

OTKA grant K 108974

Communication: badges, attention seeking and survival games

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31/01/2018

Research Report

The goal of the project was to study the mechanism of honest signalling in various contexts including aggressive communication, sexual selection and parent-offspring communication with the tools of game theory and survival games (kin demography).

Attention seeking displays (ASD). (i) We have shown that giving and listening to attention seeking displays can be evolutionarily stable (Számadó, 2015). (ii) We have investigated the evolution of ASDs in a spatially explicit model. We have shown that ASDs evolve to highest intensity possible with low cost and a dimorphic population evolves with high cost, where some individuals use the highest intensity ASD and others do not give ASD at all (Számadó, in preparation).

Offspring begging. (i) We have shown that honest begging of juveniles is a bet-hedging strategy in asexual populations (Garay et al., submitted to Plos One). (ii) We have shown that the seminal model of parent-offspring communication (Godfray, 1991) has infinite honest equilibria (Számadó et al., submitted to Open Science).

Aggressive communication. (i) We have investigated the role of pay-offs, parameters and seeding in a model of aggressive communication, and we have investigated the combination of these factors that promotes honest or mixed cheating strategies (Számadó, 2017). (ii) We have investigated the evolution of honest signalling in a spatially explicit game of aggressive communication. We have found a counterintuitive result: honesty did not evolve in spatially explicit settings (Számadó & Szántó, in preparation). (iii) We have proposed a potential function for soft song, a unique signal described in many bird species. This function is to help the estimation of distance between opponents. We have shown that soft song is honest cue of proximity assuming that there are potential errors in the estimation of distance between opponents (Számadó, in preparation).

General theory of signalling. (i) We have reviewed the problems with a proposed experimental approach (Polnaszek & Stephens, 2014) and with the Handicap Principle in our critique (Számadó & Penn, 2016). (ii) We have shown that the bimodal distribution of traits in a model a sexual selection is not due to the Handicap Principle as claimed (Clifton et al., 2015), instead it is a consequence of the playing-the-field assumption in the benefit function (Számadó & Penn, accepted at *Animal Behaviour*). (iii) We have shown that beneficial signals can maintain honest signalling even under conflict of interest (Számadó, in preparation). (iv) We have investigated the role of equilibrium signal cost in honest signalling with a help of an individual based simulation. We have shown that increasing equilibrium cost is only beneficial as long as it contributes to the potential cost of cheating (Számadó & Penn, in preparation).

Survival games and kin demography. (i) We have shown that cannibalism between the closest relatives can be considered as a mutualistic kin strategy when the benefit of cannibalism is

greater than the cost of it (Garay et al. 2016). (ii) We have shown that helping post-fertile grandparents will spread in the population if the cost of support to post-fertile grandparents slightly decreases the demographic parameters of fertile parents, yet it radically increases the survival rate of grandchildren (Garay et al., submitted to BMC Biology).

General game theory. (i) We have investigated matrix games under time constraints, where all different interactions may have different average time durations and different payoffs. We have shown that time constraints can change the solution of the prisoners' dilemma game (Garay et al., 2017).

There is only one study that we promised to investigate in the original research plan, but we did not do it: the metanalysis of experiments on badges of dominance. We lacked the time and manpower to carry out an extensive literature search, which would have been necessary for such study.

We promised 7 articles published in international refereed journals ranging from *Journal of Theoretical Biology*, *Animal Behaviour*, *Behavioral Ecology* to *Theoretical Population Biology*. The project has 6 published/accepted papers with a cumulative impact factor: 16,88 (*Journal of Theoretical Biology*, *Animal Behaviour* (2), *Ecological Modelling*, *Plos One*, *BMC Evolutionary Biology*). There are three more manuscripts submitted to international refereed journals (*BMC Biology*, *Royal Society Open Science*, *Plos One*). One of these received a 'minor revision' decision (*Plos One*), the revised MS will be sent back within days. We have 5 more drafts in preparation. All of the manuscripts and drafts not accepted or submitted as yet are available from bioRxiv (<https://www.biorxiv.org/>).

Detailed reports

Számadó, Sz. (2015) Attention Seeking Displays. *Plos One*. IF: 3,54

Conspicuous signals abound in nature. We propose that the function of some of these signals could be to call the attention of the receiver. We have shown that giving and searching for signals that may not signal quality but help the receiver to locate the signaller can be an ESS in a simple game of communication. There can be different equilibria depending on the preferences of the receivers: (i) only high quality signallers give attention seeking displays (ASD), in this case the signal is revealing about the quality of the signaller; (ii) both high and low quality signallers give ASDs, in this case the signal is not revealing.

