Evolutionary Game Theory Example

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One of the examples Dawkins gives in *The Selfish Gene* is about how certain birds have evolved the strategy of sneaking their eggs into other birds' nests, so they don't have to expend the energy to look after the eggs themselves. Cuckoos are an example of birds (referred to as brood parasites) that do this strategy.

One potential problem for our parasitic cuckoos, however, is that certain species of birds have evolved to be able to identify their own eggs. This means that a cuckoo unfortunate enough to lay their egg in one of these nests would not get any benefit from doing so. Guillemots are birds who can identify their own eggs, on the other hand this identification process may take a while and use energy that could otherwise be used on finding food. Finally, some species such as chickens have such a strong ingrained sense of looking after whatever is in their nest that they will sit on anything that falls into it, including fake eggs and even small animals such as kittens. Anything in their nest they treat as their own. In their naturally evolved habitat there were no brood parasites so identifying ones own eggs would not have been a particularly useful trait.

Now in a game theory setting, we assign payoffs to outcomes. We assume that sitting on an egg always causes it to hatch a chick. For every egg that hatches, the bird who laid the egg will get 5 points. For every egg that the bird has to sit on, the bird will lose 1 point. If a bird has to take the time to identify its own eggs out of all those in its nest it will lose 1 point (but if it finds any eggs that are not its own this cost will cancel out with the cost of sitting on the now destroyed egg). In our example we assume that cuckoos do not sit on eggs. We can summarise these payoffs into the following table:

Strategy	Cost/Reward
Having your own egg hatch	5
Sitting on eggs	-1 (per egg)
Identifying eggs	-1

Note that birds do not choose their actions consciously, their actions are predetermined by their genes. Chickens are simply unable to identify their eggs, they cannot adapt their strategy "on the fly", hence variations in the population dynamics will come from biology rather than the birds changing their own strategies.

The utility of any strategy is dependent on the population dynamics: a chicken in a population of chickens would gain many more points than a chicken in a population of cuckoos. Similarly, a cuckoo in a population of cuckoos would perform terribly due to the fact that no bird would be sitting on any eggs, so no eggs would be incubated. Using this observation we can calculate utility functions for each of the strategies, and then their expected utilities as functions of the current population state.

We call the 3 strategies sit (S), identify (I), and cheat (C). For now we assume that each bird only has 1 egg. We let $n :=$ number of foreign eggs in your own nest , and $x :=$ the target nest. $\mathbb{I}_{S\text{-}nest}(x)$ is a function which returns value 1 if the target nest is a sit nest, and 0 otherwise (as cheat nests and identify nests would result in no incubation for the cheater's egg).

$$U(S) = 5 - 1 - N$$
$$U(I) = 5 - 1 - 1 = 3$$
$$U(C) = 5\mathbb{I}_{\textit{S-nest}}(x)$$

Now to determine the expected value of these strategies we need to determine the distribution of the random variable N, and the probability of the event *S-nest*. Let the total number of birds in the population be T, and the proportion of each strategy be p_S, p_I, and p_C. We assume that cheaters cannot tell which nests belong to which species of birds and therefore when it decides which nest to sneak its egg into, each nest other than its own will be picked with probability $\frac{1}{T-1}$ (equal chance for each nest that isn't its own). For each nest, a cheater choosing its target is a Bernoulli random variable with probability $\frac{1}{T-1}$, where 1 represents the cheater choosing this particular nest. Now, all cheaters have the same probability of choosing an individual nest, and do so independently, hence the number of eggs in a particular nest is the sum of i.i.d Bernoulli variables, which gives

$$N \sim \text{Binomial}(T \times p_C, \tfrac{1}{T-1}) \implies \mathbb{E}(N) = p_C \frac{T}{T-1}$$

where $T \times p_C$ is the total number of cheaters in the population. The expectation of N is just *slightly* more than the proportion of cheaters in the population.

The probability of the event *S-nest* is determined by seeing that among the $T-1$ total nests available to sneak the egg into, $T \times p_S$ of them will be safe. Hence

$$\mathbb{P}(\textit{S-nest}) = p_S \frac{T}{T-1}$$

We can now determine the expected value of each strategy:

$$\mathbb{E}\left[U(S)\right] = 4 - \mathbb{E}N = 4 - p_C \frac{T}{T-1}$$
$$\mathbb{E}\left[U(I)\right] = 3$$
$$\mathbb{E}\left[U(C)\right] = 5\mathbb{E}[\mathbb{I}_{\textit{S-nest}}(x)] = 5\left(p_S \frac{T}{T-1}\right)$$

Using these expected values we can see which strategies would do better than others depending on the population state:

$$\mathbb{E}C \geq \mathbb{E}I$$
$$\implies 5\left(p_S \frac{T}{T-1}\right) \geq 3$$
$$\implies p_S \geq \frac{3}{5}\left(\frac{T-1}{T}\right)$$

$$
\begin{aligned}
\mathbb{E}S &\geq \mathbb{E}I \\
\implies 4 - p_C\frac{T}{T-1} &\geq 3 \\
\implies \tfrac{T-1}{T} &\geq p_C
\end{aligned}
$$

Which says "unless everyone is cheating identifying is a dominated strategy"

$$
\begin{aligned}
\mathbb{E}C &\geq \mathbb{E}S \\
\implies 5\left(p_S\frac{T}{T-1}\right) &\geq 4 - p_C\frac{T}{T-1} \\
\implies 5Tp_S &\geq 4T - 4 - Tp_C \\
\implies 4 - 4T &\geq T5p_C - 5p_S) \\
\implies \tfrac{4}{T} - 4 &\geq p_C - 5p_S
\end{aligned}
$$

Now, the regular definition of of an ESS doesn't particularly make sense in the case where T is a natural number, as an infinitesimal deviation is not possible when the population is of finite size, but if we let T tend to infinity we can find ESS. If $T \to \infty$ then $\frac{T-1}{T} \to 1$ and so the requirement for $\mathbb{E}S \geq \mathbb{E}I$ is always satisfied, hence sitting dominates identifying so identifiers are driven out. Now we can solve $\mathbb{E}C \geq \mathbb{E}S$ as we note that

$$p_I = 0 \implies p_C = 1 - p_S$$

and so

$$
\begin{aligned}
\mathbb{E}C &\geq \mathbb{E}S \\
\implies \tfrac{4}{T} - 4 &\geq p_C - 5p_S \\
\implies -4 &\geq -1 + p_S - 5p_S \\
\implies -3 &\geq -4p_S \\
\implies \tfrac{3}{4} &\leq p_S
\end{aligned}
$$

Now let's find the solution to the general case:

Strategy	Cost/Reward
Having your own egg hatch	h
Sitting on eggs	-e (per egg)
Identifying eggs	-i

Now when writing our utility functions we recognise that they are functions of multiple variables

$$U(S; h, e, i) = h - e(1 + N)$$
$$U(I; h, e, i) = h - e - i$$
$$U(C; h, e, i) = h\mathbb{I}_{\textit{S-nest}}(x)$$

And then we can calculate their expectations as before:

$$E(S; h, e, i) = h - e(1 + p_C)$$
$$E(I; h, e, i) = h - e - i$$
$$E(C; h, e, i) = h \cdot p_S$$

References

[Daw76] R Dawkins. *The Selfish Gene*. Oxford University Press, Oxford, UK, 1976.