Studies on the humidity and light orientation and the flying activity of Myrrha 18-guttata L. (Col., Coccinellidae).

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Introduction.

The hibernation ecology and physiology of coccinellids have been studied by a number of investigators (see e.g. CARNES 1912, EWING 1913, DOBZHANSKY 1922, BALDUF 1935, YAKHONTOV 1940, BODENHEIMER 1943, TELENGA 1948, DELUCCHI 1954, PUTMAN 1957, HODEK 1958 a and b, 1960, HODEK & CERKASOV 1958, 1960, 1961 a and b, HAGEN 1962, PULLIAINEN 1963). However, relatively little is yet known about the humidity and light orientation of these animals before and after hibernation, and very few experimental records have been published (cf. the review by HAGEN 1962).

The purpose of this paper is to place on record further observations concerning the humidity and light orientation and the flying activity of the coccinellid *Myrrha 18-guttata* (see also PULLIAINEN 1963).

Material and methods.

The studies here described were made at the Zoological Institute (in spring 1962) and the Agricultural and Forest Zoological Institute of the University of Helsinki (mainly in spring 1964). The material for laboratory experiments was acquired by two methods from a pine peat-bog situated in the western part (Haaga) of the town of Helsinki. Pine stumps about 0.5 m. long were removed from the ground (10 – 20 cm in diameter). The stumps were brought to the laboratory, where *Myrrha 18-guttata* adults emerged from crevices in the bark (method A). This took place in March and April, when there was still snow on

the ground. A lot of specimens were collected at the same time from crevices in the bark of similar pines in nature (method B). All the specimens were kept in glass jars with slightly damp blotting-paper at a temperature of about $+6°$ (to $+8°$) C. Control coccinellids were also fed on the diet recommended by SMIR-NOFF (1958). Some of the coccinellids were tested 10 minutes after they were taken from their hibernating quarters.

The apparatus used in the humidity experiments, based on those of GUNN & KENNEDY (1936) and WIGGLESWORTH (1941), was the alternative chamber described by PERTTUNEN (1953) and PERTTUNEN & LAHERMAA (1962).

13 pairs of humidities obtained with concentrated salt solutions were used (see PULLIAINEN 1963). The chemicals and the corresponding theoretical humidities at 20°C (JANISCH 1938) were as follows:

H_2O	100 % R.H.	$Ca(NO_3)_2$	56 % R.H.
KH_2PO_4	97 % R.H.	$MgCl_2$	34 % R.H.
KCl	87 % R.H.	Silica gel	0 % R.H.
NaCl	77 % R.H.		

The dishes with salt solutions were set up at least half an hour before the beginning of the experiments.

The animals were inserted into the apparatus through the hole in the lid, ten at a time, and their positions recorded at 15-minute intervals for two hours. For every alternative the number of specimens tested was 100.

The desiccation of the adults took place at 25°C over silica gel in little capsules made of wire gauze, 5 — 10 specimens in each capsule.

In the experiments aimed at elucidating the mechanism of the humidity reaction, one insect at a time was put into the alternative chamber. These experiments were carried out beneath a lamp placed at a height of 70 cm centrally above the chamber. Measurements showed that the light intensity in the chamber was about 400 Lux. Round the chamber there was a cardboard cylinder 5 cm high without a cover.

The behaviour of each coccinellid was observed for 15 minutes. When the insect moved in the chamber its track was copied onto the paper on the natural scale. The lengths of the tracks were measured with the aid of a map-measurer. The speed and the time spent in each half were also determined.

The apparatus used in the light experiments was a dark-light alternative chamber described by PERTTUNEN (1958) and PERTTUNEN & LAHERMAA (1958). The following light intensities were used: 10, 100, 1000 and 10 000 lux (measured with a Metrawatt light meter, type Tavolux 2) on the lighted side of the chamber. The sources of light above the chamber were the following lamps: Airam 220 – 230 V 25 W G 9, Airam 220 – 230 V 60 W F 8, Airam 230 V 100 W D 11 and Philips

HPLR 400 W Typ 57225 G/93. The light given by the three first-mentioned lamps is called long-wave light (see Table 1) and the light of the fourth lamp correspondingly short-wave light (see Table 1).

For the experiments on the interference between the light and humidity reactions, a combined humidity and light choice chamber was used.

The animals were inserted into the apparatus through the hole in the lid, twenty at a time, and their positions recorded at one-minute intervals for 30 minutes. For each alternative, this was repeated five times with new individuals; thus for every alternative the number of specimens tested was 100.

Most of the experiments were carried out at a temperature of about 20°C. Some experiments were also carried out at temperatures of +10°C and +30°C. The humidity in the chamber was kept constant with a concentrated solution of $MgCl_2$ beneath the false floor, which produces an air humidity only varying from about 30 % R.H. to 40 % R.H. (see also JANISCH 1938). In some experiments 0 % R.H. was used throughout the temperature scale.

The insects were not sexed before testing. The sex ratio was determined for a number of batches of beetles and found not to vary to any significant extent from 50 : 50.

The results here described are based on ca. 1500 specimens and 100 000 position records.

Results.

Humidity reactions.

Group experiments. The intensity of the humidity reaction is expressed as the percentage on the moister side, $\dfrac{100\ (W\text{-}D)}{N}$ (cf. PERTTUNEN 1953), where W represents the number of animals (position records) on the moister side, D the number of records on the drier side, and N the total number of position records,

Table 1. The relative spectral light distribution used in these experiments. Calculated according to LAMPI (1964, p. 15) and the data of Philips.

The so-called long-wave light:

Wave-lengths	3800–4300 Å	4300–4850 Å	4850–5050 Å	5050–5300 Å	5300–5600 Å	5600–5900 Å	5900–6200 Å	6200–7900 Å
%	0.3	2.5	3.2	3.7	5.3	6.5	15.5	63.0

The so-called short-wave light:

