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A sheep in wolf's clothing: do carrion and dung odours of flowers not only attract pollinators but also deter herbivores?

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Carrion and dung odours of various flowers have traditionally been considered an adaptation for attracting the flies and beetles that pollinate them. While we accept the role of such odours in pollinator attraction, we propose that they may also have another, overlooked, anti-herbivore defensive function. We suggest that such odours may deter mammalian herbivores, especially during the critical period of flowering. Carrion odour is a good predictor for two potential dangers to mammalian herbivores: (1) pathogenic microbes, (2) proximity of carnivores. Similarly, dung odour predicts faeces-contaminated habitats that present high risks of parasitism. These are two new types of repulsive olfactory aposematic mimicry by plants: (1) olfactory feigning of carcass (thanatosis), a well-known behavioural defensive strategy in animals, (2) olfactory mimicry of faeces, which also has a defensive visual parallel in animals.

Keywords: aposematic odour; carrion; defence; dung; herbivory; mimicry; thanatosis

Certain plants carry in their flowers a very strong carrion or dung odour, often regarded as a deceptive odour for attracting fly and beetle pollinators that exploit carcasses and dung for reproduction, e.g.[1–10] Of this group of plants, the best known for carrying a carrion odour are members of the parasitic genus, *Rafflesia*, with the largest known flowers,[2] *Aristolochia grandiflora*[1] and *Helicodiceros muscivorus*, commonly known as dead-horse arum.[4,7] Dung odour is well exemplified by *Stapelia* sp.,[1,9] *Arum italicum*[5] and many other *Arum* species.

Although many flower characteristics, especially colour and odour, function in attracting pollinators,[1] evidence of their defensive function has also been theorised. Hinton[11] proposed that bright colours of poisonous flowers are aposematic. Pellmyr and Thien[12] in a broad theoretical study on the origin of angiosperms proposed that floral fragrances originated from chemicals serving as deterrents against herbivore feeding. In a much more focused study of flower defence in the genus *Dalechampia*, Armbruster[13] and Armbruster *et al*[14] proposed that defensive resins have evolved into a pollinator-reward system, and that several defence systems have evolved from such advertisement systems. However, the possibility of dual signalling systems, serving simultaneously to attract some animals and repel others, has not received much research attention. Pollen odours in certain wind-pollinated plants that do not attract pollinators are rich in defensive molecules such as α-methyl alcohols and ketones.[15] The dearomatised isoprenylated phloroglucinols may visually attract pollinators of *Hypericum calycinum* by their UV pigmentation properties, but at the same time the plant may use this pigmentation as a toxic substance against caterpillars, defending the flowers from herbivory.[16] Herrera *et al*.,[17] proposed that plants that possess a particular combination of traits that simultaneously enhances pollination and defends against herbivores, enjoy a disproportionate fitness advantage over plants possessing individual traits of such combinations. The dual action of attracting pollinators while deterring other animals was also found in other taxa, e.g. *Catalpa speciosa* and *Aloe vryheidensis*.[18–20] Thus, floral scents may have a defensive role[21] in addition to the known attracting function.

A general question related to the operation of defensive systems in organisms is whether levels of attack are correlated with the levels of risk. It is commonly noted that since there are no attacks there are no risks, e.g.[22–24] implying that no defence is needed. While in certain cases this view is probably true, the reality may be different in others. This issue has recently been addressed for the occurrence of summer-green plants in the dry Negev desert of Israel,[25] light-coloured coastal and dune plants[26] and red and yellow autumn leaves.[27] The fact that certain organisms are not attacked is not an *a priori* indication that there is no such risk. It has been argued that in many cases the risks exist but it might well be that the low levels of attack simply indicate that defences are strong, and that the defended organisms have

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successfully deterred possible enemies.[25–28] An example of such a situation is found in the desert plants that form green islands in the dry summer when all surrounding plants have turned yellow and many of them have been grazed to their roots. Even under such extreme grazing pressure those green plants are repeatedly ignored by the Bedouin's large flocks of sheep and goats that pass them daily. These summer-green plants are characterised by being poisonous or thorny as protection against herbivory. Under the dry summer conditions in the desert, green is as conspicuous and contrasts with the background, as do yellow, red and black colours in "greener" ecosystems.[25] The lack of attacks on these green plants is a clear indication of their very good defensive and deterrent qualities rather than of a low level of risk.

