Why are there so many and so few white flowers?

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Though the world we see appears to be rich in white flowers, this is not the case for animals, such as insects, with ultraviolet (UV) receptors. In fact, flowers that appear white to insects are very rare. We analyse this phenomenon to highlight new discoveries in the mechanisms of insect vision that may have influenced the evolution of flower colour. Our analysis reveals that an understanding of biological signalling requires a comprehensive understanding of sensory physiology and perceptual psychology. An evaluation of UV signals alone may not be helpful, as this can be as inaccurate as models based solely on the human visual system. We interpret floral colours and their frequency in nature from the more relevant perspective of insect colour vision.

Flowers contain the reproductive organs of angiosperms. Their primary function is in allowing the export and import of pollen – the male reproductive material – to and from other members of the same species, in order to ensure recombination, genetic variability and thus adaptability to changing environmental conditions. Most angiosperms employ pollinators to facilitate the transport of pollen[1]. The most important pollinators are insects, and particularly bees (Hymenoptera: Apoidea)[1]. Floral signals are the means by which insect visitors detect, recognize and memorize flowers as potential food sources. Here we focus on the visual cues, colours and patterns of flowers. Colour is considered to be the most important cue for the detection and recognition of flowers at a distance[2–5]. Pattern becomes important only at close range, because the insect spatial resolution is roughly 100 times poorer than our own[6].

Insect vision differs fundamentally from that of human beings. This is true for the visual spectrum – all insects so far tested see UV light – but also the ways in which colour and pattern information are integrated in the insect brain[7]. The fact that bees and other insects perceive something we cannot has led to the idea that UV is particularly meaningful for its receivers and thus constitutes an attractive signal by itself[8]. However, closer inspection reveals that UV reflections are no more special than those in other parts of the insect visual spectrum[9] and that UV reflecting flowers either fail to convey signalling information or even provide cryptic clues for insect pollinators. This article analyses the current research on insect perception and the possible consequences of this for floral colouration.

Why we see white flowers as white, and why insects don't

The visual spectrum of all insects extends into the UV, in most cases down to 300 nm (Ref. 7). At the long wavelength end of the scale, most insects, including most bees, see only into the near red (630 nm), although there are several species (e.g. in the Lepidoptera) with a visual range extending further into the far red than our own[7]. We refer henceforth to the bee's visual spectrum, meaning the most common case, which comprises a range from 300 to 630 nm.

Many flowers that appear to us as red, blue, or yellow reflect UV light[4,5,10–14]. However, 'human-white' flowers are almost always UV absorbent[4,5,10–14]. Such flowers are achromatic to our eyes because they reflect more or less evenly and strongly across the human visual spectrum thus stimulating all three types of photoreceptors (blue, green and red) and producing a 'white' sensation. However, because such flowers are almost all UV absorbing, they are not 'bee-white' but strongly chromatic. A true bee-white flower would have to have equiproportionate reflectance across the bee's visual spectrum[4,5,12]. Such true bee-white flowers are very rare and it has even been proposed in the past that they do not exist[10,15] (Fig. 1).

What makes the flowers coloured?

Floral colours result from the selective absorption and reflection of ambient light in the tissues of flower petals.

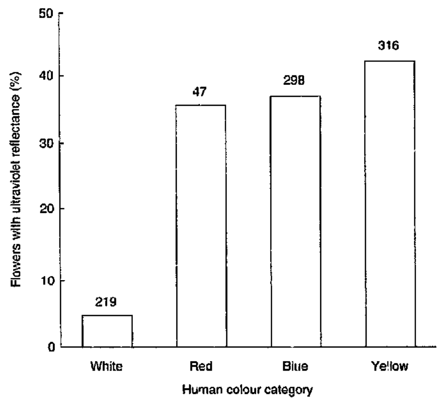

Fig. 1. The percentages of differently coloured flowers that reflect ultraviolet light. Data were sampled from a large variety of habitats[14]. Numbers above columns indicate how many species were evaluated.

