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An animal model for collective behavior in humans: the impact of manipulated trust and aggression

David Eilam

TEL AVIV UNIVERSITY
RESEARCH AUTHORITY
RAMAT AVIV
TEL AVIV 69978 ISRAEL

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TEL AVIV UNIVERSITY
RESEARCH AUTHORITY
RAMAT AVIV
TEL AVIV 69978 ISRAEL

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14. ABSTRACT

Final report for EOARD Grant FA8655-11-1-3050. There were four objectives identified for this research. This report documents the findings for each of these objectives. The status of these objectives is: 1. To measure the collective response in same-gender compared with mixed-gender groups. 2. To identify the social rank of initiators and followers individuals, and test whether the followers adopt the behavior of the initiators, thereby resulting in the uniform collective behavior. 3. To support the data of collective behavioral responses with measurements of physiology by tracking corticosteroids that provide a robust index of anxiety level. 4. To administer oxytocin or testosterone to dominant or subordinate males and females in same-gender and mixed-gender groups. This will modify the social status of the respective individuals, and in consequence will alter the collective behavior of the entire group. The results of each of these objects are published separately. During the conduct of this research, we also identified a need to evaluate whether the voles suffer symptoms observed in post-traumatic-stress disorder (PTSD). Our hypothesis is that the PTSD effect would not be contagious like the acute response to the threat. PTSD trials revealed a wash-out of the stress induced by life-threat one week before the PTSD test. This result has been combined and will be published with those of Objective #3.

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TEL AVIV UNIVERSITY אוניברסיטת תל-אביב
GEORGE S. WISE FACULTY OF LIFE SCIENCES הפקולטה למדעי החיים ע"ש ג'ורג' ס. וייז
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Final Report

An animal model for collective behavior in humans: the impact of manipulated trust and aggression

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Table of contents

A. The following objectives were introduced in the original application. The subsequent sections include a summary of achievements on each of these objectives.

1. *Measure the collective response in same-gender vs. mixed-gender groups (status: published)*
2. *Identifying the social rank of initiators and followers individuals, and testing whether the followers adopt the behavior of the initiators to form uniform collective behaviour (status: submitted for publication).*
3. *Supporting the data of collective behavioral responses with physiological measurements, namely by tracking corticosteroids as a robust index of anxiety level (status: in preparation for publication)*
4. *To administer oxytocin or testosterone to dominant or subordinate males and females in same-gender and mixed-gender groups. This will modify the social status of the respective individuals, and in consequence will alter the collective behavior of the entire group (status: in progress).*
5. *To evaluate whether the voles suffer symptoms observed in post-traumatic-stress disorder (PTSD). Our hypothesis is that the PTSD effect would not be contagious like the acute response to the threat.*

B. Publications resulting from the grant (attached)

Eilam D. Zadicario P. Genossar T. and Mort J. The anxious vole: the impact of group and gender on collective behavior under life-threat. *Behavioral Ecology and Sociobiology* 66 (2012): 959-968

Kleiman M., Bodek S. and Eilam D. Who is the boss? Discriminating between leaders and followers in the behavior of voles under owl attack. *Behavioral Ecology and Sociobiology (A revised version which is currently under review)*

A. Summary of the achievements in each of the above aims

1. *To measure the collective response in same-gender compared with mixed-gender groups.*

Status: published; attached as Appendix I

A paper on the results of thiswas already published (attached). This study followed our previous AFRL-supported study in which we documented conformist (consensus) behaviour in groups of voles under threat. Here we found that anxiety was affected by both the social context and the gender of the tested individuals. In same-gender groups, both female and male voles reduced their activity in unprotected areas following owl attack. The same applied for females and the majority of males in mixed-gender groups. However, few males in mixed-gender groups displayed a behavior that represents an exceptionally low anxiety, by moving in exposed and unprotected areas. We suggest that these males were probably individuals of high social rank, and their response reflects their natural protective role, as previously described in social voles.

Impact for the Department of Defence: In this animal model we found that natural groups that comprise both males and females are better able to cope with life-threat compared with same-gender groups.

Appendix A

2. *To identify the social rank of initiators and followers, and test whether the followers adopt the behavior of the initiators, thereby resulting in the uniform collective behavior.*

Status: submitted for publication (see Appendix B)

We found that under threat, the behavior of the group conforms to the mid-range and not to the extremes. The mid-range behaviour is of the voles with high social rank while the extremes are voles with low-social rank. Under life threat, the extremes converged to the behaviour of the high-ranked voles whereas the highly-ranked voles were more stable in their behavior. Accordingly, the highly-ranked voles acted as "stabilizers" in the group by setting the group behavioral code, with the other voles conforming to this code. In light of these results, we suggested that individuals were not necessarily predisposed to be leaders or followers, but having grown in size and by virtue of their experience and physical strength they assumed responsibility for leading and stabilizing their groups. We also suggested that behavioral propagation in hierarchical groups is faster compared to in non-hierarchical groups.

Impact for the Department of Defence: Previous models suggest ‘self organization’ as a fast mechanism by which uniform group behavior emerges. In contrast, the present animal model of voles demonstrates that an even faster mechanism could be the propagation of information in a “military-like hierarchy”. Specifically, while self-organized behavior is based on copying the nearest neighbor. In voles’ social hierarchy, information (behavior) is transmitted within the group from the leaders to the low-ranked individuals and between groups from any individual in the delivering group to the leaders of the receiving group (but not from low-ranked individuals in the delivering group to low-ranked individuals in the receiving group).

We suggest that this model for bi-dimensional transmission of social information is faster than neighbour copying, where individuals respond to their single nearest neighbor, under the assumption that responding to more neighbors is costly in time and information processing.

Appendix B

3. ***To support the data of collective behavioral responses with measurements of physiology by tracking corticosteroids that provide a robust index of anxiety level.***

   Status: In preparation for publication

This is a follow-up of the experiment in Objective #2, but with measuring corticosteroids along with the behavior. Experiment, data acquisition and analysis were completed and the study is in final preparation for publication. The main findings are listed below (part of these are described in more details in Appendix C).

i. The highly-ranked animals that lead the group are those with greater body mass (older and more experienced individuals.
ii. In agree with the previous finding, we found that leaders (hi-mass individuals) have lower levels of corticosterone (a Pearson correlation coefficient revealed a significant negative link between corticosterone body mass; $r = -0.22$, $p = 0.022$). This reconfirms the results obtained in the experiment of Objective # 2, that there is a direct link between social rank, behaviour and corticosterone level, and the behavior of group leaders is more stable whereas the extremes are the low-ranked voles (= low-mass voles).
iii. Baseline levels of stress were tremendously higher in females compared to males.
iv. Surprisingly, socially isolated females and males had a lower level of corticosteroids - an enigmatic results since social isolation is conventionally considered as a stressor.

Appendix C

4. ***To administer oxytocin or testosterone to dominant or subordinate males and females in same-gender and mixed-gender groups. This will modify the social status of the respective individuals, and in consequence will alter the collective behavior of the entire group.***

   Status: In progress (no further experimentation needed)

We faced unexpected difficulties in this part of the study for two technical reasons: (i) there were no reliable kits to measure testosterone level in voles. Application of the available kits for rodents and humans revealed very low levels (virtually nil). Even more surprising is the fact that administration of testosterone, even at very high dosage, did not affect the behavior of the subjects. (ii) Similarly, administrating oxytocin to leaders or to follower and then assessing the impact of these treatments on the behavior of the group under life threat revealed so far no behavioral changes compared to controls. We continue to analyse these experiments but at present it is not clear whether these results would merit publication.

5. ***To evaluate whether the voles suffer symptoms observed in post-traumatic-stress disorder (PTSD). Our hypothesis is that the PTSD effect would not be contagious like the acute response to the threat.***

   Status: Completed

As illustrated in Appendix C, PTSD trials revealed a wash-out of the stress induced by life-threat one week before the PTSD test. This result has been combined and will be published with those of Objective #3.

Appendix C

Eilam D. Zadicario P. Genossar T. and Mort J.

The anxious vole: the impact of group and gender on collective behavior under life-threat.

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ORIGINAL PAPER

The anxious vole: the impact of group and gender on collective behavior under life-threat

David Eilam · Pazit Zadicario · Tom Genossar · Joel Mort

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Abstract Social animals behave collectively in order to maintain a cohesive group. This collective behavior is often led by a few individuals of specific gender, social rank, or spatial physical location in the group (i.e., perimeter or front). We examined how individual social voles (*Microtus socialis*) in same-gender compared with mixed-gender groups respond to an owl attack. We found that anxiety level, as measured by the time that each individual spent in less-sheltered sectors (open arms of elevated plus-maze and center of open arena), was affected by both the social context and the gender of the tested individuals. While both female and male voles generally reduced their activity in the open following owl attack, males in mixed-gender groups were exceptional in dichotomizing into those that spent a short period and those that spent a long period in the open arms of the plus-maze. Based on the similar responses of the same-gender groups, we suggest that anxiety is contagious, and based on the lower anxiety level of the mixed-gender groups, we suggest that natural groups that comprise both males and females are better able to cope with life-threat compared with same-gender groups. Finally, we suggest that the differential responses of males in the mixed-gender groups were due to a few males that displayed a low level of anxiety. These males were probably individuals of high social rank, and their response reflects their natural protective role, as previously described in social voles.

Keywords Predation risk · Defensive behavior · Collective behavior · Contagious fear · Transmission · Predator–prey interactions

Introduction

Individuals in social groups need to display a certain level of collective behavior in order to maintain group cohesion (Conradt and List 2009). In the framework of a group, individuals tend to act differently to how they might have acted individually under otherwise identical circumstances. In collective behavior, individuals in a group display an alignment of behaviors without any apparent centralized coordination (Carere et al. 2009). In humans, collective behavior is an influential and well-documented behavior (e.g., in the stock market, in political choice, in consumer preferences, etc.). Numerous terms and theories have been posited in order to explain this group effect (‘Herd morality’; ‘Herd behavior’; ‘Crowd behavior theory’; ‘The maddened crowd’, ‘Contagion theory’; ‘Group mind’; ‘Mob behavior’; etc.). In a review of these theories, from their emergence in the eighteenth century until the present, it is noted that current models for collective behavior in humans have focused on patterns, not on individuals, relying on physical properties such as distances and velocities rather than on emotional states (Raafat et al. 2009). In other words, current models do not refer to individuals as the basic unit of the group. Moreover, most human studies are based on a posteriori analyses, suggesting different and sometimes conflicting underlying mechanisms for collective behavior. For example, the ‘Contagion

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David Eilam and Joel Mort are visiting professors at the Department of OTANES, University of South Africa.

D. Eilam (✉) · P. Zadicario · T. Genossar
Department of Zoology, Tel-Aviv University,
Ramat-Aviv 69978, Israel
e-mail: eilam@post.tau.ac.il

J. Mort
Trust and Human Interaction Branch, US Air Force Research
Laboratory, Wright-Patterson Air Force Base,
Dayton, OH, USA

theory' states that grouping causes individuals to act in a certain way, whereas the 'Convergence theory' states the opposite: Individuals who wish to act in the same way come together to form groups. Uncovering the impact of individuals in a group is a prerequisite for comprehending and, if possible, predicting the seemingly self-organized group behavior.

Like humans, animals may also behave collectively, whether a migrating herd of buffalo (Molszewski 1983), a hunting pack of wolves (Schmidt and Mech 1997), an aerobating flock of birds (Davis 1980), or a swimming school of fish (Parrish et al. 2002). At the level of performance, there are striking similarities between the collective behavior of humans and other animals, and research on these similarities has been flourishing recently, as illustrated in a set of articles on group decisions in humans and animals (*The Philosophical Transactions of the Royal Society*, vol. 364, 2009). This is not to say that humans and animals have the same cognitive capacities but that various components of collective behavior, especially the more automated and ancestral, are similar in both. These common patterns may also be controlled by the same mechanisms. At the very least, principles derived from animal collective behavior can be used as a "search image" in studying human collective behavior. On the basis of collective animal behavior, three main questions have been posed by Conradt and Roper (2005): (1) Are there specific individuals that lead the decision on a specific collective behavior? (2) How does the collective behavior spread across the group? and (3) What do individuals in the group gain by behaving collectively? In addition to their value in unveiling the structure of the fascinating behavior of large animal groups and the underlying governing mechanisms, studies in collective animal behavior may also shed light on reminiscent behavior in humans. For example, studies on collective cognition in animal groups have revealed that minor behavioral changes in a few individuals may propagate and result in a major behavioral change of the entire herd or flock (Couzin 2008; Conradt et al. 2009; Guttal and Couzin 2010). Collective behavior, which is considered as self-organized with no central control, has been mathematically modeled, and these models could explain the behavior of pedestrians and in crowd disasters (Moussaïd et al. 2011). Other studies (Conradt 2008; Conradt et al. 2009; Conradt and List 2009; Conradt and Roper 2003, 2010) have scrutinized decision-making in groups of animals and paralleled them with daily group decisions in humans (for review, see Conradt and List 2009). Although these same underlying principles may apply to humans to the same extent as to other animals, in humans, there are additional factors that shape their collective behavior, such as cultural and religious constraints, thus making the study of collective animal behavior more suitable for unraveling the mechanisms governing such behavior.

The present study is based on our previous study, in which male social voles (*Microtus socialis*) were exposed as a group (with their cage-mates) to owls that attacked their cage (Izhar and Eilam 2010; Eilam et al. 2011). The large individual variability in anxiety, as measured in male voles before the attack, was significantly reduced after the owl attacks, and all group members displayed a relatively similar level of anxiety. It was suggested that this collective behavior of the male voles is reminiscent of the social response seen in humans following a disaster, when a uniform behavioral code dominates, and there is reduced behavioral variability (Izhar and Eilam 2010; Eilam et al. 2011). Notably, male voles that had been individually exposed to owls preserved their variability in anxiety level (Izhar and Eilam 2010; Eilam et al. 2011). While the above studies scrutinized all-male groups, the present study was based on comparing the behavior of individuals in same-gender groups (males or females) and mixed-gender groups. The theory behind studying both mixed and same-gender groups was that the behavior of animals in groups, especially birds and mammals, reflects the behavioral pattern of specific individuals in these groups. For example, specific individuals (usually experienced adult individuals of one gender) were found to shape the behavior of the entire group (Black 1988; Prins 1996; Byrne 2000; Graw and Manser 2007; Hay et al. 2008). Accordingly, we set out to test whether the impact of owl attacks on the anxiety levels of voles would be similar in groups of only males, only females, or mixed-gender groups. We examined whether individuals in a same-gender group behave as voles do in a mixed-gender group under the same circumstances and which social structure better copes with a threatening ordeal.

