

VISUAL SENSITIVITY AND FORAGING IN SOCIAL WASPS

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INTRODUCTION

A substantial amount of experimental work has been concerned with the properties of the compound eye of insects, particularly of honey-bees. Most such studies are either of visual sensitivity, or of brightness or colour discrimination of flying insects, but only when these are sessile and working at the lower limit of their sensitivity. Little attention has been paid to the possibility that functional threshold illuminations for a flying insect in actual flight may be substantially higher than for a sessile insect. The luminosity thresholds for the cat (1×10^8 millelamberts) and for man (5.5×10^7 mL.) as determined by GUNTER (1951), provide local illuminations much below that at which these mammals are able to negotiate objects at speed.

WOLF and ZERRAHN-WOLF (1936) find that the eye of the honey-bee, light-adapted at 142 mL. failed to respond to a moving strip pattern at luminosities equivalent to 1-2 mL. After some 30 min. dark adaptation, the strip pattern could be detected at about 2×10^3 mL. BARLOW (1952) has suggested that, in order to be continuously visible to a honey-bee, a barely distinguishable mark must be subjected to at least a thousand times the illumination necessary for human sight to distinguish it. BARLOW also showed that the sensitivity of the hymenopterous eye was approximately proportional to the length of the eye, so that larger insects should be the more sensitive.

The sensitivity of the hymenopterous eye as a whole seems to depend on the largest number of ommatidia aligned in any one direction (the length of the eye being the greatest such distance) provided that the interommatide angle is kept just below the limiting resolving power of each ommatidium. Evidently, such a limitation restricts the number of facets in an eye of a given size. Barlow discusses the possible advantages to an insect of increasing either of these competing attributes. TEISSIER (1926) had earlier found that, over a wide range of insects including the Vespinae, the allometric growth of the insects is such that the surface area of a facet is proportional to the number of ommatidia in an eye. This relationship presumably reflects the optimum balance between the two desiderata noted above. Since this relation holds even among the different instars of the mainly nocturnal *Blatta orientalis* L. it is unlikely to be a characteristic of diurnal insects alone, though there are specialized insects for which this relation may not hold. The nocturnally foraging South American wasp *Apoica* has smaller eyes than have Vespinae, but the shape of the eye is different and the ocelli are more developed (RICHARDS and RICHARDS, 1951). Differences in the foraging periods of social hymenoptera may be related to their visual sensitivities. The hornet for instance, continues to forage in moonlight (WOOD, 1872) whereas the writer knows of no such records for British wasps. The object of this paper is to present the evidence which establishes the relation between the duration of foraging activity and functional visual sensitivity, on a quantitative basis, for some of the social hymenoptera.

EXPERIMENTAL

Records of the horizontal illumination were taken at dusk, or at dawn, when foraging ceased or commenced. The first practical difficulty was to establish the end-points of activity. The second was to decide whether to record the luminosity of the nest entrance and flight markers, often in shade, or the general horizontal illumination in the open. Neither difficulty proved severe.

Two end-points were found to be reproducibly observable at dusk: the refusal of potential foragers to leave the nest, and the return of the last forager. Refusal to forage was usually preceded by abortive flight just sufficiently far from the nest for the worker to obtain a clear view of the sky. When perhaps half a dozen such flights had resulted in the workers hesitating, and returning to the nest, no further sorties were observed. The manner in which these decisions were made by the workers determined the choice of horizontal illumination as a measure of light intensity rather than nest luminosity.

Exception might be taken to the recording of the illuminations when the last forager returns, on the grounds that, once sorties have ceased, the normal duration of a foraging trip will decide what illumination obtains when the last entry is made. This duration would, stochastically, tend to increase with the number of foragers out at the time. However, there is evidence that worker wasps do not always return to the nest at night (GAUL, 1952; BLACKITH, 1957) though how general this tendency may be is not clear. The last workers at the nest entrance fly slowly from one minor reference mark, such as a twig or leaf, to another, and collisions with leaves or blades of grass or with other workers are common. This behaviour, together with the sudden cessation of activity at a clearly defined level of illumination, leaves little doubt that the last entrants are flying at the effective limit of their visual sensitivity. There are interesting specific differences in the behaviour of wasps trying to locate the nest entrance at dusk. *V. rufa* hovers until it can lower itself into the hole, but *V. germanica* lands impetuously near the nest and half crawls, half flies, to the hole. *V. vulgaris* resembles *V. germanica* in this respect.