  1360 - 1385/96/$15.00 PII S1360 - 1385(96)20008-1

Colouration is achieved through only a few classes of pigments: flavonoids (including anthocyanins, chalcones, aurones and flavonols), carotinoids (including xanthophylls and carotenes) and betalaines (including betaxanthins and betacyanins). Within these classes there is great diversity, which allows for the wide variety of floral colours and colour combinations that humans so appreciate. Carotinoids and some anthocyanins are known to produce UV reflectance, but flavonoids appear to be generally UV absorbing[16]. Pigments that give rise to white flowers also generally absorb UV light[17] (Fig. 2). The few bee-white flowers that do exist reflect UV by special structural adaptations (air-filled intracellular structures or starch grains) of the epidermal cells[11]. Plants of many families can actually produce a bee-white colouration, as shown by the reflectance of some white fruits with colouration presumably adapted to the visual system of vertebrates[18]. Also, floral parts not exposed to the scrutiny of the insect eye (such as within flowers of *Lupinus*) may be bee-white[14]. Why then do plants eliminate the UV component when using white signals (as they appear to humans) to address insects?

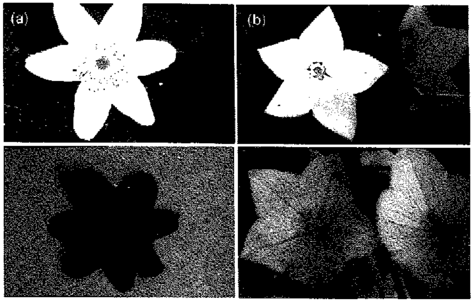

Fig. 2. White flowers differ in their capacity to reflect ultraviolet (UV) light. (a) *Anemone nemorosa* under daylight (upper panel) or UV light (lower panel) and (b) *Platycodon grandiflorum* under daylight (upper panel) or UV light (lower panel). *Photographs kindly supplied by W. Barthlott.*

White flowers with ultraviolet reflectance and backgrounds are the same colour to bees

To interpret this phenomenon, it is first necessary to understand how, and if, white flowers (with and without UV reflectance) contrast with common background materials. Flowers bloom against backgrounds of vegetation, bark, soil and stone. What is generally not recognized about these materials is that they are all similar in having more or less uniform, but weak, spectral reflectances in the insects' visual spectrum, so that they appear rather 'dull'[4,6,12–14]. There is no major difference between leaf and non-leaf backgrounds because both differ only in their absorbance in the red, which is only in the periphery of the visual spectrum of most insects. Furthermore, the insect eye adapts to the background of the objects it is perceiving so that the spectral reflectance of the background becomes the neutral standard against which the colours of the flowers are compared[19]. This means that 'bee-white' flowers have much the same chromatic appearance as most natural backgrounds: they are uncoloured in the bees' visual spectrum (Fig. 3).

It has been suggested that nocturnally blooming white flowers should reflect UV to maximize reflectance in a low-light environment[11]. That suggestion followed an intuitive argument based on our own human vision: for us, a white object is certainly easier to detect in dim light than an object that reflects only part of the spectrum. However, white flowers that bloom nocturnally and are attended by moths are not insect-white because they too lack UV reflectance[20]. Moreover, hawkmoths avoid artificial flowers with insect-white reflectance, independently of their brightness[20]. This again indicates that, even for some nocturnal and crepuscular pollinators, and pollinators of deeply shaded habitats, the argument that insect white may be a useful flower signal, because of its brightness in a dark environment, does not apply. Rather, it seems that insect-white flowers are at a disadvantage in comparison with coloured ones, and are therefore rare in nature.

White flowers are brighter than their background – so why is it difficult for bees to see them?

The lack of colour contrast between target and background is not a problem for a human observer, so long as the two differ in their brightness. Colour is perceived by humans on the basis of three perceptual attributes called hue, saturation and brightness[21]. Hue is the attribute that permits a colour to be classified as red, yellow, green and so forth. Saturation describes a colour's similarity to a neutral grey or white within the context of its hue: a grey object with a small reddish tint has little saturation, whereas a red object with a little white or grey is highly saturated. Brightness tells us about the relative ordering of an object on the dark-to-light scale. Because of our capacity for perceiving brightness differences, we can easily detect a white target on a grey background. However, this is not the case for bees. The first evidence that bees were different from human beings in their perception of colour, not only in terms of their visual spectral range, was reported by Hertz[22,23] and Engländer[24]. Both found that bees were almost untrainable to bee-white (i.e. an achromatic stimulus). It has now been confirmed by several psychophysical studies that brightness is not used by bees, wasps or flies in the context of feeding[25–30]. Insects judge two signals as being equal if they differ strongly in brightness, but not in colour, and easily distinguish between them if their spectral reflections differ by only a few nanometers[25–30]. In short, bees have great difficulty in detecting targets that differ from their background only in terms of brightness, and have little capacity to learn such stimuli in association with a reward. Thus, bee-white flowers would not be detectable against their background, despite the difference in brightness they may present to human observers.

