

REPORT DOCUMENTATION PAGE			Form Approved OMB NO. 0704-0188		
<p>The public reporting burden for this collection of information is estimated to average 1 hour per response, including the time for reviewing instructions, searching existing data sources, gathering and maintaining the data needed, and completing and reviewing the collection of information. Send comments regarding this burden estimate or any other aspect of this collection of information, including suggestions for reducing this burden, to Washington Headquarters Services, Directorate for Information Operations and Reports, 1215 Jefferson Davis Highway, Suite 1204, Arlington VA, 22202-4302. Respondents should be aware that notwithstanding any other provision of law, no person shall be subject to any penalty for failing to comply with a collection of information if it does not display a currently valid OMB control number. PLEASE DO NOT RETURN YOUR FORM TO THE ABOVE ADDRESS.</p>					
1. REPORT DATE (DD-MM-YYYY) 10-12-2021		2. REPORT TYPE Final Report		3. DATES COVERED (From - To) 5-Dec-2016 - 5-Jun-2020	
4. TITLE AND SUBTITLE Final Report: A general theory of social structure integrating demography and decisions on social networks			5a. CONTRACT NUMBER W911NF-17-1-0017		
			5b. GRANT NUMBER		
			5c. PROGRAM ELEMENT NUMBER 611102		
6. AUTHORS			5d. PROJECT NUMBER		
			5e. TASK NUMBER		
			5f. WORK UNIT NUMBER		
7. PERFORMING ORGANIZATION NAMES AND ADDRESSES University of Pennsylvania Office of Research Services 3451 Walnut Street, 5th Floor Philadelphia, PA 19104 -6205			8. PERFORMING ORGANIZATION REPORT NUMBER		
9. SPONSORING/MONITORING AGENCY NAME(S) AND ADDRESS (ES) U.S. Army Research Office P.O. Box 12211 Research Triangle Park, NC 27709-2211			10. SPONSOR/MONITOR'S ACRONYM(S) ARO		
			11. SPONSOR/MONITOR'S REPORT NUMBER(S) 69191-MA.15		
12. DISTRIBUTION AVAILABILITY STATEMENT Approved for public release; distribution is unlimited.					
13. SUPPLEMENTARY NOTES The views, opinions and/or findings contained in this report are those of the author(s) and should not be construed as an official Department of the Army position, policy or decision, unless so designated by other documentation.					
14. ABSTRACT					
15. SUBJECT TERMS					
16. SECURITY CLASSIFICATION OF:			17. LIMITATION OF ABSTRACT UU	15. NUMBER OF PAGES	19a. NAME OF RESPONSIBLE PERSON Erol Akcay
a. REPORT UU	b. ABSTRACT UU	c. THIS PAGE UU			19b. TELEPHONE NUMBER 650-644-5412

RPPR Final Report
as of 24-Feb-2022

Agency Code: 21XD

Proposal Number: 69191MA

Agreement Number: W911NF-17-1-0017

INVESTIGATOR(S):

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DUNS Number: 042250712

EIN: 231352685

Report Date: 05-Sep-2020

Date Received: 10-Dec-2021

Final Report for Period Beginning 05-Dec-2016 and Ending 05-Jun-2020

Title: A general theory of social structure integrating demography and decisions on social networks

Begin Performance Period: 05-Dec-2016

End Performance Period: 05-Jun-2020

Report Term: 0-Other

Submitted By: Erol Akcay

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Distribution Statement: 1-Approved for public release; distribution is unlimited.

STEM Degrees:

STEM Participants:

Major Goals: The major goals of this project were to (i) model the processes structuring social networks in animal and human societies, (ii) study how social network structure affects individual behavior and social traits, and (iii) study how social networks coevolve with social behaviors.

Accomplishments: See attached pdf.

Training Opportunities: Nothing to Report

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Results Dissemination: We have published 14 papers from the work supported by the grant, and plan to submit at least one more paper, as described below. We have also disseminated our results at various meetings as oral presentations, including specifically the annual Evolution meetings and numerous workshops and symposia.

