

Review

The effects of predator odors in mammalian prey species: A review of field and laboratory studies

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Abstract

Prey species show specific adaptations that allow recognition, avoidance and defense against predators. For many mammalian species this includes sensitivity towards predator-derived odors. The typical sources of such odors include predator skin and fur, urine, feces and anal gland secretions. Avoidance of predator odors has been observed in many mammalian prey species including rats, mice, voles, deer, rabbits, gophers, hedgehogs, possums and sheep. Field and laboratory studies show that predator odors have distinctive behavioral effects which include (1) inhibition of activity, (2) suppression of non-defensive behaviors such as foraging, feeding and grooming, and (3) shifts to habitats or secure locations where such odors are not present. The repellent effect of predator odors in the field may sometimes be of practical use in the protection of crops and natural resources, although not all attempts at this have been successful. The failure of some studies to obtain repellent effects with predator odors may relate to (1) mismatches between the predator odors and prey species employed, (2) strain and individual differences in sensitivity to predator odors, and (3) the use of predator odors that have low efficacy. In this regard, a small number of recent studies have suggested that skin and fur-derived predator odors may have a more profound lasting effect on prey species than those derived from urine or feces. Predator odors can have powerful effects on the endocrine system including a suppression of testosterone and increased levels of stress hormones such as corticosterone and ACTH. Inhibitory effects of predator odors on reproductive behavior have been demonstrated, and these are particularly prevalent in female rodent species. Pregnant female rodents exposed to predator odors may give birth to smaller litters while exposure to predator odors during early life can hinder normal development. Recent research is starting to uncover the neural circuitry activated by predator odors, leading to hypotheses about how such activation leads to observable effects on reproduction, foraging and feeding.

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1. Introduction

There has been a notable recent upsurge of interest in the study of predator–prey relationships. This interest emanates from many different scientific disciplines. For example, while ethologists are interested in the intrinsic nature of predator–prey interactions in nature, psychologists and psychiatrists increasingly regard predator-induced defenses in animals as potentially useful models of human emotional disorders. On the other hand, neuroscientists and endocrinologists increasingly see predator cues as useful tools in acquiring fundamental information about how the brain and endocrine system of mammals respond during acute or chronic stress.

Prey species have developed specific behaviors to facilitate recognition, avoidance and defense against predators. Such anti-predator behavioral systems are fundamental to survival. In many cases anti-predator defense involves the detection and response to specific chemical cues that predators produce.

In this manuscript, we will review studies examining the effects of predator odors on prey behavior and physiology. We will discuss results from laboratory experiments, small-scale enclosure experiments and field studies, noting similarities and differences in the outcomes obtained using these different approaches. We will highlight species differences in predator odor effects and also note differences in responsivity of prey species towards fur, urine, feces and anal gland derived odors. Towards the end of the article, the neural and endocrine correlates of predator odor effects on behavior and reproduction will also be reviewed and discussed.

The review will largely focus on small mammals and their ground predators, with particular attention to the chronic effects of exposure to predator odors.

2. The relationship between predator and prey

2.1. Primary vs. secondary defenses

There is a long-standing differentiation in ethology (Edmunds, 1974; Kruuk, 1972; Robinson, 1969) between

primary defenses, those operating on a continuing, chronic basis, and *secondary defenses*, those that come into play when a predator is present. Many of the primary defenses, especially in invertebrates, are structural in nature. These include crypsis, mimicry, and protective features such as spines or armor that act to conceal or protect the animal from predation. Behaviors consonant with these features are necessary in order for them to be functional, e.g. leaf-mimicry does not succeed if the animal moves around or makes frequent cries. Primary defenses may also be behavioral, particularly in mammals. These may include an array of action patterns that make the individual prey animal less available to its predators, such as sleeping in a different tree every night (Reichard, 1998), utilization of a home base that affords concealment and protection (e.g. a burrow), or living in a flock or herd.

The traditionally clear distinction between primary and secondary defenses breaks down at the border where predators are detected, and where this detection can produce a chronic change in the expression of what might otherwise be regarded as primary defenses (Peacor and Werner, 2001).

The major behavioral mechanism facilitating predator detection is an activity pattern labeled ‘vigilance’ in the ethological literature, and ‘risk assessment’ in the psychological literature. It involves a number of species-typical behaviors with a focus on detection, localization, and identification of predators, in which different species may selectively utilize particular sensory modalities. Thus ungulates commonly use vision as a major sensory avenue for detection of predators; a use greatly facilitated by the relative lack of concealment in habitats favored by ungulates, and permitting, in turn, ungulate-appropriate secondary defenses such as flight to be initiated while the prey is far enough from the predator for this to be effective (Mitchell and Skinner, 2003).

Responsivity to auditory signals of danger, such as sounds of predators or alarm cries of conspecifics, is particularly important among group-living animals that cannot fully utilize vision, such as fossorial or nocturnal species (Warkentin et al., 2001). The value of predator

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