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Mistakes and the evolution of copying

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Mistakes by either copiers or those they emulate can affect the evolution of copying behavior. Here, I present a series of game-theory models that examine the evolution of Copier and Chooser strategies, where individuals adopting a Chooser strategy assess the resources in question, but pay a cost for doing so. I consider three versions of this model in which: (i) Choosers err, (ii) Copiers err, and (iii) both Choosers and Copiers err. A number of findings emerge from this family of models. Increasing the search cost that is associated with the Chooser strategy increases the frequency of the Copier strategy. Decreasing the fidelity of copying — i.e., decreasing the proportion of times that Copiers correctly emulate Choosers — decreases the frequency of the Copier strategy. In addition, increasing the mistake rate of Choosers increases the frequency of Copiers. Lastly, and somewhat surprisingly, Copier is more likely to be an ESS when the difference between the value of resources in the environment is small.

KEY WORDS: copying, mistakes, evolutionarily stable strategy.

INTRODUCTION

When making decisions, both humans and nonhumans are affected by the actions of those around them. One manifestation of this is copying behavior. Copying — a form of social learning — has been defined in many different ways, but it most commonly refers to a situation in which an observer repeats the action of a model (HEYES 1994). Although psychologists have been studying copying since the work of George Romanes (ROMANES 1884, 1889, 1898), with the exception of work on “imprinting,” ethologists and evolutionary biologists have only recently begun studying this subject in earnest. This lag time may be due in part to the lack of a sound theoretical framework for the evolution of copying behavior. Over the last 20 years this framework has emerged, as population geneticists, anthropologists, and evolutionary ecologists have begun developing models for the evolution of cultural transmission, including copying (CAVALLI-SFORZA & FELDMAN 1981; BOYD & RICHERSON 1985, 1995, 2002; ROGERS 1988; FINDLAY 1991; BIKHCHANDANI et al. 1992, 1995; KIRKPATRICK & DUGATKIN 1994; LALAND 1994a, 1994b, 2004; SOLTIS et al. 1995; LALAND et al. 2000; HEINRICH & BOYD 2001; READER & LALAND 2003; CASTRO & TORO 2004). Social learning, particularly via copying, is ubiquitous in humans, but has also been found in nonhumans in the context of foraging in rats (see GALEF 1976, 1996 for reviews) and fish (LALAND & WILLIAMS 1997, LALAND & READER 1999), song learning in birds (CATCHPOLE & SLATER 1995, SLATER 2003), mate choice in birds and fish (see DUGATKIN 1996, 2000 for reviews), and a variety of other situations (BONNER 1980; CAVALLI-SFORZA & FELDMAN 1981; BOYD & RICHERSON 1985; ZENTALL & GALEF 1988; HEYES & GALEF 1996; BLACKMORE 1999; RENDELL & WHITEHEAD 2001; READER & LALAND 2002, 2003; BROWN & LALAND 2003; LALAND & HOPPITT 2003).

When individuals attempt to copy the behavior of a model, errors can occur (CAVALLI-SFORZA & FELDMAN 1981, BOYD & RICHERSON 1985) in at least two distinct ways. First, the model being observed may make an error. For example, imagine that the model has learned that resource A is preferable to resource B. At times, models may incorrectly choose resource B over resource A. If an observer is watching on these occasions, such mistakes will affect not only the model, but the observer as well. Second, even when models choose correctly, copiers themselves may make mistakes. For example, a copier may see a model choose resource A, but may incorrectly choose resource B itself. Once again, this may affect the evolution of the copying strategy. Below, I present a series of game-theoretical models that examine the evolution of copying, when: (i) models err, (ii) copiers err, and (iii) both models and copiers err.

MATHEMATICAL MODELS AND RESULTS

Imagine two resources, A and B. For example, A and B could be patches of different quality, mates of different qualities, etc. A and B provide resources in quantities a and b, such that A is a more profitable resource than B, and hence $a > b$. Further assume that A and B exist in proportions x and $1 - x$. Following (PRUETT-JONES 1992), let k = the cost associated with searching for resources A and B.

Imagine a game with a strategy set of two — Copier and Chooser. Choosers assess the resources available, pay the search cost k, and if correct in their assessment, receive the benefits associated with the more profitable resource. Copiers, as the name implies, copy the choice of Choosers (but copy only one Chooser). To determine evolutionarily stable strategies (ESS) for games involving Copiers and Choosers, let E{i,j} be the expected payoff to strategy i when pitted against strategy j. In our two-strategy game, Copier is an ESS when E {Copier, Copier} > E{Chooser , Copier}. If E{Copier, Copier} = E{Chooser, Copier}, then Copier is an ESS when E{Copier, Chooser} > E{Chooser, Chooser}. Similarly, Chooser is an ESS when E{Chooser, Chooser} > E{Copier, Chooser}. If E{Chooser, Chooser } = E{Copier, Chooser}, then Chooser is an en ESS when E{Chooser, Copier} > E{Copier, Copier}.