Methods

Subjects

Social voles, also called Guenther's vole or Levant voles (*Microtus socialis guentheri*) are burrow dwellers, weighing 37–50 g, and 11 cm in length plus a 2-cm tail. They are distributed in southeast Europe and the northern Middle East, where they feed on seeds and green vegetation (Mendelssohn and Yom-Tov 1999). Social voles live in extended families (parents and the offspring of two to three consecutive litters), under a social hierarchy that correlates with age and size, with several families sharing a complex burrow system and the males displaying extensive parental care, along with protecting and maintaining the burrow-system (Libhaber and Eilam 2002). Social voles were selected for this study not only for being highly social, as attested by their name, but also for being predated upon by many carnivores and raptors and mainly by owls. Indeed, voles comprise

40–70% (sometimes over 90%) of the diet of barn owls (*Tyto alba*) and tawny owls (*Strix aluco*) (Mikkola and Willis 1983; Martin and Busby 1990; Selaas 1993; Mendelssohn and Yom-Tov 1999). In Israel, they are the most common prey of barn owls, comprising 20% to 50% of their diet, as revealed by the owls' pellets in various agricultural and urban environments (Charter et al. 2007, 2009).

Thirty-eight male and 25 female voles were obtained from breeding colonies at the I. Meier Segals Garden for Zoological Research at Tel-Aviv University. Voles were kept in groups of four to nine without mixing individuals from the original families due to aggression of family members toward stranger voles. From the original families, the tested voles were selected in same-gender or mixed-gender groups, as follows: (1) 24 adult males in three all-male groups; (2) seven adult females in one all-female group; (3) 14 adult males and 18 adult females in four mixed-gender groups. The number of animals in each group, including the relatively small number in the all-female group, was limited by gender composition in the original groups of our vole colony. Each group was kept in a metal cage (60×30×20 cm) with a wire-mesh roof. Before testing, voles were marked individually by shaving a specific part of their fur and then acclimated for 2 weeks in their cages inside a quiet air-conditioned room (24°C) with 10:14 h light/dark cycle. Voles were provided daily with ad libitum standard rodent pellets, sunflower seeds, and fresh vegetables.

Apparatus

Elevated plus-maze This maze is a standard and common apparatus for assessing anxiety (Wall and Messier 2001). It comprised a black-painted aluminum cross-shape, each bar 70×70 cm in length. The maze was placed horizontally 50 cm above the ground, with the sides of two arms closed by 20-cm-high aluminum walls. The other two arms of the cross-shape were bordered with a 5 mm low wall, to prevent the animals from falling off. The more time an animal spends in the open arms of the elevated plus-maze, the less anxious that animal is. The elevated plus-maze was placed in a quiet dark room. A video camcorder (Sony DCR-SR35) and an infra-red light source, with an 830 nm filter that emits light not visible to the voles (Tracksys, UK) was placed above the maze to provide a top view of the behavior of the tested vole.

Open field The 'open field' is the most common apparatus in experimental psychology (Walsh and Cummins 1976). In the present experiment, this was a 2×2 m arena with 50 cm Plexiglas walls, illuminated by a dim light. The open field was also illuminated with an infra-red light source (Tracksys, UK), in order to provide a vivid picture for a video camera (Ikegami B/W ICD-47E, Tokyo, Japan) that was placed above the arena center to provide a top view of the entire arena. The apparatus was placed in an empty quiet air-conditioned room, and the video signal was wire-transmitted to an adjacent room, where it was stored onto a computer for further analysis. For the assessment of anxiety, it is assumed that the more time the tested animal spends away from the walls of the 'open field' apparatus, the less anxious it is (Prut and Belzung 2003; Whishaw et al. 2006).

Procedure

Pre-OWL test After 2 weeks of acclimation in the quiet room, each individual vole underwent a pre-exposure test in the open field and the elevated plus-maze. Each vole was first tested for 15 min in the open field, and 1 h later, the same vole was tested for 5 min in the plus-maze. These testing durations follow the common procedures that are practiced in these apparatuses (Wall and Messier 2001; Eilam 2003). Time in the open was measured in the elevated plus-maze as the time spent in the open arms during the 5 min test (Wall and Messier 2001). Similarly, time in the open in the 'open field' was measured as the time spent at least 20 cm away from the arena walls (Prut and Belzung 2003; Whishaw et al. 2006). All testing started at dusk, a peak activity time in the social vole (Mendelssohn and Yom-Tov 1999), and terminated before midnight. In both tests, the experimenter transferred an individual vole to the apparatus inside a plastic jar and gently released it into the center of the plus-maze or into the near right corner of the open field. The experimenter then left the room until the end of the trial. Each vole was then returned to its cage and cage-mates. After testing every individual in a cage, the cage was returned to the quiet acclimation room.

Exposure to the owls The day after testing in the open field and plus-maze, just before dusk, voles were exposed as a group to owl attacks. For this, the voles' home-cages were transported to the center of a barn-owl aviary (6×6×4 m), in which two of the owls could fly freely. The owls had been 1-day food-deprived prior to the test day. The owls' food (dead mice or chicks) was then placed on the wire-mesh roof of the voles' cage. Thus, when the owls swooped down on the vole cage to feed, they threatened the voles but could not reach them through the wire-mesh. The next morning, after spending overnight in the owls' aviary, the voles' cages were returned to the quiet acclimation room for 12 h.

Post-OWL test At dusk, about 12 h after being removed from the owls' aviary, each vole underwent the same procedure of the pre-OWL test in the open field and plus maze.

Data acquisition and analysis

Behavior of voles in the open field was analyzed by means of Ethovision software (by Noldus Information Technologies, NL), which tracks the progression of the vole in the arena, providing five times per second the time and the location of the center of the vole's image against the background of the brighter arena floor. From Ethovision, we obtained the *distance moved* (meters), which was the cumulative distance traveled by a vole during a 15 min trial; *velocity* (meters per second), which was the mean speed of travel in the open field; and *center duration* (seconds), time spent in the center of the open field, at least 20 cm away from the arena walls. Behavior of voles in the plus-maze was scored during playback of the video files, as follows: *open-arm time*, which was the cumulative time spent in the open arms; and percentage of open-arm entries, which was the number of open-arm entries divided by total arm entries. Arm exit (either closed or open) was scored whenever the rodent stepped out of an arm with at least two legs, while arm entry (either closed or open) was scored whenever the rodent stepped into an arm with all four legs.

Statistics

Statistical analysis was performed using Statistica 8.0 by StatSoft Inc, USA. Unless noted otherwise, data were compared by means of repeated-measure two-way ANOVA, with two between-group factors (gender and grouping composition, where grouping composition was same-gender or mixed-gender group) and one within-group factor (pre-OWL and post-OWL data; repeated measures for each vole). If data deviated from normal distribution in a Kolmogorov–Smirnov test, they were transformed (square-root or log) to reach normality. Proportions were also transformed (square-root of arcsin) for analysis. Alpha level was set to 0.05.

Results

All voles, regardless of gender, showed a decrease in the time spent in the open sector during the post-OWL compared with the pre-OWL trials (two-way ANOVA with repeated measures; $F_{1,46}=36$; $P<0.0001$ for the plus-maze and $F_{1,46}=21$; $P<0.0001$ for the open field; Table 1). Furthermore, as shown in Table 1, the decrease in same-gender groups was greater than in mixed-gender groups, in both the plus-maze and the open field ($F_{1,46}=5.9$; $P=0.019$ and $F_{1,46}=15$; $P<0.001$, respectively). The effect of gender and the interaction between gender and group were not significant in the elevated plus-maze but were significant in the open field (see Table 1). In addition to the obvious

Table 1 Mean (±SEM) time (seconds) spent in the open arms of the elevated plus-maze (left) and away from the walls of the open field (right), before exposure to the owls (pre-Owl), after exposure to the owls (post-OWL), and the mean delta (difference between post-OWL and pre-OWL), depicted for females (top) and males (bottom) in same-gender and in mixed-gender groups

		Elevated plus-maze			Open field		
		Pre-OWL	Post-Owl	Delta	Pre-OWL	Post-Owl	Delta
Females	Same-gender	37.00±6.87	10.29±2.48	27.86±7.50	19.43±4.42	5.66±3.28	18.40±4.00
	Mixed-gender	44.72±7.12	22.13±5.41	26.08±5.62	16.72±2.00	7.84±1.71	11.58±1.83
Males	Same-gender	37.50±4.46	22.58±6.62	27.17±4.31	53.78±7.03	28.86±3.40	30.72±5.30
	Mixed-gender	54.92±10.02	35.26±7.56	29.73±7.18	15.60±2.63	6.60±1.43	11.91±2.72
$F_{1,46}$; *P* value		Within-group (gender) 1.4; 0.244	Between-group (grouping) 5.9; 0.019	Interaction 0.5; 0.465	Within-group (gender) 12.6; <0.001	Between-group (grouping) 15.4; <0.001	Interaction 14.9; <0.001

The results of a two-way ANOVA are depicted at the bottom for the effect of gender, grouping, and the interaction of gender×grouping impact of the owls, there was also a robust impact of grouping conditions.

Behavior of female and male voles in a mixed-gender group

To further examine the effect of the owls on the different groups, data for individual voles on the night before and the night after exposure to the owls were compared. As shown in Fig. 1, most of the high scores during the post-OWL test are of males. Moreover, the males in the mixed group appear to have dichotomized into two types: those that spent a long period in the open arms, and those that converged at the lower range, where most of the females aggregated. A comparison of the number of females and males above and below the mid-range line of the mixed group revealed a significant difference (χ_1^2=4.23; P=0.04). The post-OWL scores of male and female voles in the mixed group did not differ significantly (t_{25}=1.46; P=0.07), due to the score of the female at the top of the range (marked with an arrow in Fig. 1) being more than twofold that of the second highest female. When the top-range female was excluded from the comparison as outlier, however, the post-OWL behavior of males and females in the mixed-gender group significantly differed (t_{18}=2.19; P=0.02). Altogether, female voles in the mixed group in general reduced their time in the open arms of the elevated plus-maze and converged together into a relatively narrow range whereas male voles in the mixed group diverged into those that behaved similarly to the females and those that spent a relatively long period in the open arms. This divergence, however, is not apparent in the time spent at the center of the open field (Fig. 2), where both male and female voles in mixed-gender groups seem to have equally reduced their activity in the open following exposure to the owl.

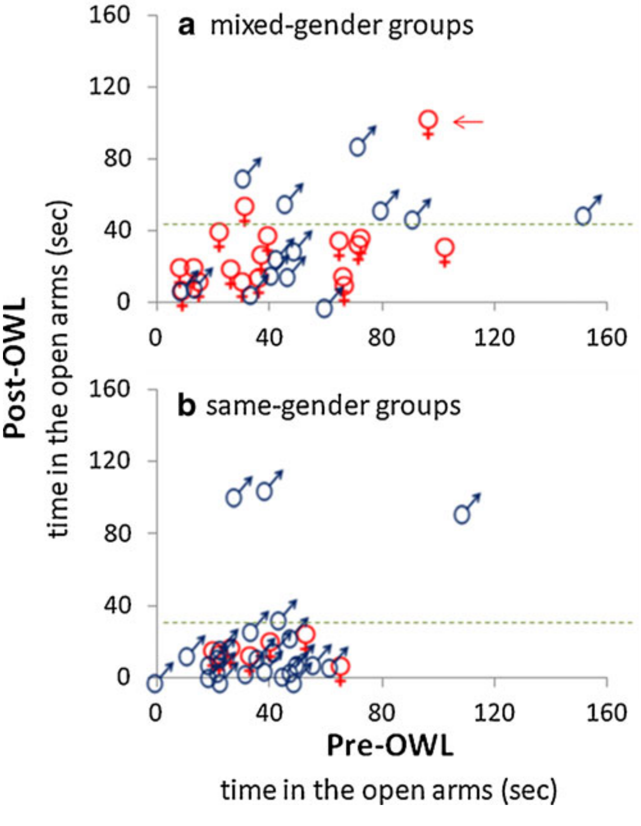

Fig. 1 The time spent in the open arms of the elevated plus-maze by each female and male vole after owl attack (y-axis) compared with the behavior of the same individual before owl attack (x-axis). The *dashed horizontal line* represents the middle of the post-OWL response in all individuals (the midrange between the longest and shortest time spent in the open). As shown, in both mixed-gender groups (*top*) and same-gender groups (*bottom*), individuals in the upper range during the post-OWL test were males. The female at the top of the range (*marked with an arrow*) was more than twofold that of the second highest female and was therefore excluded from the comparison as outlier

Behavior of female and male voles in same-gender groups

The behavior of female and male voles in same-gender groups is depicted in Fig. 1b for the elevated plus-maze and in Fig. 2b for the open field. For each individual vole, post-OWL behavior (Y-axis) is depicted as a function of the

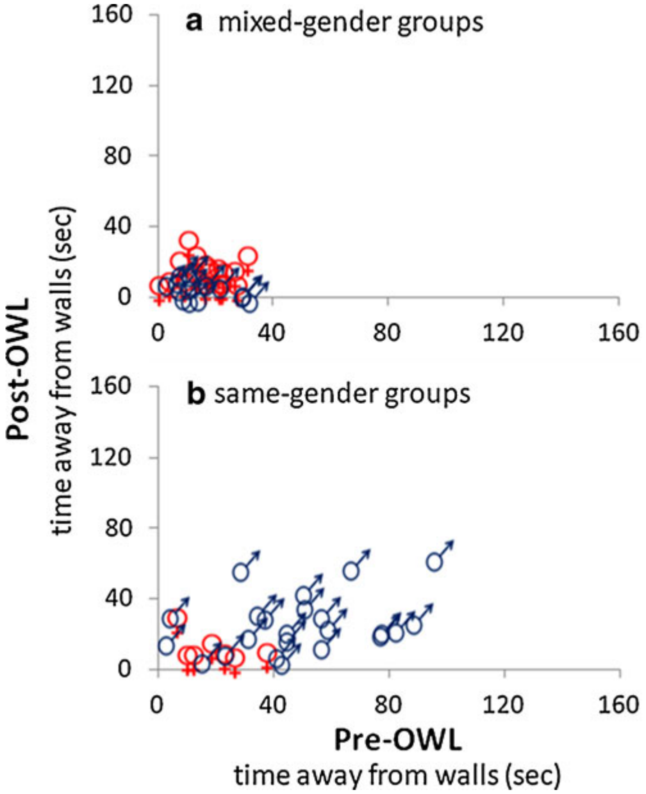

Fig. 2 The time spent in the center (away from the walls) of the open-field by each female and male vole after owl attack (y-axis) compared with the behavior of the same individual before owl attack (x-axis). As shown, in mixed-gender groups (*top*), all males and females spent a short period at the center of the open field. Males and females in same-gender groups also spent a short period in the center of the open field, but male scores were scattered over a wider range

pre-OWL behavior (*X*-axis). As shown, female scores aggregated in the low range of the *Y*-axis, whereas male scores were scattered over a greater range. In the elevated plus-maze, males dichotomized into those with low and those with high score. Overall, all the high scores are of males.

