



Original Article

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

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Received 20 August 2013; revised 28 November 2013; accepted 19 December 2013; Advance Access publication 13 February 2014.

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

Key words: game theory, intraspecific arms race, social foraging, social intelligence hypothesis.

INTRODUCTION

Recent decades have seen great interest in social cognition and its evolution, due largely to the nontrivial nature of such abilities (e.g., considering the intentions of others), as well as the idea that coping with social challenges may underlie the evolution of general intelligence (Shettleworth 2010). Indeed the latter suggestion, known as the “social intelligence hypothesis” (Jolly 1966; Humphrey 1976; Byrne and Whiten 1988), relies heavily on the finding that species exhibiting advanced cognitive abilities often maintain elaborate social structures. Although this hypothesis initially referred to humans and other primates, it has also been related to advanced cognition in other species, including corvids (Emery and Clayton 2004), hyenas (Holekamp 2007), and cetaceans (Marino 2002). However, regardless of such elaborate social structures, group-living animals face a more fundamental

challenge that is often ignored in this context: social foraging (Giraldeau and Caraco 2000).

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).

Although scrounging saves the time and energy that must be invested in order to produce resources, it requires a sufficiently high frequency of producers in the population to be beneficial. The negative, frequency-dependent selection operating on these 2 strategies results in a mixed evolutionarily stable strategy (Barnard and Sibly 1981; Barnard 1984; Giraldeau and Caraco 2000; Giraldeau and Dubois 2008). In such populations, selection can be strong enough to give rise to a suite of scrounging avoidance tactics by producers and consequent counter tactics by scroungers (Barnard

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1984; Coussi-Korbel 1994; Emery and Clayton 2001; Flynn and Giraldeau 2001; Bugnyar and Kotrschal 2002; Held et al. 2002; Bugnyar and Heinrich 2006; Shaw and Clayton 2013). Thus, selection on social foragers to outsmart each other can lead to an intra-specific evolutionary arms race (Dawkins and Krebs 1979) that results in increased cognitive abilities (Barnard 1984; Bugnyar and Kotrschal 2002; Grodzinski and Clayton 2010).

In many species of social foragers, the PS game may have selected for cognitive adaptations that involve plastic responses to the presence of others (an “audience effect”) (Barnard 1984; Byrne and Whiten 1988; Coussi-Korbel 1994; Norris and Freeman 2000; Emery and Clayton 2001; Flynn and Giraldeau 2001; Bugnyar and Kotrschal 2002; Held et al. 2002; Bugnyar and Heinrich 2006; Shaw and Clayton 2013). For example, in spice finches, as well as pigs and gorillas, producers keep their distance from potential scroungers (Byrne and Whiten 1988, Chapter 16; Flynn and Giraldeau 2001; Held et al. 2002); in mangabeys and chimpanzees, producers lead scroungers away from food (Byrne and Whiten 1988, Chapter 16; Coussi-Korbel 1994); scrub jays return to re-cache, in private, food items they have been observed by conspecifics to have been hiding (Emery and Clayton 2001); Eurasian jays attempt to prevent auditory information of their caching activities from reaching potential scroungers (Shaw and Clayton 2013); scrounging ravens watch caching from a distance and delay their approach until the cacher (producer) has left (Bugnyar and Heinrich 2006), and scrounging chimpanzees may hide to watch conspecifics recover food, and emerge from hiding to steal it (Byrne and Whiten 1988, Chapter 16). Although success in the PS game may be influenced by a number of traits, from body size to dominance ranking (Giraldeau and Beauchamp 1999), these observations suggest that potential targets for adaptation are likely to include data processing and decision-making abilities. However, the cognition underlying such abilities is likely to entail a cost, which may be developmental, physiological, and/or derived from prolonged data processing (Burger et al. 2008). Previous interspecific comparative analysis has found a correlation between food-stealing behaviors and residual brain size (Morand-Ferron et al. 2007), but the use of brain size as a proxy for cognitive abilities remains somewhat controversial (Healy and Rowe 2007).

Here, we examine the conditions under which mutations in the cognitive apparatus that increase performance in the PS game provide sufficient benefit to outweigh such costs and analyze the consequences of evolving general versus strategy-specific cognitive abilities. As the nature of the cognitive abilities involved in the aforementioned examples is far from clear, it is impossible to model them in any detail without restricting the generality of the model. To avoid this, we model these cognitive abilities simply as traits affecting the performance of producers and scroungers competing against each other (as detailed below). Consequently, our model is in fact much more general and concerns any such traits, and not necessarily only cognitive ones (e.g., size or aggressiveness). For consistency, we will keep referring to a “cognitive trait” throughout the description of the model and its results, and we will return to the plausibility of these traits being cognitive in the discussion.

We compare a situation in which the PS interaction involves a single cognitive ability to one in which each foraging strategy employs a separate, strategy-specific ability. Using mathematical analysis and agent-based simulations, we show that strategy-specific cognitive abilities are unable to support a consistent arms race and result either in scroungers’ extinction or in a race to decrease cognitive level (a “backwards race”). In contrast, a single, general cognitive ability used by both foraging strategies exhibits a persistent arms race.

