

On the Role of Light in the Mating Behavior of *Drosophila subobscura*

Wilhelm Pinsker

Universität Tübingen, Institut für Biologie II, Lehrstuhl für Populationsgenetik, Auf der Morgenstelle 28, D-7400 Tübingen

and

Elfriede Doschek

Universität Wien, Institut für allgemeine Biologie

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Unlike other related species wild flies of *Drosophila subobscura* require light for successful mating. Two explanations for the influence of light on the reproductive behavior could be suggested:

- 1) Light increases sexual activity.
- 2) Light mediates the transmission of visual courtship elements.

In order to decide this question the mating success of wild-type and mutant flies was tested at light of different wave-lengths. It turned out that mutant flies with reduced ommochrome component of the eye pigment were not able to copulate at wave-lengths above 570 nm whereas the other strains still copulated at wave lengths close to the limit of their spectral sensitivity. Since spectral sensitivity of the photoreceptors is assumed to be the same in all strains tested the difference in mating success must be ascribed to effects caused by the lack of pigment. Thus an investigation of the optomotor response was carried out. It revealed that mating success is clearly correlated with the ability to discriminate contrast. From this result it can be concluded that the exchange of visual signals and not merely the perception of light is essential for the courtship of *Drosophila subobscura*. Optical stimuli may be important at two different stages of mating behavior: at the beginning, when the male is activated by the sight of a female, and during the wing dance, where the movements of the partners are coordinated optically.

Introduction

Wild flies of the species *Drosophila subobscura* are not able to mate in complete darkness. This fact was pointed out first by Philip *et al.* [1]. Since that time several authors have tried to find some explanation for this strange feature of the sexual behavior which is not found among other closely related species of the *Drosophila obscura*-group [2]. There are two main theories about the reasons for this light dependence of *Drosophila subobscura* in reproduction:

- 1) The general activity of *Drosophila subobscura* is highly reduced in darkness and as a consequence the mating activity is also suppressed.
- 2) Light is necessary for the flies to exchange visual stimuli during courtship.

Experimental support exists for both theories. Wallace and Dobzhansky [3] tried to watch how the

flies behave in the dark, using observation chambers illuminated by light of wave lengths above 610 nm. Light of this range of the spectrum is very near to the limit of sensitivity of the *Drosophila* eye [4 – 6]. On these light conditions flies of the species *Drosophila subobscura* turned out to be quite motionless, showing neither courtship behavior nor other activities. With the related species *Drosophila pseudoobscura*, however, no change in behavior could be observed in the same experimental conditions. The flies moved and copulated as they do in normal light. From this result one may suggest that *Drosophila subobscura* needs light to trigger its general activity. This would offer a reasonable explanation for the light dependence in its mating behavior.

There are, however, also strong arguments for the second theory. Investigations of Rendel [7], Milani [2], Spieth [8], Mynard Smith [9] and Brown [10] revealed that during the courtship of *Drosophila subobscura* the wings of the male serve as a visual signal to stimulate the females. Grossfield [11] could show that males of *Drosophila subobscura* failed to

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copulate after amputation of their wings whereas with males of *Drosophila melanogaster* and *Drosophila auraria* the same amputation did not reduce the mating success remarkably. This finding might be interpreted in such a way that in the courtship of *Drosophila subobscura* visual signals are very important. The fact that these signals cannot be transmitted in darkness may account for the necessity of light during mating in this species. In this connection it should be mentioned that in *Drosophila subobscura* courtship lacks characteristic acoustic elements. Unlike in many other species of the genus sound producing wing vibration could not be observed and no courtship song could be recorded [12]. It can be assumed that the loss of acoustic courtship signals played a decisive role in the speciation process of *Drosophila subobscura* leading to the evolution of a species-specific nonacoustic courtship behavior with predominance of visual elements and thus to the peculiarity of light dependent mating.

One way to decide the question which of the two explanations is right, could be to design experimental conditions which allow the flies to perceive only the brightness of light but not the shapes and movements of their sexual partners. If copulation took place in such a test this result would prove the first theory to be true. If not, the dependence of mating on visual courtship elements becomes highly probable.