When this behaviour was seen, a reading was rapidly taken with a "Lumeter" photometer. By pre-setting the instrument to the expected range, and keeping it as near the nest as the shading effect of trees, etc. permitted, only a few seconds elapsed before attention was again transferred to the nest to ensure that activity had ceased. The low reflectivity coefficient of nest entrances is noteworthy; it usually lies between 0.1 and 0.05.

The identification of the wasps was in each instance confirmed by excavating the nests and extracting the males and females at the end of the season.

RESULTS

Two facts support the contention that illumination is by far the most important single factor in determining the duration of foraging in the Vespinae. One of these facts is the close agreement between the foraging thresholds at dawn and at dusk.

When considering this agreement the normal range of diurnal variation is worth bearing in mind. Full summer sunlight provides some 8-10,000 lumens/sq.ft., whereas a starlit but moonless night provides about 0.002 lumens/sq.ft. Within this wide range we find that, for *V. germanica* (Nest A) in Table I, the mean illumination at dawn for the first sortie is 0.15 lumens/sq.ft. and in the evening the last forager returns when the illumination falls to 0.25 lumens/sq.ft.

TABLE I.—*V. germanica*.

DATE.	NEST.	AIR TEMP. °C.	ILLUMINATION (LUMENS/SQ. FT.) AT			WEATHER NOTES.
			<i>First sortie.</i>	<i>Last sortie.</i>	<i>Last entry.</i>	
—	—	—	—	—	—	—
5 ix '55	A	16.1	—	5.78	0.21	Clear skies after rain.
6 ix '55	A	15.0	—	2.89	0.35	Clear skies.
7 ix '55	A	6.1/16.7	0.18	1.73	0.30	Clear skies, dawn and dusk, mist at dawn.
8 ix '55	A	17.2	—	2.60	0.35	Clear skies.
9 ix '55	A	12.8/13.6	0.17	3.32	0.36	Clear skies dawn and dusk.
13 ix '55	A	11.1/10.6	0.14	8.08	0.36	Heavy cloud, rain at dawn.
14 ix '55	A	7.8	0.21	—	—	Clear skies.
16 ix '55	A	13.3	—	2.02	0.19	Heavy cloud.
26 ix '55	A	12.2	—	6.91	0.23	Light cloud.
30 ix '55	A	13.3	0.12	—	—	Cloudy.
6 x '55	A	11.1/11.1	0.11	1.77	0.24	Light cloud, strong winds dawn and dusk.
11 x '55	A	15.6	—	2.26	0.12	Light cloud.
14 x '55	A	11.7	—	2.74	0.09	Clear skies.

TABLE II.—*V. rufa*.

DATE.	NEST.	AIR TEMP. °C.	ILLUMINATION (LUMENS/SQ. FT.) AT			WEATHER NOTES.
			<i>First sortie.</i>	<i>Last sortie.</i>	<i>Last entry.</i>	
—	—	—	—	—	—	—
31 vii '52	B	17.8	—	2.20	0.19	Broken cloud
6 viii '52	B	12.8/17.2	0.12	1.39	0.28	Thin cloud dawn; thick cloud dusk, after rain.
24 viii '55	C	13.3/22.2	0.40	5.78	0.78	Cloudy dawn and dusk: light mist dawn.
26 viii '55	C	18.9	—	2.02	0.72	—
29 viii '55	C	15.6	—	4.04	0.86	Clear skies.
30 viii '55	C	18.3	—	3.17	0.37	—
1 ix '55	C	12.2/20.0	0.60	2.02	0.26	Clear skies dawn; cloudy dusk.
2 ix '55	C	16.1	—	6.37	0.99	—

TABLE III.—*V. vulgaris*.

DATE.	NEST.	AIR TEMP. °C.	ILLUMINATION (LUMENS/SQ. FT.) AT		
			<i>First sortie.</i>	<i>Last sortie.</i>	<i>Last entry.</i>
—	—	—	—	—	—
13 viii '52	D	17.2	—	4.00	0.39
14 viii '52	D	15.6	—	1.38	0.35
15 viii '53	E	15.4	—	1.33	0.17
19 viii '53	F	15.4	—	2.50	0.30
21 viii '53	G	11.7	—	0.95	0.12
24 viii '53	G	14.4	—	1.50	0.13
26 viii '53	G	13.9	—	1.33	0.20
27 viii '53	G	14.4	—	1.17	0.12

TABLE IV.—*V. crabro*.

