Proposal Title: Linking individual behavior, social networks, and dispersal in a wild bird population

Key Words: Social network, Social behavior, Social structure, Network dynamics

Research Area: Ecology

Research Sub Area: Behavioral Ecology

Project Period: 1 years

Budget Requested For the Project Period: 23,935 (Euro)

Budget Distribution:
1st year : 23,935 (Euro)

Personal Details of all researchers active in this proposal:

<table>
<thead>
<tr>
<th>Name</th>
<th>PI/CI</th>
<th>Institution and Department</th>
<th>Signature</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dr. Ilany Amiyaal</td>
<td>PI</td>
<td>Faculty of Life Sciences Faculty of Life Sciences Bar Ilan University - BIU, Israel</td>
<td></td>
</tr>
</tbody>
</table>

Institutional Stamp and Signature:
Linking individual behavior, social networks, and dispersal in a wild bird population

Scientific abstract
Recent studies have emphasized the importance of social structure to components of fitness, including longevity and reproductive success, and also to processes such as pathogen and information transmission. The role of social structure in the evolution of cooperation has also been recognized. Evidence suggests that social structure can be influenced by environmental, genetic, individual, and structural factors. There is accumulating support for the notion that individuals are socially bonded with similar others, with respect to traits such as age class, dispersal status, and personality. It is not clear yet whether individuals adjust their behavior to match the social environment (behavioral plasticity), or choose a social environment that matches their personality. In this study, we will link individual behavior with social network structure in a wild population of the cooperative breeder Arabian babbler, that has been monitored for the last 40 years. This one-year study will facilitate an extensive study linking individual behavior, social structure, and population dynamics. We will use a population of 20 groups including approximately 200 babblers with well-known life histories, all marked and habituated to human presence. Using focal observations, we will record individual behavior to quantify repeatability and inter-individual differences. We will then link these behaviors to social network positions of the same individuals, and also to the overall group structure. Specifically, we will record allopreening, allofeeding, and play interactions among all group members, to create networks describing three facets of social structure. Finally, we will record all dispersal events. This study will advance the understanding of social network structure and dynamics, and also the knowledge about how personality is linked to social structure in natural settings, and specifically in cooperative breeders. The proposed research will help to answer how personality and social structure interact to affect population dynamics.
Linking individual behavior, social networks, and dispersal in a wild bird population

1. Background and preliminary results

**Background:** The transition to sociality is one of the major shifts in evolution. Social structure is an important selective factor, affecting both reproductive success (Silk et al. 2003) and survival (Silk et al. 2010; Barocas et al. 2011; Archie et al. 2014). In humans and other animals, sociality affects individual health, demographic processes, and evolutionary fitness via multiple mechanisms, such as pathogen transmission (Mossong et al. 2008; Hamede et al. 2009) and the promoting or impeding of particular social behaviors (Ohtsuki et al. 2006; Santos et al. 2008; Rand et al. 2014). The social structure of a population summarizes the social bonds of its members (Hinde 1976). Hence, understanding the processes that generate variation in social structure across populations and species is crucial to elucidating the impacts of sociality on a range of processes and individual fitness.

Personality describes behavioral differences between individuals that are consistent across time and context (Sih et al. 2004; Réale et al. 2007). Since personality is characterized by limited behavioral plasticity, it was suggested that individuals may prefer environments that match their behavioral types (Holtmann et al. 2017). For example, bolder dunnocks (*Prunella modularis*) were shown to settle in areas with higher levels of human disturbance, when compared to shy individuals (Holtmann et al. 2017). This idea can be extended to include the social environment, a dynamic factor that is both a result of individual behavior and in turn affects individuals’ behavior and life history (Krause et al. 2010; Barocas et al. 2011; Ilany et al. 2015). Studies in several species demonstrate assortativity in animal societies, where individuals are found to be bonded with similar individuals, with respect to size, behavioral tendencies, age, sex, and dispersal status (e.g., Croft et al. 2005; Wolf et al. 2007; Ilany et al. 2015). We are aiming to test whether individuals assort by behavioral profiles, implying limited behavioral plasticity, or, alternatively, they change their behavior to match that of their social connections. Both options will result in an observed pattern of assortativity, but only longitudinal measurement of individual behavior and social network structure will allow us to uncover the underlying processes.

