Carrion odor and cattle grazing: Evidence for plant defense by carrion odor

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Introduction

Carrion odors of various flowers have traditionally been considered an adaptation for attracting the flies and beetles that pollinate them.1,2 In addition to this classic reproductive signaling, Lev-Yadun et al.3 proposed that it may also have another, overlooked, anti-herbivore defensive function. They suggested that such odors may also deter mammalian herbivores, especially during the critical period of flowering, since carrion odor is a good predictor for two potential dangers to mammalian herbivores: (1) pathogenic microbes, and (2) proximity of carnivores. While theoretically plausible,4,5 there is a strong need to examine the possibility that mammalian herbivores are indeed deterred by carrion odor and that it reduces herbivory. This in turn will serve as a very good indication that carrion odor of various flowers has a defensive signaling potential.

Fear of the dead is common in many if not all human cultures, and carcasses are repulsive to most people, but this issue has not been addressed in depth concerning mammalian herbivores. The gruesome details of carcass decay processes over time6 and their bad odors seem to explain why carrion avoidance by mammalian herbivores has not attracted much research attention.7,8 Avoidance of dead animals owing to risk of pathogens is well known in ants and bees9-11 and this risk is also the reason for strict laws and regulations related to handling animal carcasses and meat residues in many countries.

An opportunity to examine the potential of carrion odor as defense from herbivory emerged by examining the behavior of cattle toward carcasses in two long grazing experiments set up to study the influence of various levels of cattle stocking density on the vegetation,12-18 conducted in two adjacent paddocks, each containing a cattle carcass dumping plot. It shows a probable defensive behavior in cattle that has been overlooked, and which might represent the behavior of other large mammalian herbivores. The deterrence from carrion odor shown here is a very good indication for the potential defensive role of carrion odor, primarily signaled by plants toward potential pollinators, as was recently proposed on theoretical grounds.3

Materials and Methods

The two long grazing experiments, one for 8 y, from 1982 to 1989, and the other for 7 y, from 1994 to 2000, were conducted at the Karei Deshe Range Station, just north of the Sea of Galilee in Israel (32°55′N, 35°35′E, altitude 150 min a.s.l.). The soil is brown basaltic proto grumosol,19 usually not deeper than 60 cm, with rock cover of about 30%. The climate is typical eastern Mediterranean, characterized by mild wet winters with mean minimum and maximum average temperatures of 7°C and 14°C, respectively. Average annual (winter-spring) rainfall is 570 mm. The summers are hot and dry, with mean minimum and maximum average temperatures of 19°C and 32°C, respectively. The herbaceous vegetation consists of 166 species.17 The experiments were conducted primarily to examine the impact of various stocking levels on vegetation. The repeated avoidance

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of the carcass dumping area by cattle came as a surprise. In the first, eight-year experiment, each of the 16–18 heads of cattle that took part in the experiment had an area of ca. 20,000 (range 19,000–21,000) m² (total area 338,000 m²) (Table 1), while in the other, seven-year experiment, each of the 21–26 heads had only ca. 9,000 (range 8,000–10,000) m² per head (total area 215,000 m²) (Table 1). In both experiments 28–100% of the heads were replaced each year (Table 1). A new herd of the first year is considered 100% replacement, but in the first experiment 100% of the heads were replaced in 1986 (Table 1). A plot within each paddock, ca 2,000 m² in area, was used repeatedly to dump cattle carcasses of the whole experimental herd of ca. 650 cows. Several carcasses were dumped there every year, but the carcasses, which were at least five m apart, never formed a pile that could block grazing either by not allowing passage or by visually hiding the forage from the grazing cattle. Dumping carcasses in the plot began with the onset of the first experiment. The dumping area was chosen because it was less stony, so the tractor that pulled the carcasses had easy access. Each of the two adjacent paddocks used for the two experiments was surrounded by a fence, but there were no internal fences that separated the carcass dumping area from the rest of the paddock or any other obstacle to prevent cattle from approaching that area and grazing in it. In its vegetation composition, the carcass dumping area was no different from anywhere else in the paddock. The borders of the carcass dumping area were created by the lower type of giving-up density. The question is whether this behavior is adaptive and whether it represents a general phenomenon. As far as we know, this is probably an overlooked phenomenon. We suggest that this effect is adaptive. Volatiles originating in the decomposition of the carcasses very likely alert the grazing cattle and various other mammalian herbivores to various potential dangers in the carcass dumping area. The succession of odors emitted from the carcass dump. The cattle grazed much less on the carcass dump.

### Results

The cattle grazed much less on the plot that was used to dump the dead cattle. The lower consumption of fodder in the two carcass dumps compared with the rest of the paddocks was obvious in each of the 15 y of the experiments (Table 1). There were no signs of local effects of fertilization around the carcasses. In the first experiment, the average grass biomass at the end of the season was 124.6 gr/m² for the regular grazing area and 236.5 gr/m² for the grazing area used as the carcass dump. Using a paired t test we found the differences highly significant (t = 14.0, df = 6, p < < 0.01). In the second experiment the average grass biomass at the end of the season was 61.7 gr/m² in the after carcass area, and 153.7 gr/m² for the grazing area used as the carcass dump. The differences were again highly significant (t = 15.5, df = 6, p < < 0.01).