DATE.	NEST.	AIR TEMP. °C.	ILLUMINATION (LUMENS/SQ. FT.) AT		
			<i>First sortie.</i>	<i>Last sortie.</i>	<i>Last entry.</i>
—	—	—	—	—	—
14 viii '53	H	13.3	—	0.0133	0.0033
21 viii '53	H	12.2	—	0.0130	0.0025
24 viii '53	H	14.4	—	0.0160	0.0042
26 viii '53	H	10.6/10.6	0.010	0.0180	0.0020
27 viii '53	H	13.3	—	0.0150	0.0017

Secondly, when the illumination approaches the threshold in the evening, the workers are plainly flying at the limit of their visual sensitivity. Typically, they collide with one another and with twigs, leaves, and blades of grass and navigate to the nest by way of a series of minor reference marks which are not searched for during the day even though the wasps may in fact be using them as reference points.

Similarly, for hornets (table IV) there is good agreement between the illumination at which they refuse to forage and that at which they recommence foraging. These insects, apparently, do not need to refrain from leaving the nest at an illumination higher than their visual threshold, as do wasps, because their visual threshold is so much lower. For large hymenoptera, the foraging thresholds lie within ranges of illumination at which predicted dark-adaptation should be complete, in the hornet this range corresponds roughly with that found on a moonlit night. Direct observation, both visual and aural, confirms the continued nocturnal foraging of hornets recorded by Wood (1872). If a cloud passes across the moon, foraging is suspended and restored with the moonlight, suggesting that changes of illumination are readily discovered by the workers. Moreover, these thresholds are much the same whether the moon is full, but lightly obscured by cloud (a diffuse source), or whether it is only three quarters full (virtually a point source).

There is now good evidence that the function of the workers stationed at night near the nest entrance is more closely connected with the perception of light intensity than with defence. Negative evidence is that such workers are often so cold after a few hours in this position that they are capable only of clumsy movements, such as a feeble hostile separation of the mandible when prodded and they fail to respond to a suspended live worker from another nest. Nevertheless, shortly before the foraging threshold illumination is reached at dawn, these workers crawl out to the platform of bare earth and excavated particles common round wasps nests and then back into the nest. The inference that the onset of foraging is prepared by the return of the workers, often loosely regarded as sentries, seems reasonable, though no doubt the information conveyed is no more specific than generalized activity. On only one occasion has a foreign insect been observed to enter a nest. At first light on 11.X.'55 a flying *Geotrupes stercorarius* landed on the entrance of the *V. germanica* nest, and half walked, half fell, inside. The workers at the entrance made no response other than the usual swaying of the body which can be evoked by prodding them with a stick. Not until the beetle had been in the nest for about a minute was there any demonstration by the wasps, but the noise of the eventual disturbance was considerable, though no wasps left the nest during it. When this nest was excavated a week later the dismembered integument of the beetle was found below the nest. Badgers, too, seem able to excavate wasps' nests at night with impunity, although the eyes and nose are exposed to stings. A noticeable feature of the activity of badgers at Silwood Park, where 7 of the 9 known nests were destroyed by them during 1955, is that nests of more than about 3-500 workers are rarely attacked. Several workers have pointed out that wasps in larger nests become more aggressive than those in less populous nests.

Changes of apparent threshold values with number of foraging insects.

The difficulty of defining a threshold in terms of the behaviour of the first or last insect to perform an action is that the vagaries of an individual are substituted for the average behaviour of a group of insects. Nevertheless, these vagaries are themselves predictable. Generally, the more workers there are foraging the sharper will these thresholds be defined. Although we know that the sorties from, and entries to, a nest follow the negative binomial distribution, we may consider the low foraging densities for which the frequencies become indistinguishable from the Poisson expectations (Blackith, 1957). It is for such low frequencies that the problem of estimating the thresholds becomes most acute.