Számadó, Sz. & Penn, D.J. (2015) Why does costly signalling evolve? Challenges with testing the handicap hypothesis, *Animal Behaviour*. IF: 2,86

We published a critique of the study made by Polnaszek & Stephens (2014) on measuring the relationship between signal cost and honesty. We raised these caveats regarding the theoretical background, interpretations and conclusions of the study by Polnaszek and Stephens (2014) to emphasize the problems with the handicap hypothesis and the challenges with testing this idea.

Future studies should consider the theoretical objections with the handicap hypothesis, or provide more convincing justifications for why these critiques can be ignored. We suggest that the jay study provides evidence that uncheatable constraints can enforce honesty (index signal hypothesis), but studies are needed to find an explanation for the evolution of such constraints.

Garay József, Varga Zoltán, Gámez, Manuel, Cabello, Tomas (2016) Sib cannibalism can be adaptive for kin. *Ecological Modelling* IF: 2,36

Sib cannibalism seems to be paradoxical behaviour, since it decreases the survival rate of the closest relative juveniles, so the rate of sib cannibalism changes the demography of the cannibal phenotype. In the general kin demographic selection model presented here, the long-term growth rate of a phenotype is determined by a Leslie matrix that depends on the life history strategy, and a uniform density-dependent selection process takes place, keeping the total population size at the level of the carrying capacity. Using this model, where different phenotypes are described by different Leslie matrices, we point out that the phenotype optimizing the phenotypic long-term growth rate will select out any other optimizing phenotype. We find that sib cannibalism is adaptive if the sib cannibal can decrease its developmental time, and the shorter development time can increase the rate of survival from sib cannibal juvenile to adult, and also when sib cannibalism increases fecundity in the adult stage. Cannibalism between the closest relatives can be considered as a mutualistic kin strategy when the benefit of cannibalism is greater than the cost of it.

Garay, J., Csiszár, V. & Móri, T.F. (2017) Evolutionarily stability for matrix games under time constraints. *Journal of Theoretical Biology*. IF: 2,04

In ecology, since actions need different time durations, the time constraints decrease the number of active individuals, and so the number of interactions, as well. Based on that, we introduce a matrix game under time constraints, where all different interactions may have different average time durations and different payoffs. We adapt Maynard Smith's concepts of evolutionary stability for this class of game. The time constraints can change the solution of the prisoners' dilemma game, namely, the cooperator strategy is evolutionarily stable strategy (ESS) if the time durations of defector strategy are long enough. The cooperator strategy is also ESS in the introduced prisoners' sharing game, where the time constraints are given by the original version of prisoners' dilemma and the payoff matrix defines how to share the common plunder, i.e., if the cooperator remains silent, and defector betrays the cooperator, then the cooperator will get the bigger part of plunder.

Számadó, Sz. (2017) When honesty and cheating pays-off: the evolution of honest and dishonest equilibria in a conventional signalling game. *BMC Evolutionary Biology*. IF: 3,22

Mixed cheating where some individuals signal honestly yet some other cheat can be found in nature. Recently the validity of the models used to understand this observation was questioned (Hegelsen et al., 2013). We re-run the Szalai and Számadó (2009) simulations with the extended strategy set proposed by Hegelsen et al. (2013) using the same parameter range as Szalai and Számadó (2009).

Communication and polymorphic strategy sets with honest and cheating strategies evolved though not as frequently as in the original study (Szalai and Számadó, 2009); it is not surprising given the much larger strategy set introduced by Hegelsen et al. (2013). We have shown that the differences between the current results and the results of Hegelsen et al. (2013) –where no communication evolved at all- can be explained by two factors: (i) choice of parameter range: Hegelsen et al. (2013) used a restricted range, two orders of magnitude smaller than the original study and (ii) different seedings used for the initial populations. Strategy set had a small effect; pay-offs had little effect in honest regions.

Számadó, Sz. & Penn D.J. (Accepted in Animal Behaviour) Does the handicap principle explain the evolution of dimorphic ornaments? *Animal Behaviour*. IF: 2,86

Dimorphic ornaments are characteristic and puzzling traits that can be observed in males of many species. Clifton et al. (2016) in recent paper argue that the handicap principle can explain the evolution of bimodal ornament distributions. Számadó and Penn (accepted Animal Behaviour) provide a critique of this claim. We point out that the results of the Clifton et al. (2016) depends on a specific assumption about the benefits of ornamentation, namely the fact that this benefit function has an inflection point at the average ornament size. Thus, the handicap principle is neither necessary nor sufficient to explain bimodal ornament distributions.