Wave-lengths	4000–4200 Å	4200–4400 Å	4400–4600 Å	4600–5100 Å	5100–5600 Å	5600–6100 Å	6100–6600 Å	6600–7200 Å
%	0.016	0.42	0.052	0.75	44.5	45.0	8.2	0.91
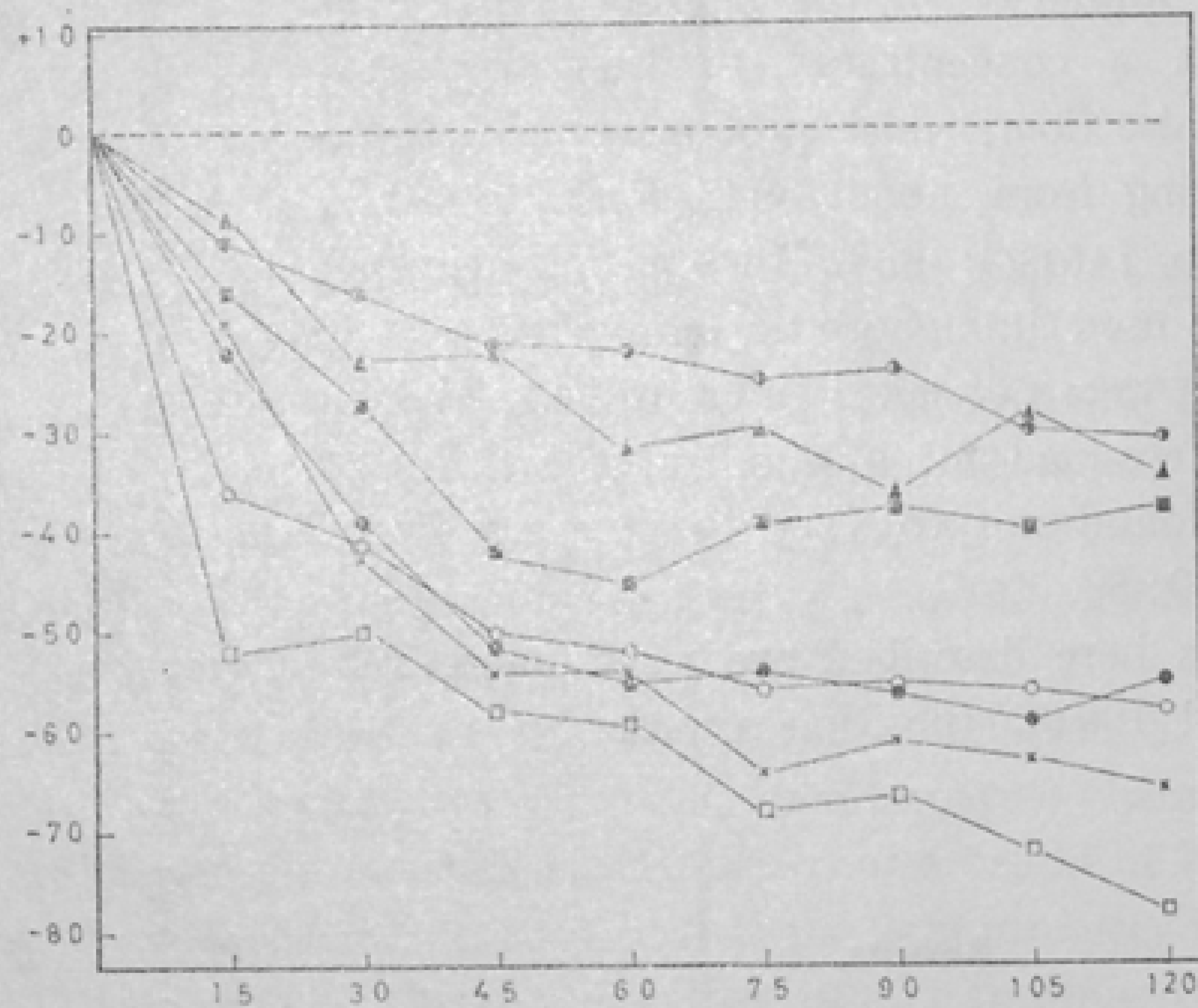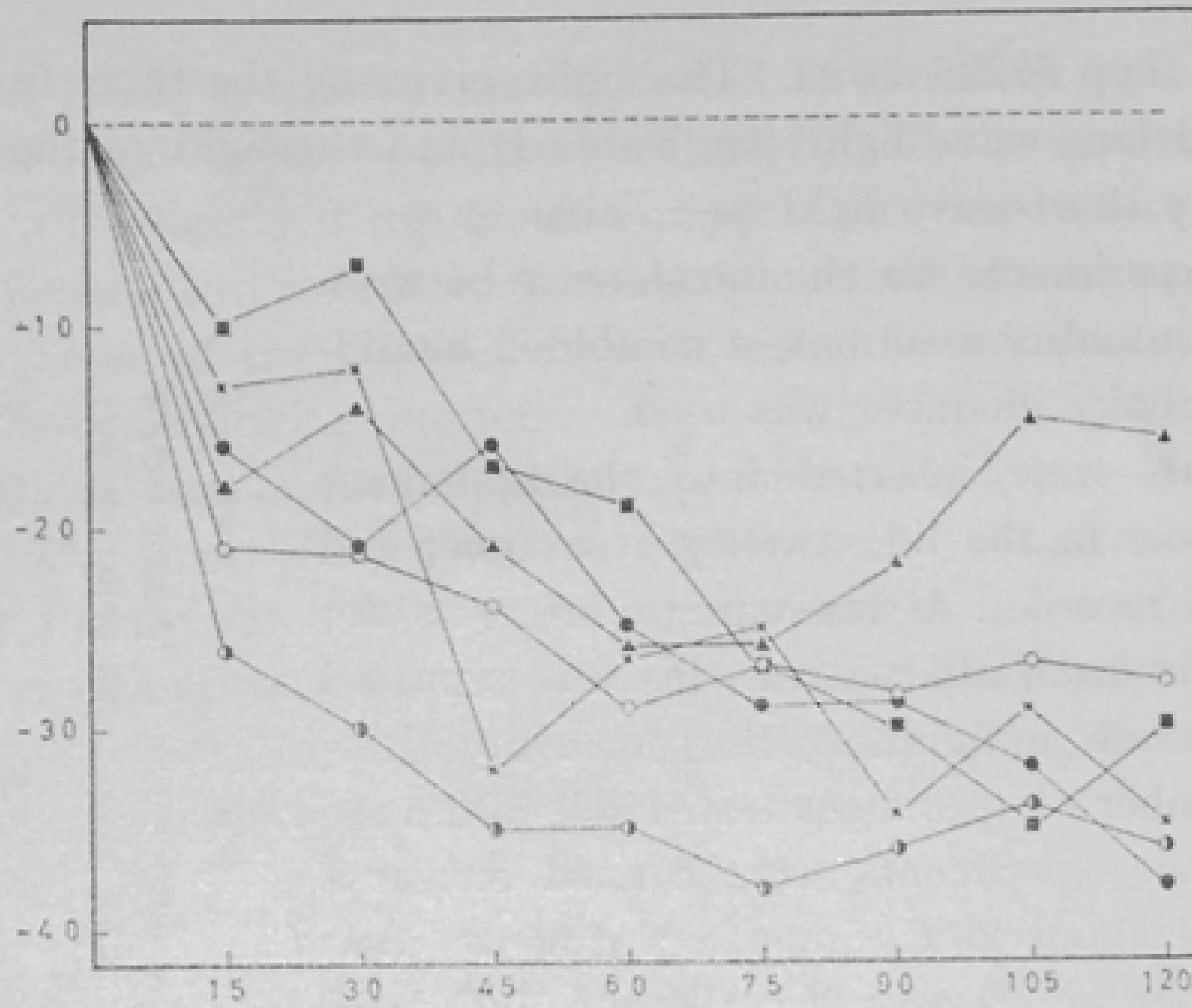
Figs. 1—2. Reactions of *Myrrha 18-guttata* specimens to different humidity alternatives according to Pulliainen (1963). Ordinate: Intensity of reaction $\dfrac{100\ (W-D)}{N}$. Abscissa: time in minutes.

Fig. 1 (above). —▲— 77-56 % R.H., —■— 87-34 % R.H., —◐— 56-0 % R.H., —×— 77-34 % R.H., —●— 56-34 % R.H., —○— 34-0 % R.H.

Fig. 2 (below). —◐— 87-56 % R.H., —▲— 87-77 % R.H., —×— 100-34 % R.H., —●— 100-87 % R.H., —○— 100-56 % R.H., —■— 100-97 % R.H., —□— 100-77 % R.H.

including the small number in the narrow middle zone. The broken line at 0 is the zero line of no reaction, the percentages above this (+) indicating a reaction towards moist, and the percentages below it (—) a reaction towards dry.

Figs. 1 – 2 show the reactions of *Myrrha 18-guttata* specimens to various alternative humidities. These results were already represented in an earlier paper by the author (PULLIAINEN 1963). The undesiccated beetles showed a reaction towards the drier side of the chamber when different humidity alternatives were offered. When the higher alternative was 100 % R.H., the beetles could perceive a difference of 3 per cent.

Experiments with single individuals. In order to make more exact observations on the humidity behaviour of *M. 18-guttata* and to determine the mechanism of the reaction, experiments were carried out on individuals. The method used has been described earlier (p. 118). Humidity alternatives of 100 and 34 % R.H. were used. In Figure 3 a typical track of a beetle can be seen.

Table 2. Analysis of the behaviour of *M. 18-guttata* beetles in the alternative chamber. For further explanation, see text and SYRJÄMÄKI (1962, p. 8).

1. No. of turnings		2. No. of crossings		3. No. of halts		4. No. of mom. crossings		5. Time spent in inactivity		6. Distance travelled, cm		7. Time spent in motion, min.		8. Speed cm./sec.	
D	W	D-W	W-D	D	W	D	W	D	W	D	W	D	W	D	W
18	8	3	4	0	0	0	3	0	0	208	135	11	4	18.9	33.8
29	7	3	4	0	1	0	1	0	1	220	22	11	3	20.0	7.3
23	1	0	1	0	0	0	0	0	0	206	1	15	0	13.7	0.0
32	0	0	0	1	0	2	0	1	0	198	0	14	0	14.1	0.0
1	0	0	0	1	0	0	0	14	0	17	0	1	0	17.0	0.0
3	0	0	0	2	0	0	0	13	0	13	0	2	0	6.5	0.0
23	0	0	0	3	0	2	0	7	0	158	0	8	0	19.8	0.0
2	0	0	0	1	0	0	0	14	0	12	0	1	0	12.0	0.0
5	1	1	1	5	0	0	0	9	0	22	4	6	0*	3.7	24.0
5	0	0	0	1	0	0	0	13	0	35	0	2	0	17.5	0.0
Σ 141	17	7	10	14	1	4	4	71	1	1089	162	71	7	15.3	23.1

* time = 10 sec.