While open-field behavior of individuals in the all-male groups extended over a wide range, behavior of some males in the mixed-gender groups converged to the relatively narrow range of the females (Fig. 1). In the elevated plus-maze, the dichotomy of the behavior of males is apparent in both the mixed-gender and the all-male groups (Fig. 1). However, while in the mixed-gender groups, there were six males above the mid-range and eight males below it; in the all-male groups, there were only three males in the high range and 21 in the low range. Unlike the males, the behavior of females in both the elevated plus maze and in the open field in both the mixed-gender groups and the all-female groups was similar in the sense that in each social group they aggregated in the low range.

The differential social effect on females and males

In order to highlight the behavioral differences between females and males, we categorized the period spent in the open as short (20 s or less), intermediate (between 20 and 40 s), or long (more than 40 s), and the number of voles in each category is provided in Fig. 3. As shown for the elevated plus-maze during the pre-OWL test, most of the males in the mixed group spent long periods in the open arms, whereas males in the all-male group spent either intermediate or long periods in the open arms. The same trend, but with a minor shift to the lower ranges, was apparent in females during the pre-OWL test in the elevated plus-maze, while in the post-OWL test the females showed an overall trend of reduced activity in the open arms. This is clearly displayed in the high number of females that spent only a short time in the open and the decrease in the number of females that spent a long time in the open, regardless of grouping status. Interestingly, males in the same-gender group reacted like the females during the post-OWL test, with the majority of males in the same-gender groups spending a short time in the open, a few spending an intermediate time, and none spending a long time. This behavior in the all-male groups is in contrast with that of males in the mixed-gender groups, which displayed a bi-phasic distribution, with many individuals spending either a short or long period in the open, but only a few spending an intermediate period there. In the plus-maze, there were thus more active-in-the-open females and males in the mixed-gender groups compared with the respective same-gender groups.

Applying the same comparison for the time spent away from the walls of the open field revealed that during the post-OWL test there were more males and more females that spent less time away from the walls then during the pre-owl test. This was most striking in the mixed-gender groups, where 90–100% of the voles aggregated in the short-time bin. Comparing the behavior of each gender in the two sets of apparatus reveals that more males than females spent a long period in the open during the pre-OWL test, and that the subsequent decrease in time spent in the open was more marked in females compared with males. The behavior of females, regardless of grouping condition, was consistent in the two sets of apparatus, whereas males seemed to be more sensitive to grouping conditions. In the elevated plus-maze, individuals in the all-male groups displayed marked decrease in activity in the open arms in the post-OWL test, whereas in the open-field, decreased activity characterized the males in the mixed-gender groups.

Discussion

In the present study, we induced anxiety in social voles by exposing them to attacks by barn owls and compared their behavior before and after exposure to the owls under two social situations: (1) voles in same-gender groups and (2) voles in mixed-gender groups. Below, we discuss whether: (1) anxiety in groups under stress is contagious and (2) which social structure, mixed-gender, or same-gender group better withstands life-threat. Finally, in considering the finding that a few males displayed a low level of anxiety, we suggest that these were individuals of high social rank and that the response of these individuals reflects the natural division of labor in social voles.

Social groups have emerged as a means against predation threat (Hamilton 1971). They are preserved as long as individuals in the group take similar action; otherwise, the group may split (Conradt and Roper 2005). Predation threat has been suggested as '*prime mover of social evolution*' (Wilson 1975), resulting in precaution behavior (vigilance). Generally, the larger the group, the lower the required level of individual vigilance and the greater the collective vigilance (Elgar 1989; Dehn 1990; Bednekoff and Lima 1998). Nevertheless, vigilance vary among individuals: It is higher in those at the perimeter of herds than those in the center (Elgar 1989; Quenette 1990). In many social species, a few individuals guard the group while the others forage (e.g., hyraxes: Kotler et al. 1999; babblers: Bergstrom and Lachmann 2001; and meerkats: le Roux et al. 2009). This seems to be the case of the present study with mixed-gender groups, in which all females and some males displayed high anxiety, while other males displayed low anxiety. In contrast, in the unnatural social structure of same-gender groups, the above difference in males vanished, and all individuals displayed a high level of anxiety. It should be noted that studies on collective behavior are often constricted by the large size of

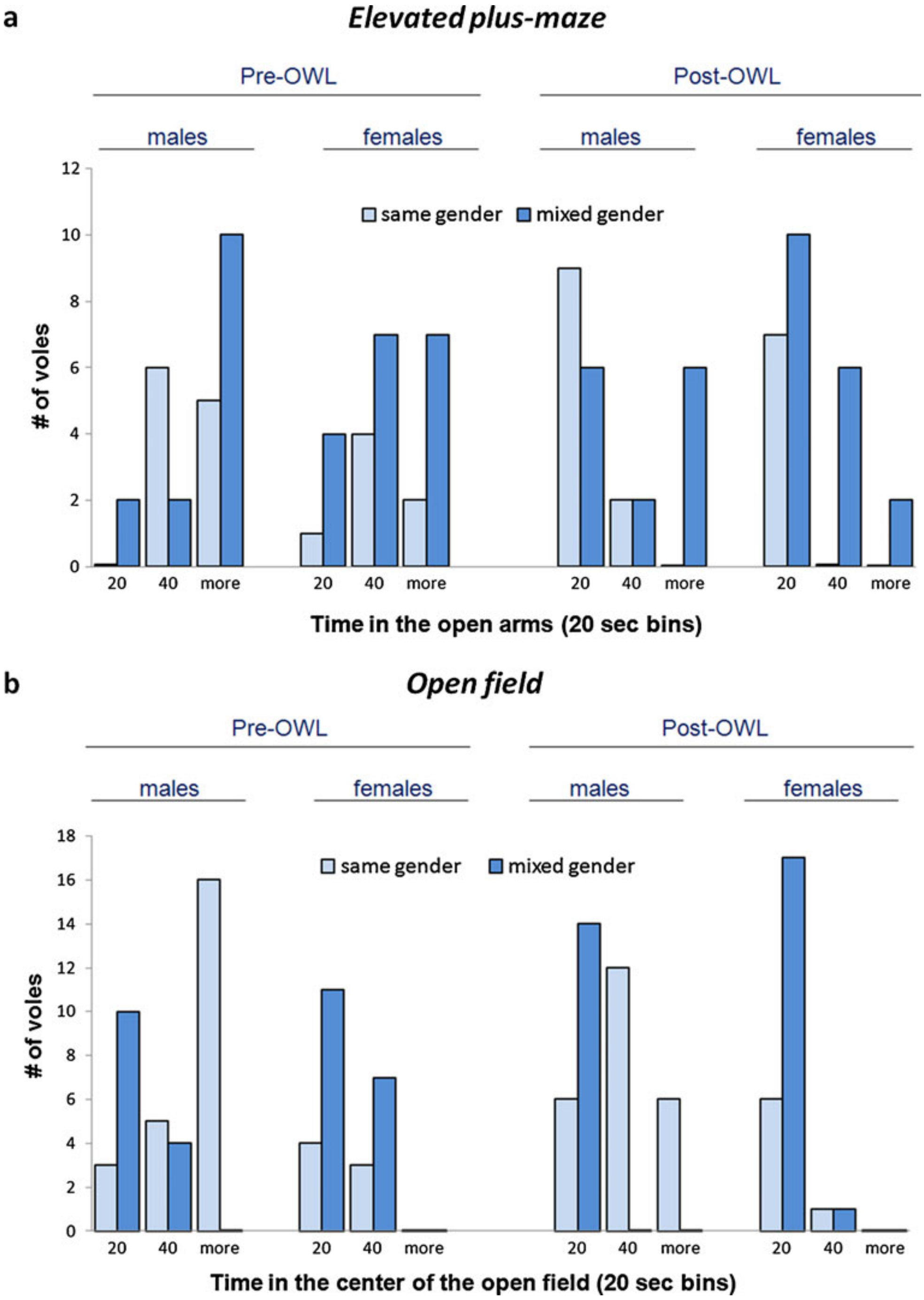

Fig. 3 The number of voles (*y*-axes) that spent a short (20 s or less), intermediate (more than 20 but less than 40 s), and long period (more than 49 s) in the open sectors of the apparatus (*x*-axes) are depicted for the elevated plus-maze (**a**) and the open field (**b**). **a** During the pre-OWL test (*left*), most males and females spent intermediate or long periods in the open arms of the elevated plus-maze, irrespective of grouping condition. However, during the post-OWL test, males in mixed groups dichotomized to those that spent a short period and those that spent a long period in the open arms. In females of the mixed-gender groups, there were more individuals in each rank compared with the respective rank for females in the same gender groups. In contrast, in both males and females in same-gender groups, most individuals spent only a short period in the open arms. **b** In both males and females, most individuals spent a short period in the center of the open field during the post-OWL test (*right*) compared with the pre-OWL test (*left*)

the group (for example, several millions in starlings) and thus focus on the presumed self-organized behavior of the entire group (Couzin and Krause 2003; Ballerini et al. 2008; Bajec and Heppner 2009; Carere et al. 2009; Daruka 2009) rather than analyzing the behavior of grouped individuals. Wherever the behavior of individuals was noted, it was revealed that the behavior of even a few individuals may lead the collective behavior of the group (Couzin 2009; Procaccini et al. 2011; Townsend et al. 2011).

The present results demonstrate that variability in anxiety levels among female voles decreased after a stressful event, whether the females were grouped with males or with other females. The same was found for males grouped with other males but not for males grouped with females. The adoption of a relatively similar level of anxiety by all group members reconfirms our previous studies with male social voles that underwent the same testing procedure as that of the present study (Izhar and Eilam 2010; Eilam et al. 2011). The similarity between the present and previous results further supports the notion that anxiety is contagious, resulting in the similarity of behavior displayed among individuals in the above groups of voles. Indeed, being among a group of vigilant, watchful, and worried conspecifics might exert a contagious effect, and, in consequence, other individuals may also become vigilant, watchful, and worried (Sirot and Touzalin 2009). Behavioral templates may propagate from one individual to the next by automatic contagion (Raafat et al. 2009). This could be the process that occurred in the female voles and in the males that were grouped in all-male groups, when individuals adopted the same behavior and displayed a relatively homogenous group response (collective behavior).

A hypothesized mechanism for adopting the same behavior is that of the ‘mirror neurons system’ (Rizzolatti and Craighero 2004; Bonini and Ferrari 2011). This system is based on automatically mimicking the motor behavior of others (Bien et al. 2009). Such a mechanism enables individuals to learn via observation from the experience of others by mere imitation, and the result is a contagious effect in which some individuals mimic the behavior of one or several other individuals. It was suggested that mirror neurons are involved in collective behavior (Lee and Tsai 2010), where such a mechanism could have the potential for executing fast and time-saving decisions (Ecksteina et al. 2012), and this is critical in the face of a life-threat. Perceived threat has been shown to increase synchronization (Bode et al. 2010), and a mechanism like that of the mirror neurons could account for the relatively similar levels of anxiety that were measured in the voles, acquired by some individual voles automatically mimicking the behavior of others.

The present results have revealed that female and male voles were affected differently by the exposure to owl attacks. There was also a differential effect on males and females in same-gender compared with mixed-gender groups. Following owl attack, females in the all-female groups revealed higher anxiety levels than females grouped with males, and males that were grouped with females displayed lower anxiety levels than those in all-male groups. In the context of the above notion of a mirror neurons system, this system was found to be more active in females than in males (Cheng et al. 2006), thus females were considered to be more sensitive to emotional contagion (Lee and Tsai 2010). This fits well with the present data, where females were found to display higher levels of anxiety, regardless of group composition, despite the lower anxiety of females grouped with males compared with females grouped with females. This raises the issue of the reciprocal impact of gender on the response to owl attack.