We will use the same population of the cooperative breeder Arabian babbler (*Turdoides squamiceps*), that has been studied by Amotz and Avishag Zahavi for over 40 years. The goal of the current proposal is to lay the foundations to continue Zahavi’s work by developing and testing theory and introducing new technologies to track individuals and their social interactions. In the future, we are aiming to collaborate with scientists from various fields, such as genetics and microbiology, to add new dimensions to the study of social behavior and population dynamics in this excellent system.
**Preliminary results:**

To date we have made progress with the analysis of archived data, as well as with developing protocols for quantifying individual behavior and social networks in Arabian babblers.

**Individual behavior:** We developed a protocol to collect data on a set of individual behaviors, by following habituated groups including marked birds. These behaviors include foraging, guarding, preening, and playing, and will be expanded to include additional types of behavior, for example ones that are expressed during the breeding season. We have started to create individual profiles based on inter-individual variation in the amount of time allocated to these behaviors (Fig. 1).

**Figure 1:** Behavioral profiles of two individuals, as measured during focal observations. Distance from the center is proportional to the amount of time allocated to specific behaviors.

**Social networks:** We defined three types of networks, based on 1) allofeeding, a directed behavior in which one babbler is offering a food item to another (Kalishov et al. 2005); 2) allopreening, an undirected behavior, when two or more babblers are preening each other (commonly happens in both directions) (Dattner et al. 2016); and 3) social play, when two or more babblers are chasing or jumping on each other with no aggressive intentions and consequences (Pozis-Francois et al. 2004). The advantage of these social behaviors is that they are clearly and easily defined, in contrast, for
example, to proximity. These behaviors allow us to quantify social relationships in multiple orthogonal ways (Fig. 2).

**Population dynamics**: Figure 3 presents the dispersal events among 52 groups of babblers over 12 years. Our archived records, collected during the long-term study led by the late Prof. Amotz Zahavi, include data from 28 additional years.

![Figure 3: Population dynamics in Arabian babblers over 12 consecutive years. Groups are depicted as colored ribbons, with width proportional to group size. Dispersal events are depicted as lines linking origin and destination groups.](image)

2. Objectives

The main goal of our research is to link individual behavior, social structure, and population dynamics, by using data from a long-term study of a cooperative breeder, documenting fine-scale individual and social behavior, and conducting accompanying manipulative experiments. Our short-term goals, for the one year time-frame of this grant, are to explore between-individual differences in a range of behaviors (aim 1), and to link these behaviors to individual- and group-level variation in social networks (aim 2). The successful conclusion of these specific aims will constitute the foundation for a full research proposal based on collaborative work with a German laboratory, aspiring to develop and test general theory of the individual/group/population axis in cooperative breeders.

The results of the research described in this proposal should yield important insights into 1) the fine-scale structure of Arabian babbler groups, as depicted by three different measures of social connectivity, namely allopreening, allofeeding, and play; 2) the repeatability of specific types of
behavior; and 3) the influence of individual repeatable behavioral profiles on social networks. Taken together, these results will facilitate an extensive study linking individual and social behavior with population dynamics, contributing to understanding of social, ecological, and evolutionary processes in cooperative breeders and possibly in other species.

3. Work plan

We collaborate on this project with Dr. Oded Keynan, a researcher at the Dead-Sea & Arava Science Center, who has been studying this babbler population for the last seven years. We have recruited a PhD student, Nikola Dragic, with experience in both field work and computational methods. We are planning to hire a field technician that will manage the project logistics, and will assist in data collection in the field. Each of the 20 marked groups will be observed three times a year, during different seasons, for eight days (total of 24 days per group). During observations, we will collect all individual behaviors, social interactions, and demographic events such as breeding, dispersal, and death.

4. Methods

**Study area and species:** The study will be conducted at the Shezaf Nature Reserve, a 40 km² area in the Arava region, Negev desert, southeast Israel (30°48ʹN, 35°13ʹE). A long-term research project on the social behavior of the cooperatively breeding Arabian babbler (T. squamiceps) has been conducted in the area since 1971 by Amotz and Avishag Zahavi (Zahavi and Zahavi 1999). The area is an extremely arid desert savanna with mean annual rainfall of 35mm (Keynan and Yosef 2010). The site’s flora is dominated by Acacia trees (Acacia tortilis and Acacia raddiana) and scattered shrubs (Zilla spinosa, Lycium shawii, and Haloxylon persicum).