THE MODEL

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. Symbols for all variables and parameters used in the model are listed in Table 1.

Basic model and the scrounging success probability function

Each generation consists of multiple rounds of foraging, and in each round, some fraction of producers finds food. A producer that finds food will sometimes (with probability f) face a scrounging attempt, and if this attempt is successful, half of the found food will be lost to the scrounger. The probability that a scrounging attempt is successful, σ , is determined by the difference d in cognitive abilities between the scrounger and the producer: scroungers with relatively advanced cognitive abilities are more often successful at obtaining food, whereas producers with relatively advanced abilities are more often successful at avoiding loss of food to scroungers. It is then reasonable that σ should increase monotonically with the cognitive 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 extent to which scrounging success is influenced by cognition: It represents the lowest possible scrounging success 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 is weak and scrounging is likely to succeed regardless of the difference in cognitive abilities. We assume that the probability of successful scrounging is determined partly, but not solely, by cognitive abilities (i.e., $0 < a < 1$). The parameter s determines the size of the effect that a single cognitive mutation has on the probability of successful scrounging: Each mutation changes σ by $\sim s$ until it saturates at some maximum or minimum value for $|sd| \gg 1$. The

Table 1
Symbols used in the mathematical analysis and computer simulations

Symbol	Meaning
a	Lowest probability of successful scrounging
C	Cognition gene (GCM)
C_p	Producing cognition gene (SCM)
C_s	Scrounging cognition gene (SCM)
d	Difference in cognitive level between scrounger and producer
F	Social foraging strategy gene
f	Probability that a producer who found food will face a scrounging attempt
n	Population size
s	Cognitive mutation effect size
T	Number of time steps in one generation
w_p	Producer’s fitness
w_s	Scroungers’ fitness
α_p	Selective advantage of a (+1) cognitive mutation in producers
α_s	Selective advantage of a (+1) cognitive mutation in scroungers
γ	Fitness cost associated with cognitive level
δ	Change in cognitive level
μ	Mutation rate (for all genes)
ρ	Producer’s probability of finding food
σ	Scrounging success probability
φ	Fraction of pure scroungers in the population

effects of these assumptions can be seen in Figure 1, which shows scrounging success probability as a function of d for different values of a and s .

We consider 2 possibilities for the influence of cognition on the PS game. In the 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. In the Specialized Cognition Model (SCM), one trait, C_s , determines scrounging ability, whereas another, C_p , determines the ability of producers to avoid being scrounged.

Mathematical analysis

Effect of cognitive mutations on fitness

We want to find the selection coefficient of cognitive mutations, which is given by [mutant fitness – wild-type fitness]/[wild-type fitness] or (mutant fitness)/(wild-type fitness) – 1. Suppose a producer has a mutation that increases its cognitive ability by δ , it will find food at the same rate as a wild-type producer and face a scrounging attempt with the same probability f , but the probability that the scrounger succeeds in taking 1/2 of its food will be just $\sigma(d - \delta)$, instead of the wild-type probability $\sigma(d)$. However, the mutant will have to pay the cost of additional cognition, reducing its net payoff by a factor $e^{-\delta\gamma}$. If we give a food item the value 1, then combining the above, the relative fitness advantage α_p of the mutation is $\alpha_p(\delta) = e^{-\delta\gamma} \left[\frac{1 - f\sigma(d - \delta)/2}{1 - f\sigma(d)/2} \right] - 1$. Similarly, the advantage α_s of a mutation that changes scroungers’ cognitive ability by δ is given by $\alpha_s(\delta) = e^{-\delta\gamma} \sigma(d + \delta)/\sigma(d) - 1$.

Computer simulations

The population

We simulated a population of $n = 100$ haploid social foragers. Foragers’ PS behavior was determined by their genotype at the F gene, which controls their probability to play the producer strategy. A pure producer carries an F allele 1, a pure scrounger carries 0; an agent with an F genotype of, for example, 0.7 plays producer with probability 0.7 at any given foraging step, and scrounger with probability 0.3. We ran both pure strategy simulations, where the only possible F alleles were 0 and 1, and mixed strategy simulations, where there were 11 possible alleles: 0, 0.1, 0.2 ... 1. Alleles

included in the simulation were assigned equal frequencies in the population’s first generation.

Cognitive ability was determined by the C gene in the GCM and by the C_p and C_s genes in the SCM. In both models, foragers’ cognitive level in the first generation was set to 0, that is, in the GCM, all foragers had the 0 allele in the C gene, and in the SCM, all foragers carried the 0 allele at both the C_p and C_s gene. We assume that a higher cognitive level incurs a cost, γ , which may be developmental, physiological, or derive from the possibly longer processing times associated with a higher cognitive level. We use a cost proportional to the agent’s cognitive level (C in the GCM or both C_p and C_s in the SCM), which is a fractional deduction from the final accumulated payoff. For example, maintaining cognitive level $C = 10$ resulted in a deduction of 10% from the payoff; maintaining $C_p = 10$ and $C_s = 2$ resulted in a deduction of 12% of payoff, regardless of whether the PS strategy was mixed or pure.