As shown in Figs. 1, 2, and 3, the behavior of individuals in mixed-gender groups differed from that in the same-gender groups. In the elevated plus-maze, males dichotomized to those that reduced their activity in the open to the same low level as that of the females in their group, and those that maintained a high level of activity in the open (Figs. 1 and 2). In the plus maze, females that were grouped with males displayed greater activity in the open area compared with females that were grouped with females. Notably, this differential effect was not preserved in the open field, where both females and males minimized their activity away from the arena walls (Fig. 2). While the greater activity in the open of the females in the mixed-gender groups could be explained as a contagious effect of the more active males, the dichotomy of behavior in the males is puzzling. This dichotomy of behavior after a life-threatening event reinforces our past finding that defensive response in social voles is heterogeneous, with some individuals freezing, others fleeing, and yet others alternating between freezing and fleeing (Edut and Eilam 2004; Eilam 2005). Social voles that fled in the face of life threat also possessed lower levels of corticosterone compared with voles that froze, implying that fleeing voles are less anxious (Eilam et al. 1999). In the same vein, males in other vole species have also been found to be more susceptible to owl predation than females, perhaps since they traveled more in the open and more risky habitats (Koivunen et al. 1996). Ostensibly, the bold behavior of some males when grouped with females, but not when grouped with males, could be wrongly interpreted as a ‘macho’ response. In the case of social voles, this is even more piquant, considering that social male voles force their females to babysit (Libhaber and Eilam 2002), as if this species is the exemplar for male chauvinism. However, we suggest that the observed behavior of the voles simply reflects the natural division of labor in social voles, where males have a protective role, and therefore travel more in the more risky areas, as found in other vole species (Koivunen et al. 1996). Compared with other species of voles, male social voles display extensive parental care along with protecting and maintaining the burrow-system in which they live in large groups (Libhaber and Eilam 2004). Altogether, the present results indicate that the more natural group structure of both females and males was better able to cope with stressful events, with some of the males performing their protective role, being less anxious compared with individuals in the same-gender groups. Further observations on social voles are required in order to reveal the social status of these less-anxious males.

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Ethical standards The experiments in this study comply with the current laws in Israel and were performed under permission of the Institutional Committee for Animal Experimentation at Tel-Aviv University.

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Appendix B

Kleiman M., Bodek S. and Eilam D.

Discriminating between leaders and followers in the behavior of voles under owl attack.

Behavioral Ecology and Sociobiology

A revised version, submitted on Feb 2014

Discriminating between leaders and followers in the behavior of voles under owl attack

Michal Kleiman*, Sivan Bodek* and David Eilam

Department of Zoology, Tel-Aviv University, Ramat-Aviv 69978, Israel

*Equally contributed in all phases of this study

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Correspondence:
David Eilam, Ph.D.
Professor of Zoology
Department of Zoology, Tel-Aviv University, Ramat-Aviv 69978, Israel
Phone: +972 36406471; Fax: +972 36409403; e-mail: Eilam@post.tau.ac.il

ABSTRACT

The study of group behavior has not as yet provided an inclusive answer to the question of whether the behavior is self-organized and spontaneously emergent or led by specific individuals. Since it is impossible to track many animals simultaneously, research has dichotomized into (i) modeling behavior while assuming that individuals are equal and ignoring the possible impact of individual variability; and (ii) studying individuals in the context of relatively small groups while assuming that, albeit weaker, similar interactions also occur in large groups. The latter approach was used here, addressing the question of whether specific individuals lead the behavior of voles after owl attack. We hypothesized that since social groups are usually hierarchical, the influence of specific individuals should differ according to social status. Based on previous studies, we used body mass as a proxy for social rank (greater mass represents higher social rank), have found that many low-mass individuals increased their activity in open areas after owl attack. In contrast, voles with high mass reduced their activity in the open and were the more stable social component, establishing the “behavioral code” for the group and reducing diversion. Accordingly, we suggest that individuals in the present study were not necessarily predisposed to be leaders or followers, but that, having grown in size and by virtue of their experience and physical strength, they assumed responsibility for leading and stabilizing their groups. We also suggest a hypothetical model for the propagation of behavior in hierarchical groups.

Key words: Collective behavior; Sociality; Anti-predator behavior; Animal personality; Synchronization; Self-organization.

INTRODUCTION

The term collective behavior was coined by Blumer (1951) and has been at the focus of human sociology and anthropology for centuries (MacKay 2004; originally published in 1841). In animals, the study of collective behavior is flourishing (see special issue of *The Philosophical Transactions of the Royal Society*, vol. 364, 2009). Collective behavior refers to a large group of individuals, all displaying coordinated action; for example, an aerobating flock of birds (Davis 1980), a swimming school of fish (Parrish et al. 2002), or a migrating herd of buffalo (Molszewski 1983). Individuals in these groups display an alignment of behaviors without any apparent centralized coordination (Carere et al. 2009) and maintain group cohesion (Conradt and List 2009; Conradt et al. 2009). Studying collective animal behavior may shed light on similar behavior in humans, or at least infer principles that can be used as a “search image” in studying human collective behavior (e.g. in the stock market, in political choice, in consumer preferences, etc), as well as disclosing the underlying governing mechanisms of these fascinating behaviors in large animal groups.

Various theories on human collective behavior have been posited ever since the eighteenth century. These have since been reviewed, noting that the current models of collective behavior in humans have focused on physical properties such as distances and velocities rather than on emotional states (Raafat et al. 2009; see also Lopez et al. 2012 for a review on models of animal collective behavior). Since it is impossible to track the behavior of, for example, an aerobating flock of a million starlings or a maneuvering school of a thousand fish, models of collective behavior have usually assumed homogeneity of the individuals, virtually suggesting that the members of these large groups lose their individuality and entirely conform to the behavior of the group. Implicit in such assumption is that the behavior of the group is a self-organized property with no central control (Couzin and Krause 2003; Ballerini et al. 2008; Bajec and Heppner 2009; Carere et al. 2009; Daruka 2009). In other words, the collective behavior does not ensue from the behavior of specific individuals. Against this notion of conformity, there is growing evidence that group members maintain certain aspects of individuality, although the larger the group the greater the homogeneity

(Herbert-Read et al. 2013). This, together with the finding that the behavior of even a few individuals may propagate and shape the collective behavior of the entire group (Couzin 2009; Procaccini et al. 2011; Townsend et al. 2011), can be summarized in the form of three main questions in regard to collective behavior, as posed by Conradt and Roper (2005): (1) Are there specific individuals that lead the decision on a specific collective behavior? (2) How does the collective behavior spread across the group? (3) What do individuals in the group gain by behaving collectively? The present study focused on the first two questions regarding the behavior of voles after their group is attacked by owls. Although the third question was not directly addressed in the present study, if animals living in groups are to profit from sociality, individuals must conform to the behavior of the group. Otherwise, they may become isolated, and therefore exposed to a higher risk of predation (Landeau and Terborgh 1986; Szulkin et al. 2006).

The present study followed our previous studies, in which social voles (*Microtus socialis*) were exposed as a group (with their cage-mates) to owls that attacked their cage (Izhar and Eilam 2010; Eilam et al. 2011; Eilam et al. 2012). The large individual variability in behavior, as measured in the voles before the attack, was significantly reduced after the owls attacked, and group members displayed a relatively similar level of activity. In contrast, voles that had been individually exposed to owls preserved their behavioral variability (Izhar and Eilam 2010; Eilam et al. 2011). Accordingly, it was suggested that this group behavior of the voles is reminiscent of the social response seen in humans following a disaster, when a uniform behavioral code dominates and there is reduced behavioral variability (Izhar and Eilam 2010; Eilam et al. 2011). While the above previous studies focused on the behavior during the hours after owl attack, other studies on the immediate response of voles to owl attack have indicated that they retain a certain individuality, responding to the owls by various intervals of freezing or fleeing, and displaying behavioral heterogeneity (protean behavior) as a defensive strategy when confronting an attacking owl (Edut and Eilam 2004; Eilam 2005). In light of these indications of group behavior on the one hand, and individual differences on the other hand, we set out to examine conformity and individuality in groups of social voles after owl attack. We chose to study behavior after a life-threatening event since social facilitation is partly driven by an individual's perception of risk, with a strong influence of both the presence of conspecifics and cues relating to potential danger (Ward 2012). Specifically, we asked whether specific individuals affect the behavior of the group after the attack. Social voles inhabit a complex burrow system (Mendelssohn and Yom-Tov 1999) in groups that are comprised of 'extended families' of parents and several generations of their offspring (Cohen-Shlagman 1981; Libhaber and Eilam 2002). Implicit in this structure is that, at least within the family, there is an hierarchy which may affect the propagation of behavior among group members. In other words, it is predicted that socially high-ranking voles would be the leaders of the group while the socially low-ranking individuals would be the followers. Accordingly, examining the behavior of grouped social voles addressed the two outstanding questions in group behavior: Whether there are individuals that lead the behavior of the group, and how behavior propagates among group members?

METHODS

Subjects

Large groups of social voles (*Microtus socialis)* reside in branched burrows. The basic social unit in the groups is an extended family, comprising parents and several generations of their offspring. The adult body mass is usually 30-50 g; the trunk is 11 cm long with a short 1-2 cm tail. Social voles are widespread from southeast Europe to the northern Middle East, mainly inhabiting plains and low mountains. They feed on seeds and vegetables and are considered a major pest to agriculture. Voles reach sexual maturity at 30 days, pregnancy lasts 21-days, and the litter size is 6-10 pups. Life-span is about two and a half years in the wild, and four years in captivity. Voles are heavily predated upon, and in Israel they comprise about 50% of the barn owl (*Tyto alba*) diet (Mendelssohn and Yom-Tov 1999; Charter et al. 2007; Charter et al. 2009).

The present research comprised 46 voles (males and females) obtained from a captive colony in the I. Meier Segal Gardens for Zoological Research at Tel-Aviv University. Twenty-seven of these voles were studied in their original natural three groups (4,5,5 males and 5,5,3 females per group, respectively). Each group was housed in a 55x42x21 cm plastic container with a wire-mesh top, sawdust bedding, and wooden boxes (20x11x10 cm) for shelter. Another 19 voles (11 females and eight males) from two families that had been living together for several months, were separated and caged individually in standard rodent cages (41x25x15 cm) with a small shelter and kept next to each other in the same room. The latter voles were thus socially isolated in terms of a lack of physical contact with their family members, but were able to hear, smell, and even see each other through their transparent cages and wire-meshed cage tops. These conditions minimized the impact of social isolation (Leshem and Sherman 2006). Voles were kept in social isolation for a period of two weeks, a period found necessary to eliminate sociality (Chase et al. 2002). They then underwent the testing procedure as controls for the grouped voles. Following testing they were regrouped in their original families and carefully monitored by a veterinarian. Short-term aggressive interactions were noted but these ceased, with no ensuing wounds or casualties. This isolation was a necessity to uncover the impact of the group, which was the target of this study. A veterinarian continuously monitored the welfare of the socially-isolated voles according to their food consumption, physical state, general behavior, and the quality of feces, all of which were estimated to be within the normal range. Any deviation from these criteria was considered as the endpoint of the test. Cages of both the grouped and isolated voles were transferred to a quiet room (22^{o}c; 14/10 hours light/dark cycle) two weeks before experimentation. They were fed generously on alternating days with grains and diced fresh vegetables.

A colony of barn owls (*Tyto alba*) at kept in the Research Zoo of Tel-Aviv University. For the present study, a pair of these owls were allowed to fly freely in an aviary (6 x 6 x 3 m), fed with mice that were obtained dead from the animal facilities of the university after being used in other experiments, and with dead chicks obtained from chicken-hatcheries. We used live owls since our previous studies with models or owl calls as threat had revealed that these stimuli are not as effective as live owls (Edut and Eilam 2004; Eilam 2005), and since an effective threat was a prerequisite in the present study for examining the behavior of grouped voles after a life-threatening ordeal. The immediate response of voles to owl threat is either to freeze or to flee (Eilam et al. 1999); however, in the present study we analyzed their behavior 2-6 hours after the attack, when on average they only displayed reduced activity. It should be noted that the top cover of the vole cages, where owl food (slices of meat) was placed, was high enough to prevent any physical contact between owl and voles. Moreover, the owls did not seem to pay attention to the voles, and usually just stayed on the cage for about 20 sec before flying off with the food item to a perch.

Apparatus

Elevated plus-maze. This was composed of four arms, each 30 cm long, connected to form a + shape. Two opposite arms were enclosed by 20-cm high walls ("closed arms"), while the other two opposite arms were open, with a 5 mm rim along the edges ("open arms"); all four arms were connected and opened into a joint center. The maze was placed horizontally 72 cm above the floor, in a quiet room, illuminated by a dim light. A video camcorder (Sony DCR- SR35) was placed above the maze to provide a top-view of all four arms (see Lister 1987a; Ramos 2008 for further information on the elevated plus-maze).

Open field: This was an empty 2x2 m arena with 50 cm high Plexiglas walls and PVC floor, illuminated by a dim light. An infra-red light (*Tracksys*, IR LED Illuminator; UK) with 830 nm filters that emit light not visible to rodents also illuminated the arena in order to provide a vivid picture for a video camera (Ikegami ICD-47E), and was placed 2 m above the center of the arena, providing a full top-view. The open field was located in a quiet air-conditioned room (22^{o} c), and the video signal was wire-transmitted to an adjacent room, where the trajectories of the animal in the open field were tracked by means of a tracking system (*Ethovision* by Noldus Information Technologies, NL). (For more information on the open field, see Walsh and Cummins 1976; Ramos 2008).

Procedure

The present study was not aimed at examining the immediate response of voles to owl attack (which is fear in the face of a real life-threat), as had been studied previously under semi-natural conditions (Edut and Eilam, 2004). Rather, we studied the behavior of voles during the first few hours after they had experienced the owl attack, a period characterized by elevated anxiety (Izhar and Eilam, 2010; Eilam et al., 2011; 2012). The above apparatuses have been found to be reliable tools for measuring anxiety, as validated in numerous studies with anxiogenic and anxiolitic drugs (Montgomery 1958; Lister 1987). Accordingly, both grouped and socially-isolated voles underwent the trials described below, with the only difference being the social or asocial condition.

Pre-owl trial: Following a three-week acclimation period, each vole underwent testing in the elevated plus-maze and the open field in order to evaluate its basal behavioral level. For this, a vole was selected at random and caught in a glass jar, gently released into the near right corner of the open field, and its behavior was recorded for 15 minutes. After the open-field trial, the vole was allowed to rest for 60 min with its group-mates before undergoing a five-min trial in the elevated plus-maze. After this trial, the vole was returned to its home-cage and its original group. Both apparatuses were cloth-wiped with water and detergent between successive trials. Testing started at 10 am.