These experimental conditions can be provided using mutant flies with deficiencies in eye pigmentation. Kalmus [13], Götz [14] and Burnet *et al.* [15] measured the optomotor response of several eye color mutants and proved that the contrast discrimination of mutants with reduced screening pigment is remarkably lower. In wild-type flies the screening pigment is included in the primary and secondary pigment cells which surround the ommatidia of the compound eye. Lack of that pigment results in a breakdown of optical isolation between the ommatidia and therefore in a decrease in contrast discrimination whereas the sensitivity to light remains unchanged. In most eye color mutants only a certain component of the pigment is lost according to the block in the biosynthesis caused by the mutation. In the case of the mutant *white*, however, the screening pigment is almost completely absent. As a consequence *white* individuals are probably not able to recognize other flies optically but on the other hand they are not impeded in the perception of light. Hence this mutant

would ideally fulfill the requirements of the experiment described above.

Unfortunately no *white* strain exists in *Drosophila subobscura*. Several times males of the sex linked *white* mutant occurred in different laboratories [1] but they always failed to produce offspring. For that reason nobody succeeded in establishing a homozygous strain. Philip *et al.* [1] suspected that the sterility of the *white* males might be a behavioral sterility caused by defective vision.

In *Drosophila melanogaster* [16], *Drosophila pseudoobscura* [17] and *Drosophila ambigua* (Karlik, personal communication) the *white* eyed phenotype can be obtained by combining different eye color mutants. Similar experiments with *Drosophila subobscura* failed, mainly because no mutant with a complete block in the synthesis of the pteridin component was available. *Maroon*, the only mutant in question, lacks the red drospterin but instead has the precursor sepiapterin which causes a very dark pigmentation of the eye (Pinsker, unpubl.). A combination of *maroon* with the mutant *cinnabar*, which has no brown ommochrome component, resulted in flies of yellow eye color, but a few days after hatching the color turned to a dark brown. Thus also this method of producing flies with very low contrast discrimination had to be discarded.

An experimental approach to solve this problem was finally found when the fact that the components of the eye pigment differ in their absorption spectra [18] was taken into consideration. Accordingly, mutants with partly reduced screening pigment should have normal contrast discrimination only in light of wave-lengths which are absorbed by the remaining pigment. At wave-lengths, however, which are not absorbed by the pigment the contrast discrimination should be very low. In that case the experimental conditions would be ideal to investigate the importance of visual stimuli for the mating behavior of *Drosophila subobscura*.

Therefore two kinds of experiments were started. First the mating success of several eye color mutants of *Drosophila subobscura* was tested in light of different wave-lengths. If the mating behavior really depended on contrast discrimination some of the mutants should differ with respect to the wild-type on certain light conditions. To prove if these differences were due to reduced contrast discrimination a second experiment was carried out. In this experiment the optomotor response at different wave-

lengths was measured and compared with the results of the mating tests.

Materials and Methods

Strains

One wild-type strain and five mutant strains were used for the experiments. The wild-type strain was a mixture of several wild strains of different geographic origin. The mutant strain *maroon* (*ma*) has a dark-brown eye color due to the lack of the red drosopterin component in the eye pigment and the additional sepiapterin as mentioned before. With the mutants *light-red* (*ltr*), *cherry* (*ch*) and *poppy* (*pp*) the brown ommochrome component is partly reduced and completely absent in *cinnabar* (*cn*). As a result the phenotypic eye color of all these strains is light-red.

Mating experiments

For the mating tests virgin flies were prepared. Males and females were isolated 24 h after hatching and kept separated for seven days. At the age of eight days *Drosophila subobscura* flies reach their maximum sexual activity [19].

In the test groups of 3 males and 3 females were put together into a plastic vial of 10 ccm volume with some *Drosophila* food in it. Ten of these vials were placed together into a light-tight box with a glassfilter on top and a light source above. The glassfilters consisted of colored glass which transmits only a limited range of wave-lengths. As a light source a normal 60 W bulb was used. The mating success was tested in 6 different ranges of the spectrum: 400 nm (BG 12), 520 nm (VG 9), 550 nm (OG 550), 570 nm (OG 570), 590 nm (OG 590) and 610 nm (RG 610). The type of glassfilters produced by Schott is given in brackets.

Against this kind of experiment the objection could be raised that the intensity of light was completely neglected. This is true but the aim of the investigation was to find differences between strains in certain experimental conditions. For this purpose it is not important to know exactly the light intensity. The results of these experiments, however, cannot be used to compare the behavior of a particular strain at different wave-lengths to study the influence of light color on the mating.