The PS game

The lifetime of one generation included a series of 50 PS interactions, or steps, which were independent of each other and their order was unimportant. This number of steps was chosen in order to allow foragers to interact with a large sample of the population. At the beginning of each step, all foragers drew a PS strategy according to their F genotype, and those who played producer received a set payoff (e.g., 4, although the value does not matter) with a probability of 0.25. This probability was set to introduce a cost to the producer strategy and to allow an effective PS game. Foragers who play scrounger are then assigned randomly and independently to producers who found food. We assume only one scrounger can join each successful producer, and therefore if 2 or more scroungers are assigned to the same producer, only one of them will be able to attempt scrounging. This assumption is merely quantitative; it allows for a stable PS game without the need to define additional, arbitrary costs to producing and scrounging. The difference d between the (relevant) cognitive levels of the scrounger and producer involved was calculated as $d = [\text{scrounger’s } C] - [\text{producer’s } C]$ in the GCM and as $d = [\text{scrounger’s } C_s] - [\text{producer’s } C_p]$ in the SCM. In the case of successful scrounging, the scrounger receives half of the producer’s found food. It should be noted that although we do not define a finder’s share, since producers are sometimes not assigned a scrounger, they occasionally keep the

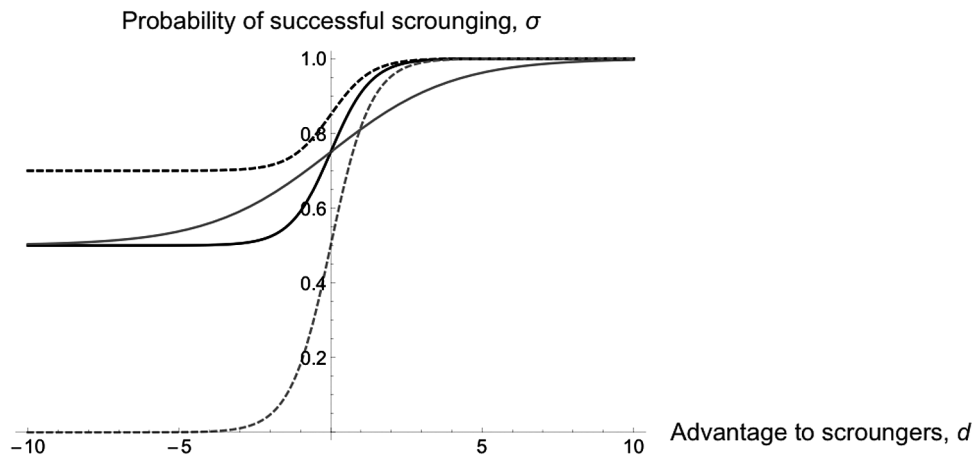


Figure 1 Successful scrounging probability, σ , for different values of cognition effect size a and cognitive mutation effect size s . Dashed black line: $a = 0.7, s = 1.5$; solid gray line: $a = 0.5, s = 0.5$; solid black line: $a = 0.5, s = 1.5$; dashed gray line: $a = 0, s = 1.5$.

full food portion to themselves. If we include in addition a finder's share, then as long as it is not too large, scrounging is maintained in the population (e.g., when $s = 1.5$, as long as the producer does not keep more than ~65% of its food finding), and the results are qualitatively similar (see also the note in the mathematical analysis in the [Supplementary Information](#)). Scrounging success baseline probability, a , used to calculate the probability of successful scrounging $\sigma(d)$, was set to 0.5 in all simulations, on one hand to allow for a stable PS game under simulation conditions, and on the other for cognition to play a significant role in determining the probability of successful scrounging. Increasing the value of a will result in lower collapse rates in the SCM; however, this contributes little to how cognitive abilities affect scrounging success and will be qualitatively similar to the case of small s . We therefore do not vary a .

Selection and reproduction

After completing 50 interactions, the foragers reproduce asexually, in proportion to their relative lifetime accumulated payoff, and immediately die (population size remains constant). Offspring are genetically identical to their parent, except for mutations, which occur in each gene at a rate of $\mu = 0.1$. Mutations in the F gene change it within the simulation's defined allele pool. In the cognition genes, a mutation changes the mutated allele by one level, either increasing (+1) or decreasing it (-1). We allowed the population to evolve for 10 000 generations; under each parameter set, we repeated the simulation 100 times.

