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

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Recently, it has been proposed on theoretical grounds that carrion odor from flowers may not only attract pollinators, but also repel mammalian herbivores. Two grazing experiments involving 16 to 26 cattle heads per year, one for eight years (1982–1989) and the other for seven (1994–2000), in a region with no large carnivores that could influence cattle behavior, show that cattle avoid areas where dead cattle have recently been dumped. They grazed much less in these unfenced plots that were used to dump dead cattle each year. In the first experiment, with an area of ca. 20,000 m^2 per head, the average grass biomass at the end of the season was 124.6 gr/m^2 for the regular grazing area, whereas it was 236.5 gr/m^2 for the carcass dumping area. In the second experiment, with a higher stocking level, with ca. 9,000 m^2 per head, the average grass biomass at the end of the season was 61.7 gr/m^2 for the regular grazing area, and 153.7 gr/m^2 for the carcass dumping area. These significant differences existed throughout the 15 y of the experiments. We propose that these results are clear evidence of necrophobia in cattle, a character that might defend them from both pathogenic microbes and predators. This in turn demonstrates that carrion odor, primarily used by plants to attract pollinators, can simultaneously defend plants from herbivory by mammals as proposed.

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 time[6] 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 bees[9-11] 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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Table 1. Cow number, paddock size, and remaining herbage in the 2 grazing experiments

Year	No. of cows	Annual cow replace-ment %	Paddock area m^2	Stocking m^2/cow	Herbage at the end of season gr/m^2 (paddock)	Herbage at the end of season gr/m^2 ("cemetery")
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					124.6 ± 16.8	236.5 ± 15.05
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					61.7 ± 9.2	153.7 ± 9.2

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) m^2 (total area 338,000 m^2) (**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) m^2 per head (total area 215,000 m^2) (**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 m^2 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 rate of cattle grazing there. The carcasses decomposed there mostly by the action of insects and microorganisms, but they were not eaten by large carnivores.

Plant biomass of patches within both the regular grazing plots and the carcass dumping area were sampled at random in April at the end of each growing season; this was done on 5 replicates of a 25 X 25 cm quadrate. Five quadrates were located within the regular grazing paddock and 5 within the carcass dumping area. Samples were cut at ground level, oven-dried at 75°C for 48 h, and weighed.[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.

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/m^2 for the regular grazing area, and 236.5 gr/m^2 for the grazing area used as the carcass dump. Using a paired t test we found the differences highly significant ($t = 11.1$, $df = 7$, $p << 0.01$). In the second experiment the average grass biomass at the end of the season was 61.7 gr/m^2 for the regular grazing area and 153.7 gr/m^2 for the grazing area used as the carcass dump. The differences were again highly significant ($t = 14.0$, $df = 6$, $p << 0.01$). Clearly, the cattle preferred to graze much less on the carcass dump.

Discussion

Giving up food at certain levels mediated by risk (giving-up density *sensu* Brown[21]) 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 dump area. The succession of odors emitted

from carcasses that attract carrion-consuming insects, reptiles, and mammals[6,8,22,23] 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.[3] 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 unexplored 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.[30] 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.[3] 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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