

Is information transfer always advantageous when food patchily distributed? A simple ESS model

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One of the potential benefits of colonial breeding may be using information on the location of food gained from other members of the colony. Obtaining this information without searching may improve the foraging efficiency especially when food occurs in rich patches whose locations are unpredictable both in space and time. A question is arising: is this efficiency really improved by the information transfer? Using the game theory we modelled the problem by two strategies: (1) Searcher looks for food actively and (2) Follower reaches the food patch by following Searchers. Investigating the equilibrium between these strategies we concluded that information transfer may increase the individuals' average foraging efficiency when the Searchers gain benefits from the exchange too.

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1. Introduction

Thirteen percent of bird species breed in colonies (Lack 1968) even though this behaviour has many disadvantages including the increased possibility of ectoparasite or disease infection (Brown & Brown 1986, 1988, Wittenberger & Hunt 1985) and intensive competition for food, nest sites, nest materials and mates (Wittenberger & Hunt 1985). One of the likely benefits from coloniality may be the possibility of using information on the location of food from other members of the colony to improve foraging efficiency (Krebs 1974).

The food of many colonial birds is located in rich patches which are distributed

in an unpredictable fashion both in space and time (Ward & Zahavi 1973, Krebs 1974). Under these conditions finding a food patch is very costly. However, if a bird can obtain information on the location of food without searching then the saving in time and energy may be spent in increasing its foraging efficiency.

The most widely accepted way of acquiring information is through the mechanism of information centre (Ward & Zahavi 1973, Mock *et al.* 1988). This hypothesis supposes that a previously unsuccessful individual can follow its successful colony mates to their previously discovered foraging site. Furthermore it is assumed that the unsuccessful birds parasitize the successful ones and that the parasites gain a net benefit while the

parasitized one suffers a slight or no cost (Krebs 1978, Evans 1982, Mock *et al.* 1988). Beauchamp & Lefebvre (1988) studied this situation using the ESS approach (Maynard Smith 1982). They found that the information gainer strategy (following strategy) can be evolutionary stable if it is difficult to find a new food patch and enough food remain in the patch after the initial discovering. However, the average feeding rate in their ESS was smaller than that would be in the case of non-following strategy. They supposed that the lower variance of feeding rate associated with the following strategy and other forms of information transfer (e.g. local enhancement or network foraging) could still explain why the birds breed colonially. Almost all of the previous studies supposed that an individual follows its colony member just after a long unsuccessful foraging trip. For example Beauchamp & Lefebvre (1988) used fixed maximum searching time for all individuals in their model. However, one can expect that some of the colony members will cheat, namely will not spend a long time searching if they have the possibility to follow other successful birds.

In this paper, using a very simple ESS model, we investigate whether these two strategies of searching and following can exist together and furthermore whether the information transfer at a breeding colony, in spite of the cheating, can alone explain the maintenance of coloniality.

2. The model

We modelled the information exchange by two strategies – Searcher and Follower. The former looks for food and the latter

waits at its nest for a successful individual and then follows it (Barta & Szép 1992). After the finding of food, both of them return to the discovered patch.

Tab. 1 shows the payoff matrix of the game. The elements of the matrix were considered to be energy intake rate which a forager experiences when it feeds with others of the given strategies. We did not distinguish between cases when the Searcher forages alone or with other Searchers. On the other hand Followers were assumed to always feed with Searchers. When a Follower plays against another Follower its intake rate was presumed to be zero since nobody searches for food. Assuming that following is more advantageous than searching, we set the energy intake rate of Follower against Searcher (c) larger than the payoff of Searcher against another Searcher (a). Let p be the proportion of Searchers in the population. Under these conditions the proportion of strategies reaches an equilibrium point where

$$p = b/(c-a+b) \quad c-a+b \neq 0 \quad (1)$$

Since 'c' was assumed greater than 'a' only a mixed ESS is the solution of this game ($p < 1$).

Tab. 1. The payoff matrix to player 1 of the game between two different foraging strategies. Searcher looks for food and Follower follows their successful colony members. Letters denote energy intake rate.