We do not posit that these carrion and dung odours are the only defence of these plants. Some of the plants known for carrying these odours have various known defence mechanisms in addition to the one proposed here. For example, many *Arum* species, like other members of the Araceae, have internal calcium oxalate needles (raphids) in their tissues associated with various toxins that penetrate the herbivore's tissues wounded by the raphids.[29,30] Moreover, these needles may insert pathogenic bacteria into the body of the herbivores.[31] Such defences protect from both invertebrate and vertebrate herbivores. For instance, in Israel, in addition to insect and snail herbivory, there was grazing impact by various ungulates throughout the Pleistocene[32–34] which were mostly replaced in the last several millennia by a greater impact by sheep, goat, cattle, horse, donkey and camel grazing.[35] In general, all the flora of the Mediterranean region, like many semi-arid and arid regions on earth, was exposed to considerable herbivory pressure, as indicated by the high incidence of spiny plants in such regions.[36]

Flowering of plants known for their carrion odour may last from days to months. For instance, in Israel, the foul-smelling *Calligonum comosum* flowers from February to April, *A. dioscoridis* from March to May, and *A. palestinum* during March and April.[37] Moreover, many of the carrion-odour-carrying plants perform vegetative reproduction, forming clones, and the long period of flowering of the sister ramets forms a niche of bad odour for long periods. In this respect, taking into account only the duration of the odourous phase of individual flowers is misleading.

We propose that plants' carrion or dung odours may concurrently serve two functions rather than fostering pollination alone. According to the classic hypothesis, these plants attract and lure to their flowers various insects that use carrion or dung for their own reproduction and use these insects as pollinators.[1,38,39] Here we propose an additional function: the volatile carrion and dung signals produced by these plants may also help to defend the plants and their flowers by deterring mammalian herbivores. In certain cases, such as in *Rafflesia*, which has only flowers above the ground, the defence may be limited to the flowers. This dual mechanism, operating in the plant's most sensitive stage of flowering, may have an advantage as it uses resources already assigned to pollinator attraction for anti-herbivore defence. As such odours are emitted only during the reproductive season, we propose that attraction of pollinators was the primary function of these chemicals. However, a more drastic possible hypothesis is that these plants evolved these odours primarily to repel herbivores, and their function in attracting pollinators is secondary. In any case, the odours function in small quantities and their production is therefore not costly.

Herbivores may be deterred by carrion odour for several ultimate and proximate reasons. Carcasses may be herbivores killed by large predators such as lions[40] and thus may indicate a proximate danger of a large predator. Carrion odour, which signals a potential free meal, is also known to attract many types of carnivores, e.g. lions, grizzly bears, hyenas, wolves, foxes, coyotes, and nearly all other carnivorous vertebrates, as all carnivores are facultative scavengers.[41] Odours of carnivore urine and faeces are known to repel herbivores.[42–47] The chemical factors that construct these foul odours are sulphurous metabolites associated with meat digestion.[42,44] Sulphur compounds dominating or found in the scent of many flowers with fetid odours[9–10] indicate a strong potential for these odours to be sensed by herbivore mammals and to repel them from the plants. A field study of the predatory lizard *Podarcis lilfordi* from the Aire islet shows a danger in the association of plants' carrion odour and carnivore attraction. The lizard hunts insects attracted to the very strong carrion odour of dead-horse arum.[48] The defensive use of volatile molecules produced by plants in response to insect herbivory by attracting predators or parasitoids of insect herbivores is a well-known phenomenon. Attacked plants may emit various volatile signals to draw predators to the attacking herbivores, their potential prey.[49–51] Olfactory aposematism, whereby poisonous plants deter mammalian or insect herbivores, has been proposed as well.[52–60] The carrion odour may thus serve the plants by attracting carnivores that may defend them just as they attract their pollinators, similar to the attraction of enemies of herbivorous insects by means of various volatiles.[49,50] Mammalian herbivores will not find such company appealing and a safe strategy for them would be to avoid carcasses, or in our case, carcass-mimicking plants. Moreover, carcasses are commonly occupied by various pathogenic microbes that may infect approaching mammalian herbivores.[41,61,62] Avoidance of dead animals because of pathogen risk is well known in ants, bees and Collembola.[63–66]

There are also solid indications for dung avoidance by mammalian herbivores because of the risk of parasites.[67–69]

Therefore, we suggest that plants with a strong dung odour may repel mammalian herbivores. Reducing predation risk while foraging, even at the cost of reducing food intake, is a widespread and well-known phenomenon[70–72] and the hypothesis we propose here is a special case of this strategy.