Though brightness apparently is not a visual cue used by bees and other insects, there is a colour-blind system that allows them to detect some objects. This system only uses the long wavelength receptor type, also called the green receptor because its sensitivity peak is in the human green region of the spectrum[31,32]. Bees and other insects may detect objects by using the excitation difference in the green photoreceptors between target and background [i.e. the contrast that the target makes with its background for the green receptor type (green contrast)]. By means of this green contrast, bees perform various visually guided tasks that are related to motion (e.g. estimation of distance from objects[33], maintaining flight paths centred between walls[34] and detection of the edges of objects[35]). Because modulations on only one receptor type are involved here, green contrast relates to an achromatic perception and is similar in many aspects to our own achromatic brightness system. The most prominent difference from the human visual system is that human perception of brightness arises because of the joint action of achromatic and chromatic visual pathways[36], whereas the green receptor in bees seems to be mutually exclusive to the chromatic pathways.

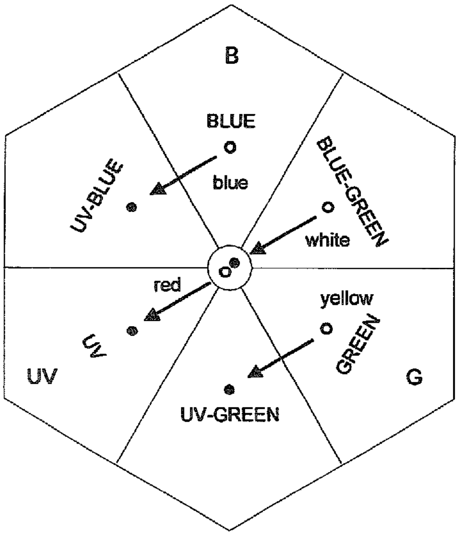

Fig. 3. Flower colours as perceived by bees and humans. The colour hexagon is a generalized colour opponent space with metrics that have been shown to be applicable to numerous species of Hymenoptera[41]. The photoreceptor excitations for the three receptor types – ultraviolet (UV), blue (B) and green (G) – in the ommatidia of the bee compound eye are shown at an angle of 120° to each other. The hexagon is divided into six equally large sectors (UV, UV-BLUE, BLUE, BLUE-GREEN, GREEN and UV-GREEN), which refer to the ways in which the bees' receptors are stimulated by given pure broad-band spectral stimuli, or with UV-GREEN, mixed spectral stimuli. Upper case letters for colour names refer to insect (bee) colours. Colour names in lower case letters refer to human colours, which, depending on whether or not, and how much, UV is reflected, occupy positions along the vectors on the colour hexagon. Open circles represent loci of colours with little or no UV reflection. Closed circles represent loci of colours that would appear the same to humans as those at the loci of the open circles, but reflect well in the UV and would, therefore, be very different from their counterparts to insects. [For example, a human-white flower lacking UV reflections is designated blue-green to insects; if it reflected well in the UV it would still be human-white, but would be insect-white instead of insect-blue-green. Similarly, a human-red flower would be colourless (achromatic and in the centre of the hexagon) unless it reflected in the UV, in which case it would be UV, but still red to humans]. The central circle in the hexagon marks the uncoloured (achromatic) area, which contains bee-white and the loci of most natural background materials[14].

Do bees use the green-contrast, achromatic signal to see white flowers?

It may be possible that bright, bee-white flowers are detected by means of the green-contrast signal that they clearly provide, because the green reflectance peak of most green leaves is generally lower than that of white flowers. However, it was recently discovered that the distance at which objects can be detected by honeybees depends both on the colour contrast and the green contrast of the target against its background[37]. The smallest visual angle for target detection (about 5°) was found when targets provided both colour and green contrast with respect to the background used (i.e. a dark grey, honeybee-achromatic paper). Targets with colour contrast but no green contrast were less well detected: the threshold was found at a visual angle as large as 15° (Fig. 4). A target with no colour (but green) contrast was not detected, and thus was not learned by the bees[37]. The human colour of the last mentioned target was rose-pink and, against the grey backdrop, was highly conspicuous to a human observer. Thus, both colour and green contrast are necessary for maximum optical range of detection. Bee-white flowers are probably disadvantaged and thus rare, because, like the pink target, they provide little or no colour contrast, green contrast notwithstanding.