The results of these experiments were tabulated (Table 2). The eight columns of Table 2 are each divided into two halves, representing the humidities of 34 and 100 % (denoted D and W, respectively). The methods used here have been described by SYRJÄMÄKI (1962, p. 8). As was seen earlier, normal undesiccated specimens exhibit a dry reaction in the group experiments. The nature of the mechanism involved can be inferred from the analysis of this dry reaction in the different columns of Table 2. In the alternative chamber a *M. 18-guttata* specimen sometimes moves and sometimes stands still. As a rule these coccinellids have a great tendency to stand still. The locomotor activity of the species will be dealt with more fully in another paper (PULLIAINEN, to be published).

From column 1 it can be seen that the turnings at the boundary are significantly
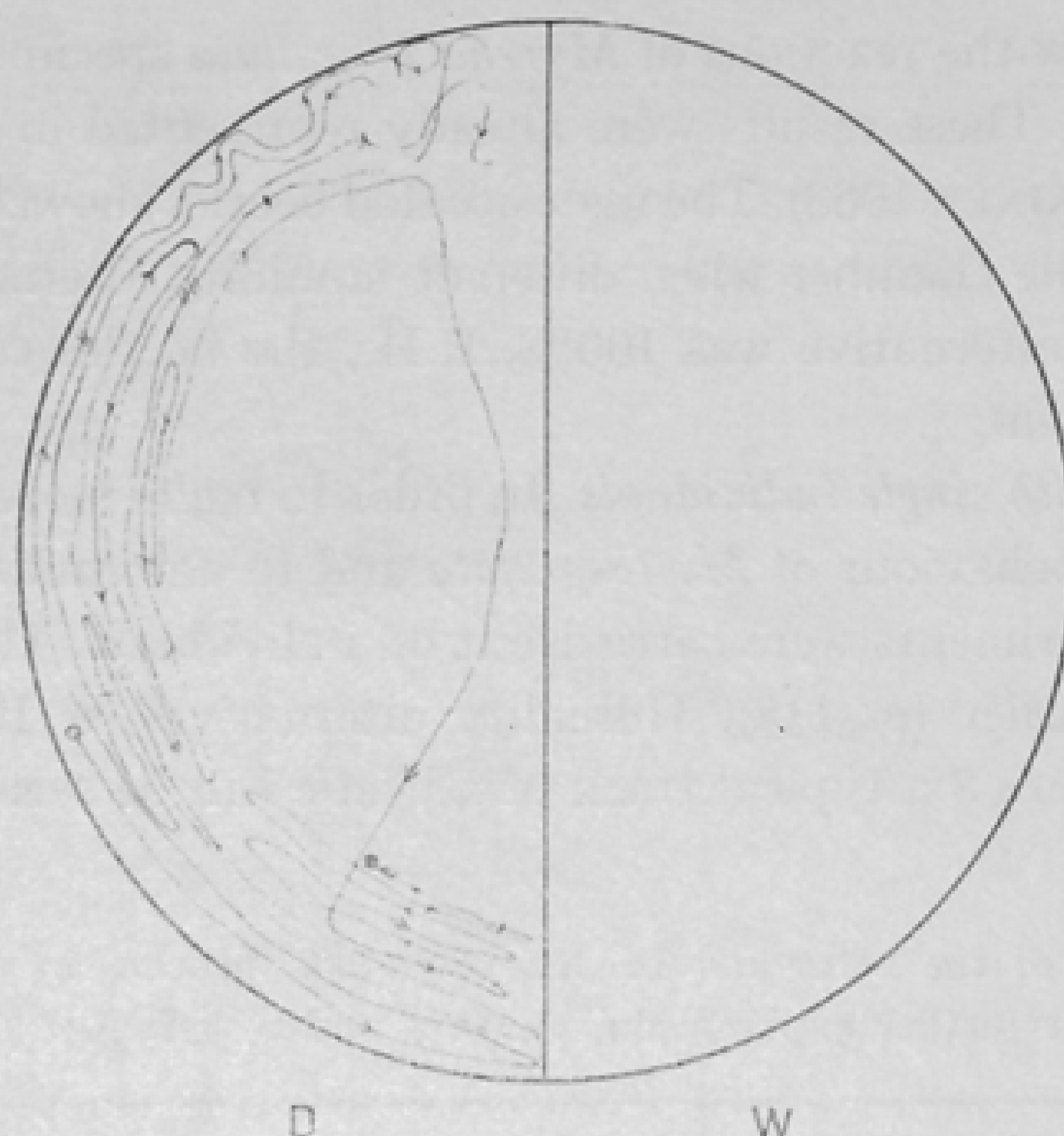
Fig. 3. Recording of a typical track of a single specimen of *Myrrha 18-guttata* in an alternative chamber. The beginning of the record is indicated by an open circle, the end with a solid circle. The arrows indicate the direction of movement of the animal. W = side with water (100 % R.H.), D = side with humidity of 34 % R.H.

more frequent on the drier side than on the moist side. The result is that the beetles tend to stay on the dry side of the chamber. Such a reaction, according to FRAENKEL & GUNN (1961), is a tactic reaction. The reaction in question is best called a klinotactic reaction. Crossings from the drier to the moist side are much less common than turnings at the boundary. In other words, the klinotactic reaction is rather effective in keeping the beetles on the dry side.

From columns 3 and 5 it can be seen that the beetles were very much more active on the moister side than on the dry side. Thus *M. 18-guttata* shows a very clear orthokinetic mechanism of reaction (according to FRAENKEL & GUNN op.cit.).