In preparation

Smolla, M. and Akçay, E. Coevolution of culture, learning, and social structure in variable environments. Manuscript in preparation.

Published

Ilany, A., Holekamp, K.E. and Akçay, E., 2021. Rank-dependent social inheritance determines social network structure in spotted hyenas. *Science*, 373(6552), pp.348-352.

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Dridi, S. and Akçay, E., 2018. Learning to cooperate: The evolution of social rewards in repeated interactions. *The American Naturalist*, 191(1), pp.58-73.

Honors and Awards: Nothing to Report

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Protocol Activity Status:

Technology Transfer: Nothing to Report

PARTICIPANTS:

Participant Type: Postdoctoral (scholar, fellow or other postdoctoral position)

Participant: Marco Smolla

Person Months Worked: 6.00

Funding Support:

Project Contribution:

National Academy Member: N

ARTICLES:

Publication Type: Journal Article

Peer Reviewed: Y **Publication Status:** 1-Published

Journal: Nature Communications

Publication Identifier Type: DOI

Publication Identifier: 10.1038/s41467-018-05130-7

Volume: 9

Issue: 1

First Page #:

Date Submitted: 9/19/18 12:00AM

Date Published: 7/1/18 8:00AM

Publication Location:

Article Title: Collapse and rescue of cooperation in evolving dynamic networks

Authors: Erol Akçay

Keywords: Cooperation, networks, social inheritance, coevolution

Abstract: The evolutionary dynamics of social traits depend crucially on the social structure of a population. The effects of social structure on social behaviors are well-studied, but relatively little is known about how social structure itself coevolves with social traits. Here, I study such coevolution with a simple yet realistic model of within-group social structure where social connections are either inherited from a parent or made randomly. I show that cooperation evolves when individuals make few random connections, but the presence of cooperation selects for increased rates of random connections, which leads to its collapse. Inherent costs of social connections can prevent this negative feedback, but these costs can negate some or all of the aggregate benefits of cooperation. Exogenously maintained social inheritance can mitigate the latter problem and allow cooperation to increase the average fitness of a population. These results illustrate how coevolutionary dynamics can constrain...

Distribution Statement: 3-Distribution authorized to U.S. Government Agencies and their contractors

Acknowledged Federal Support: Y

RPPR Final Report as of 24-Feb-2022

Publication Type: Journal Article Peer Reviewed: Y **Publication Status:** 1-Published

Journal: Proceedings of the National Academy of Sciences

Publication Identifier Type: DOI

Publication Identifier: 10.1073/pnas.1817095116

Volume: 116

Issue: 18

First Page #: 8834

Date Submitted: 10/2/19 12:00AM

Date Published: 4/1/19 4:00AM

Publication Location:

Article Title: Evolution of social norms and correlated equilibria

Authors: Bryce Morsky, Erol Akçay

Keywords: social norms, correlated equilibrium, cooperation, coordination, superstitions

Abstract: Social norms regulate and coordinate most aspects of human social life, yet they emerge and change as a result of individual behaviors, beliefs, and expectations. A satisfactory account for the evolutionary dynamics of social norms, therefore, has to link individual beliefs and expectations to population-level dynamics, where individual norms change according to their consequences for individuals. Here, we present a model of evolutionary dynamics of social norms that encompasses this objective and addresses the emergence of social norms. In this model, a norm is a set of behavioral prescriptions and a set of environmental descriptions that describe the expected behaviors of those with whom the norm holder will interact. These prescriptions and descriptions are functions of exogenous environmental events. These events have no intrinsic meaning or effect on the payoffs to individuals, yet beliefs/superstitions regarding them can effectuate coordination. Although a norm's prescriptions an

Distribution Statement: 3-Distribution authorized to U.S. Government Agencies and their contractors

Acknowledged Federal Support: Y

Publication Type: Journal Article Peer Reviewed: Y **Publication Status:** 1-Published

Journal: Scientific Reports

Publication Identifier Type: DOI

Publication Identifier: 10.1038/s41598-020-63446-1

Volume: 10

Issue:

First Page #: 10251

Date Submitted: 12/10/21 12:00AM

Date Published:

Publication Location:

Article Title: Combating climate change with matching-commitment agreements.