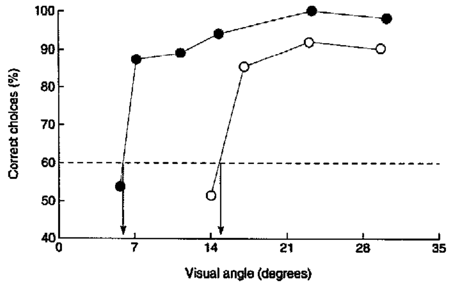

Fig. 4. Percentage of correct choices by bees as a function of the visual angle subtended by different colour stimuli. Bees were trained to enter a Y-maze with moveable back walls in its arms, and to choose a rewarding colour disk on a grey background against a stimulus-free grey background in the other[37]. The position of the coloured disk was randomized between the arms from one bee visit to the next. The back walls were progressively moved back until bees were unable to detect the colour disk and chose both arms randomly. The visual angle (α_{min}) subtended by the colour disk at the threshold of detection (60% correct choices: dashed line) was calculated for different disk diameters and distances, and for different colours (see arrows). Stimuli with colour contrast and green contrast yielded a mean α_{min} of about 5° (filled circles; in the example presented α_{min} = 5.2°, n = total of 408 choices by six honeybees). Stimuli with colour contrast but no green contrast yielded a mean α_{min} of about 15° (open circles; in the example presented α_{min} = 14.3°, n = total of 608 choices by eight honeybees) – they could be detected only from closer distances. The curves show an example for each case. Stimuli with green contrast but no colour contrast (e.g. appearing pink to human beings) could not be detected by the bees, as indicated by our not being able to train them to associate such colours with a reward. See Giurfa *et al.*[37] for details.

Alternative strategies for white flowers: how to become conspicuous without changing reflectance

Although the few bee-white, insect pollinated flowers known may be disadvantaged by their chromatic poor detectability in nature, they may compensate by exploiting other visible features. It is possible to make an object without colour contrast attractive to insects by addressing entirely different pattern perception systems. It has been shown that pattern and colour perception in honeybees constitute two separate neuronal channels with the latter dominating[38], as shown by bees being better able to learn and discriminate shape when the amount of colour information is lessened. Thus, some bee-white flowers might increase attractiveness by displaying shapes that pollinators perceive and learn particularly well. Bees and other pollinators prefer, discriminate and learn objects with highly dissected perimeters better than objects with undissected outlines[39]. Thus, some bee-white flowers, as well as those of other colours, may increase their visitations by pollinators through having highly dissected outlines. Furthermore, for bees at least, more spatial detail from a flower's image impinging on the lower part of the optical field of the compound eye would exploit the fact that bees assign special weight to this field when learning and recognizing patterns[38,40]. Most flowers display either general radial or bilateral symmetry, but the degree is variable[41]. Bees show preferences for symmetrical flower patterns over nonsymmetrical ones[42,43], behaviour which has implications for reliability of pollination and the plants' Darwinian fitness[41,43]. Thus, flowers that contrast poorly against their backgrounds may become more attractive by displaying uniformity and close perfection in symmetry. Studies are already under way to test this hypothesis.

Conclusion

Floral colours are of prime importance to many species of plants for attracting pollinators. Many pollinators are adept at learning to associate floral colours with food (mostly nectar or pollen or both). Ultraviolet reflections from some flowers impart colours that cannot be appreciated directly by human beings, and white flowers, which appear so abundant to humans, are almost all UV absorbing and so not white (equally reflective across the visual spectrum) to insects. Insect-white flowers lack colour contrast against vegetation and other backgrounds, which are more or less neutrally coloured to insects. Recent discoveries on colour perception in insects (honeybees) show that brightness is not perceived and that bees have great difficulty in learning to associate insect-white targets with food, and other pollinators avoid such targets. Thus, truly white flowers to insects could not be distinguished readily from their backgrounds, and as a result would be largely overlooked, ignored, or detected by other floral features. An understanding of both the sensory physiology and perceptual psychology of receivers is needed when examining relationships involving biological signalling: the case of white flowers and their mutualistic relationship with pollinators exemplifies the point.