Exposure to owl attack: At 8 am of the day after the pre-owl trial, a cage with either grouped voles or a socially-isolated vole was placed in a barn owl aviary (3 x 6 x 3 m). Slices of meat were placed on top of the wire-mesh roof of the cage, and the owls instantly swooped down on the meat to feed. The voles thus experienced the sense of a real-life threat although the owls could not reach them via the cage wire-meshed top. Immediately following the owl attack, the cages were removed from the aviary and returned to the quiet room for two hours.

Post-owl trial: After the two-hour rest, each vole was tested again in the open field and the elevated plus-maze, using the same procedure as in the pre-owl test. At the end of this trial, the voles were returned to the captive breeding colonies of the research zoo.

Data acquisition and analysis

Data from the elevated plus-maze trials were acquired by scoring the behavior using the *Observer* software for behavioral analyses (Noldus Information Technologies, NL). We measured the time spent in the open arms as the cumulative duration of intervals between entering (whenever a vole had all four legs in an open arm) and exiting (when at least two legs were out of the open arm) an open arm.

Data from the open-field trials were extracted from the tracking system. These comprised the total travel distance, constituting the metric distance traversed by a vole. We also measured the distance traveled in the center of the open field, with center defined as being at least 20 cm away from the open-field walls.

The rationale for extracting these variables was as follows. The total traveled distance in the open field is an index of general activity. The time spent in the open arms of the elevated plus-maze or away from the walls of the open field is commonly used as an indicator of a rodent's sense of safety, since rodents usually avoid open spaces, where predation risk is higher. Rodents also display positive tigmotaxis, and accordingly are attracted to the sense of safety provided by walls (Pickles and Hendrie 2013). In the same vein, time spent and distance traveled in open sectors is considered as a reliable measure of anxiety: the less anxious the animal, the more it stays in the open (Eilam

2003). This has been validated using anxiolitic and anxiogenic drugs that respectively increased or decreased the time spent by rodents in the open arms of a plus maze (Montgomery 1958; Lister 1987).

Assessing social rank

Social rank, personality, boldness, and dominance are complicated issues. Our preliminary attempts to assess social rank according to behavioral criteria failed due to uncontrollable factors that biased the behavioral results. For example, highly-ranked animals usually took the food first, but sometimes gave it up to young or females. Accordingly, we searched for a non-behavioral proxy for social rank. Social animals usually establish a social hierarchy, and it is commonly the larger and stronger individuals that are ranked higher than the smaller and weaker ones. Indeed, it was suggested in another species of voles that body mass, which is a product of age and strength, is a reliable predictor that well correlates with social rank (Sokolov et al. 1990) as also found in other species (for example: reindeer - Holand et al. 2004; ram - Maksimović et al. 2012; monkeys - Morgan et al. 2000). Social ranking according to body mass is implicit in the social structure of social voles, which live in "extended families" of parents and several generations of their offspring (Cohen-Shlagman 1981; Libhaber and Eilam 2004). We thus weighed the voles to obtain a proxy indication of their social rank. Each of the grouped voles was weighed (Yeshm electronic scale model YHC4162 with 1gr resolution) on alternate days during the third week of acclimation, before the pre-owl trial, and the average of the three measures was considered as the body mass of that individual, which was then used as a proxy for social rank. This procedure was not applied to the isolated voles, where *a-priori* there was no need for indication of social rank.

Statistical analysis

Unless noted differently, data underwent a two-way ANOVA with repeated measures, comparing the pre-owl and post-owl trials (within-group factor) and socially isolated vs. grouped voles (between-group factor). When data deviated from normality, a Mann-Whitney or a Wilcoxon test was used. An F-test was used to compare the variance within groups, and a χ^2 test was used to compare the number of animals in quartiles. In all tests we set the alpha level to 0.05.

RESULTS

Grouped and socially-isolated voles displayed a similar level of activity but grouped voles traveled more in the open sectors

Grouped and socially-isolated voles did not differ in their overall activity, as reflected in their total traveled distance in the open field before and after their exposure to owl attack (Figure 1a). Indeed, a two-way ANOVA with repeated measures revealed no significant difference between grouped and socially-isolated voles ($F_{1,44}$ = 1.2; P = 0.2938), a significant difference between pre- and post-owl trials ($F_{1,44}$ = 53.4; P <0.00001), and a non-significant interaction of grouping X owl ($F_{1,44}$ = 0.8; P = 0.3723). Thus, in terms of the overall traveled distance, grouped and isolated voles did not differ from each other and were similarly affected by the owls. Nevertheless, before exposure to the owls, grouped voles traveled a greater distance away from the walls of the open field compared with the socially-isolated voles (Figure 1b). A two-way ANOVA with repeated measures revealed a significant difference between grouped and isolated voles ($F_{1,44}$ = 41.7; P < 0.00001), a significant effect of the owl ($F_{1,44}$ = 22.3; P = 0.00002), but no interaction between exposure to the owls and grouping ($F_{1,44}$ = 0.8; P = 0.3723). Socially-isolated voles were also compared with grouped voles for the time spent in the open arms of the elevated plus-maze (Figure 1c). Since these data could not be normalized, they underwent a Mann-Whitney comparison, revealing a significant difference between grouped and isolated voles for the time spent in the open arms during the pre-owl trial (U = 47; P = 0.00003), and the post-owl trial ($U = 31$; $P = 0.000005$). In both the isolated and the grouped voles, there was also a significant difference between the pre- and post-owl trials (Wilcoxon text; $T = 14.0$; $P = 0.0011$ and $T = 88.0$; $P = 0.02626$, respectively). These findings imply that while the general level of activity and the impact of the owls seem similar in both grouped and isolated voles, the two tested groups significantly differ from one another, with isolated voles displaying parameters that reflect higher anxiety (less time spent in the open arms of the elevated plus-maze and away from the arena walls).

Many grouped voles with low score during the pre-owl trial increased their activity in the open during the post-owl trial

The impact of the group became apparent in the data of the individuals in the tested groups. Behavior of the voles before and after exposure to the owls (**O** and ■, respectively) was sorted from low to high according to the pre-owl phase (**O**) along the x-axis (Figure 2). This sorting resulted in an inclined order for the pre-owl data in both the isolated and grouped voles. However, for almost all individuals in both groups, the overall distance traveled in the open field (Figure 2a) decreased in the post-owl trial (■) compared with the distance traveled during the pre-owl trial (**O**). Such a decrease was also noted in the socially-isolated voles for both the distance traveled away from the walls of the open field (Figure 2b, left) and the time spent in the open arms of the elevated plus-maze (Figure 2c, left). In contrast, the grouped voles displayed a differential impact of the exposure to the owls in both the distance traveled away from the open-field walls (Figure 2b, right) and the time spent in the open arms of the maze (Figure 2c, right). Specifically, many of the grouped voles that did not travel much away from the walls during the pre-owl trial (lower median, entitled as "Low in pre-owl" in Table 1) increased their traveling away from the walls during the post-owl trial. Conversely, voles that travel greater distances away from the walls during the pre-owl trial (upper median, entitled "High in pre-owl" in Table 1) decreased their traveling during the post-owl trial (Figure 2b, right). Similar changes were noted in the time spent by the grouped voles in the open arms of the elevated plus-maze (Figure 2c, right). These changes, as summarized in Table 1, illustrate a significant increase only for grouped voles with low pre-owl traveling away from the open field walls, and for voles spending a short time in the open arms of the elevated plus maze during the pre-owl trial. These increases, together with the decreases in high pre-owl grouped voles, resulted in a convergence of most of the grouped voles to a narrower range in the post-owl trial.

Taking the time spent in the open arms of the maze and the distance traveled away from the open-field walls as a reflection of the level of anxiety, (i) grouping in voles seemed to involve lower anxiety (Figure 1); and (ii) there was a differential effect of the owls on vole activity in the open, in accordance with the behavior of individual voles before owl attack (pre-owl trial). Nevertheless, there was no difference in the variance within pre- and post-owl scores (F-test for equality of variance; $F_{50} = 1.\ 47$, $P = 0.338$; $F_{50} = 1.28$, $P = 0.536$; F_{50} 1.05, $P = 0.89$, respectively, for total distance, center distance, and time in the open arms).

The impact of social rank on group behavior

As explained in the ‘Methods’, we used the body mass of the voles as a proxy for their social status, and explored the relations between body mass and behavior during the pre-owl and post-owl trials for the socially housed voles. Figure 3a compares the total distance traveled during the pre- and post-owl trials with body mass. As shown, all the voles with mass above the median (over 37 gr) aggregated in a relatively narrow range of the distance traveled during both the pre- and post-owl trails. This is illustrated in Table 2, where the min-max values of the low-mass and high-mass voles during the pre- and post-owl trials are depicted. Indeed, a comparison of the two mass groups by F-test for equality of variance revealed that the low-mass voles had a significantly greater variance in both the pre-owl trial (F_{13}=8.67; $P = 0.0007$) and the post-owl trial ($F_{13} = 7.62$; $P = 0.0013$). Altogether, in both the pre- and post-owl trials the total distance traveled by voles with a greater body mass converged in a relatively narrow range, while the distances traveled by voles with a lower mass scattered along a wide range.

Figure 3b depicts the center distance (traveling away from the open-field walls) during the pre- and post-owl trials. As shown, low-mass voles traveled a shorter distance away from the arena walls during both the pre- and post-owl trials. High-mass voles traveled greater distances away from the walls during the pre-owl trial, while during the post-owl trial they were equally divided between the low and high ranks of the center distance (see Table 3). Indeed, a chi-square comparison of the number of high-mass and low-mass voles in each of the distance ranges (Table 3) revealed a significant difference ($\chi^2_3 = 14.1$; $P = 0.003$).

Figure 3c depicts the time spent in the open arms of the elevated plus-maze during the pre-owl and post-owl trials for high-mass and low-mass voles. As shown, in both the pre- and post-owl trials, more high-mass voles spent a longer time in the open arms whereas more low-mass voles spent a shorter time there. A chi-square comparison of the number of high-mass and low-mass voles in each of the time ranges (Table 4) revealed a significant difference ($\chi^2_3 = 8.5$; $P = 0.037$).

DISCUSSION

While owl attack had an impact on both grouped and socially-isolated voles and both displayed a similarly lower level of activity, grouped voles traveled more in the open sectors of the open-field or elevated plus-maze compared with the socially isolated voles. Moreover, while most of the latter reduced their activity in the open sectors, some grouped voles (specifically, with low pre-owl activity at the open sectors) increased their activity there. These differential changes in activity in the open sectors (increase in voles with low pre-owl activity and decrease in those with high pre-owl activity) were also described in previous studies using the same testing procedure (Izhar and Eilam 2010; Eilam et al. 2011; Eilam et al. 2012), suggesting that this is a replicable and reliable response of grouped voles to predation threat. To these past studies we add here that a midway level, a consequence of the increase and decrease, characterized voles with higher body mass, whereas those with lower body mass were mostly characterized by polarized values in the measured behavioral parameters. Based on previous studies suggesting that a greater mass reflects a higher social rank (see 'Methods'), in the following discussion we suggest that voles with high body mass were also highly ranked socially, and consistently the more stable social component that establishes the “behavioral code” for the group. This is discussed below in the context of group collective behavior, suggesting that behavior can propagate swiftly in hierarchical populations that are divided into groups that have leaders and followers.

Predation threat as the driver of sociality and establishing group behavior

Predation threat has a profound impact on behavior (Eilam et al. 1999), on its controlling mechanisms (Canteras 2002), and on essential life-cycle behaviors such as breeding (Vasilieva et al. 2000) and foraging (Kotler et al. 1992; Kotler et al. 1994; Otter 1994). It also affects population structure through the removal of specific individuals (Berger 1991; Wooster and Sih 1995). As a consequence of the above changes, the balance between prey and predator populations within the ecosystem can become altered (Abrams 1995; Turner 1997). The primer in this cascade of changes is the behavioral response of the prey, which is modulated by the strong selective pressure of predation. In the animal kingdom, social groups have emerged as a means against predation threat (Hamilton 1971). Indeed, predation threat has been suggested as a ‘*prime mover of social evolution*’ (Wilson 1975), resulting in vigilance (precaution behavior) under the assumption of “safety in numbers”: the larger the group, the lower the required level of individual vigilance and the greater the collective vigilance (Elgar 1989; Bednekoff and Lima 1998; Szulkin et al. 2006). It could perhaps be argued that the same applies to the present study; and, compared with socially-isolated voles, that grouped voles felt more safe to travel in the open (Figures $1_{b,c}$) both before and after the owl attack. However, both the grouped and the socially-isolated voles in the present study were tested individually. Therefore, if there was a group effect of “safety in numbers” in the present study, it was preserved even when they were tested individually during the period that followed the owl attack on their group. Such an effect was not observed in the socially-isolated voles removed from their original groups for three weeks prior to the owl attack. In previous studies employing the same testing procedure, we found that the effect of the group was preserved even 12 hours following exposure to the owl (Izhar and Eilam 2010; Eilam et al. 2011; Eilam et al. 2012). Consequently, it seems that the norms or sense of safety conferred by the group are preserved even when group members remain isolated from the group for several hours.

The "comfort factor" of the group

Vigilance varies among individuals: it is higher in those at the perimeter of herds than in those at the center (Elgar 1989; Quenette 1990). Moreover, defensive behavior in some herds, such as the African buffalo (*Syncerus caffer*), is based on the larger and bolder bulls taking a post at the perimeter and turning to face approaching predators, while the more vulnerable cows and calves remain in the center of the herd (Molszewski 1983). In other social species, a few individuals guard the group while the others forage (e.g. - hyraxes: Kotler et al. 1999; babblers: Bergstrom and Lachmann 2001). In the same vein, as found in other vole species (Koivunen et al. 1996), the natural labor division in social voles is that males have a protective role and therefore travel more in the more risky areas, and accordingly could be more susceptible to predation than females (Eilam et al. 2012). Altogether, predation seems to serve as a force that acts in the formation of social groups and in establishing division of labor within these groups. In this context, the present study revealed that the heavier individuals, which are presumably highly ranked socially, establish the behavioral level at which most group members converge under owl attack.

