms race, the gap between the cognitive levels of the two foraging types settles down to a roughly steady value $\hat{d}$ at which both types increase in cognitive level at the same rate. In the rare-mutation regime we are considering, this rate is given by the mutation supply times the probability that mutants with a cognitive ability increased by one unit ($\delta = +1$) will fix. Assuming that $\alpha_P(1)$ and $\alpha_S(1)$ are small compared to one, the probability of fixation is 2α (Ewens 2004). The two foraging types therefore evolve higher cognition at the same rate when

$n\left(1-\hat{\varphi}\right)\mu\left(2\alpha_P(1)\right)=n\hat{\varphi}\mu\left(2\alpha_S(1)\right)$, *i.e.*, when

$$\left(1-\hat{\varphi}\right)\alpha_P(1)=\hat{\varphi}\alpha_S(1). \qquad (11)$$

Inserting the above expression (6) for $\hat{\varphi}$, and (9) and (10) for α_P and α_S, and assuming that food is hard to find ($\rho<<1$), (11) reduces to

$$usd\sigma\left(1-\sigma\right)-1+2u\sigma\approx 2u\gamma d\sigma\left(1-u\sigma\right). \qquad (12)$$

When the cost of cognition is very low ($\gamma\approx 0$) and producers and scroungers split the food evenly ($u=1/2$), the expression simplifies further to $d\approx 2/s\sigma$, and we find that the rates of advance balance at a cognitive gap of

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

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

$$n\left(1-\hat{\varphi}\right)\mu\left(2\alpha_P(1)\right)\approx n\hat{\varphi}\mu\left(2\alpha_S(1)\right)\approx\frac{n\mu s}{10}\left(1-\frac{10\gamma}{s}\right). \qquad (14)$$

If the cost of cognition is too large (roughly, $\gamma>\frac{s}{10}$) or if the finder's share of the food is too high ($u<<1/2$), a stable race is impossible; either cognition is too costly to ever evolve, or else the pressure of scrounging on the producers is to weak to create selection to keep up with scroungers, leading to the collapse of the race.

4. Mixed strategies and sexual reproduction

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

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

$$\alpha_P(\delta) = e^{-\gamma\delta}\left[\hat{\varphi} + \left(1-\hat{\varphi}\right)\frac{1-fu\sigma\left(d-\delta\right)}{1-fu\sigma(d)}\right] - 1 \qquad (14)$$

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

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

$$\alpha(\delta) \approx \delta\left[us\sigma(1-\sigma)-\gamma\right]. \qquad (16)$$

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

$$n\mu\alpha(1) \approx n\mu\left(\frac{us}{4}-\gamma\right) \quad (17)$$

as long as cognitive levels remain roughly balanced ($|sd| << 1$, so that $\sigma \approx$ ½).

References

Ewens, W. J. 2004. Mathematical Population Genetics. P. 25. Springer, New York.

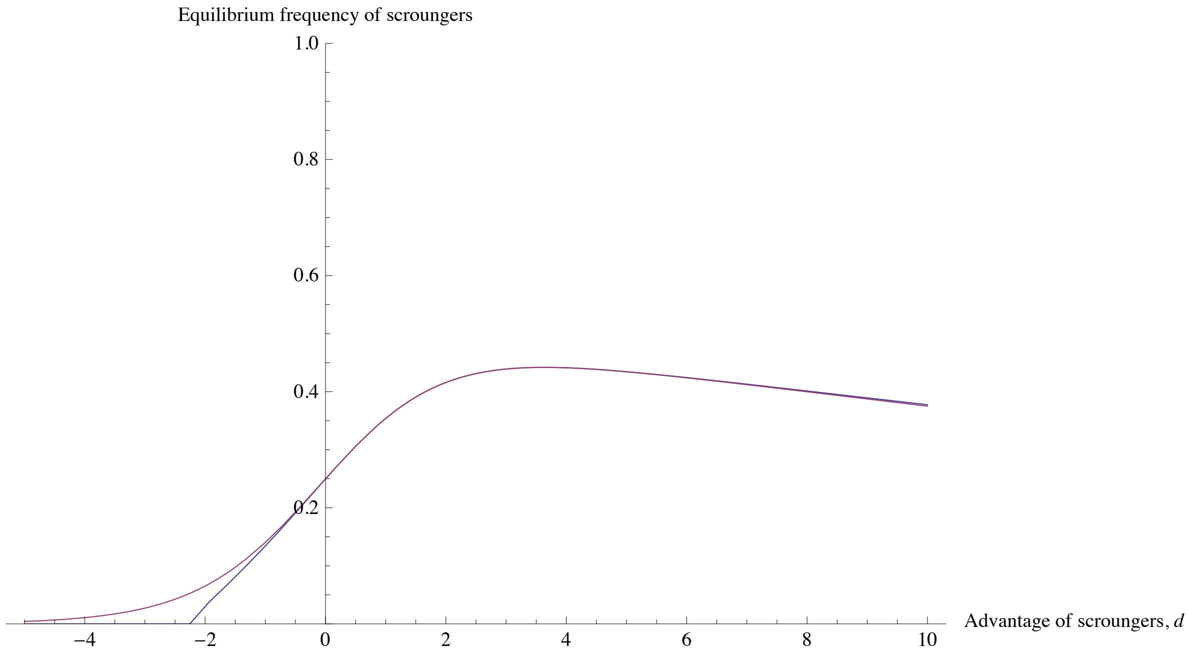

Figure S1. The equilibrium frequency of scroungers, $\hat{\phi}$, as a function of their cognitive advantage over producers, *d*. The blue curve shows the exact value obtained by solving Eqs. (3) and (4) for $w_p = w_s$, while the purple curve shows the approximate value given by Eq. (6). The other parameters 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 ($\gamma d << 1$), the frequency of scroungers is approximately $\hat{\phi} \sim \sigma / 2$.