Acknowledgements

We thank Andrew Bennett, Robert Brandt, Natalie Hempel, Randolf Menzel and Misha Vorobyev for fruitful discussions and their valuable comments on the manuscript. Special thanks are extended to W. Barthlott for use of his photographs. P.K. acknowledges the support of the Deutscher Akademischer Austauschdienst (DAAD) for study at the Freie Universität Berlin and of the Natural Sciences and Engineering Research Council of Canada (NSERC), which has made this article possible. M.G. thanks the Alexander von Humboldt-Stiftung and the International Foundation for Science (IFS) for support. L.C. was supported by the Deutsche Forschungsgemeinschaft (DFG).

References

1 Faegri, K. and van der Pijl, L. (1979) *The Principles of Pollination Ecology* (3rd edn), Pergamon Press

2 Butler, C.G. (1951) The importance of perfume in the discovery of food by the worker honey-bee (*Apis mellifera* L.), *Proc. R. Soc. London Ser. B* 138, 403–413
3 Chittka, L. and Menzel, R. (1992) The evolutionary adaptation of flower colors and the insect pollinators' color vision, *J. Comp. Physiol. Ser. A* 171, 171–181
4 Kevan, P. (1978) Floral coloration, its colorimetric analysis and significance in anthecology, in *The Pollination of Flowers by Insects* (Richards, A.J., ed.), pp. 51–78, Academic Press
5 Kevan, P. (1983) Floral colours through the insect eye: what they are and what they mean, in *Handbook of Experimental Pollination Biology* (Jones, C.E. and Little, R.J., eds), pp. 3–30, Scientific and Academic Editions
6 Wehner, R. (1981) Spatial vision in arthropods, in *Handbook of Sensory Physiology* (VII/6C) (Autrum, H.J., ed.), pp. 287–616, Springer
7 Menzel R. and Backhaus, W. (1991) Colour vision in insects, in *The Perception of Colour* (Vision and Visual Dysfunction, Vol. 6) (Gouras, P., ed.), pp. 262–293, Macmillan
8 Rosen, D. and Barthlott, W. (1991) Ökologische Aspekte der Ultraviolett-Reflexion von Blüten in Mitteleuropa, besonders in der Eifel, *Decheniana* 144, 72–112
9 Kevan, P.G. (1979) Vegetation and floral colors revealed by ultraviolet light: interpretational difficulties for functional significance, *Am. J. Bot.* 66, 749–751
10 Daumer, K. (1958) Blumenfarben wie sie die Bienen sehen, *Z. Vgl. Physiol.* 41, 49–110
11 Kugler, H. (1963) UV-Musterungen auf Blüten und ihr Zustandekommen, *Planta* 59, 296–329
12 Kevan, P. (1972) Floral colours in the High Arctic with reference to insect–flower relations and pollination, *Can. J. Bot.* 50, 2289–2316
13 Menzel, R. and Shmida, A. (1993) The ecology of flower colours and the natural colour vision of insect pollinators: the Israeli flora as a study case, *Biol. Rev.* 68, 81–120
14 Chittka, L. *et al.* (1994) Ultraviolet as a component of flower reflections, and the colour perception of Hymenoptera, *Vis. Res.* 11, 1489–1508
15 Lotmar, R. (1933) Neue Untersuchungen über den Farbensinn der Bienen mit besonderer Berücksichtigung des Ultravioletts, *Z. Vgl. Physiol.* 19, 673–723
16 Scogin, R. (1983) Visible floral pigments and pollinators, in *Handbook of Experimental Pollination Biology* (Jones, C.E. and Little, R.J., eds), pp. 160–172, Scientific and Academic Editions
17 Weevers, T. (1952) Flower colours and their frequency, *Acta Bot. Neerl.* 1, 81–92
18 Burkhardt, D. (1982) Birds, berries and UV: a note on some consequences of UV vision in birds, *Naturwissenschaften* 69, 153–157
19 Backhaus, W. and Menzel, R. (1987) Color distance derived from a receptor model for color vision in the honeybee, *Biol. Cybern.* 55, 321–331