The two types of potential odourous repellents proposed here to trick herbivores into thinking that they are heading for danger may be regarded as a special kind of olfactory aposematism, but not the regular one of poisonous plants. Since these plants are known to use olfactory deception to attract pollinators,[1,2,4–8] the deceptive use of odours for defence should be considered a logical follow-up strategy. Several cases are known, in which visual mimicry of live animals has been suggested to operate in plants to reduce herbivory[73–75] and an olfactory parallel would be a related form of the same phenomenon. Thanatosis (playing dead), and faeces mimicry (caterpillars that look like bird droppings or larva that use a faecal thatch) are well-known visual defences in animals.[76–79] Olfactory defence by faeces odour *via* the volatile skatole is known in insects belonging to the chrysopids (lacewings).[79] Fear of predation may considerably influence herbivore[44,80,81] or pollinator[82] behaviour. We propose that the plants discussed here use the ecological opportunities presented by such fears to defend themselves. It is possible to exploit such deception for a long time in evolutionary perspective if the proportion of the cheaters in the ecosystem is not too high. Such plants never became the dominant vegetation, thus they are never as common as spiny cacti in the deserts of North America or thistles in the Near East. The relatively small number of such plants in any specific ecosystem we know in the Eastern Mediterranean and elsewhere seems to accord with such a strategy. While we propose that fear ecology provides the opportunity to exploit it as defence, we are aware of the fact that this tactic probably cannot operate against all herbivores all the time. No plant defence system is perfect[83,84] and the one we propose here is no exception. Moreover, not all experiments of application of predator odours to repel their prey succeeded,[85] various herbivores react differently to the same predator odours and the same herbivore may respond differently to odours of various predators and in addition the responses vary with the season.[86–88] There is evidence that under certain conditions house mice may become habituated to specific predator odours.[89] We think that because of the patchy distribution of plants that mimic carrion and dung odours, such habituation is less probable.

We suggest that in addition to the circumstantial evidence and theoretical discussion presented here, field experiments with livestock and wild herbivores should be conducted to examine the deterrent effect of carrion and dung odours. Experimental plots with or without standard carcasses, or with application of specific odourous chemicals to odourous and non-odourous plants would serve as a logical setup for this purpose. With the current advances in volatile analysis it is possible to identify the repelling molecules, and with modern genetics it is possible to clone the genes that enable the synthesis of the specific odours. With these genes cloned, one can produce transgenic plants with much stronger odours, without odours, or with altered levels of the odours and use them for critical behavioural tests of their putative defensive role.