RESULTS

Conditions allowing an arms race

To be advantageous, the potential benefits of cognition-increasing mutations in relation to the PS game must outweigh their cost (corresponding roughly to $s \gg \gamma$), which we will assume in what follows. However, this does not guarantee that increasing cognition is always favored, because the advantage of a mutation that increases cognitive ability in a producer (scrounger) depends on its current cognitive level relative to scroungers (producers) ([Figure 2](#)). When scroungers are slightly smarter than producers (i.e., d is small and positive), producers are selected to increase their cognitive level. When producers are slightly smarter than scroungers (d is small and

negative), scroungers are selected to increase their cognitive level. Thus, small differences in cognitive level support an evolutionary arms race between social foraging strategies ([Figure 2](#)). On the other hand, cognitive differences that are too large have remarkably different consequences. If producers are substantially smarter than scroungers (d is large and negative), or vice versa (d is large and positive), the probability of successful scrounging, σ , is only slightly affected by further mutations, because it is close to either of its asymptotic values (a or 1, respectively). Because the benefit of an increased cognitive level is low in such cases, it is outweighed by the cost, and selection will favor decreased cognitive levels ([Figure 2](#)).

Effect of specialized versus generalized cognition on the race

In a population initially made up of individuals with equal cognitive abilities, the scroungers' relevant cognitive ability (C in the GCM, C_s in the SCM) initially increases in both models ([Figure 3](#)). This increases the probability that scrounging is successful, intensifying the selective pressure on producers to avoid being scrounged and leading producers' relevant cognitive ability (C in the GCM, C_p in the SCM) to rise. Improved producer cognitive ability, in turn, puts pressure on scroungers to readapt, and the consequent positive feedback loop leads to the continuing evolution of increased cognitive abilities in both producer and scrounger populations ([Figure 3](#)). The rate of this increase depends on the magnitude of cognitive mutations: Higher values of s result in faster evolutionary races (see below). In the SCM, the escalation in relevant cognitive abilities is accompanied by a slow decrease in the unused cognitive abilities (C_s for producers, C_p for scroungers), due to their cost ([Figures 3c and 4b,d](#)).

These arms races occur in both the GCM and the SCM and are temporarily stable as long as cognitive differences between foraging types are small, consistent with our analysis above showing that small d values support an evolutionary arms race. However, the arms race is interrupted when either foraging type acquires a large cognitive advantage over the other ($|sd| \gg 1$); such an advantage emerges stochastically due to the random processes in the simulation (assignment of food to producers, scrounger-to-producer assignment, selection, reproduction) and finite population size. If producers have a sufficiently large advantage, the (unsuccessful)