The flies were exposed to the colored light for 24 h. After that the females were dissected and examined for the presence of sperm in the seminal receptacle and the spermathecae. At each wave-length a total of 120 females was tested. The percentage of inseminated females was considered as a measure of the mating success. At some wave-lengths no copulation occurred in the 24 h experiment. When that happened an additional 72 h experiment was set up to make sure whether mating was possible at all in that light condition.

Contrast discrimination test

The investigation of the contrast discrimination at different wave-lengths was carried out on an apparatus which measures the optomotor response of a single fly to a striped pattern moving in the equatorial zone of the visual field. The experimental device used for this test had been planned and constructed for previous experiments by Prof. Götz and coworkers at the Max-Planck-Institut für biologische Kybernetik in Tübingen. The technical details are described at full length in the publications of Götz and Gambke [20] and Götz and Wenking [21]. Therefore it seems to be sufficient for this paper to illustrate only the most important characters of the apparatus which are essential for the understanding and the discussion of the results.

In the experiment the fly is confronted with a moving striped pattern on two screens in front of its eyes. The position of the fly with respect to the screens is kept stable by means of a tread compensator. The compensator consists of a rubber ball (15 cm in diameter) which is supported by the roller rimmed wheels of four servomotors. By means of the motors it is possible to rotate the ball about any axis of its centre.

During the test the fly is stuck to a tiny metal sledge and placed on the top of the ball. There the fly is allowed to walk freely. Any displacement of the sledge from a given position and orientation on top of the ball is registered automatically by a magnetic sensor. The sensor decomposes the displacement into its rotatory and translatory components which are converted into motions of the motor thus inducing a counterbalancing rotation of the ball. Whenever the fly walks or turns around, rotations of the ball to the contrary direction will neutralize the movement. Simultaneously the data on intensity and direction of the movement are recorded.

A periodic pattern of bright and dark stripes was presented on both screens in front of the fly. The stripe pattern was produced by a rotating cylinder with several slots around a light source behind the translucent screens. When a normal fly with undisturbed vision is exposed to a moving stripe pattern it will try to turn with the direction of the stripes. The intensity of this optomotor response can be used as a measure for the ability to perceive the stripe pattern. The aim of our investigation was to test the contrast discrimination at different wave-lengths. For this purpose the screens were covered with colored glass filters of the same type as in the mating experiments. The tests were carried out at two wave lengths: 520 nm and 570 nm. Three different strains were used for this test: the wild-type strain and the two mutant strains *maroon* and *cinnabar*.

The direction of the stripe movement changed after time intervals of five minutes, thus avoiding misinterpretation of pattern-independent unilateral rotations of the fly. The average turning reactions, measured in revolutions per time interval, refer to two intervals with opposite stripe movement. Rotation with the direction of the pattern was given a positive sign, rotation against the pattern a negative one. Generally from a particular fly the data of approximately twenty 10 minutes intervals could be collected. When the activity remarkably decreased the fly was discarded and replaced by the next. About 10 flies from each strain were used to test the optomotor response at each wave range.

Results

The results of the mating tests are given in Table I where the mating success of different strains in different light conditions is compared. It can be seen from the data that the strains don't behave equally. The wild-type strain reached the highest percentage of inseminations at wave lengths between 400 nm and 550 nm with a maximum at 520 nm. At 570 nm the mating success started to decrease. At 590 nm copulation was still possible at a low rate. 610 nm seems to be the limit for successful mating. The flies failed to copulate in both the 24 h and the 72 h experiment.

In the mutant strains the mating success was also the highest at 520 nm. The percentage of inseminated females in the strains *ma*, *ltr* and *ch* was somewhat lower than in the wild strain, in *pp* and *cn* even

Table I. Mating success of normal and mutant strains in light of different wave length: Percentage of inseminated females after 24 and 72 h ($n = 120$ for each experiment).