Authors: Chai Molina, Erol Akçay, Ulf Dieckmann, Simon Levin, Elena Rovenskaya

Keywords: Climate action, Matching commitments, Greenhouse gas emissions, International agreements, Public goods.

Abstract: Countries generally agree that global greenhouse gas emissions are too high, but prefer other countries reduce emissions rather than reducing their own. The Paris Agreement is intended to solve this collective action problem, but is likely insufficient. One proposed solution is a matching-commitment agreement, through which countries can change each other's incentives by committing to conditional emissions reductions, before countries decide on their unconditional reductions. Here, we study matching-commitment agreements between two heterogeneous countries. We find that such agreements (1) incentivize both countries to make matching commitments that in turn incentivize efficient emissions reductions, (2) reduce emissions from those expected without an agreement, and (3) increase both countries' welfare. Matching-commitment agreements are attractive because they do not require a central enforcing authority and only require countries to fulfil their promises; countries are left to choose

Distribution Statement: 4-Distribution authorized to the Department of Defense and U.S. DoD contractors only

Acknowledged Federal Support: Y

RPPR Final Report as of 24-Feb-2022

Publication Type: Journal Article Peer Reviewed: Y **Publication Status:** 1-Published

Journal: Science

Publication Identifier Type: DOI

Publication Identifier: 10.1126/science.abc1966

Volume: 373

Issue: 6552

First Page #: 348

Date Submitted: 12/10/21 12:00AM

Date Published: 7/1/21 4:00AM

Publication Location:

Article Title: Rank-dependent social inheritance determines social network structure in spotted hyenas

Authors: Amiyaal Ilany, Kay E. Holekamp, Erol Akçay

Keywords: social inheritance, spotted hyena, social network, dominance rank

Abstract: The structure of animal social networks influences survival and reproductive success, as well as pathogen and information transmission. However, the general mechanisms determining social structure remain unclear. Using data from 73,767 social interactions among wild spotted hyenas collected over 27 years, we show that the process of social inheritance determines how offspring relationships are formed and maintained.

Relationships between offspring and other hyenas bear resemblance to those of their mothers for as long as 6 years, and the degree of similarity increases with maternal social rank. Mother-offspring relationship strength affects social inheritance and is positively correlated with offspring longevity. These results support the hypothesis that social inheritance of relationships can structure animal social networks and be subject to adaptive tradeoffs.

Distribution Statement: 1-Approved for public release; distribution is unlimited.

Acknowledged Federal Support: Y

Publication Type: Journal Article Peer Reviewed: Y **Publication Status:** 1-Published

Journal: Proceedings of the Royal Society B: Biological Sciences

Publication Identifier Type: DOI

Publication Identifier: 10.1098/rspb.2020.0735

Volume: 287

Issue: 1927

First Page #: 20200735

Date Submitted: 12/10/21 12:00AM

Date Published: 5/1/20 4:00AM

Publication Location:

Article Title: Evolution of contribution timing in public goods games

Authors: Bryce Morsky, Marco Smolla, Erol Akçay

Keywords: spatial structure, social dilemma, life-history strategies, population viscosity, public goods games, timing

Abstract: Life-history strategies are a crucial aspect of life, which are complicated in group-living species, where pay-offs additionally depend on others' behaviours. Previous theoretical models of public goods games have generally focused on the amounts individuals contribute to the public good. Yet a much less-studied strategic aspect of public goods games, the timing of contributions, can also have dramatic consequences for individual and collective performance. Here, we develop two stage game theoretical models to explore how the timing of contributions evolves. In the first stage, individuals contribute to a threshold public good based on a performance schedule. The second stage begins once the threshold is met, and the individuals then compete as a function of their performance. We show how contributing rapidly is not necessarily optimal, because delayers can act as 'cheats,' avoiding contributing while reaping the benefits of the public good. However, delaying too long can put the delay

Distribution Statement: 1-Approved for public release; distribution is unlimited.