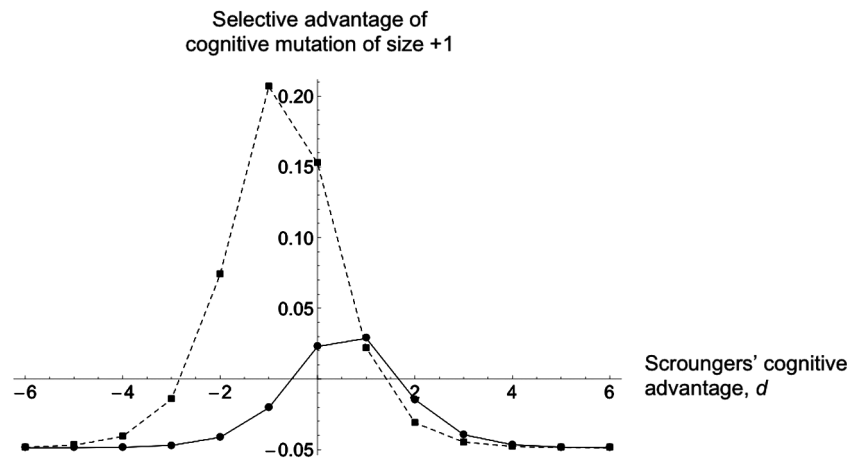
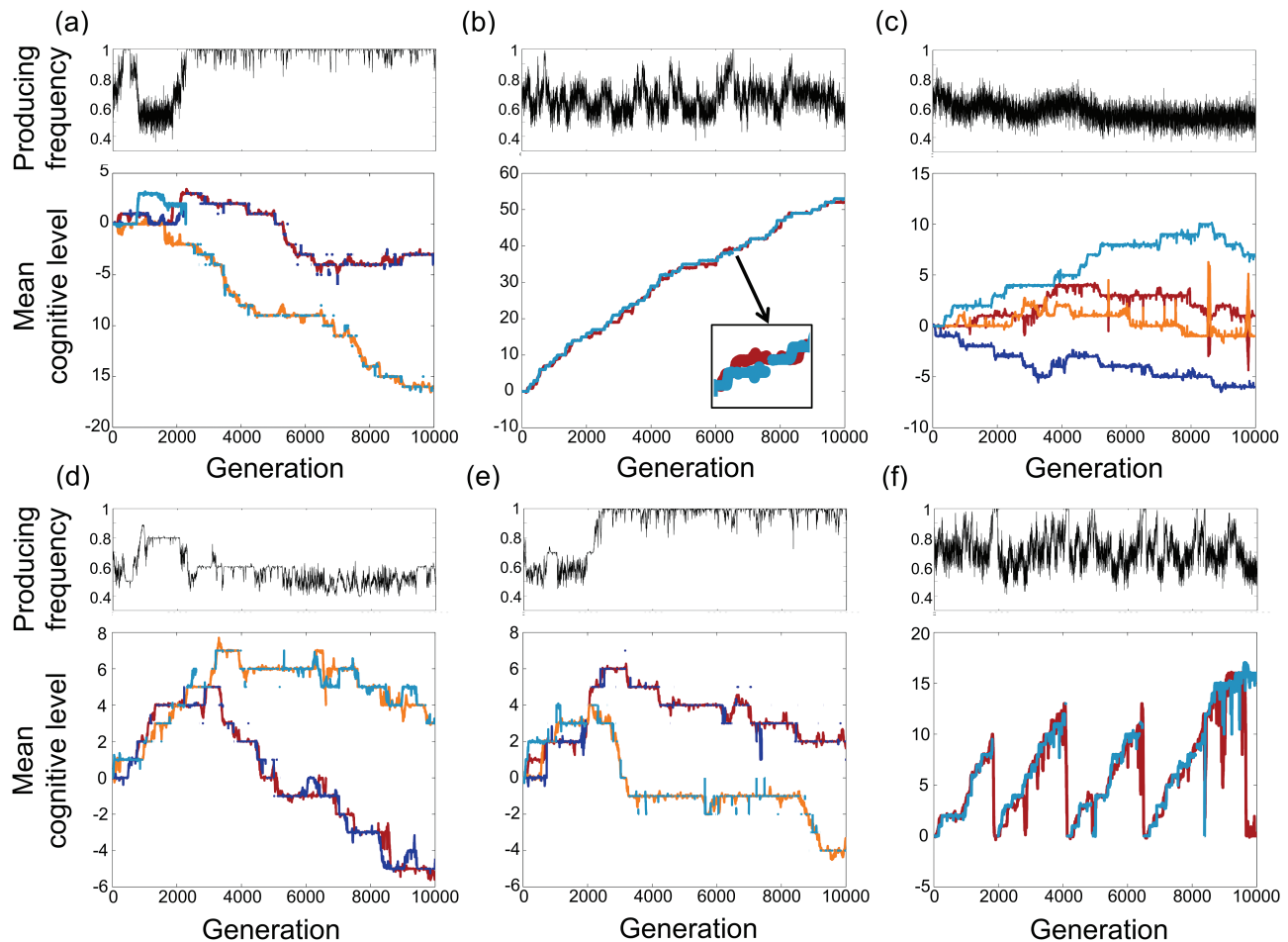


Figure 2

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


Figure 3

Examples of GCM and SCM population dynamics in agent-based simulations, under various conditions. Black and white panels show producer frequency over time; color panels show mean cognitive level over time. GCM (b and f): 2 lines representing mean C levels for producers (red) and scroungers (teal); SCM (a and c–e): 4 lines representing mean level of specialized cognitive ability for producing, C_p , in producers (red) and scroungers (blue) and mean level of specialized cognitive ability for scrounging, C_s , in producers (orange) and scroungers (teal). In mixed strategy simulations (d and e), 0–50% producing is included under “scroungers,” 60–100% producing is included under “producers.” Where red line is not visible, it is hidden 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, $\gamma = (C_p + C_s)/100$ in SCM; scrounging success baseline probability $a = 0.5$; mutation rate $\mu = 0.01$ for all genes; mutations in $C/C_p/C_s$ increase or decrease cognitive ability by 1. Note that the y axis scales in colored panels vary. (a) SCM, pure producing/scrounging (PS), $s = 1.5$. (b) GCM, pure PS, $s = 1.5$. (c) SCM, pure PS, $s = 0.5$. (d) SCM, mixed PS, $s = 1.5$. (e) SCM, mixed PS, $s = 1.5$. (f) GCM, pure PS (fixed frequencies), random inwards migration of individuals with baseline cognitive level ($C = 0$).

scroungers cannot obtain resources and are driven to extinction. Once this happens, they can only reappear through mutation that converts a producer into a scrounger. In the SCM, such mutants will have the high C_p and low C_s values typical of producers, but because this makes them unfit as scroungers, scroungers cannot recover from extinction (Figures 3a and 4). In the GCM, however, a mutant’s high cognitive ability C , inherited from its producer parent, will make it a good scrounger. This enables scroungers to reinvade the population, reestablishing the cognitive arms race from the current cognitive level of the population (Figure 3b) and continually driving up the cognitive level among both producers and scroungers (Figure 4).