		Player 2	
		Searcher	Follower
Player 1	Searcher	a	b
	Follower	c	0

Consider a population that consists of both Searchers and Followers. The payoff to Searchers is:

$$W_S^E = pa + (1-p)b \quad (2)$$

and that to Followers is

$$W_F^E = pc \quad (3)$$

When the population is in equilibrium then these payoffs are equal:

$$W_S^E = W_F^E = W^E \quad (4)$$

where W^E denotes the fitness of an average individual in the population (Maynard Smith 1982). Let us consider another population that consists of Searchers ($p=1$) only. Information transfer of food location is not allowed in this population. Now the payoff of Searchers is:

$$W_S^S = a \quad (5)$$

3. Results

Comparing the payoffs of Searchers in these populations we can evaluate the effect of information exchange on the foraging success of individuals. We can distinguish three cases on the basis of how the presence of Followers influences the payoff of Searchers.

First when the food is limited, the attendance of Followers decreases the intake rate of Searchers ($a > b$). Under these conditions the relation of payoffs is:

$$pa + (1-p)b < a \quad (6)$$

Hence the individuals in the mixed population benefit less than they would do if they live in a pure Searcher population (Fig. 1a).

In the second case the food is assumed to occur in very dense but short life-span patches which is the case of many colonial bird (Ward & Zahavi 1973). Consequently it is unlimited so the Followers do not influence the energy intake rate of Searchers ($a = b$). Now the compared payoffs have the following relationship:

$$pa + (1-p)b = a \quad (7)$$

namely the information transfer does not affect the foraging success of average individuals (Fig. 1b).

Thirdly, the presence of Followers improves the foraging efficiency of Searchers ($a < b$) when the connection between the payoffs is:

$$pa + (1-p)b > a \quad (8)$$

So the information transfer can only improve the success of birds in this case (Fig. 1c).

The effects of either kin selection or reciprocal altruism is a further possibility to increase the average foraging efficiency for an individual. They may drive the proportion of Searcher (p) from its equilibrium point toward the maximum (Fig. 1a).

4. Discussion

An evolutionary biologist should assume (i) regular changes of the roles of searching and following or (ii) an ESS mixed from these two strategies so that the in-

formation transfer at a central place can exist. In the case of the first assumption the individuals can benefit from information transfer (Barta & Szép 1992), however, the conditions of maintaining the regularity by kin selection or reciprocal altruism are often not realized under the circumstances of large crowded colonies (Waltz 1982, Mock *et al.* 1988, Galef 1991).

On the base of the presented model, when mixed ESS exists in the population, the information transfer can only improve the foraging efficiency of individuals if both Searchers and Followers gain advantages