If there are m wasps returning to the nest per minute at dusk, the probability that the minute in which the true threshold illumination is attained will have no returning foragers is e^{-m} . Thus on $1/e^m$ of the evenings on which

the last returning forager is watched, the estimated threshold will be too high by the amount by which the illumination is deteriorating per minute. Similarly, one out of every e^{2m} evenings will give estimates which are high by an amount equivalent to the deterioration of illumination during the two-minute interval. Under normal conditions, this deterioration is about 0.2 lumen/sq.ft. in two minutes. A more accurate, though less immediately useful, estimate is that the illumination decreases by a factor of 10 in 10-15 minutes. Broken cloud will produce substantial divergencies from this rate over short periods.

We can obtain some estimate of the error thus caused by considering a nest whose foragers return at the low rate of one a minute.

On an average one threshold in every three will be high by some 0.2 lumens/sq.ft. Such a bias will be much reduced by an increase of foraging strength.

Relation between eye sizes and foraging thresholds.

The simple relation propounded by Barlow (1952), that the sensitivity of the hymenopterous eye is likely to be proportional to its length, needs qualification in the present context. Barlow's examples of social wasps include measurements of the eye of a queen *V. germanica* (as evidenced by the length of 3.31 mm. plotted in his figure) and a queen of *V. crabro* (plotted eye-length 4.60 mm.). For our discussion we need the lengths of eye for workers. Moreover, some idea of the distribution of these lengths of eye is useful, because, if the range is wide and the distribution skew, an unrepresentative minority of workers may be concerned with those first sorties or last entries which determine the thresholds.

The eyelengths of 330 workers of *V. germanica* (from nest A; Table I) were found to have a mean of 2.478 mm. The standard error of the distribution was 0.13 mm. and that of the mean was 0.0070 mm. The distribution was symmetrical and showed no tendency to log-normality. The range was narrow from 2.2 to 2.8 mm. The possibility still exists that the late foragers are a biased sample of the worker force, but the importance of this possibility is much diminished. The mean length of 50 eyes from the virgin queens of this nest was 3.176 mm. (standard error of a distribution; 0.087 mm., and of the mean 0.012 mm.). The notably greater uniformity of the queens is in accordance with the experience of THOMSON, BELL and PEARSON (1910). The eyes of 100 *V. vulgaris* workers were on an average 2.337 mm. long, with standard errors of 0.096 mm. for the distribution and 0.009 mm. for the mean. Thus there is a significant discrepancy of eyelength between these two sets of workers of the two species. However, the proper sampling unit for investigations of social wasps is probably the nest rather than the individual, so that much more extensive investigation would be required

before one could say more than that the difference in size of the eyes is negligibly small for the present discussion.

Similarly, two samples of workers were taken from two different nests of *V. rufa*. Nest C (Table II) produced workers whose mean eye-length was 2.445 mm., with standard errors of 0.057 for the mean of 35 wasps, 0.315 for the distribution. Another nest not included in the tables contained workers with eyes averaging 2.366 mm. the standard errors being 0.094 for the distribution, and 0.014 for the mean of 41 individuals. The mean lengths of eye from each nest differ significantly at the 5 % level of probability, confirming the suggestion of THOMSON, BELL and PEARSON (1910) and of RICHARDS and RICHARDS (1951) that the effective sampling unit for social wasps is the nest rather than the individual.

The length of the eye of a stock of honeybees was 2.052 mm. (standard error of mean of 50 workers 0.018) a value substantially lower than that for wasps. Worker hornets, on the other hand, have eyes of average length 3.933 mm. with a standard error of 0.088 for the mean of 4 measured workers. Thus hornets, wasps and honey-bees have clearly different lengths of eye, and clearly different functional illumination thresholds, which are inversely related to the eye-lengths.

DISCUSSION

The outstanding conclusion from these experiments is that the level of illumination is at once important and different in kind from the other factors which influence foraging activity. Adverse factors other than low illumination, such as coldness, high winds, or heavy rain, may each reduce the number of workers foraging, but they do not alter the diurnal limits of this activity save in so far as these depend stochastically on the number of foragers.

Otherwise, a few workers will leave the nest at dawn even when the grass temperatures are as low as 2°C, or in winds gusting to Force 7 (about 50 km./hr.) on the Beaufort scale (moderate gale) and in steady rain. The readiness of workers to leave the nest under such conditions seems greater at dawn (first light) than at any other time.