Arabian babbler are cooperative breeders that live in territorial groups. Older babbler are dominant over younger ones (Zahavi and Zahavi 1999). Each group usually contains one dominant breeding pair, but on rare occasions subordinate individuals may also reproduce (Lundy et al. 1998). The study population currently includes 20 groups, each comprising 2-13 individuals. All individuals are ringed with a unique combination of one metal and three colored rings, and are habituated to human observers, allowing close-range observation without causing any perceivable behavioral change or stress.

**Data collection:** In each observation day, an observer spends the morning and afternoon hours (3-4 hours per session) following one group of babbler. In focal observations, a randomly selected individual is followed for 10 minutes. The behaviors, social interactions, and their durations, are noted using a custom tracking mobile phone app.

**Behavioral repeatability:** In each focal observation, the observer records the duration of all behaviors. Repeatability will be measured across both daily sessions and seasons.
Social network analysis: For each group and observation period (8 days), we will construct three networks, namely of allofeeding, allopreening, and play. The simple ratio index (Cairns and Schwager 1987) will be used to describe the strength of relationship among each pair of babblers. The three networks will be weighted and undirected, except for the allofeeding network that will be directed.

For each network, we will calculate measures at the network (group) and individual levels. We will measure network density, describing the extent to which the network is sparse or dense in contacts; network transitivity, describing the ratio of closed triads out of the total number of triads; modularity, which measures the extent to which the network can be divided into sub-groups; and assortativity, a measure of the tendency of individuals to connect to others with similar trait values.

For each individual, we will measure strength centrality, a sum of all weighted association strengths; clustering coefficient, a measure of the probability that two contacts of a focal will also be connected to each other; and betweenness centrality, which measures how individuals serve as hubs connecting different sub-components of network.

Statistical analysis: We expect to collect data from 20 groups, including a total of 200 babblers. We will use Bayesian linear mixed models with Markov chain Monte Carlo methods implemented in the MCMCglmm R package (Hadfield 2010) to evaluate the consistency of individual behaviors. Season and group name will be set as random factors. Repeatability will be calculated as the proportion of the total variance that is explained by between-individual variance (Nakagawa and Schielzeth 2010).

We will test the extent to which individual behaviors affect individual social network traits using linear mixed models. We will permute the networks to compare observed measures with those from randomized networks (Farine and Whitehead 2015). We will regress network-level measures (density, modularity, transitivity, and assortativity) against mean values of individual behaviors to evaluate the contribution of the latter to social structure.

5. Planned travel to the partner country

I plan to travel to Germany for 2-3 weeks to present my work in at least two relevant research centers: 1) the Max Planck Department of Collective Behaviour at the University of Konstanz, where collaboration with Prof. Iain Couzin and Prof. Damien Farine can lead to development of new models, statistical methods, and comparative studies of social behavior; and 2) University of Göttingen, where Prof. Peter Kappeler and Prof. Julia Fischer, among others, could be potential collaborators in the study of animal social structure and communication patterns.
Linking individual behavior, social networks, and dispersal in a wild bird population

Bibliography


## Budget Details

### Salaries

<table>
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<tr>
<th>Role in project (Name)</th>
<th>Time %</th>
<th>Months of employment</th>
<th>Justification</th>
<th>1st year</th>
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<tr>
<td>PI (Amiyaal Ilany)</td>
<td>20</td>
<td>12</td>
<td>The PI will lead the project, hire a field technician, and supervise data collection, analysis and writing of publications.</td>
<td>18,485</td>
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<tr>
<td>Field technician (To be named)</td>
<td>75</td>
<td>12</td>
<td>A field technician with a bird ringing permit will assist my PhD student, support field work and conduct observations, proposed experiments, population monitoring, and ringing of new birds.</td>
<td>18,485</td>
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<tr>
<td>PhD student (Nikola Dragic)</td>
<td>100</td>
<td>12</td>
<td>The student scholarship is provided by Bar Ilan University. No additional funds are needed.</td>
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### Non Expendable Equipment