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References

1. **Faegri K. and van der Pijl, L.,** The principles of pollination ecology. 3rd ed. Oxford, Pergamon Press, 1979.
2. **Beaman, R. S., Decker P. J. and Beaman, J. H.,** Pollination of Rafflesia (Rafflesiaceae). *Am J Bot* 1988. **75**: 1148–1162.
3. **Sakai, S.,** Aristolochia spp. (Aristolochiaceae) pollinated by flies breeding on decomposing flowers in Panama. *Am J Bot* 2002. **89**: 527–534.
4. **Stensmyr, M., Urru, I., Collu, I., Celander, M., Hansson B. S. and Angioy, A.-M.,** Rotting smell of dead-horse arum florets. *Nature* 2002. **420**: 625–626.
5. **Albre, J., Quilichini A. and Gibernau, M.,** Pollination ecology of Arum italicum (Araceae). *Bot J Linn Soc* 2003. **141**: 205–214.
6. **Seymour, R. S., Gibernau M. and Ito, K.,** Thermogenesis and respiration of inflorescences of the dead horse arum Helicodiceros muscivorus, a pseudo-thermoregulatory aroid associated with fly pollination. *Funct Ecol* 2003. **17**: 886–894.
7. **Angioy, A.-M., Stensmyr, M. C., Urru, I., Puliafito, M., Collu I. and Hansson, B. S.,** Function of the heater: the dead horse arum revisited. *Proc R Soc Lond B Biol Sci (Suppl)* 2004. **271**: S13–S15.
8. **Raguso, R. A.,** Flowers as sensory billboards: progress towards an integrated understanding of floral advertisement. *Curr Opin Plant Biol* 2004. **7**: 434–440.
9. **Jürgens, A., Dötterl S. and Meve, U.,** The chemical nature of fetid floral odours in stapeliads (Apocynaceae-Asclepiadoideae-Ceropegieae). *New Phytol* 2006. **172**: 452–468.
10. **Ollerton J. and Raguso, R. A.,** The sweet stench of decay. *New Phytol* 2006. **172**: 382–385.
11. **Hinton, H. E.,** Natural deception. In: Gregory, R. L. and Gombrich, E. H. editors. Illusion in nature and art. London, Duckworth, 1973. pp 97–159.
12. **Pellmyr O. and Thien, L. B.,** Insect reproduction and floral fragrances: keys to the evolution of the angiosperms? *Taxon* 1986. **35**: 76–85.
13. **Armbruster, W. S.,** Exaptations link evolution of plant-herbivore and plant-pollinator interactions: a phylogenetic inquiry. *Ecology* 1997. **78**: 1661–1672.
14. **Armbruster, W. S., Howard, J. J., Clausen, T. P., Debevec, E. M., Loquvam, J. C., Matsuki, M., Cerendolo B. and Andel, F.,** Do biochemical exaptations link evolution of plant defense and pollination systems? Historical hypotheses and experimental tests with Dalechampia vines. *Am Nat* 1997. **149**: 461–484.
15. **Dobson H. E. M. and Bergström, G.,** The ecology and evolution of pollen odors. *Plant Syst Evol* 2000. **222**: 63–87.
16. **Gronquist, M., Bezzerides, A., Attygalle, A., Meinwald, J., Eisner M. and Eisner, T.,** Attractive and defensive functions of the ultraviolet pigments of a flower (Hypericum calycinum). *Proc Natl Acad Sci USA* 2001. **98**: 13745–13750.
17. **Herrera, C. M., Medrano, M., Rey, P. J., Sánchez-Lafuente, A. M., Garcia, M. B., Guitián J. and Manzaneda, A. J.,** Interaction of pollinators and herbivores on plant fitness suggests a pathway for correlated evolution of mutualism- and antagonism-related traits. *Proc Natl Acad Sci USA* 2002. **99**: 16823–16828.

