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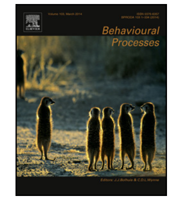

Who are the bosses? Group influence on the behavior of voles following owl attack

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ABSTRACT

Individual members of a group must conform to the group norms, as they may otherwise become isolated from the group or the group may split. On the other hand, social groups usually comprise various social ranks and display a differential division of labor and consequently different behaviors. The present study was aimed at examining how the above factors are manifested in social voles that had experienced owl attack. Here, we reconfirm the findings of past studies: that grouped voles converge to display similar behavior after owl attack. In addition, we found that high-mass voles were more active in the open sectors of the experimental set-ups both before and after the owl attack, whereas low-mass voles dichotomized to those that increased and those that decreased their activity in the open following owl attack. Taking body mass as a proxy for social rank, it is suggested that as a consequence of their larger size and of their experience and physical strength, high-mass voles both presented an exemplary model for the low-mass voles and, accordingly, assumed leadership and stabilized their group's behavior. We also suggest a hypothetical model for the propagation of behavior in hierarchical groups.

1. 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, 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 et al., 2009; Conradt and List, 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. 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 conform entirely 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 (Bajec and Heppner, 2009; Ballerini et al., 2008; Carere et al., 2009; Couzin and Krause, 2003; Daruka, 2009). In other words, the collective behavior does not ensue from the particular 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). Since group influence was still found in individuals that had been removed from the group for behavioral testing (Eilam et al., 2011; Izhar and Eilam, 2010), in the present study we sought to determine whether there are specific individuals that may influence the behavior of other group members.

The impact of the group may also extend to the behavior of its members when away from the group. Specifically, social voles (*Microtus socialis*) that were exposed as a group (with their cage-mates) to owls that attacked their cage differed in behavior from voles that had experienced owl attack as individuals (Eilam et al., 2011, 2012; Izhar and Eilam, 2010). The large individual variability in behavior, as measured in the voles before the attack, was

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significantly reduced after the owls attacked, and group members displayed a relatively similar level of activity when tested individually 2–24 h following the owl attack. Similarly, a previous study had revealed that exposure of grouped rats to a cat induced behavioral changes over a 24-h period, which included a reduction in pre-cat differences in the rats' behavior (Blanchard and Blanchard, 1989). In the tested voles, while the impact of grouping was still preserved ca. 24 h after a life-threatening event, those voles that had been individually exposed to the owls retained their behavioral variability (Eilam et al., 2011; Izhar and Eilam, 2010). Accordingly, it was suggested that this group influence in voles is reminiscent of the social response seen in humans after a disaster, when a uniform behavioral code dominates and there is reduced behavioral variability (Eilam et al., 2011; Izhar and Eilam, 2010).

In light of the above indications of group influence on the one hand, and individual differences on the other hand, we set out to examine conformity and individuality in voles following an 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). 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 extended family, there is a hierarchy which may affect the behavior of its members. In other words, it is predicted that socially high-ranking voles will influence ("lead") the behavior of low-ranking individuals ("followers"). Accordingly, examining the behavior of grouped social voles addressed two outstanding questions in group behavior: are there individuals that influence the behavior of the group; and how is behavior propagated among group members?

2. Material and methods

2.1. Subjects

Large groups of social voles (*M. socialis)* dwell in branched burrows. The basic social unit in the groups is an extended family, comprising parents and several generations of offspring. The adult body mass is usually between 30 and 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 (Charter et al., 2009, 2007; Mendelssohn and Yom-Tov, 1999).

The present research utilized 46 experimentally naïve voles (male and female) 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; 5,5; 5,3 males and females per group, respectively). Each group was housed in a 55 cm × 42 cm × 21 cm plastic container with a wire-mesh top, sawdust bedding, and wooden boxes (20 cm × 11 cm × 10 cm) for shelter. An additional 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 (41 cm × 25 cm × 15 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 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), which was maintained for a period of two weeks, a period found necessary to eliminate sociality (Chase et al., 2002). The isolated voles 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 requisite in order to uncover the impact of the group on behavior, 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; with any deviation from these criteria considered the endpoint of the test. All testing (excluding acclimation) took place within a period of two months. Cages of both the grouped and isolated voles were transferred to a quiet room (22 °C; 14/10 h light/dark cycle) two weeks before experimentation. Voles were fed generously with grains and diced fresh vegetables.

A colony of barn owls (*T. alba*) is 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 m × 6 m × 3 m), fed with dead mice obtained 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, which set out to examine 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 h following the attack, when on average they only displayed reduced activity see Appendix A. 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 mesh roof of the cage for about 20 s before flying off with the food item to a perch.

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).

2.2. Apparatus

2.2.1. 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 connected 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, 1987; Ramos, 2008 for further information on the elevated plus-maze).

2.2.2. Open field

This was an empty 2 m × 2 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