Garay, J., Varga Z., Számadó, Sz. & Szathmáry, E. Caring for parents: an evolutionary rationale. (submitted to BMC Biology)

Helping the elders is a moral commitment in many societies. We have investigated the evolutionary feasibility of such a rule using population dynamics (Leslie-type model). The heart of the problem is a three-way trade-off between fecundity, survival and helping the elders. It is possible to show that such helping behaviour will spread in the population if the cost of support to post-fertile grandparents slightly decreases the demographic parameters of fertile parents, yet it radically increases the survival rate of grandchildren. However, in general there is a threshold over which providing support to grandparents offers no evolutionary advantage.

Garay, J., Csiszár, V., Móri, T.F., Szilágyi, A., Varga, Z., & Számadó, Sz. Juvenile honest food solicitation and parental investment as a life history strategy: a kin demographic selection model (submitted to *Plos One*)

Parent-offspring conflict is a hotspot in biology. Parent-offspring communication is usually investigated with game theoretical models which have arbitrary pay-offs. Here we plan to put parent-offspring conflict and parent-offspring communication in the context of life-history models. Previous efforts mainly focused on modelling resource allocation at the expense of the dynamic interaction during a reproductive season. Here we present a two-stage model of begging where the first stage models the interaction between nestlings and parents within a nest and the second stage models the life-history trade-offs. We show in an asexual population that honest begging results in

decreased variance of collected food between siblings, which leads to mean number of surviving offspring. Thus, honest begging can be seen as a special bet-hedging against informational uncertainty, which not just decreases the variance of fitness but also increases the arithmetic mean.

Számadó, Sz, Zachar, I. & Czégel, D. One problem too many solutions: how costly is the honest signal of need? (submitted to *Royal Society Open Science*)

The “cost of begging” is one of the prominent predictions of costly signalling theory. It predicts that offspring begging has to be costly in order to be honest; more specifically it predicts that there is a single cost function - proportional to the parent’s fitness loss – that maintains honesty. Számadó investigated a classical model of begging (Godfray, 1991), he was able to show another interpretation of this cost: that this cost can be proportional to the fitness gain of the offspring, and any linear combination of these two cost functions is a solution too. Costly signalling theory cannot give a single prediction about the level of equilibrium cost in parent-offspring conflict. Measured equilibrium cost has to be compared to the parent’s fitness loss and to the fitness gain of the offspring in order to make meaningful conclusions about the role of the measured cost.

Számadó, Sz. & Penn, D.J. The role of equilibrium cost in the evolution of honest signalling: waste or optimal investment? (in preparation)

The role of cost in honest signalling is hotly debated. We investigated the role of equilibrium signal cost in the evolution of honest signals in both differential benefit and differential cost models using an agent-based simulation. We found that there is an optimal investment paid by honest individual that allows for the highest level of honesty when there is correlation between signal cost paid by low and high-quality individuals. This holds for both differential benefit and differential cost models as long there is a correlation between signal cost paid by low and high quality individuals. However, increasing equilibrium signal cost poses an obstacle and hinders the evolution of honest signalling when there is no correlation between the cost paid by low and high-quality individuals. Last but not least, we found that the potential cost of cheating is a much better predictor of honesty than the equilibrium cost paid by honest signallers.

Számadó, Sz. Soft song: help thine enemy (in preparation)

The so called “soft song” differs from the traditional territorial bird song in both structure and amplitude. As a result soft song can be detected only nearby receivers. Soft song has two other interesting characteristics: (i) out of a number signals used in aggressive context, like song type switching and song matching, only soft song predicts reliably the probability of attack, (ii) it is a low cost signal. The fact that such a low cost signal can still be a reliable indicator of aggressive intent caused a lot of speculation in the literature. We show with the help of game theoretical models that the possible function of soft song is to signal the proximity of the signaller to the rival. In turn it is this ‘proximity risk’ –the risk of a rival that can mount a successful attack- that maintains the honesty of this low amplitude, low cost signal.

Számadó, Sz. Honesty needs no cost: beneficial signals can be honest and evolutionarily stable. (in preparation)

The role of signal cost is hotly debated in biology. The handicap principle claims that honest signals have to be costly at the equilibrium and this cost is a theoretical necessity. Accordingly, the handicap principle further claims that signalling is fundamentally different from any other adaptation because honest signalling would collapse in the absence of cost – which is a “necessary evil” for other traits. We investigated this claim in a simple action-response game where signals do not have any cost. We have shown that beneficial signals can be honest and evolutionarily stable. These signals are beneficial to both high and low quality signallers independently of the receiver’s response, yet they can maintain honest signalling just as much as costly signals. Signal cost –in or out of equilibrium- is not a necessary condition of honesty.