18. **Stephenson, A. G.,** Toxic nectar deters nectar thieves of Catalpa speciosa. *Am Midl Nat* 1981. **105**: 381–383.
19. **Johnson, S. D., Hargreaves A. L. and Brown, M.,** Dark, bitter-tasting nectar functions as a filter of flower visitors in a bird-pollinated plant. *Ecology* 2006. **87**: 2709–2716.
20. **Hansen, D. M., Olesen, J. M., Mione, T., Johnson S. D. and Müller, C. B.,** Coloured nectar: distribution, ecology, and evolution of an enigmatic floral trait. *Biol Rev* 2007. **82**: 83–111.
21. **Knudsen, J. T., Eriksson, R., Gershenzon J. and Ståhl, B.,** Diversity and distribution of floral scent. *Bot Rev* 2006. **72**: 1–120.
22. **Holopainen J. K. and Peltonen, P.,** Bright autumn colours of deciduous trees attract aphids: nutrient retranslocation hypothesis. *Oikos* 2002. **99**: 184–188.
23. **Wilkinson, D. M., Sherratt, T. N., Phillip, D. M., Wratten, S. D., Dixon A. F. G. and Young, A. J.,** The adaptive significance of autumn leaf colours. *Oikos* 2002. **99**: 402–407.
24. **Schaefer H. M. and Wilkinson, D. M.,** Red leaves, insects and coevolution: a red herring? *Trends Ecol Evol* 2004. **19**: 616–618.
25. **Lev-Yadun S. and Ne'eman, G.,** When may green plants be aposematic? *Biol J Linn Soc* 2004. **81**: 413–416.
26. **Lev-Yadun, S.,** Defensive functions of white coloration in coastal and dune plants. *Isr J Plant Sci* 2006. **54**: 317–325.
27. **Lev-Yadun S. and Gould, K. S.,** What do red and yellow autumn leaves signal? *Bot Rev* 2007. **73**: 279–289.
28. **Lev-Yadun S. and Gould, K. S.,** Role of anthocyanins in plant defense. In: Gould, K. S., Davies, K. M. and Winefield, C. editors. Life's colorful solutions: the biosynthesis, functions, and applications of anthocyanins. Berlin, Springer-Verlag, 2008. pp 21–48.
29. **Franceschi V. R. and Horner, H. T., Jr.**, Calcium oxalate crystals in plants. *Bot Rev* 1980. **46**: 361–427.
30. **Franceschi V. R. and Nakata, P. A.,** Calcium oxalate in plants: formation and function. *Annu Rev Plant Biol* 2005. **56**: 41–71.
31. **Lev-Yadun S. and Halpern, M.,** External and internal spines in plants insert pathogenic microorganisms into herbivore's tissues for defense. In: Van Dijk, T. editor. Microbial ecology research trends. New York, Nova Scientific Publishers, Inc., 2008. pp. 155–168.
32. **Tchernov, E.,** Quaternary fauna. In: Horowitz, A. editor. The Quaternary of Israel. New York, Academic Press, 1979. pp 257–290.
33. **Bar-Oz, G.,** Epipalaeolithic subsistence strategies in the Levant: A zooarchaeological perspective. The American School of Prehistoric Research (ASPR) Monograph Series. Boston, Brill Academic Publishers Inc., 2004.
34. **Steiner, M. C.,** The faunas of Hayonim Cave (Israel): A 200,000-year record of Paleolithic diet, demography and society. Cambridge, Peabody Museum of Archaeology and Ethnology, 2005.
35. **Perevolotsky A. and Seligman, N.,** Role of grazing in Mediterranean rangeland ecosystems. Inversion of a paradigm. *Bioscience* 1998. **48**: 1007–1017.
36. **Grubb, P. J.,** A positive distrust in simplicity - lessons from plant defences and from competition among plants and among animals. *J Ecol* 1992. **80**: 585–610.
37. **Feinbrun-Dothan N. and Danin, A.,** Analytical flora of Eretz-Israel. Jerusalem, Cana Publishing House Ltd. (in Hebrew), 1991.
38. **Dafni, A.,** Mimicry and deception in pollination. *Annu Rev Ecol Syst* 1984. **15**: 259–278.
39. **Jersáková, J., Johnson S. D. and Kindlmann, P.,** Mechanisms and evolution of deceptive pollination in orchids. *Biol Rev* 2006. **81**: 219–235.
40. **Schaller, G. B.,** The Serengeti lion: a study of predator-prey relations. Chicago, University of Chicago Press, 1972.
41. **DeVault, T. L., Rhodes O. E., Jr, and Shivik, J. A.,** Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathways in terrestrial ecosystems. *Oikos* 2003. **102**: 225–234.
42. **Müller-Schwarze, D.,** Leading them by their noses: animal and plant odours for managing vertebrates. In: MacDonald, D. W., Müller-Schwarze, D. and Natynczuk, S. E. editors. Chemical signals in vertebrates 5. Oxford, Oxford University Press, 1990. pp 585–598.
43. **Pfister, J. A., Müller-Schwarze D. and Balph, D. F.,** Effects of predator fecal odors on feed selection by sheep and cattle. *J Chem Ecol* 1990. **16**: 573–583.
44. **Nolte, D. L., Mason, J. R., Epple, G., Aronov E. and Campbell, D. L.,** Why are predator urines aversive to prey? *J Chem Ecol* 1994. **20**: 1505–1516.