Choosers make mistakes

To examine the case in which Choosers make mistakes, let $\mu_1 =$ the probability that Choosers make mistakes and select the less valuable resource (B). It is important to note here that the “cost” to making a mistake (and selecting the inferior resource) is above and beyond the cost (k) that Choosers always pay for earching. If our population is made up almost completely of Choosers, and Copiers are at mutation frequency, the payoff to each is:

Payoff to Chooser = $\mu_1 b + (1 - \mu_1)a - k$ (1)
Payoff to Copier = $\mu_1 b + (1 - \mu_1)a$ (2)

Since (2) is always greater than (1), Chooser is not an ESS.

If our population is made up almost completely of Copiers, and Choosers are at mutation frequency, the payoff to each is:

Payoff to Chooser = $\mu_1 b + (1 - \mu_1)a - k$ (3)
Payoff to Copier = $xa + (1 - x)b$ (4)

Equations (3) and (1) are equal, as the payoff to Chooser does not depend on the frequency of each strategy in the population. Equation (4) differs from equation (2) because in a world full of Copiers, each individual Copier is copying other Copiers who have no good knowledge about which resource is preferable, as there are virtually no Choosers to copy. As such, the payoff in equation (4) represents that of choosing randomly with respect to their proportion in the environment.

Copier is an ESS if:

$$k > (a - b)(1 - x - \mu_1) \quad (5)$$

Equation 5 demonstrates that Copier is an ESS when: (i) k — the search cost that Choosers pay — is high, (ii) the difference between the more profitable and less profitable resource (a-b) is small, (iii) the more profitable resource (A) is at a relatively high frequency, and (iv) the error rate of Chooser is high.

Finally, a mixed ESS, containing both Copiers and Choosers, exists when: $k < (a - b)(1 - x - \mu_1)$. To calculate the expected frequencies at the mixed ESS, let p = frequency of Choosers, and (1 – p) = frequency of Copiers. The expected payoff for Choosers = p* E(Chooser, Chooser) + (1 – p)* E(Chooser, Copier) = $\mu_1 b + (1 - \mu_1)a - k$, and the expected payoff for Copiers = p* E(Copier, Chooser) + (1 – p)* E(Copier, Copier) = $p(\mu_1 b + (1 - \mu_1)a) + (1 - p)(xa + (1 - x)b)$. Setting these payoffs equal to one another and solving for the frequency of Choosers and Copiers, we obtain:

$$p = 1 - \frac{k}{(\mu_1 + x)(b - a) + a - b}, \text{ and } 1 - p = \frac{k}{(\mu_1 + x)(b - a) + a - b} \quad (6)$$

Copiers make mistakes

Now consider the case in which Copiers, not Choosers, make errors. Let μ_2 = the fidelity of copying, such that when $\mu_2 = 0$, Copiers correctly copy the action of a Chooser, and when $\mu_2 = 1$, Copiers always err, and select the resource not selected by the Chooser.

If our population is made up almost completely of Choosers, and Copiers are at mutation frequency, the payoff to each is:

$$\text{Payoff to Chooser} = a - k \tag{7}$$
$$\text{Payoff to Copier} = \mu_2 b + (1 - \mu_2)a \tag{8}$$

As such, Chooser is an ESS if:

$$\mu_2(a - b) > k \tag{9}$$

From Equation 9, we see that Chooser is an ESS when: (i) the error rate of Copier is high, (ii) the difference between a and b increases, and (iii) search costs are small.

In a population of Copiers, with Choosers at mutation frequency, the payoff to each is:

$$\text{Payoff to Chooser} = a - k \tag{10}$$
$$\text{Payoff to Copier} = xa + (1 - x)b \tag{11}$$

Copier is an ESS when:

$$k > (a - b)(1 - x) \tag{12}$$

Equation 12 shows that Copier will be an ESS when: (i) the search time for Chooser is high, (ii) the difference between a and b is small, and (iii) the relative frequency of A is high.

When $(a - b)(1 - x) > k > \mu_2 (a - b)$, a mixed ESS exists and the equilibrial frequencies of Choosers and Copiers are:

$$p = \frac{(a-b)(1-x)-k}{(a-b)(1-\mu_2-x)}, \text{ and } 1-p = 1-\frac{(a-b)(1-x)-k}{(a-b)(1-\mu_2-x)} \tag{13}$$

Copiers and Choosers make mistakes

Now, suppose that both Copiers and Choosers make mistakes. If our population is made up almost completely of Choosers, and Copiers are at mutation frequency, the payoff to Choosers is (as before):

$$\text{Payoff to Chooser} = \mu_1 b + (1 - \mu_1)a - k \tag{14}$$

Copier could find itself in one of four situations: (i) Copier does not err, Chooser errs, (ii) Copier doesn't err, Chooser doesn't err, (iii) Copier errs, Chooser errs, and (iv) Copier errs, Chooser doesn't err. The payoff for these scenarios is $(1 - \mu_2)(\mu_1 b + (1 - \mu_1)a) + \mu_2 (\mu_1 a + (1 - \mu_1)b)$. This simplifies to:

$$\text{Payoff to Copier} = a(1 - \mu_1\text{-}\mu_2 + 2\mu_1\mu_2) + b(\mu_1 + \mu_2 - 2\mu_1\mu_2)$$

Chooser is an ESS when:

$$(a - b)(\mu_2(1 - 2\mu_1)) > k \tag{15}$$

In other words, Chooser is an ESS when either: (i) the search cost is relatively low, (ii) the error rate for Copiers is high, or (iii) the difference between a and b is large.