Desiccation. The specimens for desiccation were taken from their hibernation quarters. The mean weight of 250 undesiccated specimens after hibernation was 9.32 mg (range 6.33 mg – 12.19 mg). Fig. 4 shows the loss of weight of *Myrrha 18-guttata* on desiccation. It is surprising that these beetles lose 26 per cent of their weight during the first 24 hours of desiccation. After this rapid decrease the subsequent loss of weight is fairly steady. »Reflex bleeding» (see WIGGLESWORTH 1947, p. 232) in unfavourable conditions may remarkably accelerate the decrease of weight during the first hours of desiccation (=unfavourable condition). During 144 hours of desiccation these coccinellids lost 50 per cent of their weight. During desiccation no food was given to the coccinellids so that they also suffered from starvation during this time.
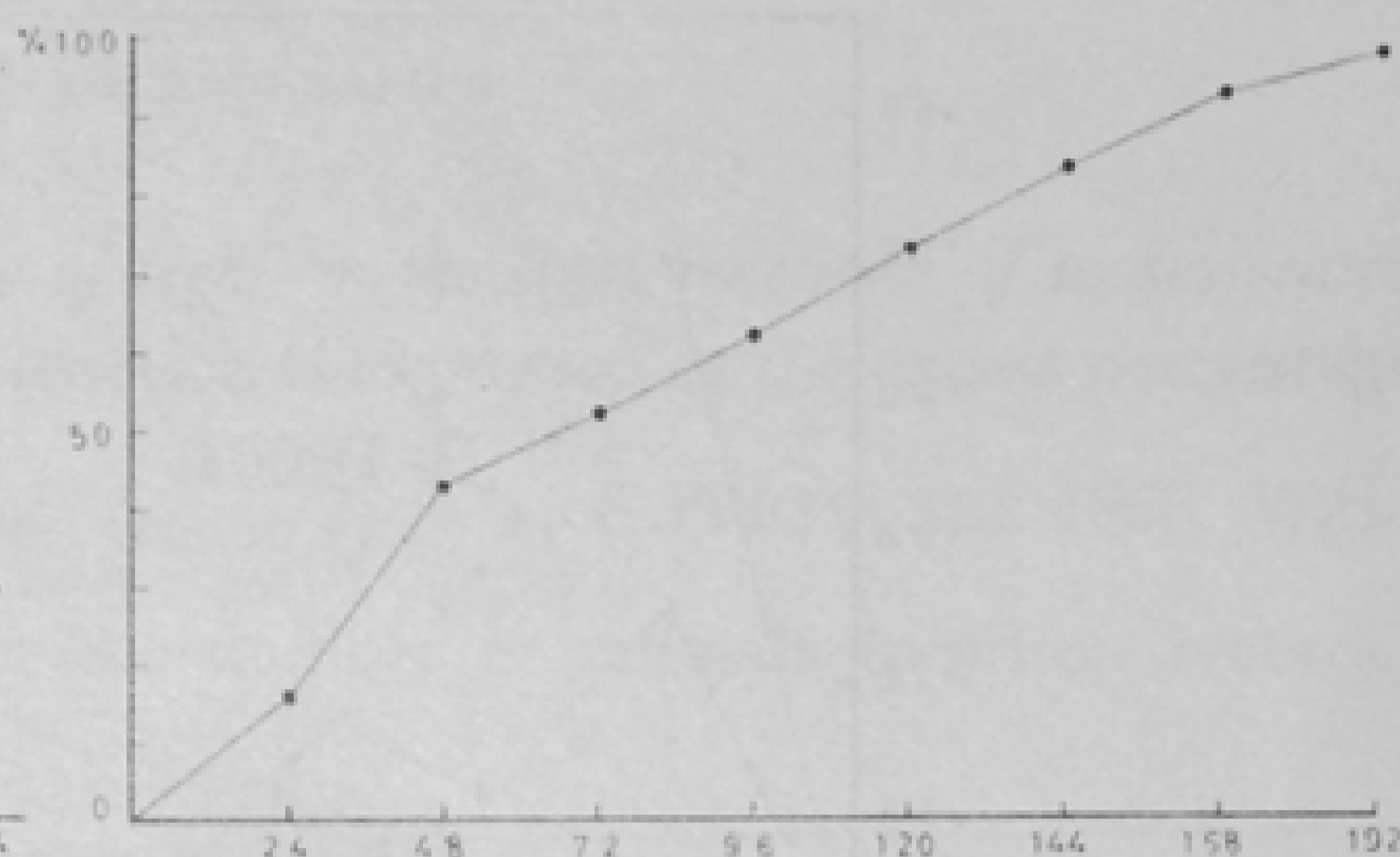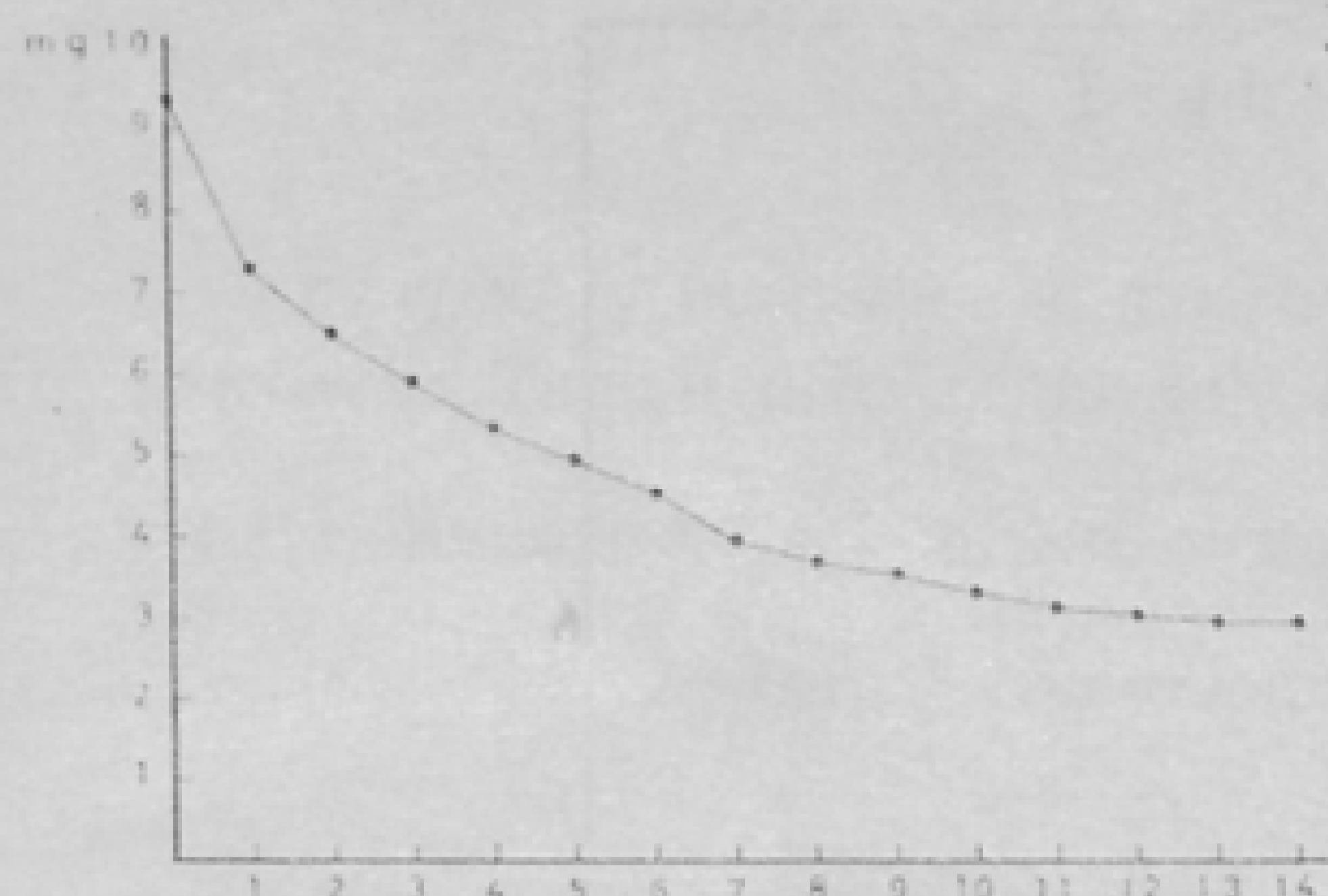
Fig. 4. The loss of weight of a specimen of *Myrrha 18-guttata* on desiccation (+25°C, 0 %
R.H.). Ordinate: weight (mg) of a specimen. Abscissa: time in days.

Fig. 5. The death rate of *Myrrha 18-guttata* on starvation and desiccation (+25°C, 0 %
R.H.). Ordinate: percentage mortality. Abscissa: time in hours.

Death rate on starvation and desiccation. Fig. 5 shows the death rate of *Myrrha
18-guttata* during continuous starvation and desiccation at 25°C and 0 % R.H.
The results were obtained in two different ways. At first the dead specimens
were removed from the desiccation capsules at 24-hour intervals.   Animals
which failed to react to repeated tactile stimulation were considered dead. During
these tests for signs of life the beetles were placed for a short time in 30 – 40 %
R.H. In another case the numbers of coccinellids were investigated after 72 and
144 hours' continuous desiccation. Both methods gave exactly the same result.
After 192 hours (8 days) of desiccation almost all the specimens were dead.

Humidity reactions of desiccated specimens. The humidity alternatives used in
the experiments with desiccated specimens were 34 % and 100 % R.H. Figs.
6 and 7 show the humidity reactions of undesiccated and desiccated specimens
of *Myrrha 18-guttata.* Undesiccated specimens show a very clear hygronegative
reaction (intensity of reaction —60, mean of 45 – 120 min.). After desiccation
for 24 hours the reaction has already become indifferent (the intensity of the
reaction —4). The control tests (34 % R.H./34 % R.H.) gave the same value.
After desiccation for 72 and 96 hours a clear hygropositive reaction is visible
during the first minutes of the experiments, but soon becomes indifferent. Fig.
8 shows the reversal of the clear hygronegative reaction by desiccation to indiffer-
ent. However, the coccinellids showed a hygropositive reaction after desiccation
for 144 hours (for 45 – 120 min. the difference is statistically significant, $x^2 =$
5.582). We must also remember that the insects are very fatigued by desiccation
for the above-mentioned time.