Acknowledged Federal Support: Y

RPPR Final Report as of 24-Feb-2022

Publication Type: Journal Article Peer Reviewed: Y **Publication Status:** 1-Published

Journal: Philosophical Transactions of the Royal Society B: Biological Sciences

Publication Identifier Type: DOI

Publication Identifier: 10.1098/rstb.2020.0049

Volume: 376

Issue: 1828

First Page #:

Date Submitted: 12/10/21 12:00AM

Date Published: 5/1/21 4:00AM

Publication Location:

Article Title: Not by transmission alone: the role of invention in cultural evolution

Authors: Susan Perry, Alecia Carter, Marco Smolla, Erol Akçay, Sabine Nöbel, Jacob G. Foster, Susan D. Healy

Keywords: creativity, innovation, cultural evolution, invention, individual differences

Abstract: Innovation—the combination of invention and social learning—can empower species to invade new niches via cultural adaptation. Social learning has typically been regarded as the fundamental driver for the emergence of traditions and thus culture. Consequently, invention has been relatively understudied outside the human lineage—despite being the source of new traditions. This neglect leaves basic questions unanswered: what factors promote the creation of new ideas and practices? What affects their spread or loss? We critically review the existing literature, focusing on four levels of investigation: traits (what sorts of behaviours are easiest to invent?), individuals (what factors make some individuals more likely to be inventors?), ecological contexts (what aspects of the environment make invention or transmission more likely?), and populations (what features of relationships and societies promote the rise and spread of new inventions?). We aim to inspire new research by highlighting

Distribution Statement: 1-Approved for public release; distribution is unlimited.

Acknowledged Federal Support: Y

Publication Type: Journal Article Peer Reviewed: Y **Publication Status:** 1-Published

Journal: Philosophical Transactions of the Royal Society B: Biological Sciences

Publication Identifier Type: DOI

Publication Identifier: 10.1098/rstb.2020.0259

Volume: 376

Issue: 1828

First Page #:

Date Submitted: 12/10/21 12:00AM

Date Published: 5/1/21 4:00AM

Publication Location:

Article Title: Underappreciated features of cultural evolution

Authors: Marco Smolla, Fredrik Jansson, Laurent Lehmann, Wybo Houkes, Franz J. Weissing, Peter Hammerste

Keywords: cultural systems, human evolution, cultural evolution, cumulative culture, evolutionary biology

Abstract: Cultural evolution theory has long been inspired by evolutionary biology. Conceptual analogies between biological and cultural evolution have led to the adoption of a range of formal theoretical approaches from population dynamics and genetics. However, this has resulted in a research programme with a strong focus on cultural transmission. Here, we contrast biological with cultural evolution, and highlight aspects of cultural evolution that have not received sufficient attention previously. We outline possible implications for evolutionary dynamics and argue that not taking them into account will limit our understanding of cultural systems. We propose 12 key questions for future research, among which are calls to improve our understanding of the combinatorial properties of cultural innovation, and the role of development and life history in cultural dynamics. Finally, we discuss how this vibrant research field can make progress by embracing its multidisciplinary nature.

Distribution Statement: 1-Approved for public release; distribution is unlimited.

Acknowledged Federal Support: Y

RPPR Final Report as of 24-Feb-2022

Publication Type: Journal Article Peer Reviewed: Y **Publication Status:** 1-Published

Journal: Philosophical Transactions of the Royal Society B: Biological Sciences

Publication Identifier Type: DOI

Publication Identifier: 10.1098/rstb.2019.0422

Volume: 375

Issue: 1805

First Page #: 20190422

Date Submitted: 12/10/21 12:00AM

Date Published: 6/1/20 4:00AM

Publication Location:

Article Title: Capuchin monkey rituals: an interdisciplinary study of form and function

Authors: Susan Perry, Marco Smolla

Keywords: play, capuchin monkeys, bond-testing, social relationships, social networks, ritual