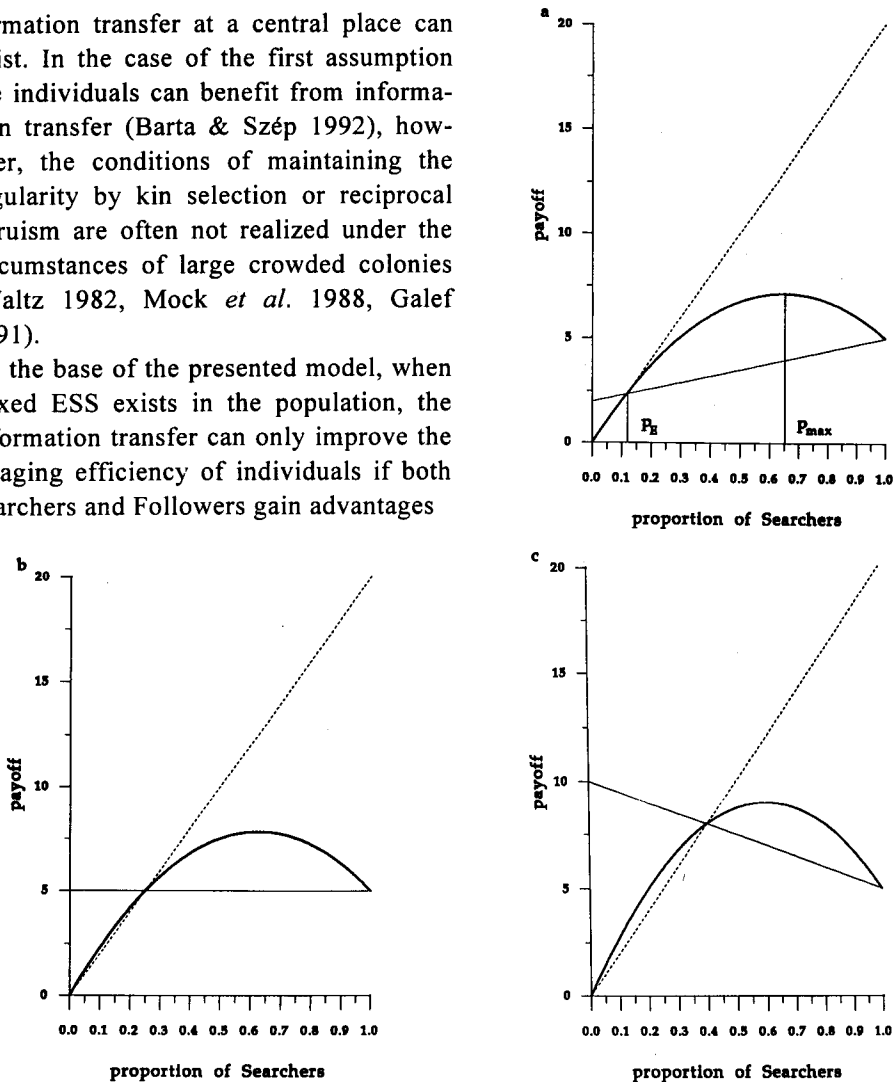


Fig. 1. Graphic presentation of the foraging game. Solid line indicates payoff of Searcher, dotted line marks payoff of Follower and heavy line shows the payoff of an average individual. The payoff of an average individual in a pure Searcher population is equal to 5. Arbitrary parameters of the games are given in brackets.

a. The Followers decreased the payoff of Searchers. The population can reach the maximum average payoff due to the effects of kin selection or reciprocal altruism which may drive p from p_E to p_{max} . p is the proportion of Searchers, p_E is the equilibrium proportion of Searchers and at p_{max} an average individual reaches maximum payoff ($a=5, b=2, c=20$).

b. The Followers did not influence the payoff of Searchers ($a=5, b=5, c=20$).

c. The Followers increased the payoff of Searchers ($a=5, b=10, c=20$).

from the exchange. However, these benefits of Searchers may be caused by factors outside of information transfer, e.g. social foraging (Götmark *et al.* 1986) and anti-predation advantages (Mock *et al.* 1988). Therefore, one may conclude that the information transfer alone may not be able to maintain the colonial nesting in the common cases (e. g. large crowded colonies). In other words, the widely used condition of patchily distributed food for the advantage of information transfer may not be sufficient, and it would be needed to amplify with the benefits of Searchers. When we do not assume benefits for Searchers, the information transfer could decrease the foraging success of individuals (Vickery *et al.* 1991, Caraco & Giraldeau 1991).

The most widely cited field studies of information transfer are those of Brown (1986, 1988) and Greene (1987). Both studies were able to demonstrate the improvement of information exchange on foraging efficiency of colony members. In the osprey colony studied by Greene (1987) close relatives lived together so the kin selection may be responsible for the benefits of information transfer. On the other hand, the degree of relatedness in cliff swallow colonies was very low (Brown 1986). Brown (1986) supposed that both Searcher and Follower cliff swallows benefit from information transfer which may be supported by their food sharing call (Brown *et al.* 1991). One of the possible benefits may be that the Searcher can more easily find the food patch with the aid of Followers on its subsequent trip. This is so of the swallows, since the food patch (aerial swarms of insects) can easily move away during a short time (Emlen & Demong 1975, Brown *et al.* 1991).

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Összefoglalás

Előnyös-e mindig az információ átadás foltszerű táplálék esetén? Egy egyszerű ESS modell

A telepes fészkelés egyik lehetséges előnye a teleptársak által gyűjtött, a táplálék helyéről szóló információ felhasználása. Ennek az információnak keresés nélküli megszerzése növelheti az egyedek táplálkozási hatékonyságát, különösen, ha a táplálék ritka, de gazdag foltokban fordul elő, és a foltok helye időben jósolhatatlan. Egy kérdés merül fel: tényleg növeli-e az információ-átadás a táplálkozási hatékonyságot? A játékelmélet eszközeit használva két táplálkozási stratégiával modelleztük a problémát: (i) a Kereső aktívan keres a táplálékfoltok után, (ii) a Követő a Keresőt követve éri el a táplálékfoltot. A két stratégia között beállt egyensúlyt vizsgálva, az a következtetés vonható le, hogy az információ-átadás csak akkor növeli a táplálkozási hatékonyságot, ha a Keresőknek is előnyös az átadás.

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