45. **Terlouw, E. M. C., Boissy A. and Blinet, P.,** Behavioural responses of cattle to the odours of blood and urine from conspecifics and to the odour of faeces from carnivores. *Appl Anim Behav Sci* 1998. **57**: 9–21.
46. **Fendt, M.,** Exposure to urine of canids and felids, but not of herbivores, induces defensive behavior in laboratory rats. *J Chem Ecol* 2006. **32**: 2617–2627.
47. **Russell B. G. and Banks, P. B.,** Do Australian small mammals respond to native and introduced predator odours? *Austral Ecol* 2007. **32**: 277–286.
48. **Pérez-Mellado V. and Riera, N.,** 2004. Unique interactions of insular lizards and plants. The case of the dead horse arum (Dracunculus muscivorus) and the Balearic lizard (Podarcis lilfordi). Procedings of the Fifth International Symposium on the Lacertids of the Mediterranean Basin, Lipari, Aeolian Islands, Sicily, Italy, 7–11. May 2004. Firenze: Firenze University Press. 33–34.
49. **Kessler A. and Baldwin, I. T.,** Defensive function of herbivore induced plant volatile emissions in nature. *Science* 2001. **291**: 2141–2144.
50. **Kappers, I. F., Aharoni, A., van Herpen, T. W. J. M., Luckerhoff, L. L. P., Dicke M. and Bouwmeester, H. J.,** Genetic engineering of terpenoid metabolism attracts bodyguards to Arabidopsis. *Science* 2005. **309**: 2070–2072.
51. **Baldwin, I. T., Halitschke, R., Paschold, A., von Dahl, C. C. and Preston, C. A.,** Volatile signaling in plant-plant interactions: ''talking trees'' in the genomic era. *Science* 2006. **311**: 812–815.
52. **Eisner, T.,** Catnip: Its Raison d'Être. *Science* 1964. **146**: 1318–1320.
53. **Levin, D. A.,** The role of trichomes in plant defense. *Q Rev Biol* 1973. **48**: 3–15.
54. **Rothschild, M.,** Secondary plant substances and warning colouration in insects. In: van Emden, H. F. editor. Insect/plant relationships. Symposia of the Royal Entomological Society of London Number six. Oxford, Blackwell Scientific Publications, 1973. pp 59–83.
55. **Atsatt P. R. and O'Dowd, D. J.,** Plant defense guilds. *Science* 1976. **193**: 24–29.
56. **Wiens, D.,** Mimicry in plants. *Evol Biol* 1978. **11**: 365–403.
57. **Eisner T. and Grant, R. P.,** Toxicity, odor aversion, and ''olfactory aposematism''. *Science* 1981. **213**: 476.
58. **Harborne, J. B.,** Introduction to ecological biochemistry. London, Academic Press, 1982.
59. **Launchbaugh K. L. and Provenza, F. D.,** Can plants practice mimicry to avoid grazing by mammalian herbivores? *Oikos* 1993. **66**: 501–504.
60. **Provenza, F. D., Kimball B. A. and Villalba, J. J.,** Roles of odor, taste, and toxicity in the food preferences of lambs: implications for mimicry in plants. *Oikos* 2000. **88**: 424–432.
61. **Janzen, D. H.,** Why fruits rot, seeds mold, and meat spoils. *Am Nat* 1977. **111**: 691–713.
62. **Putman, R. J.,** Carrion and dung: the decomposition of animal wastes. Southampton, Edward Arnold, 1983.
63. **Trumbo, S. T., Huang Z.-Y. and Robinson, G. E.,** Division of labor between undertaker specialists and other middle-aged workers in honey bee colonies. *Behav Ecol Sociobiol* 1997. **41**: 151–163.
64. **Hart, A. G., Bot A. N. M. and Brown, M. J. F.,** A colony-level response to disease control in a leaf-cutting ant. *Naturwiss* 2002. **89**: 275–277.
65. **Nilsson E. and Bengtsson, G.,** Death odour changes movement pattern of a Collembola. *Oikos* 2004. **104**: 509–517.
66. **Franks, N. R., Hooper, J., Webb C. and Dornhaus, A.,** Tomb evaders: house-hunting hygiene in ants. *Biol Lett* 2005. **1**: 190–192.
67. **Lozano, G. A.,** Optimal foraging theory: a possible role for parasites. *Oikos* 1991. **60**: 391–395.
68. **Cooper, J., Gordon I. J. and Pike, A. W.,** Strategies for the avoidance of faeces by grazing sheep. *Appl Anim Behav Sci* 2000. **69**: 15–33.
69. **Hutchings, M. R., Gordon, I. J., Kyriazakis I. and Jackson, F.,** Sheep avoidance of faeces-contaminated patches leads to a trade-off between intake rate of forage and parasitism in subsequent foraging decisions. *Anim Behav* 2001. **62**: 955–964.
70. **Kats L. B. and Dill, L. M.,** The scent of death: Chemosensory assessment of predation risk by prey animals. *Ecoscience* 1998. **5**: 361–394.
71. **Brown J. S. and Kotler, B. P.,** Hazardous duty pay and the foraging cost of predation. *Ecol Lett* 2004. **7**: 999–1014.