In contrast, a large cognitive advantage for scroungers will not lead producers to extinction, due to the frequency dependence of the PS game. Instead, mutations that decrease producers’ cognitive level will be favored because the benefits in reducing cognitive costs will outweigh their effect on scrounging avoidance success (which is minimal under these conditions because scroungers are much

smarter). Once producers’ cognitive levels are reduced, selection will act on the scroungers to follow suit for similar cost-saving reasons, resulting in a “backwards” race. This “backwards” race scenario is likely to occur and escalate in SCM populations, in cases where the size of cognitive mutation effect s is small and selection is therefore not as harsh (Figures 3c and 4). However, in GCM populations, a large cognitive advantage for scroungers will quickly be reduced by scroungers mutating into producers while retaining their high C levels, thus reestablishing the race.

Mixed strategies

So far, we have considered pure producers and pure scroungers. In nature, however, the PS trait is usually manifested as a mixed strategy, and individuals have been observed to employ both strategies to varying degrees based on their personal tendencies and previous experience, as well as on physiological, social, and environmental conditions (Mottley and Giraldeau 2000; Lendvai et al. 2004; Lendvai et al. 2006; Katsnelson et al. 2008; Tóth et al.

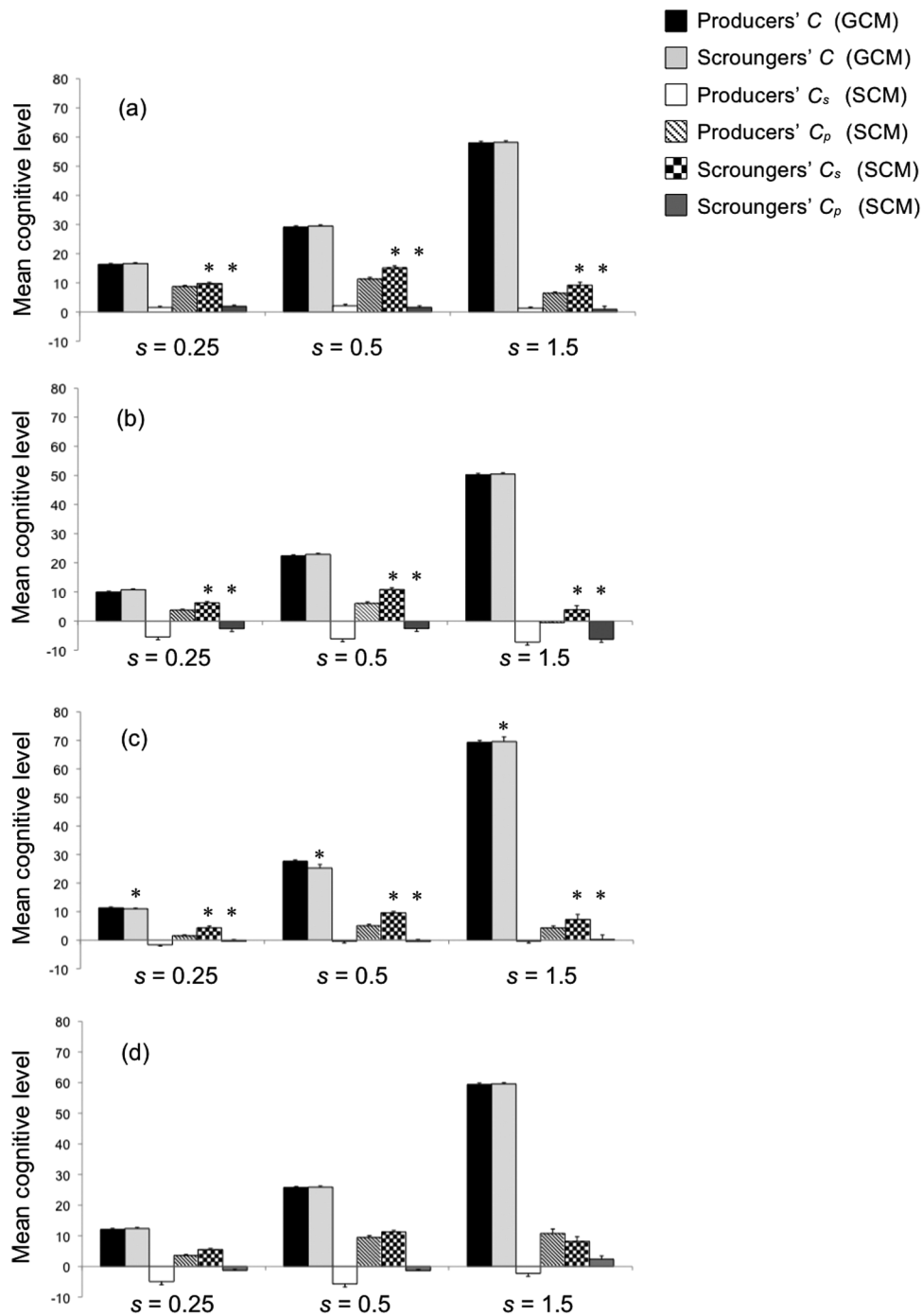


Figure 4

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 9901–10000, for 100 repeats of each simulation. Columns marked with (*) are means calculated for less than 90 repeats, that is, 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 3 column groups in each subfigure correspond 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, $G = 10000$ 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 > 0.5 alleles 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); $\gamma = C/100$.