Behavior of high-mass voles in both pre- and post-owl trials was within a range 2-3-fold smaller than that of the low-mass voles (see min-max values in Table 2). Thus, the high-mass voles may be acting as “stabilizers” of the group by displaying a moderate range of behavior at which the low-mass voles converge, and by establishing a sort of social support in the threatened group (Leshem and Sherman 2006). While hierarchies assign priority to resources such as food, space, and mates (Hoffmeyer 1982), here we show that part of the high-mass voles’ contribution to the group could lie in their establishing stability and preventing the divergence of group behavior to the extremes.

Contagious vigilance

The present results confirm those of previous studies with social voles that underwent the same test procedure. It was suggested that activity in the open sectors of the open field and elevated plus-maze reflects the level of anxiety; and, accordingly, that group members adopt a relatively similar level of anxiety following owl-attack (Izhar and Eilam 2010; Eilam et al. 2011). The increase in activity in the open areas by grouped voles with low pre-owl behavior and its decrease in voles with high pre-owl behavior, further support the notion that anxiety is contagious. Thus, being among a group of vigilant, watchful, and anxious conspecifics might exert a contagious effect, with other individuals also becoming vigilant, watchful, and anxious (Sirot and Touzalin 2009; Beauchamp et al. 2012), and vice versa. While the mechanism for such propagation of behavioral templates from one individual to the next could be that of automatic contagion (Raafat et al. 2009) or neighbor copying (Pays et al. 2007), the present results demonstrate that the low-mass and presumably lower-social ranking animals converged to display the behavior of the high-mass and presumably high-ranking individuals. This is reminiscent of the social integrative responses seen in human behavior following a disaster, responses that usually involve solidarity, altruism, loyalty, and volunteering (Tierney et al. 2001). These types of social integrative responses were found to similarly emerge among a large spectrum of individuals who differed in age, occupation, income, ethnic background, gender, and sexual preferences (Lowe and Fothergill 2003).

Leaders, followers, and propagation of collective behavior from one individual to the next

The adoption of a similar behavioral code is prevalent in collective behavior, in which all individuals adopt the same behavioral pattern, usually characterized by a sudden change in their direction of movement (Couzin et al. 2002; Conradt and Roper 2003, 2005, 2010; Bajec and Heppner 2009; Conradt et al. 2009; Couzin 2009; Conradt 2011; Lopez et al. 2012). Collective behavior has been modeled in some cases by assuming that the individuals are identical and the propagation of behavior is caused by the mechanism of “neighbor copying” (Deneubourg and Goss 1989; Viscido et al. 2005; Herbert-Read et al. 2011; Katz et al. 2011). Implicit in these presumptions is: (i) the homogeneity of all individuals; and (ii) that the influential factor is the proximity of the neighbor regardless of its identity or its characteristic behavior. Under these assumptions, collective or group behavior has been considered as a self-organized property that emerges spontaneously. According to this notion, individuals in a group behave differently than they would otherwise behave when socially isolated under the same circumstances (Couzin and Krause 2003; Conradt and List 2009). In contrast, an opposite notion suggests that group behavior could be affected by specific individuals, such as “leaders” that establish the behavioral code of the group, or “cowards” that start running and trigger the escape of the entire herd. Another possibility could be that a group displays an average consensual behavior, to which the extremes converge in order to avoid standing out from the group. All in all, an outstanding question in the study of collective behavior is whether there are specific individuals that establish the behavior of the group or whether group behavior is a self-emergent property (Conradt and Roper 2005). This has been the general perspective of the above discussion of whether vigilance is homogenous or differential among group members. The question remains as to whether, by virtue of conformity, group members lose their individuality and behave homogenously.

A seminal study on the role of individuality in collective behavior (Herbert-Read et al. 2013) tackled the question of how group members balance individuality against the need to conform to the group, and how this balance is affected by group size and group composition. Studying relatively small groups, those authors suggested than group members do not lose their individuality, and rather than a dichotomy to conformity or individuality, there is a conformity gradient: the larger the group, the greater the conformity and the loss of individuality. In other words, group members lose aspects of their individuality with the increase in group size. While individuality is maintained to some degree, because group members need to conform to the group, individuals behave more similarly to each other in social rather than in asocial contexts (Herbert-Read et al. 2013). The results of the present study, which were also obtained for relatively small groups of 8-10 voles, concur with those of Herbert-Read and his colleagues, in showing that grouped individuals displayed a certain conformity along with maintaining a certain individuality.

To the outstanding question of which are the specific individuals that lead the behavior of a group (Conradt and Roper 2005), the present study offers an inclusive answer: that in this case these are the voles with higher body-mass. Since body mass in voles, as in some other species, correlates with social rank (see Methods), we suggest that socially high-ranked voles are those that affect the behavior of the low-mass group members. Indeed, before experiencing owl-attack, voles with a low body mass displayed a larger range in the measured behavioral parameters than after the attack, when most of them converged to the range of the high-mass individuals. This division into leaders and followers was also revealed in other studies with other species, where specific individuals, usually experienced adults, were found to shape the behavior of the entire group (Black 1988; Prins 1996; Byrne 2000; Graw and Manser 2007; Hay et al. 2008; Harcourt et al. 2009). These latter studies, like the present one, differ from yet other previous studies that have suggested that animal “personality” or “behavioral signature” differentiates between leaders and followers (Harcourt et al. 2009; Webster and Ward 2011; Burns et al. 2012; Carter et al. 2012; Dingemanse and Wolf 2013). These latter studies found that specific individuals were predisposed to be the leaders regardless of their size, color, and other physical properties (Burns et al. 2012). In this context, the present study introduces body mass as an overt and easy-to-measure discriminator between leaders and followers. Nevertheless, the two notions, that of predisposition and that of growing into leadership, are not mutually exclusive. Different combinations of these two notions may exist in different species and, therefore, the present finding regarding the impact of body mass should not be generalized but rather considered as another possible influential factor when determining the impact of specific individuals.

Neighbor copying has been a suggested mechanism for the propagation of behavior among group members, and thereby for the emergence of similar behavior in all individuals (Deneubourg and Goss 1989; Viscido et al. 2005; Herbert-Read et al. 2011; Katz et al. 2011). Implicit in this mechanism is that the proximity to another individual is the key element in the propagation of behavior within the group. To this, the present study adds that, at least in the context of small groups, it is not just proximity but also the identity of the neighbor that influence behavioral copying. Specifically, the low-mass voles copy the behavior of the high-mass voles, and not necessarily the behavior of the nearest vole. An evocative effect was described in baboons, where 'follow-a-friend' was the social affiliation that explained their collective movements (King et al. 2011). Considering that individuality declines with the increase in group size, it is questionable whether the present finding in groups of about 10 voles is also applicable for larger groups. Nevertheless, the social structure of vole populations introduces another possible, and perhaps swift-acting, mechanism for behavioral transmission among group members. In harvest fields, large populations of voles inhabit a complex network of burrows shared by several "extended families" of parents and several generations of their offspring. Accordingly, it is possible that the recombinant unit for behavioral propagation is the extended family and not the individuals. In other words, behavior does not propagate from one individual to the next, but undergoes a two-stage propagation: (i) from one extended family to the high-mass individuals of the neighboring extended family; and (ii) within the extended family, from the high-mass individuals to the low-mass individuals, as revealed in the present study (Figure 4). Such propagation in a hierarchical population, which could be termed 'leader copying', could be faster than simple neighbor copying, and this could perhaps be vital under life threat. In the present study, it is possible that the voles could be recognizing their conspecifics' social status simply by their size (a reflection of body mass) and by their familial bonds, since the extended family of parents and their several successive litters is the basic social unit in the large populations of this species of voles. This hypothetical model of 'leader copying' (or 'follow the leaders') offers a potential search image tool when studying group behavior in the wild.

The complexity of behavior at the individual level rests on two effectors: (i) individual traits; and (ii) group dynamics (Bezzi and Groenevelt 2006). The present study is in line with recent studies in demonstrating that, at least in the context of relatively small groups, members may preserve their individuality along with displaying a certain group conformity (see Herbert-Read et al., 2012). This seems to be preserved as long as the population features several social ranks. While previous studies have suggested that group members could be predisposed to being leaders or followers (Burns et al. 2012), our results concur with those of other studies in suggesting that the larger, and perhaps the older and more experienced, individuals are those that establish the behavioral code of the group. Notably, while body mass seems a reliable proxy for social ranking in voles, other features may be required to characterize social ranking in other species. From a broad perspective, the trade-off between conforming to other group members and maintaining individuality seems to be an important selective factor in the evolution of social groups and collective behavior (Herbert-Read et al. 2013). To this, we suggest that individual voles in the present study were not necessarily predisposed or born as leaders or followers, but simply grew in size and, by virtue of their experience and physical strength, took the responsibility of leading and stabilizing their groups.

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ETHICAL STANDARDS

This study and the maintenance conditions for the voles and owls were carried out under the regulations and approval of the Institutional Committee for Animal Experimentation at Tel-Aviv University (permit # L-11-047) and by the USAF Animal Use Programs (Proposal AFOSR-2012-008A).

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TABLES

Table 1: The number of voles that increased or decreased their behavior in the post-owl trial is depicted for each behavioral parameter in the socially-isolated and the group voles. For each, the voles were divided at the median into those with low scores in pre-owl trial and those with high scores in the pre-owl trial.

	Low in Pre-OWL *(below median)*		***High in Pre-OWL*** *(median and above)*		$\chi^2_{(1)}$	P
Socially-isolated voles	Increased	Decreased	Increased	Decreased		
Traveled distance	3	6	0	10	3.96	0.047
Center Distance	0	9	2	8	2.01	0.156
Time in the open	1	8	1	9	0.01	0.937
Grouped voles						
Traveled distance	2	11	0	14	2.33	0.127
Center Distance	**9**	**4**	1	13	11.1	0.001
Time in the open	**8**	**5**	2	11	5.85	0.016

Table 2: Range (min – max values) of traveled distance (m.) in low-mass voles (less than 37 gr.) and high-mass voles (more than 37 gr.).

	Low-mass voles		***High-mass voles***	
	Min-Max	Mean	Min-Max	Mean
Pre-OWL	44.0 - 221.9	131.9	110.8 - 168.5	134.7
Post-OWL	55.7 - 181.2	101.3	71.0 - 119.5	97.3

Table 3: The number of high-mass and low-mass voles that traveled a greater distance (above median) and shorter distance (below median) away from the open-field walls during the pre-owl and post-owl trials.

	Pre-OWL		***Post-OWL***	
	Greater distance	Shorter distance	Greater distance	Shorter distance
High Mass	11	2	6	7
Low Mass	3	11	2	12

Table 4: The number of high-mass and low-mass voles that spent a greater time (above median) and shorter time (below median) in the open arms of the elevated plus-maze during the pre-owl and the post-owl trials.

	Pre-OWL		***Post-OWL***	
	Greater time	Shorter time	Greater time	Shorter time
High Mass	8	5	11	2
Low Mass	5	9	5	9

FIGURE CAPTIONS

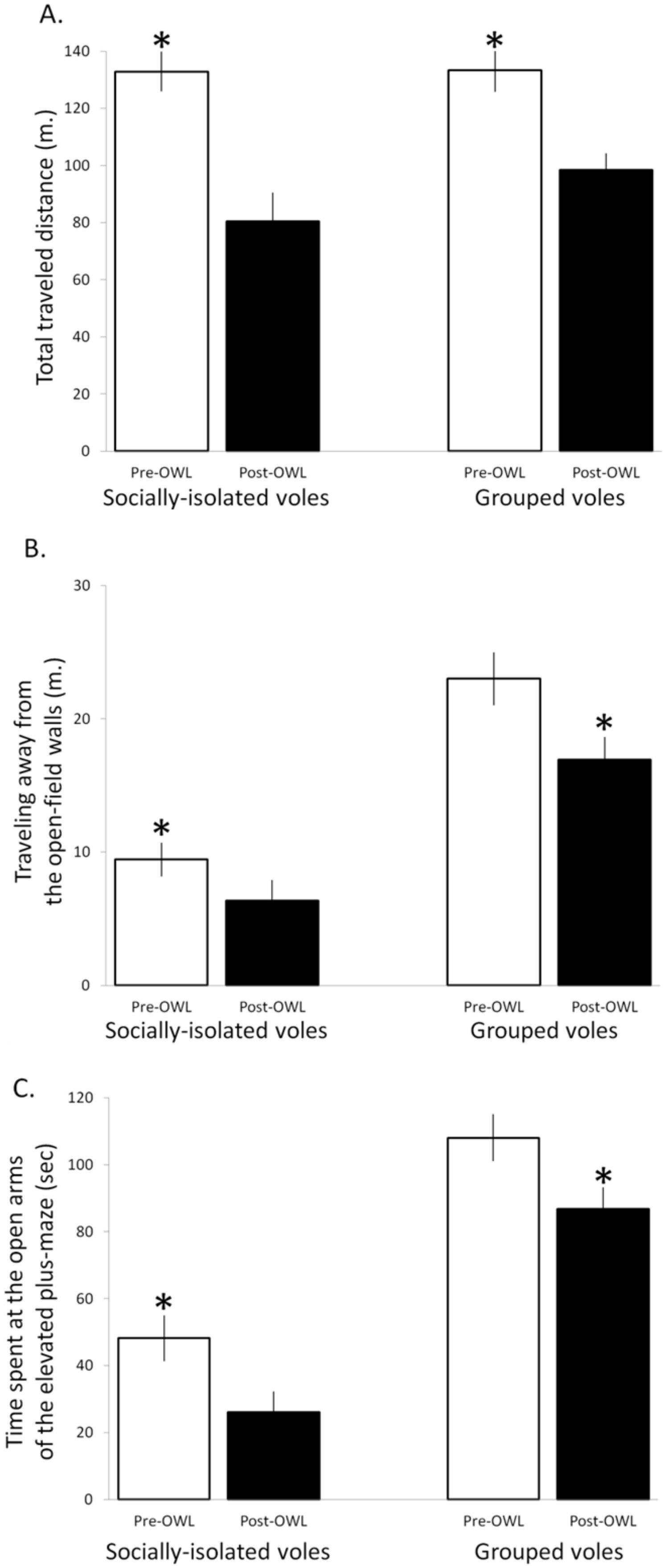
Figure 1: The effect of owl attack on grouped compared with socially-isolated voles. The effect on the total travel distance (A) was similar in both grouped and isolated voles. In both * indicates a significant difference between the total distance traveled before the owl attack (☐) compared to after the owl attack (■). In contrast, the distance traveled away from the walls of the open field (B) and the time spent in the open arms of the elevated plus-maze (C) were greater in grouped voles than in socially-isolated voles (bars marked with * were differed significantly from the all other bars in B and C).

