

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

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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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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 (\pm 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 \pm 6.87	10.29 \pm 2.48	27.86 \pm 7.50	19.43 \pm 4.42	5.66 \pm 3.28	18.40 \pm 4.00
Mixed-gender	44.72 \pm 7.12	22.13 \pm 5.41	26.08 \pm 5.62	16.72 \pm 2.00	7.84 \pm 1.71	11.58 \pm 1.83
Males						
Same-gender	37.50 \pm 4.46	22.58 \pm 6.62	27.17 \pm 4.31	53.78 \pm 7.03	28.86 \pm 3.40	30.72 \pm 5.30
Mixed-gender	54.92 \pm 10.02	35.26 \pm 7.56	29.73 \pm 7.18	15.60 \pm 2.63	6.60 \pm 1.43	11.91 \pm 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 \times 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 ($\chi_1^2=4.23$; $P=0.04$). 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

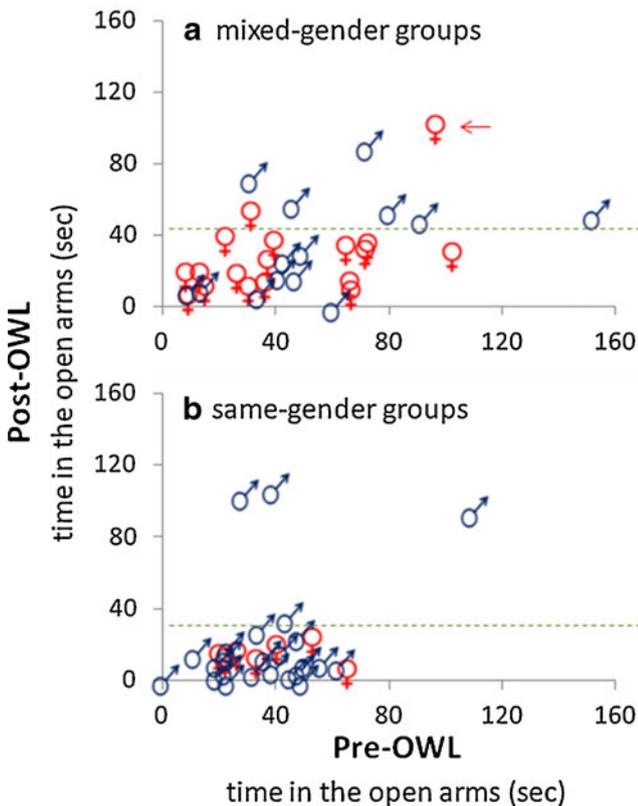


Fig. 1 The time spent in the open arms of the elevated plus-maze by each female and male vole after owl attack (*y*-axis) compared with the behavior of the same individual before owl attack (*x*-axis). The *dashed horizontal line* represents the middle of the post-OWL response in all individuals (the 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

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.

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

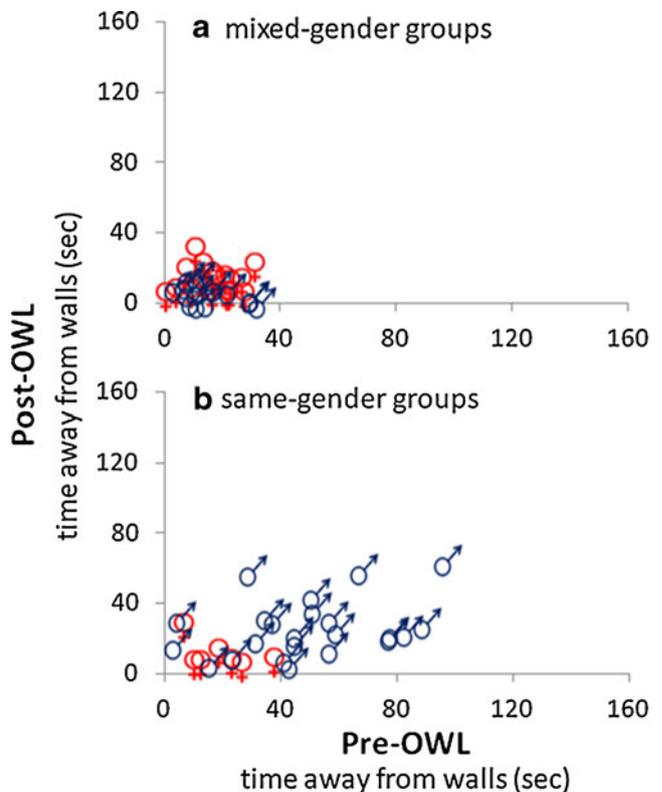


Fig. 2 The time spent in the center (away from the walls) of the open-field by each female and male vole after owl attack (*y*-axis) compared with the behavior of the same individual before owl attack (*x*-axis). As shown, in mixed-gender groups (*top*), all males and females spent a short period at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