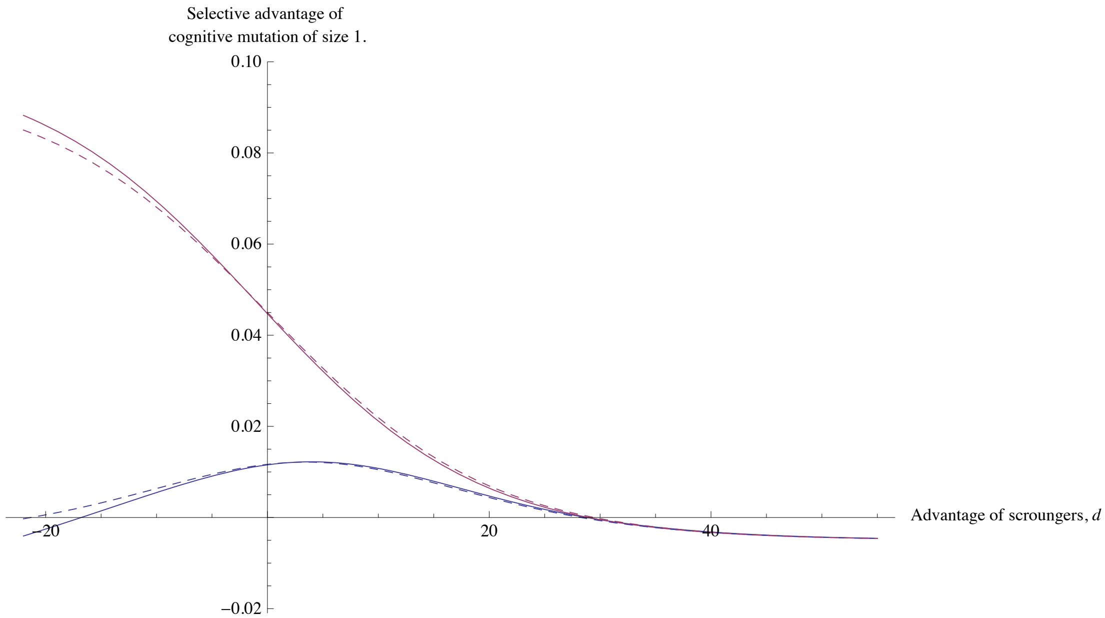

Figure S2. The selective advantage α for a mutation increasing the relevant cognitive ability by one unit in producers (blue) and scroungers (pink), as a function of the cognitive advantage of scroungers, *d*. The solid curves show the exact equations (7) and (8), while the dashed curves show the approximations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

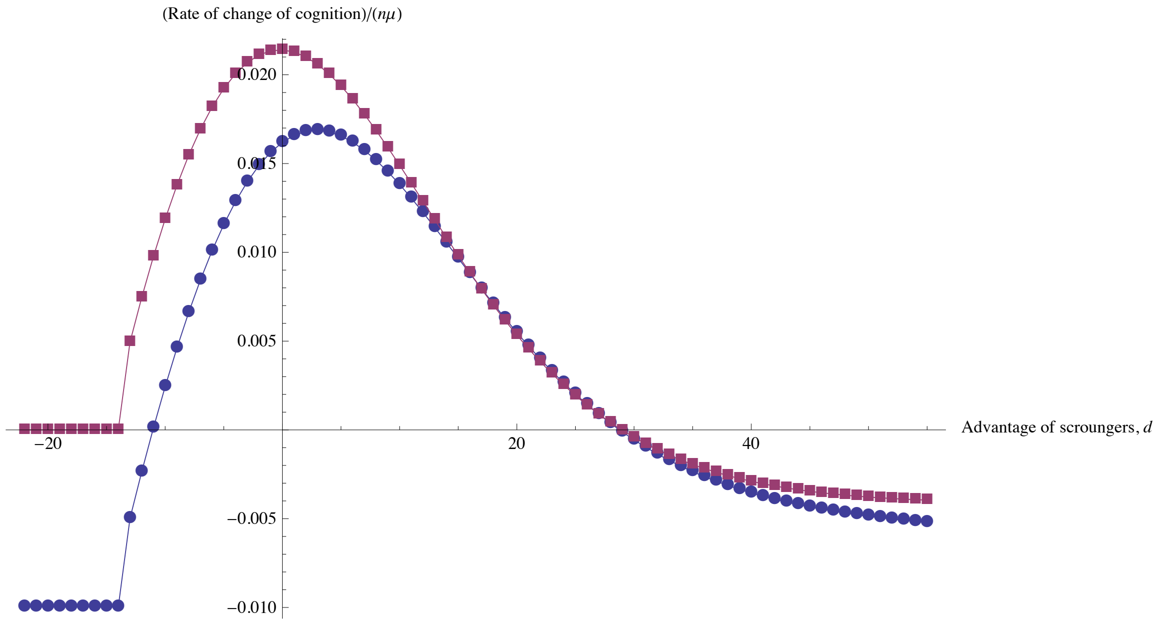

Figure S3. The rate at which mutations increasing cognitive ability are fixed, divided by $n\mu$, the number of mutations in the population per generation, as a function of the cognitive advantage of scroungers, *d*. The rate for producers is shown in blue, and for scroungers in pink. When the scroungers' 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 $a = 0$, $s = 0.1$, $\gamma = 0.005$, $r = 0.1$.