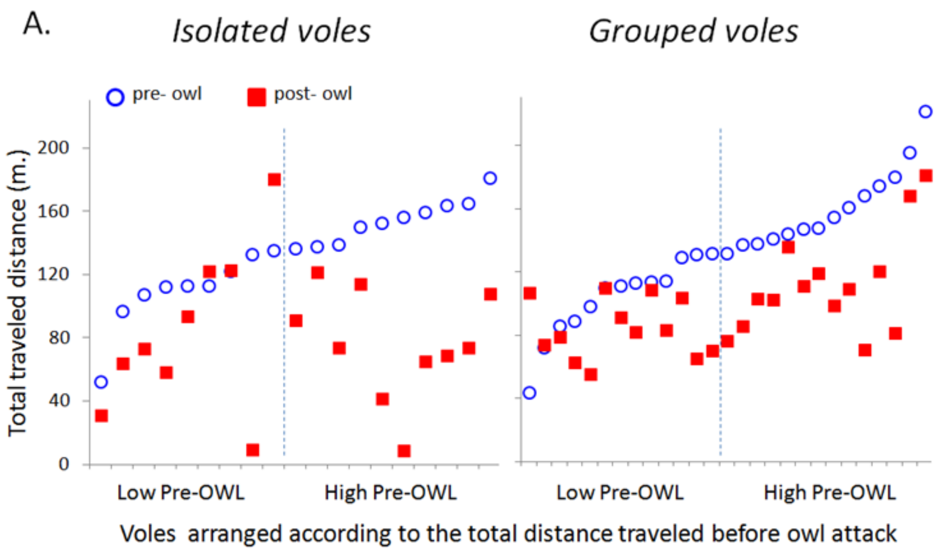
Figure 2: The impact of the group on the total traveled distance (A), the distance traveled away from the walls of the open field (B), and for the time spent in the open arms of the elevated plus-maze (C). In each of these behaviors, socially-isolated voles (left) and grouped voles (right) are depicted along the X-axis ordered from low to high according to their behavior during the pre-owl trial (O), resulting in inclined sequence. The respective post-owl scores for each individual vole (■) are depicted at the same pre-owl order, so that the behavior of the same vole is aligned vertically for the pre- and post-owl trials. Vertical dashed line marks the median of the pre-owl trial. As shown, most voles consistently displayed lower scores in the post-owl compared to the pre-owl trial. However, the scores of below-median grouped voles (Low Pre-OWL) for the distance traveled away from the open field walls (B, right inset) and the time spent in the open arms of the elevated plus maze (C, right inset) revealed different patterns. Specifically, many scores of these voles rose in the post-owl trial (see Table 1).

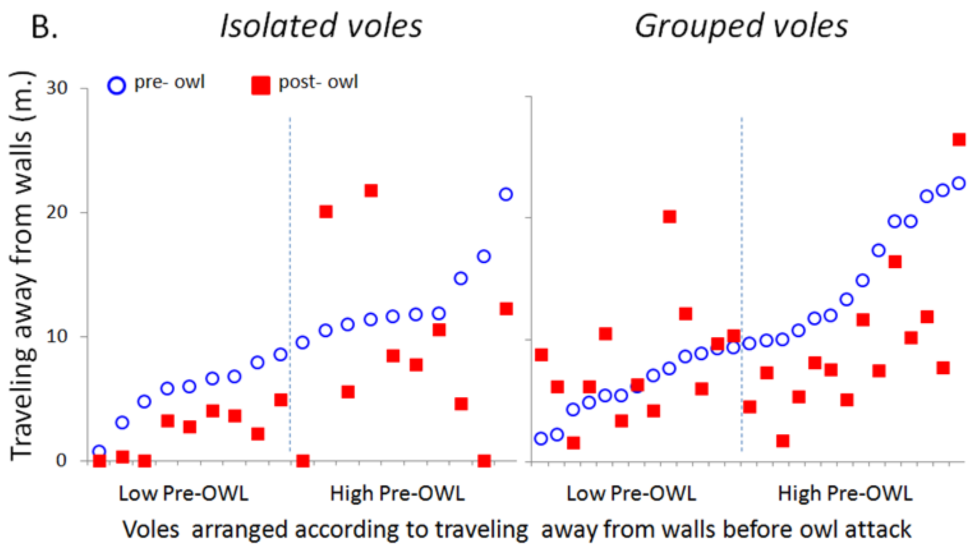
Figure 3: The interrelations between body mass and pre- and post-owl trials for the total traveled distance (A), the distance traveled away from the open field walls (B) and the time spent in the open arms of the elevated plus-maze (C). For the distance traveled, dashed line represents the median body mass value. For the distance traveled away from the walls and the time spent in the open arms, dashed lines represent the median values in the pre- and post-owl trials. Note that the order of axes layout in inset A differs from that of insets B and C for clarity of presentation.

Figure 4: “Leader copying” - a hypothetical model for bi-dimensional transmission of social information in an hierarchical population. The presumptions in this model are: (i) information could be transmitted between groups from any individual in the origin group to only the high-ranking individuals in the receiving group (transmission to a low-ranking individual in the receiving group is meaningless because the high-ranked individuals would not copy them); (ii) information within the receiving group passes from the high-rank to the low-rank individuals; (iii) under the above two limitations, individuals only respond to their single nearest neighbor, under the assumption that responding to more neighbors is costly in time and information processing (Herbert-Read et al. 2011).

Fig 1


A.
Total traveled distance (m.)
0
20
40
60
80
100
120
140
*
*
Pre-OWL
Post-OWL
Pre-OWL
Post-OWL
Socially-isolated voles
Grouped voles
B.
Traveling away from
the open-field walls (m.)
0
10
20
30
*
*
Pre-OWL
Post-OWL
Pre-OWL
Post-OWL
Socially-isolated voles
Grouped voles
C.
Time spent at the open arms
of the elevated plus-maze (sec)
0
20
40
60
80
100
120
*
*
Pre-OWL
Post-OWL
Pre-OWL
Post-OWL
Socially-isolated voles
Grouped voles


A.
Isolated voles
Grouped voles
pre- owl
post- owl
Total traveled distance (m.)
0
40
80
120
160
200
Low Pre-OWL
High Pre-OWL
Low Pre-OWL
High Pre-OWL
Voles arranged according to the total distance traveled before owl attack


B.
Isolated voles
Grouped voles
pre- owl
post- owl
Traveling away from walls (m.)
0
10
20
30
Low Pre-OWL
High Pre-OWL
Low Pre-OWL
High Pre-OWL
Voles arranged according to traveling away from walls before owl attack

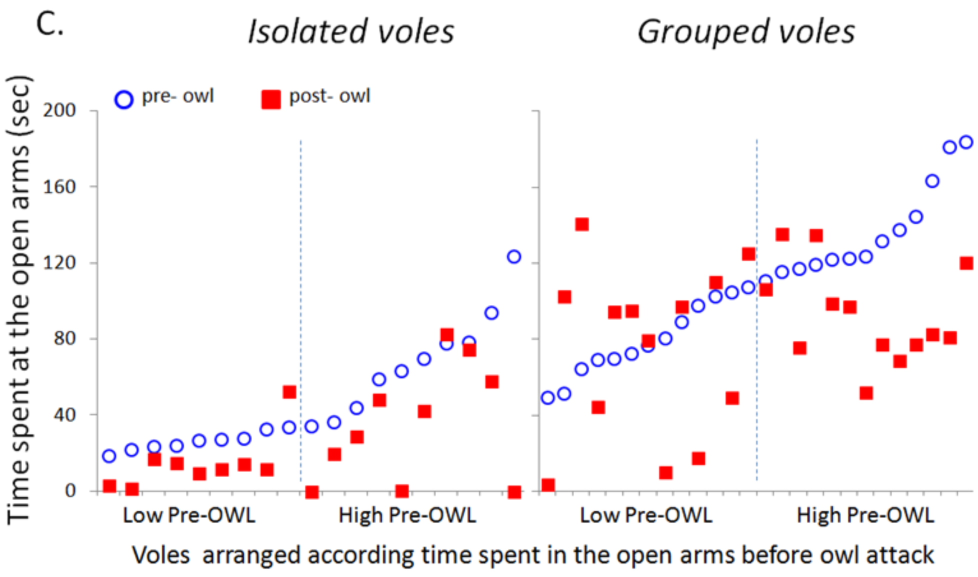

C.
Isolated voles
Grouped voles
pre- owl
post- owl
Time spent at the open arms (sec)
0
40
80
120
160
200
Low Pre-OWL
High Pre-OWL
Low Pre-OWL
High Pre-OWL
Voles arranged according time spent in the open arms before owl attack

Fig 3

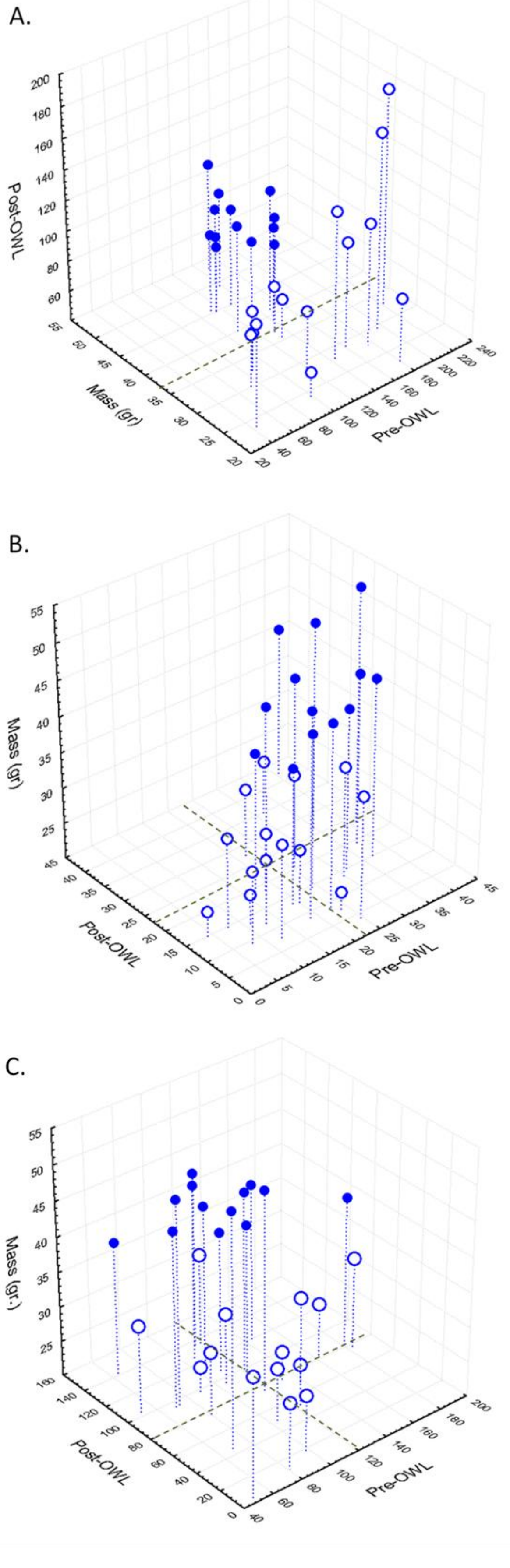
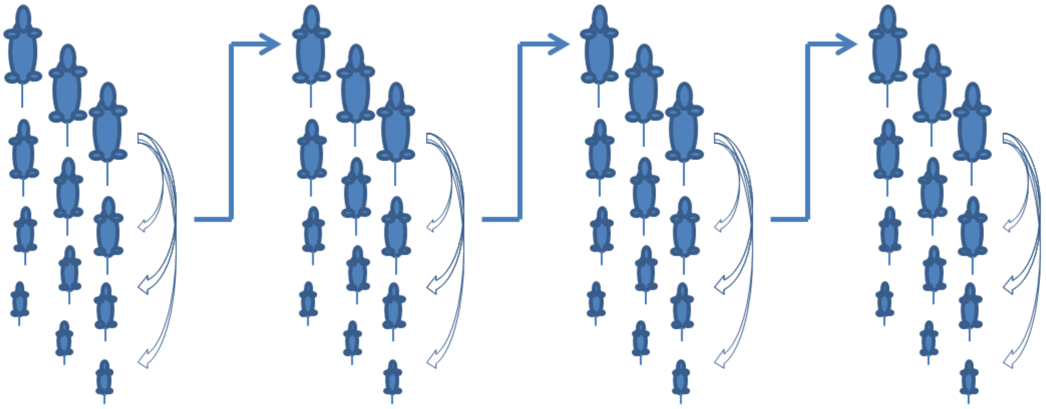

A.
Post-OWL
200
180
160
140
120
100
80
60
Mass (gr)
55
50
45
40
35
30
25
20
Pre-OWL
20
40
60
80
100
120
140
160
180
200
220
240
B.
Mass (gr)
55
50
45
40
35
30
25
Post-OWL
45
40
35
30
25
20
15
10
5
0
Pre-OWL
0
5
10
15
20
25
30
35
40
45
C.
Mass (gr.)
55
50
45
40
35
30
25
Post-OWL
160
140
120
100
80
60
40
20
0
Pre-OWL
40
60
80
100
120
140
160
180
200

