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Revisiting the "visible burrow system": The impact of the group, social rank, and gender on voles under owl attack

Sivan Bodek, David Eilam *

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

HIGHLIGHTS

- Corticosterone was higher in voles after than before life-threat (owl attack).
- Corticosterone levels were also higher in females than in male voles.
- Contagious fear may account for higher corticosterone levels in grouped voles.
- Voles with higher body mass had lower corticosterone than low-mass voles.
- Being less stressed by the owls, high-mass voles lead and stabilize their groups.

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ABSTRACT

In the present study, corticosterone levels and behavior were compared between voles (*Microtus socialis*) that were attacked by a barn owl (*Tyto alba*) and voles that did not experience such attack. Both female and male voles were exposed to the owl either together with their groupmates or when socially isolated. As hypothesized, corticosterone levels were higher in voles after the owl attack, and were higher in females than in males. However, blood corticosterone was higher in voles that experienced the attack in groups compared with the socially-isolated voles. The latter result seems enigmatic, since group members usually benefit from the "social buffering" conferred by their group-mates. It is suggested that contagious vigilance among group members accounts for the higher mean corticosterone level in grouped compared to socially-isolated voles, overshadowing the possible impact of social buffering. We also found a negative correlation between body mass and corticosterone level, with more high-mass voles showing low corticosterone levels compared with low-mass voles. This finding accords with a previous study in which the behavior of high-mass voles was less affected by owl attack compared to low-mass voles. The novelty of the present results therefore lies in supporting, at the hormonal level, past behavioral findings in rats and voles, and in demonstrating that high-mass voles, by virtue of their physical strength and perhaps also their life experience, are less stressed by the owl attack and become the leaders and stabilizers of their groups.

Dedicated to Bob (in memoriam) and Caroline Blanchard, my mentors for academic life and research.

1. Introduction

Predation is a strong selective pressure considered as a driving force in the formation of social groups. Several notions have been presented to interpret why being in a group is advantageous for prey species ('safety in numbers' — [1–3]; 'the selfish herd' [4,5]; etc.). Like many other aspects of defensive behavior, the response of individuals in groups under life threatening contexts was also scrutinized in Bob and Caroline Blanchard's study of the behavior of eight rats that inhabited the 'visible burrow system' apparatus [6]. In this apparatus, composed of sheltered burrows and chambers that connect to an open surface area, rats were found to display differential responses when encountering a cat. Specifically, dominant male rats were least affected by the cat compared with subordinate male rats, while female rats displayed an in-between response in all the measured behavioral parameters (Table 2 in Ref. [6]). Moreover, after experiencing exposure to the cat, a convergence to a similar behavior characterized the 12 groups of rats that were tested in the visible burrow system. In other words, differences between females, subordinate males, and dominant males, as noted during the pre-cat period, diminished following exposure to the cat [6]. The present study examined the response of groups or

* Corresponding author.
E-mail address: eilam@post.tau.ac.il (D. Eilam).

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of socially-isolated voles (*Microtus socialis*) to attack by their main natural predator, the barn owl (*Tyto alba*). For this we followed-up the footprints of the above study of Blanchard and Blanchard, as well as their other studies on the impact of social rank and gender on plasma corticosterone levels in stressed animals [7]. Specifically, we set out to show that, following owl attack, voles would display higher plasma corticosterone levels, and these levels would be higher in females than in males. We also predicted that as social animals, socially-isolated voles would have higher corticosterone levels than grouped voles, both before and after owl attack. Finally, in light of a previous study [8], we predicted that high-mass voles would have lower corticosterone levels than low-mass voles. The rationale for these hypotheses is as follows.

The response to a life-threat comprises concomitant behavioral and physiological changes. Of the latter, the change along the hypothalamic–pituitary–adrenal axis, which is manifested as an increase in plasma corticosteroid level, is a reliable indication of stress [9–11]; for review see Ref. [12,13]. Moreover, corticosterone has been shown to increase even in response to specific stimuli of predation threat, such as the sight of a predator [14], owl calls [15], or predator odors [12,16,17]. Owls are a major threat for voles, which comprise 40–70% (sometimes over 90%) of the diet of barn owls and tawny owls (*Strix aluco*) [18–21]. In Israel, voles 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 [22,23]. Accordingly, it was hypothesized in the present study that plasma corticosterone levels would rise in voles immediately after they experienced a real life-threat — the attack of a live owl.