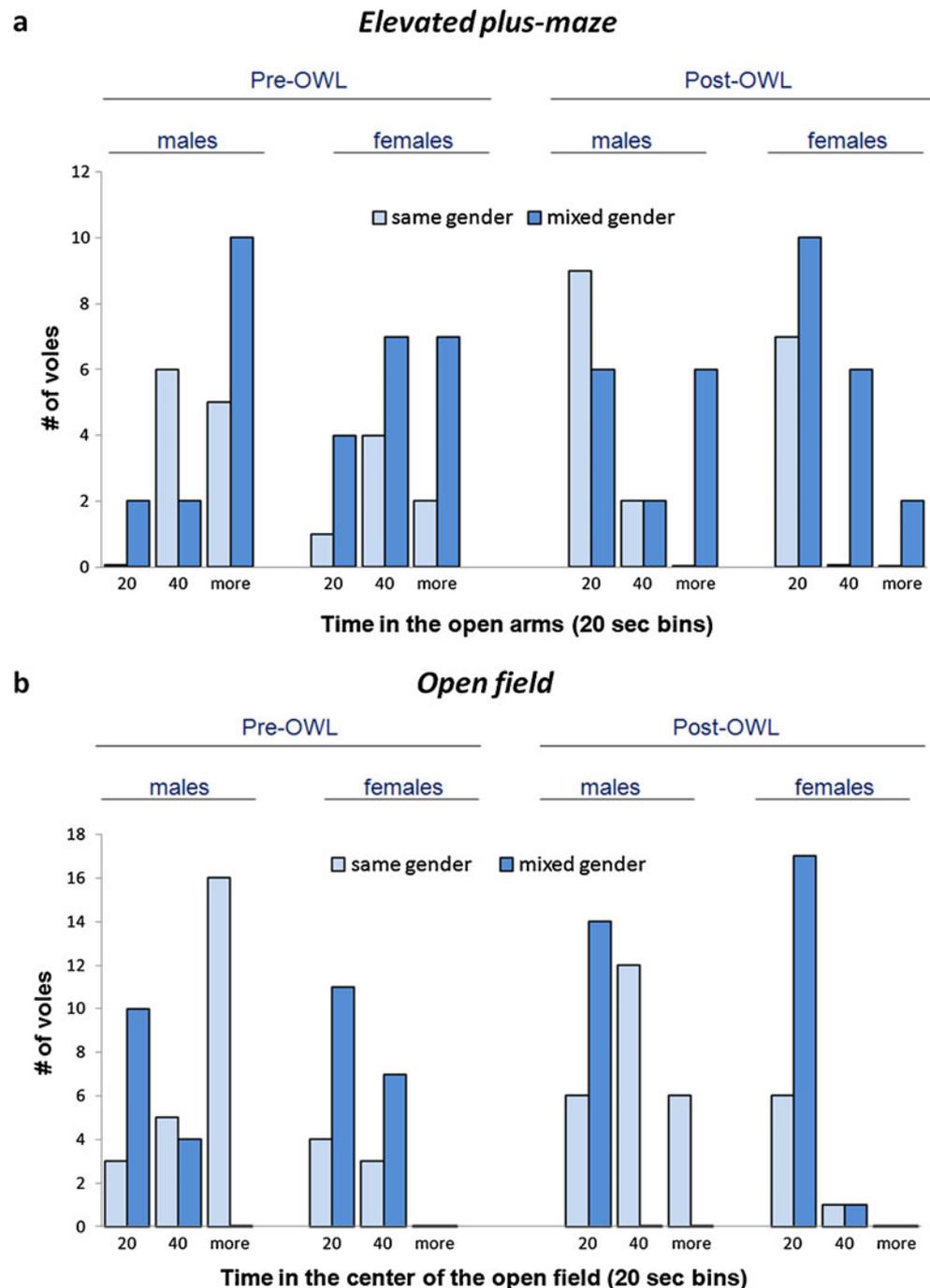
spent less time away from the walls than during the pre-owl test. This was most striking in the mixed-gender groups, where 90–100% of the voles aggregated in the short-time bin. Comparing the behavior of each gender in the two sets of apparatus reveals that more males than females spent a long period 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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