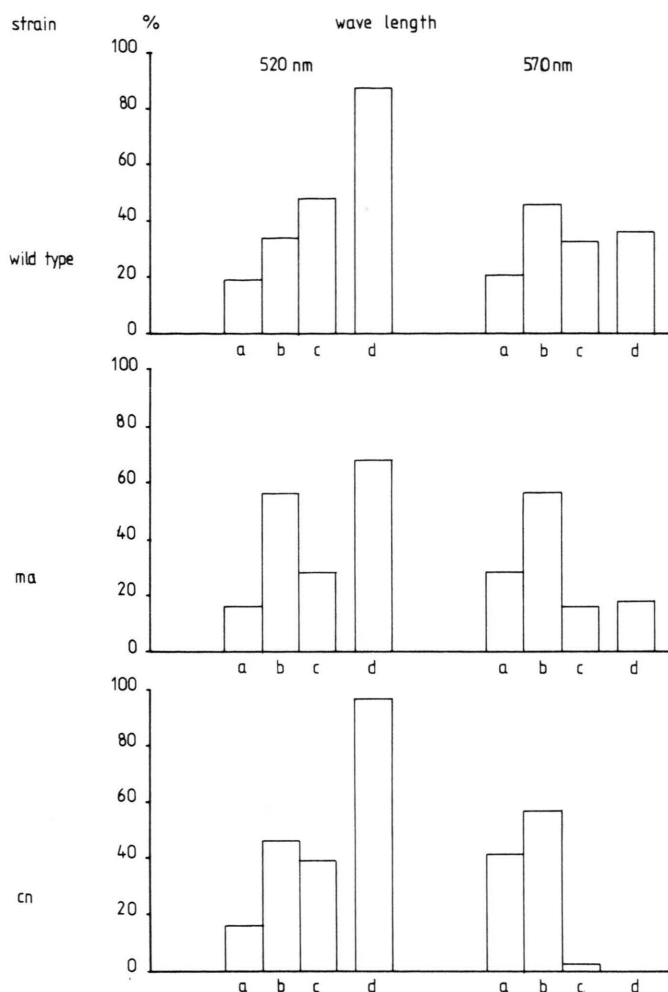
Strains	Hours	Wave length					
		400	520	550	570	590	610
wild-type	24	71	87	73	36	1	0
	72	—	—	97	88	19	0
<i>ma</i>	24	14	68	—	—	—	—
	72	—	—	35	18	0	—
<i>ltr</i>	24	14	63	—	—	—	—
	72	—	—	11	3	0	—
<i>ch</i>	24	7	75	8	0	—	—
	72	15	—	35	0	—	—
<i>pp</i>	24	75	96	45	—	—	—
	72	—	—	66	0	—	—
<i>cn</i>	24	31	97	—	—	—	—
	72	—	—	13	0	—	—

higher. This variation could be partly due to differences in the general mating activity of the strains. An effect of increased light sensitivity of the under-pigmented mutants [22] on the mating success seems quite unlikely. It has been shown by Marinković and Andjelković [23] that changes in light intensity in the wide range between 10 lux and 1000 lux do not alter the insemination rate of *Drosophila subobscura* remarkably.

At the other wave-lengths mating success was remarkably lower in the mutant strains than in the wild-type. In blue light of about 400 nm the decrease of mating success in the mutant strains does not clearly correspond to the lack of a particular component of the eye pigment. In the wave range between 550 nm and 610 nm, however, a direct correlation between insemination rate and the degree of pigmentation seems to be obvious. In all mutant strains the decrease of mating success started already at about 550 nm. The most extreme reduction was found in *cn* which has the poorest pigmentation of all mutants. At about 570 nm only two of the mutants were able to copulate: the brown eyed strain *ma* and the darkest of the red eyed mutants *ltr*. At about 590 nm no successful insemination could be observed among the mutants.

It can be seen from these data that at certain wave-lengths the mating success of the mutant strains is severely reduced compared with the wild-type. To find out whether this lower insemination rate could be due to insufficient contrast discrimination, the optomotor

Fig. 1. Optomotor response and mating success of the wild-type strain and the mutant strains *ma* abd *cn* in light of 520 nm and 570 nm. a – c: Frequency distribution of the average turning reactions measured after 10 minute periods; a = weak negative response (< 1 rotation/10 min); b = weak positive response (< 1 rotation/10 min); c = strong positive response (> 1 rotation/10 min); d: Mating success (percentage of inseminated females).



response of three different strains at two different wave-lengths was investigated. The wave-lengths chosen for these tests were 520 nm and 570 nm. At 520 nm mating was optimal in all strains whereas at 570 nm the most obvious difference was found between the wild-type and the mutant strains. The experimental strains were chosen according to their pigmentation: the wild-type strain with complete brown and red eye pigment, the mutant *ma* which lacks the red drosoperin and the mutant *cn* which lacks the brown ommochrome pigment. In the mating tests at wave length 570 nm *ma* showed the smallest deviation from the wild-type, *cn* the largest deviation (Table I).