In previous studies we had found that groups of male voles that were exposed to owl attack displayed a reduction in the individual differences among the members of the attacked group [24]. In mixed-gender groups of voles, males dichotomized to those that increased their activity in open areas and those that, like females, reduced it [25]. Furthermore, it was suggested that as a consequence of their larger size, their experience, and their physical strength, high-mass voles were the exemplars for the low-mass voles and, accordingly, provided leadership and stabilized their group's behavior [8]. This finding was in line with other studies in which fearful rats were socially supported by the presence of non-fearful rats when tested together, compared to fearful rats that were tested alone [26]. In the same vein, it was found that the stress status of a rat influenced the behavior of co-tested rats [27]. Taking an increase in plasma corticosterone as a reliable response to predatory threat, we predicted that when a group of social voles would be exposed to owl attack, the high-mass voles that had been previously found to display a mild behavioral response to owl attack compared to the low-mass voles [8], would also have lower corticosterone levels than the latter.

Social isolation is stressful for group-living species but not for solitary ones [28]. During times of stress, the mutual support among group members ('social buffering') reduces corticosterone response to a conditioned stimulus, perhaps by suppressing the activation of the hypothalamic–pituitary–adrenal axis [26,29]. Indeed, taking activity in open areas, away from sheltered areas, as an index of anxiety level, it was found that after experiencing owl attack, socially-isolated voles displayed greater anxiety than grouped voles [8,25,30]. In light of these earlier studies, it was hypothesized in the present study that following owl attack, socially-isolated voles would display a higher level of plasma corticosterone compared to grouped voles.

Previous studies have reported a considerable gender difference in the response to stress and activation of the hypothalamic–pituitary–adrenal axis, manifested in higher plasma corticosterone level [31–35]. Accordingly, we expected that when female and male voles would experience owl attack, the former would reveal higher plasma corticosterone levels compared with the latter. Employing a test with high ecological validity, based on the interaction of a natural predator and its common prey, we posited four hypotheses: (i) voles would have higher corticosterone after owl attack compared to that before the attack; (ii) female voles would have higher corticosterone levels than male voles; (iii) socially-isolated voles would have higher corticosterone levels than grouped ones; and (iv) high-mass voles would have lower corticosterone level than low-mass voles.

2. Materials and methods

2.1. Subjects

The social vole (*M. socialis*) is a monogamous species that lives in extended families of parents and several generations of their offspring, with several families occupying together a network of branched burrows [10,21,36–38]. An adult weighs about 30–50 g, body length is 11 cm and tail length is about 1–2 cm. They are found from south-east Europe to the northern Middle East. They feed on vegetation and seeds, causing major damage to agricultural crop. Social voles may reach sexual maturity as early as 30 days of age. Pregnancy lasts about 21 days and the common litter size is 6–10 pups. In the wild, their life span is ca. two and a half years, while in captivity it may extend up to four years. Voles are preyed upon by a variety of predators, including barn owls (*T. alba*) for which voles comprise about 50% of their diet [21–23].

This study comprised a total of 92 voles (female and male), originating from a captive colony raised in the *I. Meier Segals Garden for Zoological Research* at Tel-Aviv University. In the present experiment, 45 voles (referred to below as 'grouped voles') were kept in their five original groups (5,4; 5,5; 3,5; 3,8; 4,3 female and male, respectively). Each group was housed in a plastic container (55 × 42 × 21 cm), covered by a wire-mesh top. An additional 24 females and 23 males (referred to below as 'socially-isolated voles') were separated from their original groups three weeks before testing, and each was caged separately (41 × 25 × 15 cm). This study was carried out under the regulations and approval of the Institutional Committee for Animal Experimentation at Tel-Aviv University (permit # L-11-047) and of the USAF Animal Use Programs (Permit # AFOSR-2012-008A).

2.2. Apparatuses

2.2.1. Elevated plus maze

This comprised an apparatus with four horizontal arms (each 30 cm long) connected to form a ✚ shape. Two opposite arms were enclosed by 20 cm high walls ("closed arms"), whereas the other two arms were bordered by a 5 mm high ridge ("open arms"). The elevated plus-maze apparatus was placed on a 72 cm high leg (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 Ref. [39,40] for further information on the elevated plus-maze).

2.2.2. Open field

This was an empty 2 × 2 m arena with 50 cm high Plexiglas walls and a PVC floor, illuminated by a dim light. A video camera (Ikegami ICD-47E), that was placed 2 m above the center of the arena, provided a full top-view of the arena. 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 and thereby facilitate tracking of the rodent. The open field was located in a quiet air-conditioned room (22 °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 Ref. [40,41].