Fig 4

Hierarchical neighbor copying

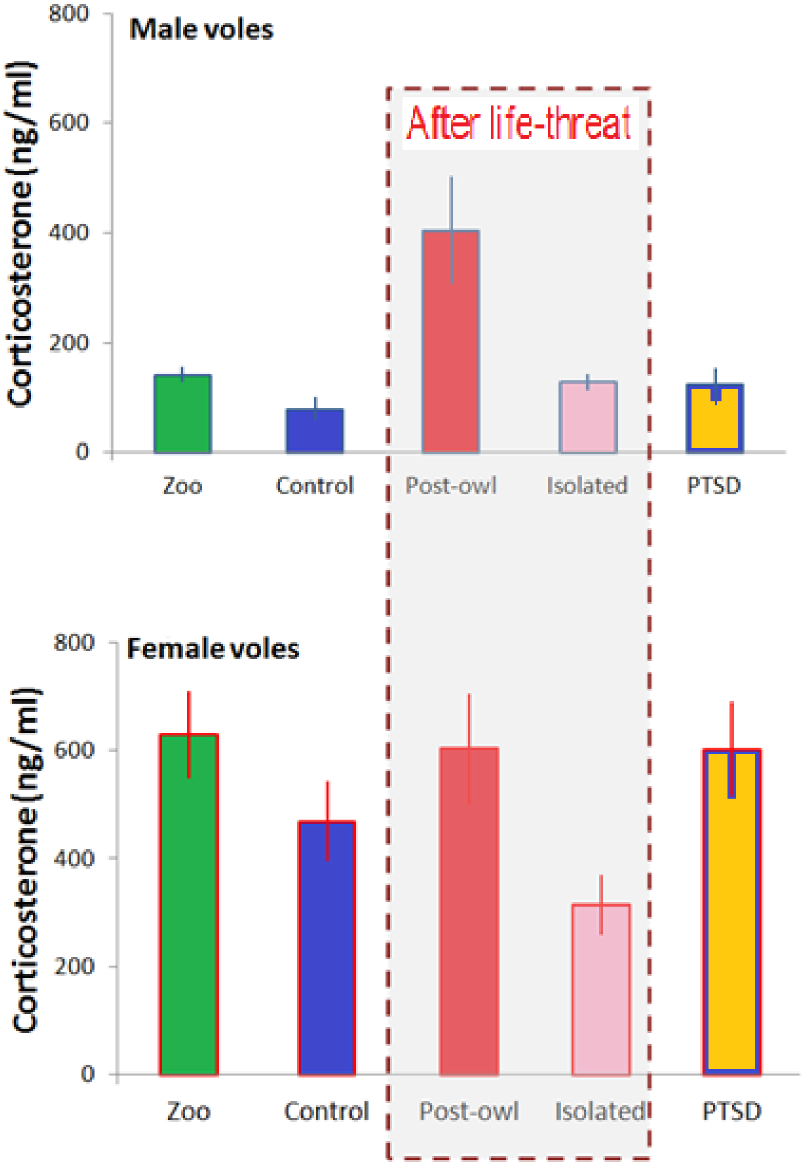
(neighbor copying followed by copying high-mass individuals)



Appendix C

Collective behavioral responses and corticosteroids: The conspicuous impact of gender and grouping

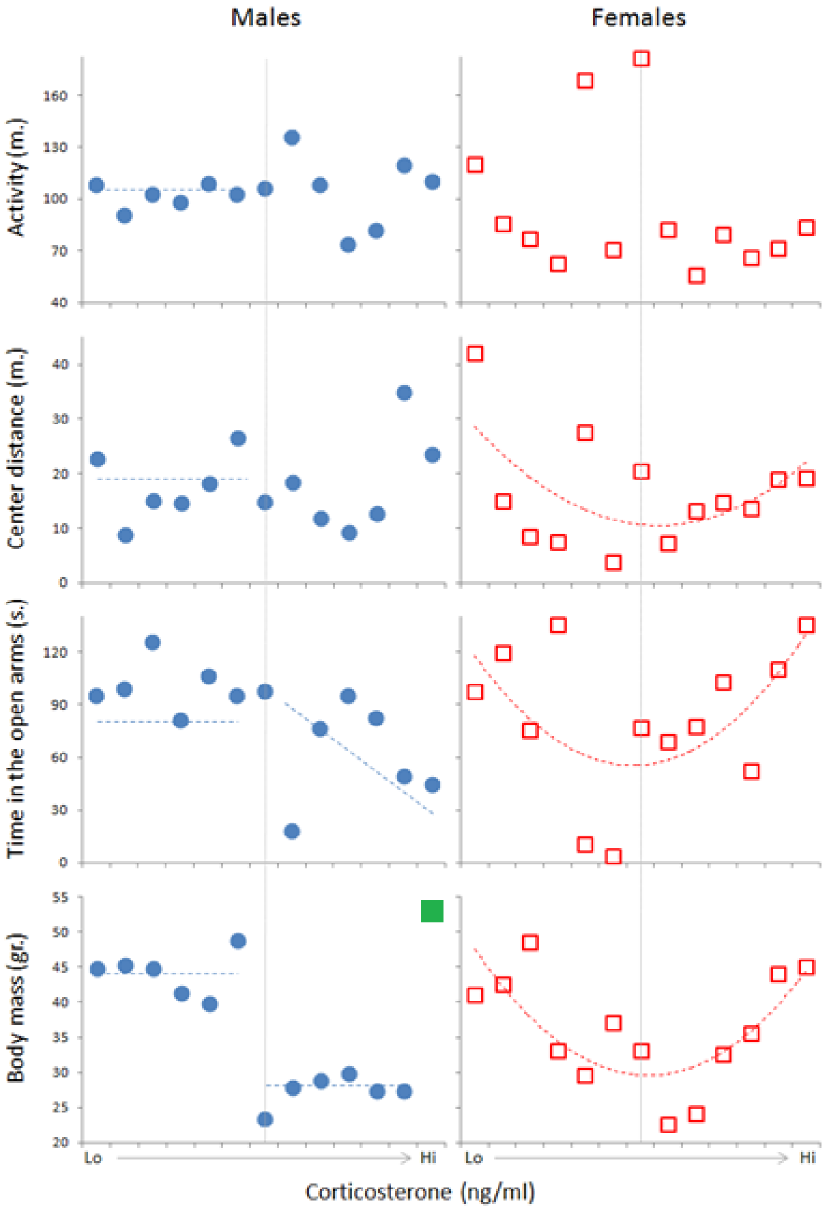
Figure 1



This figure describes corticosterone levels in males (top) and females (bottom). As shown in males, the levels of corticosteroids were low and the only substantial increase was after grouped voles were exposed to life threat (red bar). Exposing voles as individuals to the same threat did not affect their corticosterone level (pink bar). Finally, there was not impact of housing and testing conditions as reveled in controls (blue bar) compared with voles that live in "natural" colonies in our zoo (green bar). The effect seen under owl attack (red bar) had been washed out a week later (PTSD, orange bar). The puzzling result is of course the lack of effect of life threat on isolated male voles (pink bar) compared with the impact of the same life threat on grouped male voles (red bar). We suspect that this was due to behavioral contagion (or "coward" effect) in the grouped male voles, and no scrutinize the behavioral data in order to check out this possibility.

Female voles (bottom inset) display an inversed pattern. First, their corticosterone levels were on average three fold those of males. Second, their cortticosterone was as high in their “natural” colonies in the zoo (green bar) as after experiencing life threat (red bar). These high levels were also measured in controls for testing procedures (sans life threat) and after a wash-out time interval of one week (PTSD, orange bar). Therefore, it is as if grouped female voles were stressed continuously, and that their corticosterone level was so high that it could not get higher after life threat (ceiling effect). Strikingly, the only time that female voles displayed significantly low levels of corticosterone was when they were socially isolated and experiencing life threat alone and not in the group (pink bar). This echos the above finding that socially isolated male voles do not respond to life threat, compared to grouped male voles. This further indicates that the obtained puzzling impact of social isolation was not an occasional outlier result, and therefore, further scrutiny of the behavior of isolated voles (males and females) is required along with comparing them with grouped voles.

Figure 2

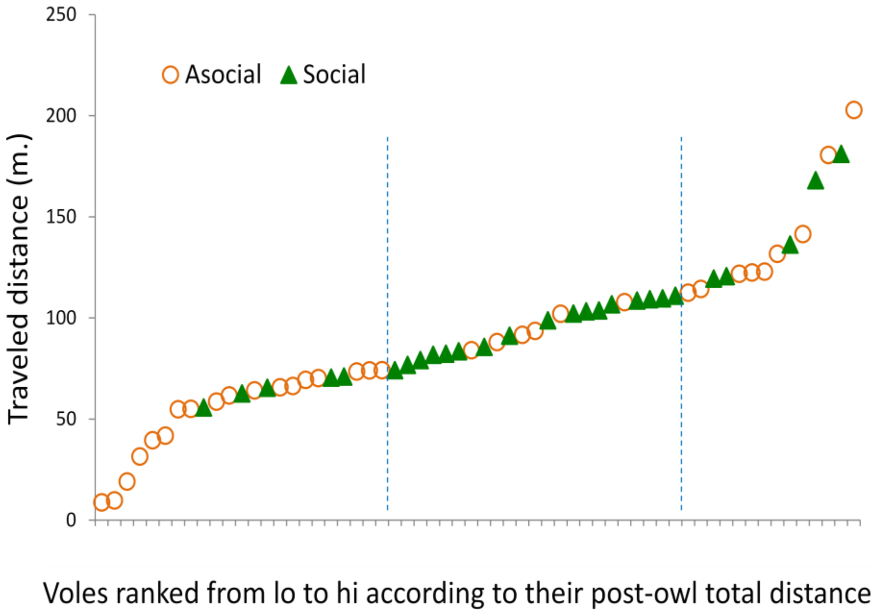


This figure describes the data for each individual male (left-hand column, blue circles) and female (right-hand column, red squares) voles as a function of their corticosterone levels. For these, males and voles were separately ranked from low to high according to their corticosterone levels (x-axis) and the corresponding body mass and behavioral scores for each individual were depicted above the respective rank of corticosterone. The vertical grey line in each inset represents the median rank of corticosterone.

As shown in males (left-hand column), the low ranks of corticosterone (lower median) characterized the high-mass (and presumably high socially-ranked males as detailed in Appendix B). On the other hand, male voles at the high corticosterone levels were all with all with low body mass (and presumably low socially-ranked males as detailed in Appendix B). The only exceptional male was the one with the highest body mass (🟧) that also had the highest corticosterone level. This exception, however, is in agree with other studies where it was demonstrated that the dominant male has high anxiety/stress level due the continuous need to preserve its social status. The behavioral measures of time at open sectors reconfirm from a physiological perspective the findings of Appendix B, that the behavior of high rank individuals is in a narrow range and that they are the stabilizers of group behavior.

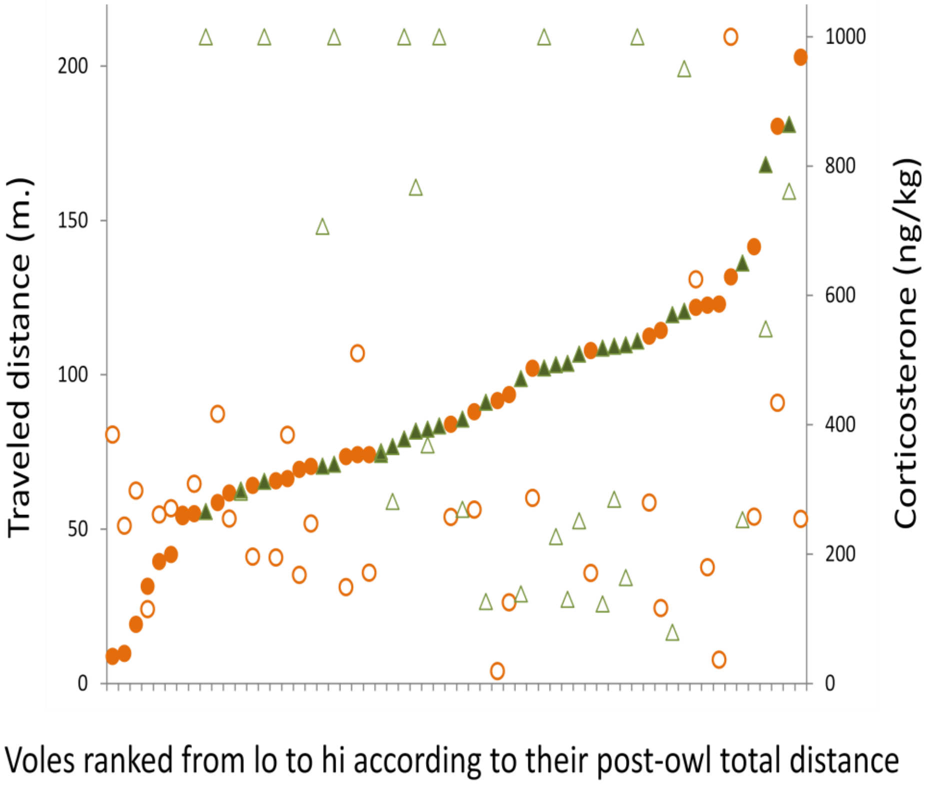
Unlike males, the results in females (right hand column) show that the females with high body mass (and presumably high socially-ranked, as detailed in Appendix B) dichotomized on one hand to the low corticosterone ranks (like high socially-ranked male voles), and on the other hand to the high ranks of corticosterone. According to these results, in addition to social rank (as reflected in body mass), there is another factor that affects corticosterone level in females. We are now searching for this factor. Altogether, the results of the present study will highlight how group behavior is determined by the social structure of the group, and the role of social rank in setting the behavior of a group of individuals.

Figure 3



Traveled distance, which is a general index of activity and animal condition, in social (▲) compared with asocial (O) voles. Both social and asocial voles were rank-ordered together from low to high along the abscissa according the distance they traveled after the life threat (owl attack). As shown, the mid ranks are mostly of social voles whereas the low and high ranks are of the asocial voles ($\chi^2_{(2)} = 13.3$; p = 0.001). This illustrates the divergence of behavior is asocial animals compared with the convergence of social animals to the mid ranks.

Figure 4



This is a replication of Figure 3, with the addition of corticosterone levels (right-hand ordinate) for each vole that are ranked along the abscissa. As shown, all the very high (maximal) corticosterone levels were of grouped voles (△). Otherwise, there is a general trend of inverted relations: the greater the travel distance, the lower corticosterone level.