Abstract: Many white-faced capuchin monkey dyads in Lomas Barbudal, Costa Rica, practise idiosyncratic interaction sequences that are not part of the species-typical behavioural repertoire. These interactions often include uncomfortable or risky elements. These interactions exhibit the following characteristics commonly featured in definitions of rituals in humans: (i) they involve an unusual intensity of focus on the partner, (ii) the behaviours have no immediate utilitarian purpose, (iii) they sometimes involve 'sacred objects', (iv) the distribution of these behaviours suggests that they are invented and spread via social learning, and (v) many behaviours in these rituals are repurposed from other behavioural domains (e.g. extractive foraging). However, in contrast with some definitions of ritual, capuchin rituals are not overly rigid in their form, nor do the sequences have specific opening and closing actions. In our 9260 h of observation, ritual performance rate was uncorrelated with amount

Distribution Statement: 1-Approved for public release; distribution is unlimited.

Acknowledged Federal Support: Y

Publication Type: Journal Article Peer Reviewed: Y **Publication Status:** 1-Published

Journal: Cooperation and conflict: The interaction of opposites in shaping social behavior

Publication Identifier Type: ISBN

Publication Identifier: 1108475698

Volume:

Issue:

First Page #: 26

Date Submitted: 12/10/21 12:00AM

Date Published: 1/2/21 12:25AM

Publication Location: Cambridge, UK

Article Title: Internalizing cooperative norms in group-structured populations

Authors: Erol Akcay, Jeremy Van Cleve

Keywords: social norms, norm psychology, internalization, punishment

Abstract: Social norms play a crucial role in human behavior, especially in maintaining cooperation within human social groups. Social norms might be self-enforcing or be enforced by the threat of punishment. In many cases, however, social norms are internalized and individuals have intrinsic motivations to observe norms. Here, we present a model for how intrinsic preferences to adhere to cooperative norms can evolve with and without external enforcement of compliance. Using the methodology of preference evolution, we model how cooperative norms coevolve with the intrinsic motivations to follow them. We model intrinsic motivations as being provided by guilt, a kind of internal "punishment" that individuals feel for falling short of cooperative norms, and show that the shape of this internal punishment function plays a crucial role in determining whether and how much internalization can evolve. We find that internal punishment functions that eventually level off with the deviation from the norm c

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Acknowledged Federal Support: Y

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Partners

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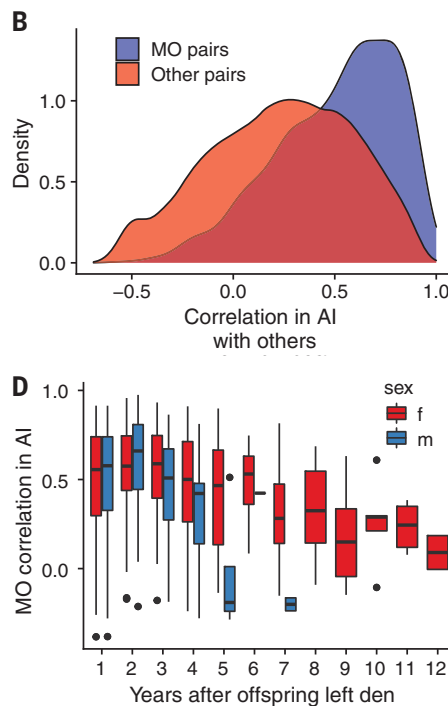
Signature: Erol Akcay

Signature Date: 12/10/21 2:30PM

Main scientific accomplishments

Social inheritance in animal societies

We proposed a general model of social network formation and dynamics based on simple demographic processes, and a process we called “social inheritance” where newborn offspring make social connections that are similar to those of their parents. In a recent paper (Ilany et al. 2021), we presented the first direct test of the hypothesis that social networks in animal societies can be structured by social inheritance. Using a long-term dataset on spotted hyenas (*Crocuta crocuta*) collected by Kay Holekamp’s group at Michigan State University, we showed that new offspring’s social connections indeed resemble those of their mothers. Moreover, we showed that social inheritance is rank-dependent: higher ranked mothers’ offspring resemble their connections more strongly, while offspring of lower ranked mothers have connections less similar to their mothers. The similarity of mothers’ and their offspring’s social connections remains stable over several years, even as direct association between mother and offspring



Documenting social inheritance in spotted hyenas by quantifying the similarity of parents’ and offspring’s connections with third parties in the group. Panel B (from Ilany et al. 2021) shows that mother-offspring pairs’ correlation between association indices (AI) with third parties are significantly higher than random pairs. Panel D shows that this high correlation persists through several years, despite mother-offspring association itself declining over this period (not shown here).