Before the investigation of the optomotor response could be started the optimal speed of the stripe

movement had to be determined in a preliminary test. For this purpose the optomotor response of the wild-type strain was studied at wave length 570 nm using different speeds of stripe movement. The angular velocity of the pattern was measured in Hz. 1 Hz denotes 1 pattern period (= 1 bright and 1 dark stripe) per second. The angular width of one pattern period seen from the position of the fly was 28° which is readily resolved by the compound eye of *Drosophila* [21]. The results of this test are shown in Table II. It can be seen that the highest values for the turning reaction could be obtained at speeds between 1.5 and 6 Hz. Therefore a speed of 3 Hz was used in the further experiments.

The results of the optomotor response tests with 3 different strains at 2 wave-lengths are given in Ta-

Table II. Optomotor response of the wild-type strain in light of 570 nm using different speeds of stripe movement. (Number of flies tested = 12, + = rotation with the stripe pattern, - = rotation against the stripe pattern).

Speed of stripe movement [Hz]	Full rotations of the fly	Exposure time [h]	Rotations per h
0.8	+ 14.15	5 h 30'	2.6
1.5	+ 46.24	5 h 40'	8.2
3.0	+ 32.27	5 h 30'	5.9
6.0	+ 44.25	5 h 20'	8.3
12.0	+ 21.86	5 h 40'	3.8
24.0	+ 22.11	5 h 20'	4.1
48.0	- 16.74	5 h 40'	-2.9

Table III. Optomotor response of the wild-type strain and the mutant strains *ma* and *cn* in light of 520 nm and 570 nm. (Speed of the stripe pattern = 3 Hz.)

Wave range	Strain	Number of flies	Full rotations	Exposure time	Rotations per h
520	wild-type	5	603.38	34 h 20'	17.6
	<i>ma</i>	13	152.48	33 h 50'	4.5
	<i>cn</i>	11	245.62	30 h 40'	8.1
570	wild-type	20	299.72	35 h 40'	8.4
	<i>ma</i>	13	75.97	31 h 20'	2.4
	<i>cn</i>	10	16.47	33 h 30'	0.5

ble III and Fig. 1. In Table III the average turning reactions (in rotations per hour) can be compared. It can be seen that all three strains showed a stronger optomotor response in light of 520 nm. At 570 nm contrast discrimination seems to be reduced in the wild-type as well as in both mutants. This decrease in the ability of contrast discrimination at wavelengths above 550 nm is in good accordance with the data of Heisenberg and Buchner [6] who studied the spectral sensitivity of the optomotor response in *Drosophila melanogaster*. In the wild-type and in the mutant *ma* the average turning reaction at 570 nm measures about half the value recorded at 520 nm. In *cn*, however, an extreme decrease of the optomotor response can be observed: from 8.1 at 520 nm to almost zero at 570 nm.

As it has been mentioned above the average turning reaction was measured in 10 minutes intervals. These single measurements can be classified to 3 different groups: a) weak negative, b) weak positive and c) strong positive response. The frequency dis-

tribution of these classes in the six experiments are presented in Fig. 1. In five of the experiments the predominance of the positive reactions (b + c) becomes obvious. Only in the test with the *cn* strain at 570 nm the number of positive and negative reactions seems to be more or less the same thus indicating that the flies were not able to perceive the moving pattern. A χ^2 -analysis, however, proves a slight deviation from random distribution around zero ($\chi^2 = 6.1$, $df = 1$, $p < 0.05$).