In order to be sure that the reversal of the humidity reaction was really due
to desiccation, specimens of *Myrrha 18-guttata* were kept for 144 hours (6 days)
at 25°C without food but with access to drinking water; these specimens still
showed a strong hygronegative reaction. Starvation for six days did not change
the humidity reaction.
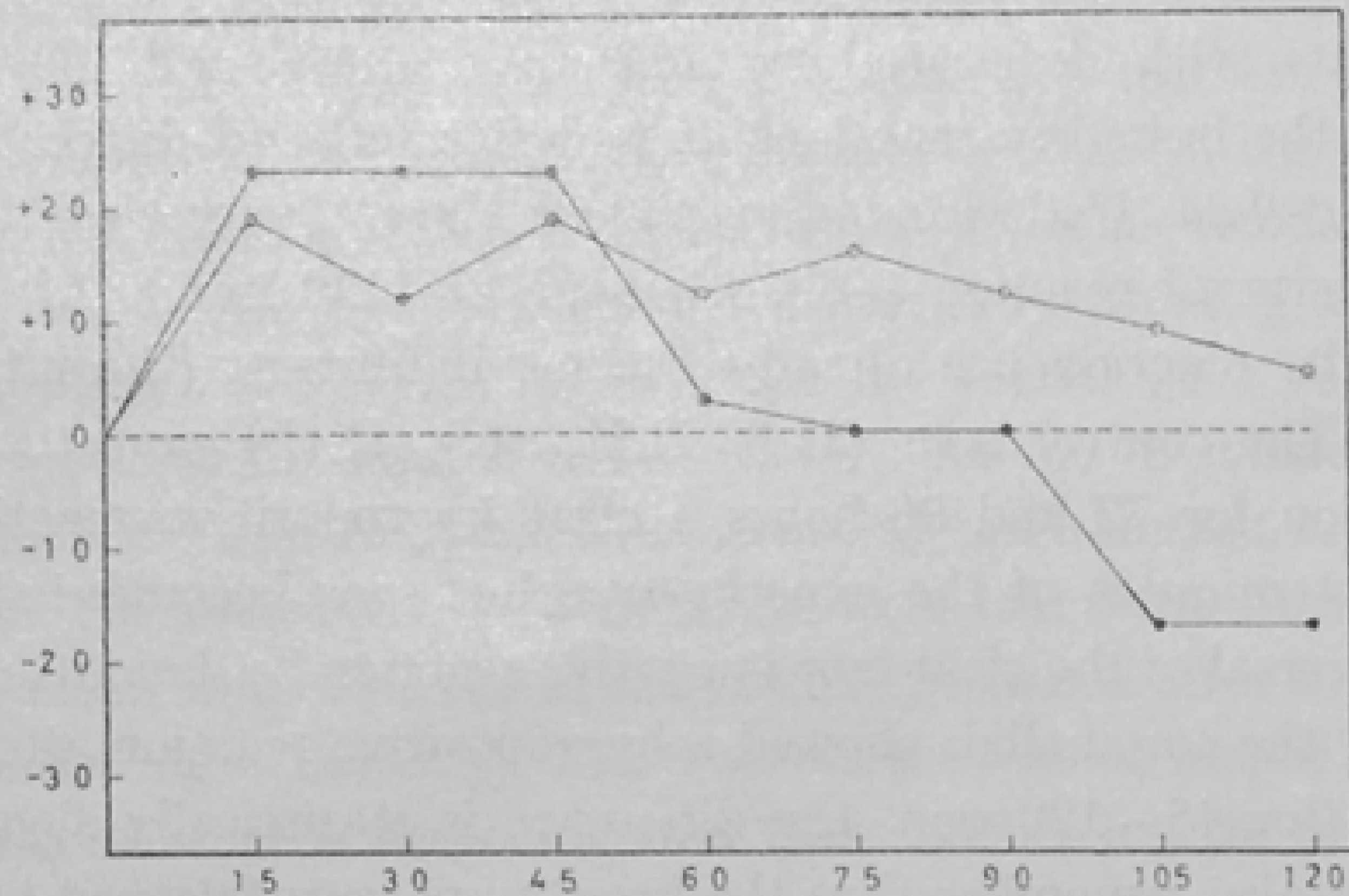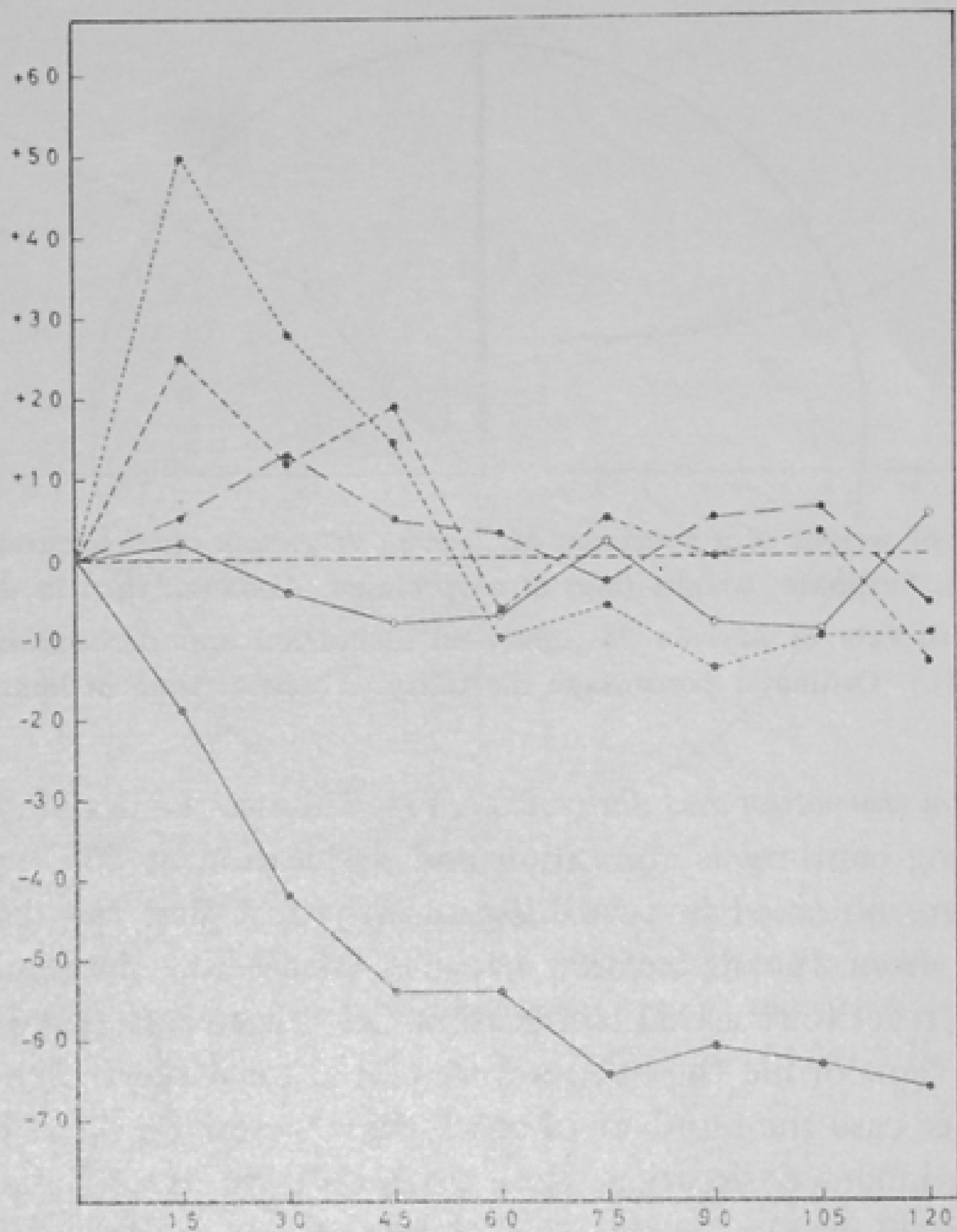
Figs. 6—7. Humidity reactions of undesiccated and desiccated *Myrrha 18-guttata* specimens in the alternatives of 34—100 % R.H. Ordinate: Intensity of reaction $\dfrac{100\ (W\text{-}D)}{N}$. Abscissa: time in minutes.

Fig. 6. (above). —●— reactions of undesiccated specimens, —○— reactions after desiccation for 24 hours, —●— reactions after desiccation for 48 hours, ——●—— reactions after desiccation for 72 hours, ---●--- reactions after desiccation for 96 hours.

Fig. 7 (below). —●— reactions after desiccation for 120 hours, —○— reactions after desiccation for 144 hours.

Light reactions.