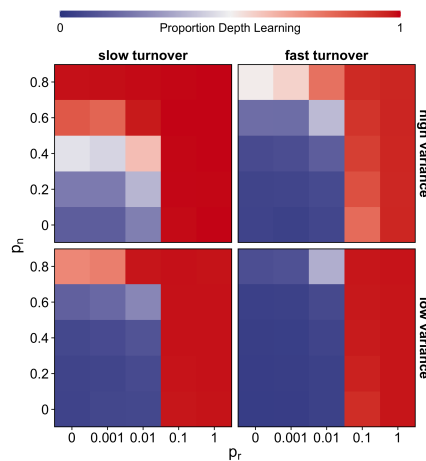
declines.

Cultural evolution and social network structure

We also investigated how social network structure affects behaviors and how these in turn affect social network structure. An earlier result (Akçay, 2018) showed that cooperative behaviors on dynamic social networks are favored when these networks form with few random

(non-inherited) connections, but once cooperation evolves, it creates selection to make more random connections. In this way, cooperation undermines itself by changing network structure.

Further work investigated the spread of socially learned behaviors and skills on dynamic and evolving social networks (Smolla and Akcay, 2019). We found that selection on different kinds of socially acquired skill sets (specialist vs. generalist) creates different kinds of social networks (densely vs. sparsely connected, respectively). In a paper about to be finished, we are exploring the coevolution of cumulative culture, social learning strategies, and social networks in varying environments (Smolla and Akcay, in prep; see Figure). We find that learning strategies favoring breadth (learning a lot of different things) vs. depth (learning few things very well) favor sparse and dense social networks, respectively, and the converse is also true. The positive feedback between learning strategies and social structure locks populations into different cultural regimes.



Evolution of different learning strategies in varying environments and dynamic networks: each panel in the figure corresponds to a different environment where the payoffs from different skills vary a lot or a little (top vs. bottom) and the payoffs change over time slowly or fast (left vs. right). Within each panel the evolved proportion of agents that prefer to engage in depth learning (getting better in skills they already know) as a function of the network-structuring parameters: p_n , the probability of social inheritance, and p_r , the probability of making random connections. The figure shows that slow turnover and high variance environments favor depth learning, but across all environments, denser networks (high p_n and/or p_r) also favor depth learning.

Evolution of norm psychology and timing of contributions to public goods

Other recent work funded through the grant considered the how the human capacity of internalizing social norms and feeling guilt about violating them might evolve in structured populations (Akcay and Van Cleve 2021). We found that biological propensity for norm internalization can evolve in group-structured populations as a way to avoid external punishment and that it can sustain cooperation in public goods settings. Earlier work (Morsky and Akcay, 2019) investigated how inherently meaningless, random signals can evolve to have normative meaning for observers because they allow coordination of actions. These models point to different ways in which human norm psychology can evolve.

We also considered how the temporal spread of public goods production changes the evolutionary dynamics of contributions (Morsky et al. 2020). We found that when the timing of contributions is under positive frequency dependence, as individuals living in the same group are selected to coordinate the speed of their contributions.

General outlook

I have published a synthesis paper that puts the overall thrust of this project in the general context of what is next for social evolution theory (Akçay, 2020): in particular, results from this project point to an emerging direction for social evolution theory where the setting in which social behaviors co-evolves with the behaviors themselves. The results above show such coevolution can lead to unexpected dynamics and can explain the diversity and functioning of social systems in nature and human societies. In addition, we contributed to several other review papers dealing with cultural evolution and social learning.

Publication list

In preparation

Smolla, M. and Akçay, E. Coevolution of culture, learning, and social structure in variable environments. Manuscript in preparation.

Published

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