The low contrast discrimination of the *cn* strain in light of 520 nm can be explained from the absorption spectrum of the red eye pigment. According to Heyman *et al.* [24] the optical transmission of the red drosoperin has its minimum at wave-lengths between 480 nm and 490 nm but is very high at wave-lengths above 550 nm. This means that in *cn* flies the optical isolation of the ommatidia is sufficient at wave-lengths of about 520 nm. Light of 570 nm, however, is able to penetrate the red pigment. Thus isolation becomes ineffective and therefore *cn* flies are contour-blind in light of that wave-length. In the wild-type strain and in the mutant strain *ma* optical separation of the ommatidia is effected by the brown ommochrome pigment at 570 nm as well as at 520 nm.

The results of the present investigation can be compared with the results of the mating tests (Fig. 1). High insemination rates and strong optomotor response were found with all three strains in light of 520 nm. At 570 nm the mating success as well as the intensity of the reaction to the moving stripe pattern were obviously reduced. The wild-type strain and the mutant strain *ma*, however, were still able to copulate successfully at a low rate and a clear optomotor response could be detected too. *cn* flies on the other hand could hardly perceive the moving stripes in the test and failed completely in the mating experiment. From these data it can be concluded that in *Drosophila subobscura* the ability to react to a moving pattern and the ability to mate are correlated. Further evidence for this assumption can be obtained from comparing the behavior of the two mutant strains *ma* and *cn*. At 520 nm both mating success and optomotor response were higher in *cn* than in *ma*. At 570 nm both values were lower in *cn*. It seems therefore highly probable that the mating success in *Drosophila subobscura* depends on the contrast discrimination rather than the subjective brightness background.

Discussion

The aim of our study was to find out whether the mere perception of light or the exchange of visual courtship signals is necessary for successful mating in *Drosophila subobscura*. The correlation between insemination rate and contrast discrimination indicates that the second explanation is right. This result does not refute the importance of light intensity on sexual activity which has been proved by Kekić and Marinković [25]. Visual stimuli, however, seem to be essential.

It should be discussed now which elements of the courtship of *Drosophila subobscura* are light dependent. The mating behavior of *Drosophila subobscura* has been described by Rendel [7], Milani [2], Spieth [8], Maynard Smith [9] and Brown [10]. According to these authors and our own observations males of *Drosophila subobscura* indicate their readiness to mate by opening and closing the wings in a scissor-like movement. As soon as a male recognizes a possible sexual partner he approaches her from the side and starts tapping her with the front legs. This part of the courtship could be regarded as tactile or chemical recognition. After that the male moves to a position in front of the female and spreads his wings. The female responds with side steps while the male tries to maintain his frontal position. In this way female and male step aside several times to the left and to the right remaining face to face. This part of the courtship is called wing-dance. If the female is ready to mate she suddenly stops the dance and the male circles round to the rear, jumps and attempts genital contact.

According to this description the courtship of *Drosophila subobscura* is possibly light dependent at two different stages. The first stage could be the initial recognition of the female by the male before physical contact. As it was shown by Milani [2] males respond to quite unspecific optical stimuli like wax-models. Hence it can be assumed that the males need the sight of a female or of something that looks like a female to get stimulated for courtship. The second stage could be the wing-dance. During this dance the male has to follow the movements of the female, a behavior which requires optical control.

The spreading of the wings by the males on the other hand could be a visual stimulus for the female possibly decisive for the acceptance of the male as a species specific partner. This would mean that both sexes need light for courtship: The males for visual orientation and for the wing-dance, the females for recognizing the signal of the spreaded wings presented by the males.

The question which of the courtship elements is responsible for the light dependence of the mating behavior cannot be decided yet. It is imaginable that courtship cannot start at all in complete darkness since visual recognition of the female by the male is an essential stimulus. If courtship could be initiated, however, by other stimuli like taste or smell it could proceed only to the wing-dance where vision is needed by both partners.

The methods for a detailed analysis of this problem are already offered by the results of the contrast discrimination tests. Up to now observation of *Drosophila subobscura* behavior in darkness was performed directly without infrared conversion devices in red light of more than 610 nm. Since the *cn* strain proved to be almost completely contour-blind at 570 nm observation of the behavior after cutting off all visual courtship elements has become easier. Moreover, as *cn* flies are able to perceive light intensity at this wave-length, general activity might be higher and thus offer the possibility of recording unsuccessful courtship attempts. Finally *cn* flies could be put together with wild type flies which have normal contrast discrimination at 570 nm to study in detail whether the courtship of males or females or both sexes is light dependent.

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