The effect of intensity and quality of light on the light reactions of undesiccated specimens. The intensity of the light reaction is expressed as the excess percentage on the illuminated side of the chamber, $\dfrac{100\ (L\text{-}D)}{N}$ (cf. PERTTUNEN 1958, WELLINGTON 1960), where L represents the number of animals (position records)
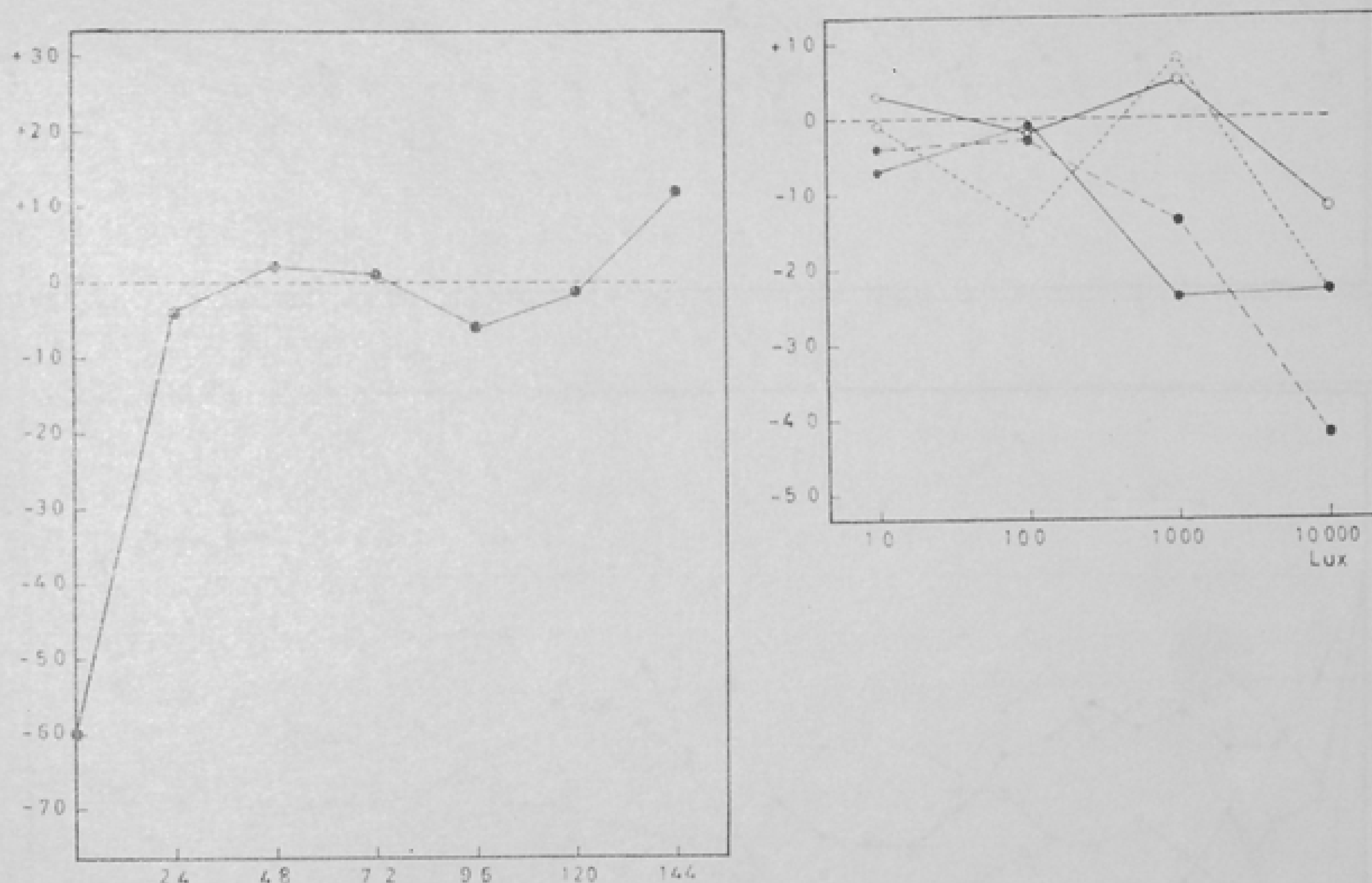

Fig. 8. Humidity reactions of undesiccated and desiccated *Myrrha 18-guttata* specimen
Ordinate: intensity of reaction $\dfrac{100\ (W\text{-}D)}{N}$. Abscissa: time in hours.

Fig. 9. Effect of light intensity and light quality on the light reactions of *Myrrha 18-guttata* specimens in the different humidity conditions. –●– 0 % R. H., –○– 34 % R.H., ––●–– 77 % R.H., ––○–– 100 % R.H. Long-wave light was used in the experiments with intensities of 10, 100 and 1000 lux and short-wave light with the intensity of 10 000 lux (cf. Fig. 10). Ordinate: intensity of reaction $\dfrac{100\ (L\text{-}D)}{N}$. Abscissa: light intensity on the illuminated side of the choice chamber. The curves are based on altogether 1000 specimens and 48 000 position records.