2009; Kurvers et al. 2010; Morand-Ferron and Giraldeau 2010; Katsnelson et al. 2011). In simulations of both of our models, inclusion of mixed strategies yields qualitatively similar results to those described above: GCM races persist, whereas SCM races

are bound to collapse. As in the pure strategy case of the SCM, gaps between C_p and C_s arise stochastically. If C_s becomes much larger than C_p , the latter decreases (as in the pure case) to avoid cognitive costs, resulting in a “backwards race” (Figure 3d). If C_p

becomes much larger than C_s , selection favors foraging strategies that produce as often as possible, and scrounging disappears from the population (Figure 3e), as in the pure case. This disappearance of scrounging from the population as its adaptive value decreases is plausible given that in nature, social foraging strategies can be adjusted to provide better adaptation to changing environmental conditions (Mottley and Giraldeau 2000).

Cognitive mutation effect size (s)

When s is large, a single mutation that increases the cognitive level of a scrounger (producer), when the cognitive difference between producers and scroungers is small or 0, entails a significant increase in the probability of successful scrounging (successful scrounging avoidance). Such a mutant has a relatively large advantage over other individuals and the mutation is therefore likely to spread rapidly. This spread, in turn, provides a background on which a counter-mutation will have a large advantage, in the same manner. On the other hand, the difference in cognitive level does not need to be high (relative to smaller values of s) in order for the effect of a single cognitive mutation to be negligible. This can be illustrated, for example, by comparing the probability of successful scrounging represented by the 2 solid lines in Figure 1: When $d = 3$ or $d = -3$, decreasing the difference by one mutation to $d = 2$ or $d = -2$ will confer a change in scrounging success probability that is close to 0 for $s = 1.5$ (black line), but for $s = 0.5$, it will be much more effective (~ 0.05 ; grey line). In the GCM, because the emergence of large differences in cognitive level is quickly overcome, larger values of s result in faster races (Figure 4). In the SCM, which is sensitive to large cognitive differences for the reasons detailed previously, larger values of s led to a higher rate of race collapse and backwards races (Figure 4).

Cognitive cost (γ)

It is not surprising that setting the cognitive cost to 0 (as shown in Figure 4a) resulted in faster races (compared with that shown in Figure 4b). In SCM populations, it also caused the cognition genes, which were irrelevant to the foraging strategy (C_s for producers and C_p for scroungers) to drift rather than decrease in level, 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 (Figure 4a; see Table 2).

Evolution in the F gene

In simulations where the F gene was free to evolve, the frequency of producers and scroungers fluctuated; the F gene inevitably coevolves with the genes determining cognitive level, but the interaction is

complex due to the negative frequency dependence that is inherent in the PS game. To examine the effect of these fluctuations on the arms race, and to explore the nature of arms races in SCM populations where scroungers cannot become extinct, we ran a set of simulations with no fluctuations by holding the frequencies of producers and scroungers constant, at 0.7 and 0.3, respectively. This ratio was based on the frequencies observed in our simulations where the cognitive level was held at 0 with no cognitive mutations, while the F gene was allowed to evolve (producer frequency for the last 100 of 10 000 generations was 0.697 ± 0.009 mean \pm SD; population size $n = 100$, $s = 1.5$; 100 simulation repeats). To still allow transfer of cognitive abilities between producers and scroungers (a key feature of the GCM) while keeping PS frequencies fixed, we allowed F gene mutations (at a rate of $\eta\mu = 0.1$) that changed one producer into a scrounger and one scrounger into a producer (retaining their cognitive levels). Incidentally, the effective mutation rate was thus doubled.

The arms race in GCM populations was faster under constant PS frequencies (Figure 4d), which can be expected given the higher mutation rate. This result does, however, indicate that the fluctuations in PS frequencies that are typical of the PS game are not the driving force behind the arms race, as might have been hypothesized. Interestingly, the fact that scroungers could not go extinct did not promote consistent arms races in SCM populations. Instead of extinction, once a large gap formed in cognitive abilities between producers and scroungers, scroungers decreased their cognitive level and the race did not progress (Figure 4d).