20 White, R. *et al.* (1994) Wavelength discrimination and the role of ultraviolet vision in the feeding behavior of hawkmoths, *Biotropica* 26, 427–435
21 Wyszecki, G. and Stiles, W.S. (1982) *Color Science: Concepts and Methods. Quantitative Data and Formulae*, Wiley
22 Hertz, M. (1937) Versuche über das Farbensystem der Bienen, *Naturwissenschaften* 25, 492–493
23 Hertz, M. (1937) Beiträge zum Farbensinn und Formensinn der Biene, *Z. Vgl. Physiol.* 24, 413–421
24 Engländer, H. (1941) Die Bedeutung der weißen Farbe für die Orientierung der Bienen am Stand, *Arch. Bienenkde* 22, 516–549
25 Menzel, R. (1967) Untersuchungen zum Erlernen von Spektralfarben durch die Honigbiene (*Apis mellifica*), *Z. Vgl. Physiol.* 56, 22–62
26 von Helversen, O. (1972) Zur spektralen Unterschiedsempfindlichkeit der Honigbiene, *J. Comp. Physiol.* 80, 439–472
27 Backhaus, W. (1991) Color opponent coding in the visual system of the honeybee, *Vis. Res.* 31, 1381–1397
28 Chittka, L. *et al.* (1992) Opponent coding is a universal strategy to evaluate the photoreceptor inputs in Hymenoptera, *J. Comp. Physiol. Ser. A* 170, 545–563
29 Brandt, R. *et al.* (1993) Simulation of threshold spectral sensitivity according to the color theory for the honeybee, in *Gene–Brain–Behaviour* (Heisenberg, M. and Elsner, N., eds), p. 374, Thieme
30 Troje, N. (1993) Spectral categories in the learning behaviour of blowflies, *Z. Naturforsch. Ser. C* 48, 96–104
31 Lehrer, M. (1993) Parallel processing of motion, colour and shape in the visual system of the honeybee, in *Sensory Systems of Arthropods* (Wiese, K. *et al.*, eds), pp. 266–272, Birkhäuser
32 Lehrer, M. (1994) Spatial vision in the honeybee: the use of different cues in different tasks, *Vis. Res.* 34, 2363–2385
33 Lehrer, M. *et al.* (1988) Motion cues provide the bee's visual world with a third dimension, *Nature* 332, 356–357
34 Srinivasan, M. *et al.* (1992) Range perception through apparent image speed in freely flying honeybees, *Visual Neurosci.* 6, 519–535
35 Lehrer, M. *et al.* (1990) Visual edge detection in the honeybee and its spectral properties, *Proc. R. Soc. London Ser. B* 238, 321–330
36 Krantz, D.H. (1972) Visual scaling, in *Handbook of Sensory Physiology* (Vol. VII/4) (Jameson, D. and Hurvich, L.M., eds), pp. 660–689, Springer
37 Giurfa, M. *et al.* (1996) Detection of coloured stimuli by honeybees: minimum visual angles and receptor specific contrasts, *J. Comp. Physiol. Ser. A* 178, 699–709
38 Giurfa, M. *et al.* (1995) Color and angular orientation in the discrimination of bilateral symmetric patterns in the honeybee, *Naturwissenschaften* 82, 198–201
39 Hertz, M. (1929) Die Organisation des optischen Feldes bei der Biene, I, *Z. Vgl. Physiol.* 8, 693–748
40 Wehner, R. (1972) Dorsoventral asymmetry in the visual field of the bee, *Apis mellifica*, *J. Comp. Physiol.* 77, 265–277
41 Møller, A.P. and Eriksson, M. (1994) Patterns of fluctuating asymmetry in flowers: implications for sexual selection in plants, *J. Evol. Biol.* 7, 97–113
42 Giurfa, M. *et al.* Symmetry perception in an insect, *Nature* (in press)
43 Møller, A.P. (1995) Bumblebee preference for symmetrical flowers, *Proc. Natl. Acad. Sci. U. S. A.* 92, 2288–2292
44 Chittka, L. (1992) The colour hexagon: a chromaticity diagram based on photoreceptor excitations as a generalized representation of colour opponency, *J. Comp. Physiol. Ser. A* 170, 533–543

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