on the light-exposed side, D the number of records on the dark side, and N the total number of position records, including the number of specimens observed on the narrow midline. The broken line at 0 is the zero line of no reaction, the percentages above this (+) indicate a positive reaction to light, and the percentages below it (−) a preference for the dark side of the choice chamber.
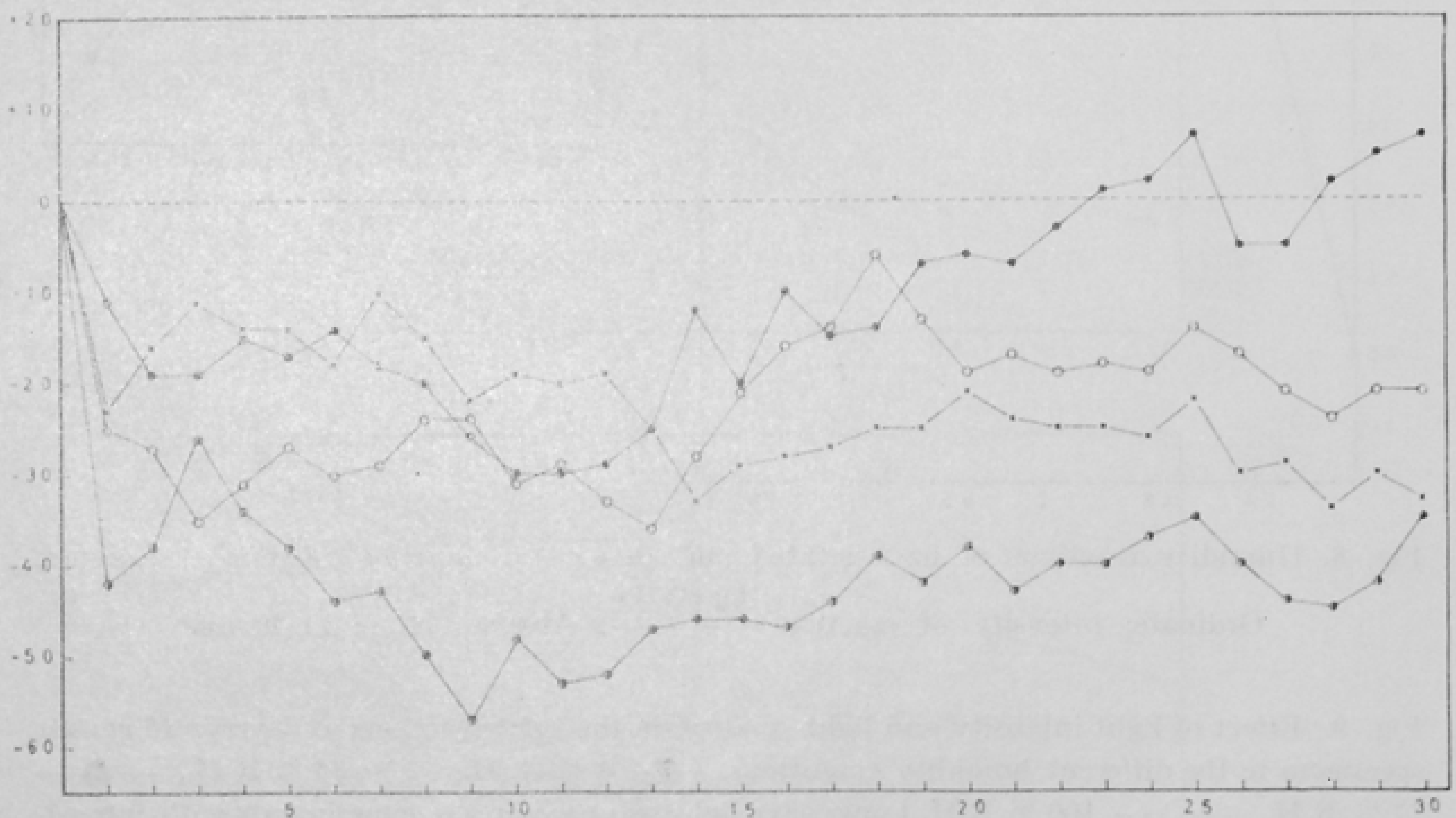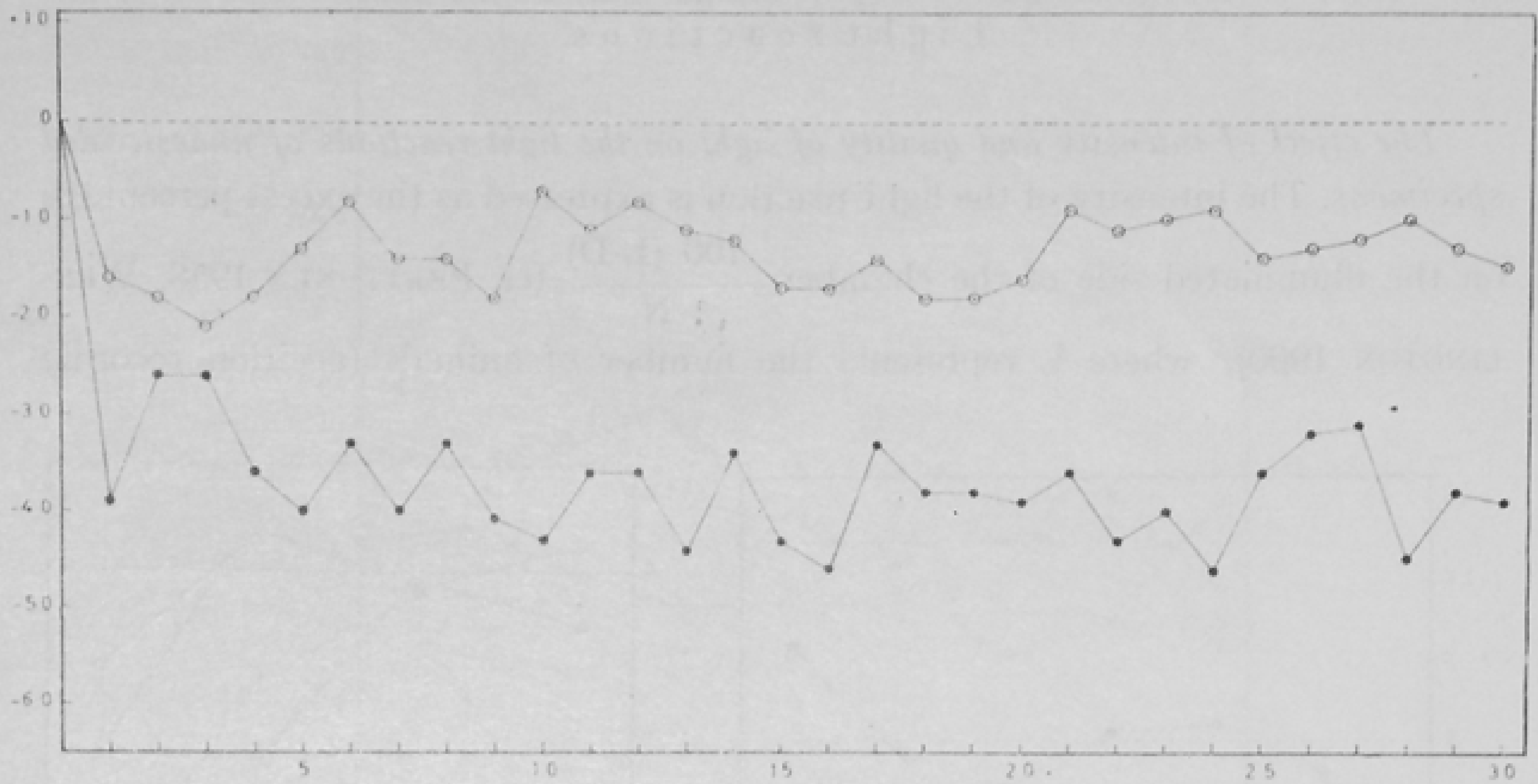
Figs. 10—11. — Fig. 10 (above). Effect of light quality (wave length) on the light reactions of *Myrrha 18-guttata* at 20°C and 77 % R.H. –●– 1000 lux short-wave light, –○– 1000 lux long-wave light. Ordinate: intensity of reaction $\dfrac{100\ (L-D)}{N}$. Abscissa: time in minutes. Fig. 11. (below). Effect of humidity conditions on the light (long-wave) reactions of *Myrrha 18-guttata*. Experiments were made at 10 000 lux and 20°C. –⊙– 0 % R.H., –●– 34 % RH., –◐– 77 % R.H., –×– 100 % R.H. Ordinate: intensity of reaction $\dfrac{100\ (L-D)}{N}$. Abscissa: time in minutes.

The specimens used in these experiments were kept in experimental light for at least an hour before the start of the experiments. Fig. 9 shows the reactions of *Myrrha 18-guttata* specimens to various light intensities. Long-wave light was used in the experiments at light intensities of 10 – 1000 lux and short-wave light in the experiment at 10 000 lux. At especially high light intensities there
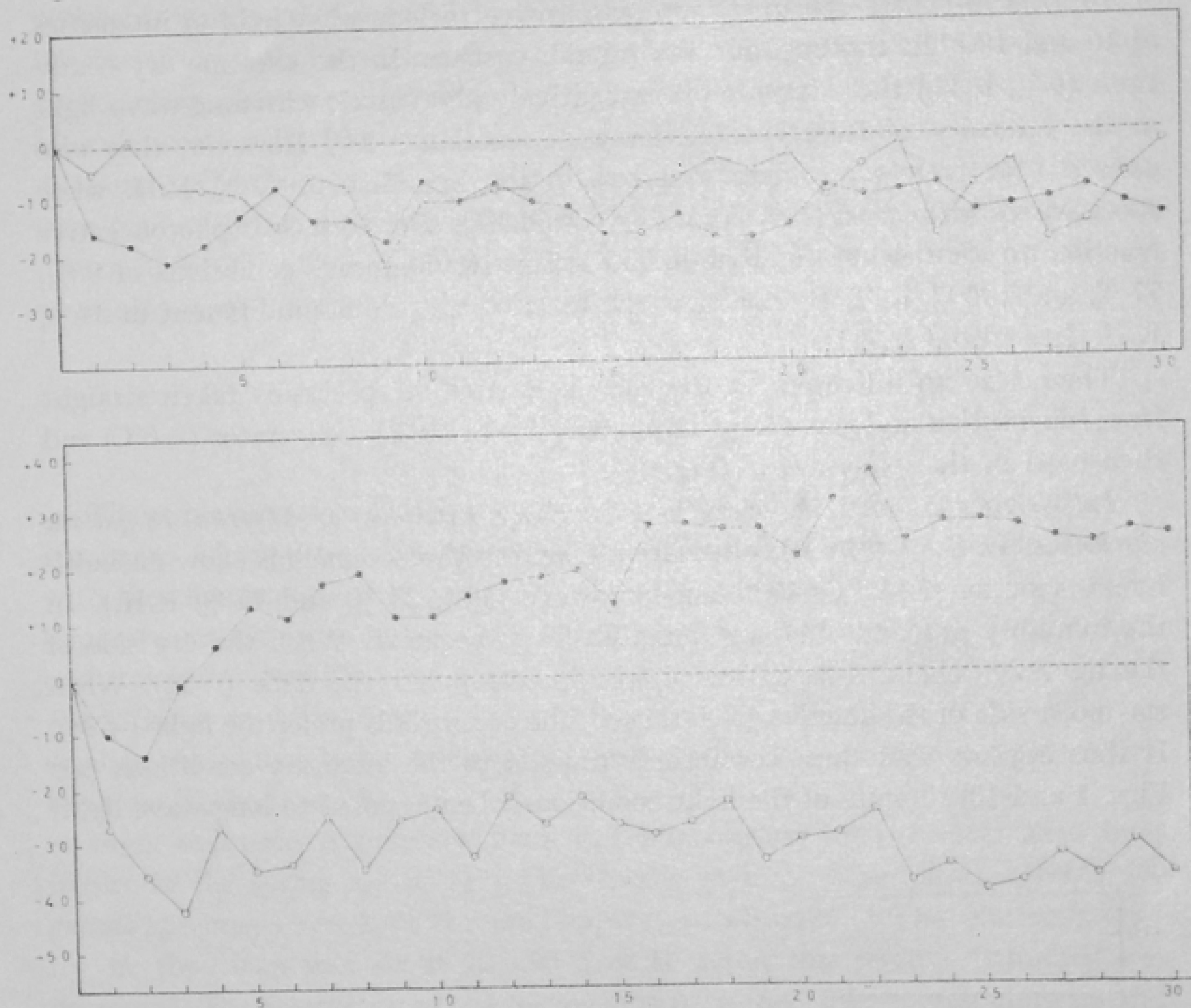
Figs. 12—13. — Fig. 12 (above). The comparison of the light reactions of *Myrrha 18-guttata* specimens kept in different conditions. The experiments were carried out at 20°C and 77 % R.H., with 1000 lux on the illuminated side of the chamber. —◯— specimens taken straight from their hibernating quarters, —●— specimens tested for weeks and stored between tests in a refrigerator at 6°C. Ordinate: intensity of reaction $\frac{100\ (L-D)}{N}$. Abscissa: time in minutes.