Ending the race

As shown above, arms races involving general cognitive abilities are not limited by the instability and short-life typical of those involving specialized cognition. However, it does not follow that these arms races will continue forever. For example, when cognition costs become too high compared with their benefits, the population may go extinct. As costs become too high, the population may also become prone to invasion by migrants with baseline cognitive levels; such an invasion is possible because these migrants, despite their poor cognitive abilities, do relatively well altogether as they do not suffer such high cognitive costs. In this case, a cyclic pattern of escalation and collapse may emerge, as the population repeatedly regresses to the cognitive baseline and then restarts the arms race (Figure 3f). Alternatively, a general cognitive ability may coevolve with other traits (such as foraging efficiency or diet, in our case), changing the very parameters considered here that govern the evolution of social cognition. Interestingly, increased general cognition resulting from the race may have pleiotropic benefits, such as

Table 2
Number of valid data points (out of 100) for mean cognitive level calculation

Simulation	s	Producers (GCM)	Scroungers (GCM)	Producers (SCM)	Scroungers (SCM)
Pure strategy, with cost	0.25	100	100	100	86
	0.5	100	100	100	62
	1.5	100	98	100	16
Pure strategy, no cost	0.25	100	100	100	75
	0.5	100	100	100	45
	1.5	100	94	100	15
Mixed strategy, with cost	0.25	99	21	100	39
	0.5	100	18	98	44
	1.5	99	19	97	21

A data point was excluded if the frequency of the social foraging strategy allele was 0 in one generation or more, between generations 9901 and 10000.

enabling the exploitation of new food sources or habitats, which could outweigh the costs of cognition. Conversely, if producers become better at exploiting food sources, producing may become much more profitable than scrounging. The consequent low frequency of scroungers will make the PS game less important, slowing down the cognitive arms race or drawing it to an end.

DISCUSSION

Our results suggest that a cognitive arms race improving performance of players in the PS game can persist and escalate, but only if it involves a general cognitive ability competing against itself. Arms races between 2 separate abilities may escalate temporarily but are bound to collapse. In the present formulation, the increased stability of arms races, when they involve generalized rather than specialized cognitive abilities, is independent of the specific details of our model. Indeed, arms races involving a single trait should generally be more stable than those between 2 (or more) traits that mutate and evolve separately, because destabilizing asymmetries will arise less frequently in the former. That intraspecific arms races should tend to persist for longer than interspecific ones is one possible implication.

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

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 relevant in the case of our model, for 2 reasons. First, as mentioned in the introduction, there is strong evidence that cognitive abilities such as information processing, learning, and decision making can have strong effects on scrounging and scrounging avoidance. Second, many other relevant traits, such as body size, are likely to be under strong stabilizing selection as the cost of increasing them becomes too high. For example, developing and maintaining a large body size requires high energy intake and may entail a higher risk of predation (Blanckenhorn 2000; Quinn et al. 2001; Rotella et al. 2003; Bonduriansky and Brassil 2005; Herczeg et al. 2009). Similarly, a large increase in levels of aggression is likely to result in high rates of injury and death; previous studies have found that aggression should be limited to an evolutionarily stable value (Maynard Smith and Price 1973; Dubois and Giraldeau 2005; Dubois and Giraldeau 2007). Improved cognitive abilities are likely to involve a fitness cost as well, as demonstrated in some species of insects (Burger et al. 2008; Snell-Rood et al. 2011). Seemingly complex abilities can be achieved through surprisingly simple neural structures (Chittka et al. 2012), but it is quite possible that brain size evolution is constrained by the energetic costs of maintenance (Isler and van Schaik 2006). However, maintaining a large body to an extent that will make a difference in success in the game, or withstanding frequent occurrence of injury as a result of heightened aggression, most probably require greater energy than maintaining a cognitive tweak that will achieve the same difference. In other words, it seems likely that cognitive

mutations that improve foragers’ performance in the PS game will tend to cost less than an increase in body size or aggressive behavior that could provide the same improvement. Thus, while our model describes a scenario applicable to many traits, cognition may be one of the few for which the benefit and cost parameters fall in the region supporting an arms race.

An intriguing possibility arising from the results of our model is that of a backwards race, a scenario observed at times in our SCM populations. It is often assumed that species tend to “become smarter” over evolutionary time, but obviously what is referred to as “high intelligence” or “advanced cognitive abilities” should not evolve unless it offers benefits in fitness. What should be the outcome of a backwards race? Although in our model specialized producing cognition and specialized scrounging cognition could potentially decrease infinitely, we may speculate that if such a scenario existed in nature, these abilities could only diminish to the point of complete degeneration or disappearance, thus leaving the population with a fixed probability of scrounging success, namely the lower limit of the scrounging success probability function (the parameter a).

When considering a situation where producers and scroungers attempt to outsmart each other, perhaps the best examples are scenarios of caching and pilfering. Still, simpler examples of PS interactions may apply. The evolution of caching and pilfering behaviors themselves may involve, at least in some cases, an escalating arms race which may be initiated, for example, by producers foraging away from potential scroungers, scroungers attempting to counter this behavior by hiding, and so on.

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

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 some social foraging systems, such as caching and pilfering, have given rise to traits such as attribution of knowledge and intentions to others in a wider range of taxa than currently suggested and, if not, what has inhibited them.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>

FUNDING

This work was supported by the National Institute of Health (GM28016 to M.W.F. and M.A.); the European Research Council (250152 to D.B.W.); and a fellowship from the Human Frontiers Science Program Organization (to U.G.).

We thank N. J. Boogert and 2 anonymous reviewers for their helpful comments on the manuscript.

Handling editor: Shinichi Nakagawa

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