If our population is made up almost completely of Copiers, and Choosers are at mutation frequency, the payoff to each is:

$$\text{Payoff to Chooser} = \mu_1 b + (1 - \mu_1)a - k \tag{16}$$
$$\text{Payoff to Copier} = xa + (1 - x)b \tag{17}$$

Copier is an ESS if:

$$k > (a - b)(1 - x - \mu_1) \quad (18)$$

Equation 18 demonstrates that Copier is an ESS when: (i) the search cost is relatively high, (ii) the error rate for Choosers is high, or (iii) the difference between a and b is small.

When $(a - b)(\mu_2(1 - 2\mu_1)) < k < (a - b)(1 - x - \mu_1)$, a mixed ESS exists. Setting the payoffs of Copier equal to Chooser, and solving for the equilibrial frequencies of Choosers and Copiers, we find that:

$$p = \frac{(a-b)(1-x-\mu_1)-k}{(a-b)(1+2\mu_1\mu_2-\mu_1-\mu_2-x)} \text{ and } 1-p = 1-\frac{(a-b)(1-x-\mu_1)-k}{(a-b)(1+2\mu_1\mu_2-\mu_1-\mu_2-x)} \quad (19)$$

DISCUSSION

With more and more evidence emerging that social learning, and its relation to genetic evolution, play an important role in animal social behavior, behavioral ecologists are beginning to develop a theoretical framework for understanding the evolution of various forms of social learning, such as copying. When mistakes are built into a game theory model for the evolution of copying, a number of general findings emerge from a two-strategy model.

Not surprisingly, increasing the search cost that is associated with the Chooser strategy decreases its frequency, and hence increases the frequency of the Copier strategy. In addition, decreasing the fidelity of copying — i.e., decreasing the proportion of times Copiers correctly emulate Choosers — decreases the frequency of the Copier strategy. Furthermore, increasing the mistake rate of Choosers increases the frequency of Copiers. At first glance this might seem like an intuitive result, in that we find a strategy (Chooser) decreasing when it is more prone to error. Keep in mind, however, that Copiers are also paying a cost when Choosers make an error, as they too are then likely to make the very same error. Copiers, however, pay a disproportionately lower cost when Choosers make mistakes, as Choosers always pay the cost of a mistake, while Copiers only pay that cost when they emulate a Chooser, and not when they emulate another Copier.

The Copier strategy is an ESS when the difference between the most profitable resource (A) and the least profitable resource (B) is small. At the same time, however, Copier is an ESS when the frequency of A is relatively high. That is, Copier does well when the most profitable resource (A) is common, but when it is not all that much more profitable than other resources (B). This somewhat surprising outcome is due to the fact that as Copier increases in frequency, its payoff approaches the average payoff for the environment (ax + b(1 – x)), while the Chooser payoff is always more heavily influenced by the most profitable resource (A), since Choosers discriminate between resource A and B in favor of A. As such, since Choosers are most often going to receive the resource A (i.e., they receive payoff a often) even when it is not common, Copiers fare best when A is common (so that they themselves will often obtain payoff a), but when a is not much greater than b (so that Choosers are not greatly benefiting from high payoffs).

The models presented here are by no means the first to consider the implications of errors for the evolution of social learning via copying (Boyd & Richerson 1985, 1995; Rogers 1988; Castro & Toro 2004). They are, however, quite different from prior models in at least two important ways: (1) Unlike other work, here I examine the case when models err, copiers err, and both err. (2). Prior work has focused on the evolution of copying when the environment is either spatially or temporally fluctuating. The models here, however, examine a very different ecological context — a single environment in which there are two different resources. Despite the differences between the models developed here and those developed earlier, it is promising that for the cases in which models are comparable, results are quite similar, suggesting that these results are robust.

The models developed here could potentially be tested in the laboratory using organisms that rely, in part, on social learning and are amenable to multigenerational studies (e.g., rats, mice, guppies). The key variables in the model — the cost of searching, the relative profitability and frequency of different resource types, and the error rates — all have the potential to be experimentally manipulated. For example, if food was the resource in question, search time could be manipulated by making it easier or more difficult to get access to various food items, resource values could be adjusted experimentally, and error rates could be manipulated by training some animals to choose inferior food types and then using such trained individuals as models for those that get information via copying. The results of such manipulations on the frequency of copiers could then be tested against the predictions of the models presented here.

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