### Discussion

Giving up food at certain levels mediated by risk (giving-up density *sensu* Brown 20) is well known, especially for granivorous rodents. Since this phenomenon of reduced cattle grazing within the carcass dumping plots occurred in each of the 15 y of the experiment, it seems to be a regular but overlooked feature, of the type of giving-up density. The question is whether this behavior is adaptive and whether it represents a general phenomenon. As far as we know, this is probably an overlooked phenomenon. We suggest that this effect is adaptive. Volatiles originating in the decomposition of the carcasses very likely alert the grazing cattle and various other mammalian herbivores to various potential dangers in the carcass dumping area. The succession of odors emitted

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**Table 1. Cow number, paddock size, and remaining herbage in the 2 grazing experiments**

| Year | No. of cows | Annual cow replacement % | Paddock area m² | Stocking m²/cow | Herbage at the end of season gr/m² (paddock) | Herbage at the end of season gr/m² ("cemetery") |
|------|-------------|--------------------------|----------------|----------------|-------------------------------------------|---------------------------------------------|
|      |             |                         |                |                |                                            |                                            |
| **First experiment** |             |                         |                |                | **First experiment**                       | **First experiment**                         |
| 1982 | 16          | 100                      | 338,000        | 21,000         | 149                                        | 280                                         |
| 1983 | 17          | 33                       | 338,000        | 20,000         | 185                                        | 290                                         |
| 1984 | 17          | 28                       | 338,000        | 20,000         | 121                                        | 210                                         |
| 1985 | 17          | 35                       | 338,000        | 20,000         | 145                                        | 220                                         |
| 1986 | 17          | 100                      | 338,000        | 20,000         | 114                                        | 200                                         |
| 1987 | 18          | 35                       | 338,000        | 19,000         | 168                                        | 290                                         |
| 1988 | 18          | 42                       | 338,000        | 19,000         | 51                                         | 212                                         |
| 1989 | 18          | 38                       | 338,000        | 19,000         | 64                                         | 190                                         |
| **Average ± SE** |             |                         |                |                | **Average ± SE**                           | **Average ± SE**                            |
|      |             |                         |                |                |                                            |                                            |
| **Second experiment** |             |                         |                |                | **Second experiment**                      | **Second experiment**                        |
| 1994 | 22          | 100                      | 215,000        | 10,000         | 54                                         | 140                                         |
| 1995 | 23          | 32                       | 215,000        | 9,000          | 68                                         | 160                                         |
| 1996 | 26          | 35                       | 215,000        | 8,000          | 65                                         | 180                                         |
| 1997 | 24          | 85                       | 215,000        | 9,000          | 29                                         | 124                                         |
| 1998 | 25          | 42                       | 215,000        | 9,000          | 105                                        | 168                                         |
| 1999 | 24          | 50                       | 215,000        | 9,000          | 41                                         | 124                                         |
| 2000 | 21          | 48                       | 215,000        | 10,000         | 70                                         | 180                                         |
| **Average ± SE** |             |                         |                |                | **Average ± SE**                           | **Average ± SE**                            |
|      |             |                         |                |                |                                            |                                            |

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20 Cattle in the Karei Deshe experimental farm suffered from no significant risk of predation, and no large carnivores that might be attracted to the carcasses were present there during the 15 y of the experiments.
from carcasses that attract carrion-consuming insects, reptiles, and mammals\(^6,8,12,23\) may signal mammalian herbivores about the existence of potential risks. Odors are known to influence food preference by mammalian herbivores.\(^24\) In terms of ecology and evolution, carcasses are reliable cues of two potential dangers to mammalian herbivores: (1) pathogenic microbes, and (2) dangerous carnivores.\(^9\) We propose that a combination of fear of diseases and fear of predators causes cattle to express the necrophobia demonstrated here.

Carcasses are commonly occupied by various pathogenic microbes, which may infect mammalian herbivores through direct contact, or when these microbes contaminate their vicinity.\(^7,8,25\) Moreover, carcasses may be the defended kills or otherwise gained food catch of large predators.\(^26\) Carcasses are known to attract many types of carnivores, e.g., lions, grizzly bears, hyenas, wolves, foxes, coyotes, and nearly all other carnivorous terrestrial vertebrates, as all carnivores may be considered facultative scavengers.\(^8\) Fear of predation is known to influence herbivore behavior\(^27-29\) in a way that may influence vegetation structure.\(^29\) For all these reasons it would be a safe strategy for cattle to distance themselves from carcasses, even when there is more fodder next to them. Since the region of our experiments had no large carnivores, this factor could not have influenced cattle behavior, hence our interpretation of it. Similarly, as there were no signs of local effects of fertilization around the carcasses, the higher amounts of grass in the carcass dumping plots can confidently be attributed to higher giving-up densities. The risk that the cattle sensed was the odor of carrion rather than that of carnivores.

We show here an unexpected aspect of necrophobia by cattle, and hypothesize that necrophobia is common in other vertebrate herbivores. We propose that this is a case of avoiding attack, one of many types of this defense strategy.\(^9\) It has been overlooked probably because scientists in general do not want to deal with the unpleasant material of decaying carcasses, a well-known human aversion.\(^8\) This, however, serves as an actual independent test of the hypothesis by Lev-Yadun et al.\(^1\) that in addition to pollination, carrion odors emitted by plants may deter mammalian herbivores.

Disclosure of Potential Conflicts of Interest
No potential conflicts of interest were disclosed.

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