Számadó, Sz. Attention seeking in a spatially explicit game of mate choice and the evolution of dimorphic ornaments (in preparation)

The evolution of conspicuous signals fascinated biologist ever since Darwin. The Handicap Principle was dominant explanation in the last decades; it proposed that exaggerated and conspicuous signals are costly signals of quality. There are other less popular explanations however, one them is that conspicuous signals function to call the attention of potential receivers. These ‘attention seeking displays’ need not reveal the quality of the signaller. There are many empirical examples and recently the idea was modelled in terms of a simple action-response game. However, action-response games model an interaction of a pair of signaller and receiver, thus they omit potential competition between signallers, which could be a crucial force behind the evolution of attention-seeking displays. Here I model this competition in a spatially explicit model of mate choice where males can give a continuous signal to call the attention of potential mates. The results show that attention-seeking displays readily evolve to the allowed maximum when the cost of signalling is low. However, dimorphism evolves when the cost of signalling is high. The population consist of two types of males at this dimorphic state: males that do not give a signals and males that give the highest intensity signal possible. The results show that variation in quality is not a necessary requirement for the evolution of dimorphic traits.

Számadó, Sz. Honest and cheating strategies in a simple model of aggressive communication: the role of spatial correlations (in preparation)

The evolution and maintenance of communication in terms of aggressive interactions is a long-debated issue. Several game theoretical models and individual based computer simulations investigated this problem in terms of a simple game of aggressive communication. So far all of these investigations focused on well mixed population of individuals. However, spatial correlations can emerge in nature where individuals or group of individuals defend resources. The extensive literature on cooperative games show that these spatial correlations can be vital in the maintenance and evolution of cooperative strategies, thus it is reasonable to expect that such correlations could play

an important role in the evolution of honest communication as well. Here we investigate a traditional game of aggressive communication in a spatially explicit context. We investigate the role of spatial correlations by comparing results of evolvability in well mixed populations with results from spatially explicit populations. Spatial correlations seem to inhibit the evolution of communication in the spatially explicit version of this game. This result is unexpected, and it requires further investigation to understand.

List of publications

Published

Számadó, Sz. (2015) Attention Seeking Displays. *PLOS one* 10(8): e0135379.

<https://doi.org/10.1371/journal.pone.0135379>

Számadó, Sz. & Penn, D.J. (2015) Why does costly signalling evolve? Challenges with testing the handicap hypothesis, *Animal Behaviour*. Volume 110, Pages e9-e12.

<http://dx.doi.org/10.1016/j.anbehav.2015.06.005>

Garay József, Varga Zoltán, Gámez, Manuel, Cabello, Tomas (2016) Sib cannibalism can be adaptive for kin. *Ecological Modelling* 334:51-59.

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Számadó, Sz. (2017) When honesty and cheating pays-off: the evolution of honest and dishonest equilibria in a conventional signalling game. *BMC Evolutionary Biology*. 17(1), 270.

<https://doi.org/10.1186/s12862-017-1112-y>

Accepted

Számadó, Sz. & Penn D.J. Does the handicap principle explain the evolution of dimorphic ornaments? (*Animal Behaviour*)

<http://real.mtak.hu/id/eprint/73702>

Submitted

Garay, J., Varga Z., Számadó, Sz. & Szathmáry, E. Caring for parents: an evolutionary rationale. (submitted to *BMC Biology*) Draft uploaded to bioRxiv.

<https://doi.org/10.1101/239285>

Garay, J., Csiszár, V., Móri, T.F., Szilágyi, A., Varga, Z., & Számadó, Sz. Juvenile honest food solicitation and parental investment as a life history strategy: a kin demographic selection model. (submitted to *Plos One*) Draft uploaded to bioRxiv.

<https://doi.org/10.1101/240416>

Számadó, Sz, Zachar, I. & Czégel, D. One problem too many solutions: how costly is the honest signal of need? (submitted to *Royal Society Open Science*) Draft uploaded to bioRxiv.

<https://doi.org/10.1101/240440>

In preparation

Számadó, Sz. & Penn, D.J. The role of equilibrium cost in the evolution of honest signalling: waste or optimal investment? (in preparation) Draft uploaded to bioRxiv.

<https://doi.org/10.1101/256370>

Számadó, Sz. Honesty needs no cost: beneficial signals can be honest and evolutionarily stable. (in preparation) Draft uploaded to bioRxiv.

<https://doi.org/10.1101/256248>

Számadó, Sz. Soft song: help thine enemy! (in preparation) Draft uploaded to bioRxiv.

<https://doi.org/10.1101/255836>

Számadó, Sz. Attention seeking in a spatially explicit game of mate choice and the evolution of dimorphic ornaments. (in preparation) Draft uploaded to bioRxiv.

<https://doi.org/10.1101/257329>

Számadó, Sz. & Szántó, A. Honest and cheating strategies in a simple model of aggressive communication: the role of spatial correlations. (in preparation) Draft uploaded to bioRxiv.

<https://doi.org/10.1101/257394>

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