72. **Trussell, G. C., Ewanchuk P. J. and Matassa, C. M.,** The fear of being eaten reduces energy transfer in a simple food chain. *Ecology* 2006. **87**: 2979–2984.
73. **Williams K. S. and Gilbert, L. E.,** Insects as selective agents on plant vegetative morphology: Egg mimicry reduces egg laying by butterflies. *Science* 1981. **212**: 467–469.
74. **Rothschild, M.,** Aide mémoire mimicry. *Ecol Entomol* 1984. **9**: 311–319.
75. **Lev-Yadun S. and Inbar, M.,** Defensive ant, aphid and caterpillar mimicry in plants. *Biol J Linn Soc* 2002. **77**: 393–398.
76. **Edmunds, M.,** Defence in animals. A survey of anti-predator defences. Harlow, Longman, 1974.
77. **Eisner T. and Eisner, M.,** Defensive use of a fecal thatch by a beetle larva (Hemisphaerota cyanea). *Proc Natl Acad Sci USA* 2000. **97**: 2632–2636.
78. **Ruxton, G. D., Sherratt T. N. and Speed, M. P.,** Avoiding attack. The evolutionary ecology of crypsis, warning signals & mimicry. Oxford, Oxford University Press, 2004.
79. **Eisner, T., Eisner M. and Siegler, M.,** Secret weapons. Defenses of insects, spiders, scorpions, and other many-legged creatures. Cambridge, Harvard University Press, 2005.
80. **Festa-Bianchet, M.,** Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. *Oecologia* 1988. **75**: 580–586.
81. **Ripple W. J. and Beschta, R. L.,** Wolves and the ecology of fear: can predation risk structure ecosystems? *Bioscience* 2004. **54**: 755–766.
82. **Dukas, R.,** Effects of perceived danger on flower choice by bees. *Ecol Lett* 2001. **4**: 327–333.
83. **Janzen, D. H.,** New horizons in the biology of plant defenses. In: Rosenthal, G. A. and Janzen, D. H. editors. Herbivores their interaction with secondary plant metabolites. Orlando, Academic Press, 1979. pp 331–350.
84. **Crawley, M. J.,** Herbivory. The dynamics of animal-plant interactions. Oxford, Blackwell Scientific Publications, 1983.
85. **Apfelbach, R., Blanchard, C. D., Blanchard, R. J., Hayes R. A. and McGregor, I. S.,** The effects of predator odors in mammalian prey species: A review of field and laboratory studies. *Neurosci Biobehav Rev* 2005. **29**: 1123–1144.
86. **Ramp, D., Russell B. G. and Croft, D. B.,** Predator scent induces differing responses in two sympatric macropodids. *Aust J Zool* 2005. **53**: 73–78.
87. **Jędrzejewski, W., Rychlik L. and Jędrzejewska, B.,** Responses of bank voles to odours of seven species of predators: experimental data and their relevance to natural predator-vole relationships. *Oikos* 1993. **68**: 251–257.
88. **Hayes, R. A., Nahrung H. F. and Wilson, J. C.,** The response of native Australian rodents to predator odours varies seasonally: a by-product of life history variation? *Anim Behav* 2006. **71**: 1307–1314.
89. **Powell F. and Banks, P. B.,** Do house mice modify their foraging behaviour in response to predator odours and habitat? *Anim Behav* 2004. **67**: 753–759.