The processes of nest-awakening, taking flight, and foraging are distinct. The first two processes are uniquely determined by the illumination, though adverse conditions may induce a high proportion of workers to refuse to forage, and at dusk the foragers will refuse at illuminations insufficient to permit the successful conclusion of a sortie. Foraging itself depends on the visibility of reference marks, and is shown to be distinct from, though naturally bound up with, illumination by the behaviour of workers in a thick mist at dawn. In these circumstances the worker will take flight as soon as the critical illumination is reached, but wander in the vicinity of the nest before returning, for a period which increases as the visibility improves. In terms of the human eye, a visibility

of about 70 yds. is needed for free foraging without refusals, but the difference between human and vespine vision may well vitiate this comparison.

The compound structure of the insect eye might lead one to expect a different threshold according to whether the illumination is diffuse or concentrated. Yet the intensity of illumination required for the foraging of hornets is the same whether it be from a full moon lightly obscured by cloud or an unobscured three-quarter moon. The behaviour of workers whose nest is among undergrowth supports the view that wasps judge when to take flight by the appearance of the sky, and are not misled by artificial (local) illumination. Such workers fly as far as is necessary to obtain a clear view of the sky, though such short trips are often observed in unobscured nests, even when no refuse is to be dropped, at dusk.

The decision to refuse or to continue foraging must depend on the sensitivity of the individual worker, but is also likely to vary with the drive to a particular form of collecting activity. BRIAN and BRIAN (1953) have shown that the predominant form of foraging activity alters during the day, and that workers engaged on one activity are but little interested in opportunities for other types of foraging. Since these drives are probably acquired during the worker's stay in the nest, their willingness to forage may be modified by the extent to which environmental conditions interfere with the several forms of activity. A forager intending to collect insect food might well be more easily deterred by low temperatures than would be one requiring building material or concerned to jettison refuse.

A noticeable feature of wasp behaviour is the greater élan with which wasps move at dawn, perhaps because the light is then improving, perhaps because they are then rested. Workers take rapid advantage of lulls in periods of inclement weather, arriving back at the nest during intervals between showers and gusts of wind where possible.

Although the main conclusions of this work are in broad agreement with those of GAUL (1952) the amplification of the scope of the work suggests that revision of his conclusions is desirable. GAUL suggests that, up to a point, higher temperatures induce activity at lower intensities of illumination, and conversely. The difference between the species studied by GAUL and those studied here may account for the present conclusion that activity is independent of temperature above 2°C, but it is also possible that GAUL made insufficient allowance for the quantitative relationship between temperature and activity, and hence the indirect stochastic dependence of the illumination threshold on the ambient temperature, without there being any direct qualitative dependence.

According to GAUL, the lowest temperature at which *Vespula maculifrons* Bey will fly is 8.5°C, and for *Dolichovespula maculata* L. it is 5°C. These values seem to be higher than for any British species of *Vespula*, whose thresholds lie between 0.1 and 1.0 lumens per sq. ft. at all temperature down to 2°C. If we ignore the supposed influence of temperature in

GAUL's experiments, his species fly at illuminations within the range quoted for the European species.

The ecological consequences of these physiological differences among Vespinae are considerable. The worker force of the hornet has, potentially, a foraging capacity out of all proportion to the numerical relation between the numbers of workers severally available to hornets and to those wasps with subterranean nests. Taking the foraging threshold at 0.01 lumens/sq.ft. there will be some 20 nights during the season throughout which hornets can forage, weather permitting. A full moon provides an illumination of about 0.013 lumens/sq.ft. and in general not all the night will be so illuminated. We do not know, however, whether rest is necessary for the workers, nor whether all types of foraging can be done at these low illuminations.

Nests of social wasps kept in the laboratory and made visible by removal of the envelope show greatly reduced activity at night. Some indication that this result is not an artefact of captivity is given by the rapid nocturnal killing of wild nests with hydrogen cyanide. On excavation some workers are found with larvae and small stones or earth in their mandibles, which fact suggests some continued activity at night.

The worker force normally increases up to the time the sexual forms are produced, but the amount of work which can be done by each worker outside the nest decreases steadily from midsummer, when about 17 hours are light enough for wasps to work, until early November, when only about 10 hours can be worked. This reduction of the effective foraging capacity is more serious for wasps than for hornets.

A few observations on honey-bees suggest that although the critical illuminations are much higher for *Apis* than for wasps, the difference between the logarithmic intensities at which sorties and entries cease is the same as it is for wasps and for hornets. This constant difference in stimulus, measured on that logarithmic scale which is appropriate to many biological stimuli, suggests that the higher illumination needed for sorties by social hymenoptera at dusk may be determined by a difference in the drive to foraging rather than by the teleologically more obvious need to allow time for a forage before return to the nest becomes impracticable. However, the drive of the honey-bee towards foraging activity is notoriously dependent on the weather, and on the honey-flow, so that this part of the investigation was not pursued.