**No Details**

### Travel Expenses

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<tr>
<th>Description</th>
<th>Justification</th>
<th>1st year</th>
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<tbody>
<tr>
<td>Travel to Germany for 2-3 weeks</td>
<td>This will give me the opportunity to present my work and meet potential collaborators with the aim of submitting a regular GIF proposal.</td>
<td>2,700</td>
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<tr>
<td>Travel expenses of PI to the field</td>
<td>To manage the project, the PI needs to visit the field site once a month. We request gas + wear and tear. Driving from Bar-Ilan University campus to Hatzeva: round trip 430km * 12 times * 0.34 Euro per km = 1750 Euro.</td>
<td>1,750</td>
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### Operating Expenses

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<td>Car maintenance + gas</td>
<td>We request 1000 Euro for gas and maintenance of the car used in the field to reach all study groups.</td>
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<td><strong>Total</strong></td>
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### Supplies, Materials and Services Expenses

**No Details**

### Miscellaneous

**No Details**
Parallel Funding
Applicant Dr. Ilany Amiyaal

Q: Have you previously received or applied for a Minerva, Alexander von Humboldt or any other Fellowship? If yes, please detail.
A: I have applied and received a postdoctoral fellowship from the National Institute for Mathematical and Biological Synthesis (NIMBioS), University of Tennessee, USA.

Q: Have you personally ever received a research grant? If yes, please detail.
A: No

Q: Did you recently submit this proposal to other funding agencies, or do you plan to submit it this year? If yes, to which funding agency?
A: No

Q: Are you currently supported by any funding agency? If yes, please detail.
A: No

Q: If the research previously received support from other sources, list rights and obligations of grantor still in effect. This research has not previously received support from other sources.
A: This research has not previously received support from other sources.

Q: If this is a continuation of any German-Israeli cooperative research, please indicate the supporting agency, duration and budget.
A: No

Q: List all previous applications to GIF by numbers:
A: None
**Curriculum Vitae**

**Current Institute:** Bar Ilan University - BIU, **Israel**

**Academic Background**

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<th>Institution</th>
<th>Area of Specialization</th>
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<td>Tel Aviv University (TAU)</td>
<td>Biology and Computer Science</td>
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<td>10/2004 - 10/2006</td>
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<td>10/2006 - 09/2012</td>
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**Previous Employment**

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<td>10/2012 - 01/2015</td>
<td>National Institute for Mathematical and Biological Synthesis, University of Tennessee</td>
<td>Biology</td>
<td>Causes and consequences of animal social network dynamics</td>
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<td>01/2015 - 07/2016</td>
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<td>Biology</td>
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**Potential Collaborators:**

1. Prof. Dr. Iain Couzin, Max Planck Department of Collective Behaviour, University of Konstanz, icouzin@orn.mpg.de, [http://collectivebehaviour.com/couzin-lab/](http://collectivebehaviour.com/couzin-lab/)

2. Dr. Damien Farine, Max Planck Department of Collective Behaviour, University of Konstanz, dfarine@orn.mpg.de, [http://collectivebehaviour.com/farine-bio/](http://collectivebehaviour.com/farine-bio/)

3. Prof. Dr. Peter Kappeler, German Primate Center, University of Göttingen, pkappel@gwdg.de, [http://www.soziobio.uni-goettingen.de/en/kappeler.php](http://www.soziobio.uni-goettingen.de/en/kappeler.php)
Publications in the past 5 years


For this paper I found the main result by analyzing data collected by the first author (MSc student).


Featured by ~40 media sources, including Science.


Requested budget for the duration of the project.

<table>
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<th>Description</th>
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<td>The PI will lead the project, hire a field technician, and supervise data</td>
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<td>collection, analysis and writing of publications.</td>
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<td>A field technician salary</td>
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TO WHOM IT MAY CONCERN

This is to confirm that the degree of Doctor of Philosophy has been conferred on Mr. Amiyaal Ilany by the plenum of the Senate of Tel-Aviv University on 13/08/2013.

The title of the thesis is: "Vocal Communication and Social Networks in the Rock Hyrax (Procavia Capensis)".

This work was carried out under the supervision of Prof. Eli Geffen.

Eitan Hoffmann
Head
Research Students Section
Tel-Aviv University
Academic Secretariat
Research Students Section
Ilan Ha-Avdat University, Ramat-Aviv
Tel-Aviv, 69978, ISRAEL