Summary.

While there is a distinction between that intensity of illumination which permits social wasps to forage, and that to which a sessile worker can respond, nevertheless illumination is the most critical of the environmental factors which control the activity of wasps. Low temperatures, high winds, and heavy rain all reduce activity but unless exceptionally

severe do not wholly stop it. At dawn, when the critical level of illumination is attained, workers leave the nest, but at dusk they will not leave should the same critical level be due in the course of the foraging flight, after which they could not return.

The three species of wasp, *Vespula vulgaris*, *V. rufa*, and *V. germanica* have a common threshold of illumination, although the hornet, *Vespa crabro* can forage in moonlight at an altogether lower illumination. Honey-bees normally need a still higher illumination than do wasps.

In all these species, the thresholds of illumination are related to the length of the compound eyes, so that species with large eyes need less light by which to forage. Moreover, there is a slight difference between the threshold at dawn when workers leave the nest, and that at dusk, when they must needs have sufficient light by which to return. This difference is almost constant for each species, when, as is customary, one measures it on a logarithmic scale.

Lastly, the estimates, which these experiments provide, of the threshold illuminations depend stochastically on the number of workers foraging. A correction for this bias is given.

Sommaire.

Parmi les facteurs du milieu qui contrôlent l'activité des guêpes, celui de l'intensité de lumière est le plus important ; toutefois on note une différence entre l'intensité de lumière qui permet aux guêpes sociales de fourrager, et celle qui produit une réponse des ouvrières sessiles.

En général, les basses températures, les vents forts, et les grandes pluies réduisent leur activité, mais ces facteurs ne l'arrêtent pas complètement, à moins qu'ils ne soient très marqués.

À l'aube, quand le niveau critique de lumière est atteint, les ouvrières quittent le guêpier, mais, le soir, si elles s'attendent à ce que la lumière vienne à s'abaisser au cours de leur sortie au-dessous du niveau critique, elles ne sortent pas.

Les trois espèces de guêpe, *Vespula vulgaris*, *V. rufa*, et *V. germanica*, réagissent au même seuil de lumière, mais le frelon, *Vespa crabro*, est capable de fourrager au clair de lune par une lumière moins intense. Normalement, les abeilles exigent une lumière plus intense que les guêpes.

Dans toutes ces espèces, le seuil de lumière se rapporte à la hauteur des yeux composés, par conséquent les espèces pourvues de grands yeux sont à même de fourrager par une lumière moins intense. De plus, il y a une légère différence entre le seuil de lumière à l'aube, quand les ouvrières quittent le guêpier, et celui du soir lorsqu'elles ont besoin d'une lumière suffisante pour rentrer. Cette différence, quand elle est mesurée à l'échelle logarithmique, comme il est d'usage, est presque constante pour chaque espèce.

Enfin, les évaluations du seuil de lumière dans ces expériences dépendent stochastiquement du nombre d'ouvrières en train de fourrager. On a tenu compte de ce fait.

Epitome.

Distinctio inter duas res fit, aut lumen idoneum est qui vespis socialibus facultatem volitare det, aut stativas vespas utcumque ututque respondere sinet. Si lux tenet, et frigus et ventus atque imber strenuitatem vesparum aegre opprimunt, nisi quum graviore sunt; sin minus, obscuritas immobilitatem importat.

Tria genera, id est *Vespula vulgaris*, *V. rufa*, *V. germanica*, supparibus liminibus lucis expergiscuntur proveniuntque, sed de crabrone, *Vespa crabro*, propter oculos longiores vespis lumen minus est, quoad lunae lumen desit. Contrarie, de apibus in alveum congerens propter oculos breviores limen superat.

Prima luce limen lucis subtiliter sed significanter deficit quod ad crepusculum attinet dum lux paulatim contabescit. Disjunctio inter haec limina in unoquoque genere constat, dummodo ad gradum logarithmicum, ut est consuetudo, disponantur. Vesperi vespae, omnia fuga, temperi commorantur, quominus permulti pabulatores, quasi in loco clarigationis, abnoctent.

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