Fig. 13. (below). Interference between the light and humidity reactions of undesiccated specimens of *Myrrha 18-guttata*. The experiments were carried out at 20° C, with 1000 lux (long-wave) on the illuminated side of the chamber. —o— the illuminated side of the chamber had the lower humidity (34 % R. H.) and the dark side of the chamber had the higher humidity (77 % R. H.). —●— the illuminated side of the chamber had the higher humidity (77 % R.H.) and the dark side lower (34 % R.H.). Ordinate: intensity of reaction $\frac{100\ (L-D)}{N}$. The percentages were thus expressed according to possible light reactions (cf. PERTTUNEN & LAHERMAA 1963). Abscissa: time in minutes.

was a small temperature difference between the illuminated side and the dark side of the chamber. This difference was at its maximum with the light intensity of 10 000 lux (about 1°C). Control tests showed that it did not affect the light reactions of the species. Fig. 10 shows the reactions of these insects to short-wave and long-wave light of the same light intensity (1000 lux).

Myrrha 18-guttata specimens were insensitive to long-wave light at intensities of 10 and 100 lux thoroughout the humidity scale. In the extreme dry conditions (0 % R.H.) these insects were negatively phototactic with long-wave light at the intensity of 1000 lux (intensity of reaction −24). However, they also gave a negatively phototactic response in the humidity of 77 % R.H. when short waves were used (1000 lux). The coccinellids showed a clear photonegative reaction to short-wave light of 10 000 lux in the humidity conditions of 0 %, 77 % and 100 % R.H. By contrast, the reaction was almost indifferent in 34 % R.H. (see also Fig. 11).

There was no difference in the light responses of specimens taken straight from hibernation and those kept for several weeks in the refrigerator (+6°C) and then used in the experiments (Fig. 12).

Interference between the light and humidity reactions of Myrrha 18-guttata specimens. In the light-dark alternative chamber the coccinellids show an indifferent reaction (+20°C, 1000 lux long-wave light, 34 % and 77 % R.H.). In the humidity gradient they are definitely hygronegative. When the dry side of the humidity chamber is darkened, the insects prefer the dark (−31). When the moist side of the chamber is darkened, the coccinellids prefer the light (+18). It thus appears that these coccinellids respond to the humidity conditions (see Figs. 1 and 13) in spite of the light conditions when exposed to long-wave light.
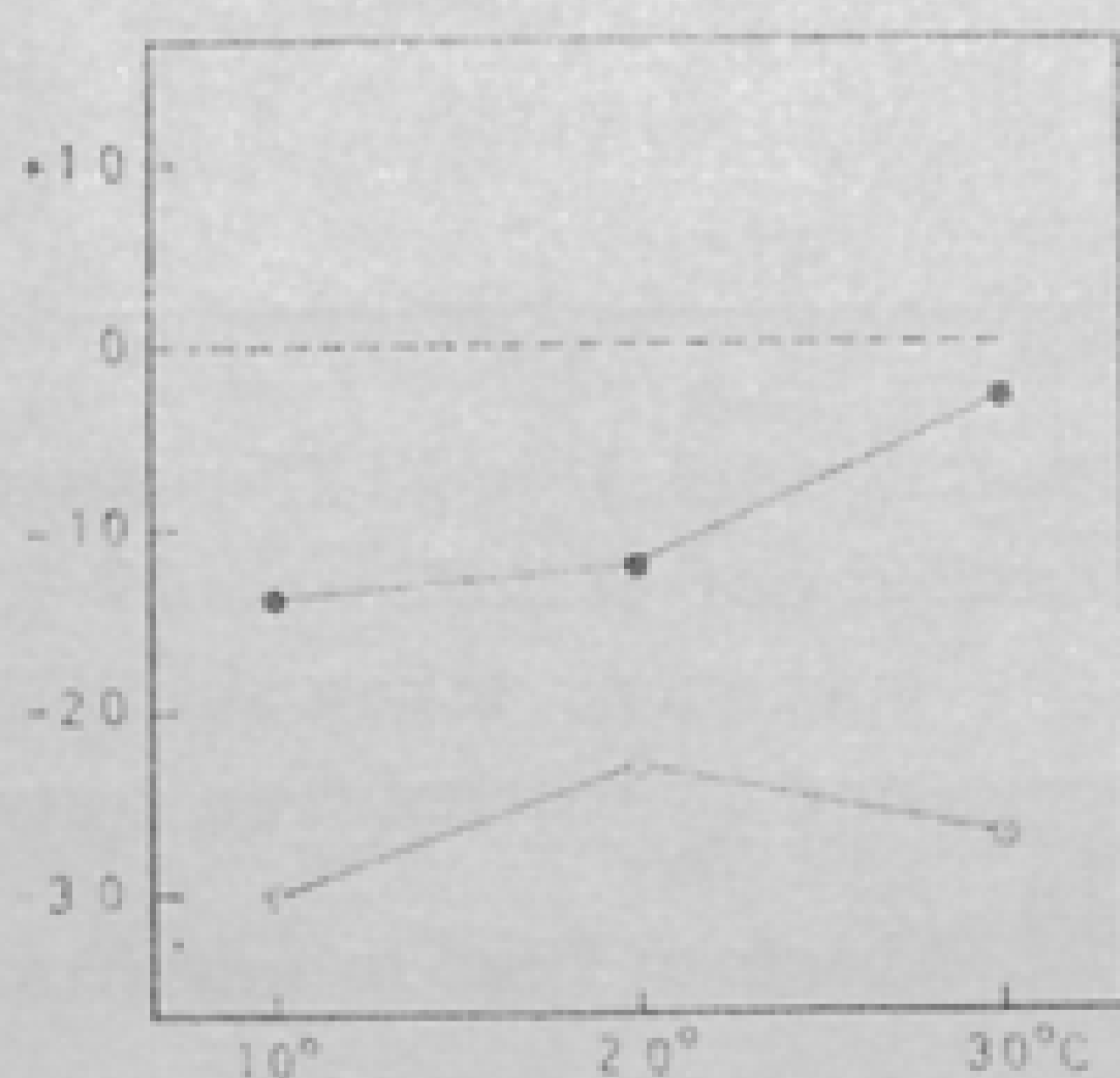

Fig. 14. Effect of temperature on the light reactions of *Myrrha 18-guttata* in different humidity conditions. Light intensity 10 000 lux (short-wave) on the illuminated side of chamber. −◯− 0 % R.H., −●− 34 % R.H. Ordinate: intensity of the reaction $\frac{100 \; (L-D)}{N}$.

Absciassa: experimental temperatures °C.

Light reactions at different temperatures. The following temperatures were used in these experiments: 10°, 20° and 30°C; and the following humidities; 0 % and 34 % R.H., with short-wave light (10 000 lux) to which the coccinellids had reacted photonegatively in the earlier experiments (see Fig. 11). Fig. 14 shows the results. In dry conditions (0 % R.H.) no difference is seen in the light

reactions at different temperatures. In 34 % R.H. the situation is not so clear but no significant trend is apparent in the light reactions at different temperatures.

The effect of desiccation on the light reactions of Myrrha 18-guttata. Figs. 15 – 19 show the light reactions of desiccated specimens of *Myrrha 18-guttata.* The experiments were carried out with long-wave light. The sensitivity of these coccinellids increases with increasing desiccation. After desiccation for 72 hours they give a clear photonegative response. The reaction seems to weaken, however, after desiccation for 120 hours. After desiccation for 144 hours there was a clear difference according to the humidity conditions under which the experiments were made. The photonegative reaction (Figs. 18 and 19) was much stronger in dry air (0 % R.H.) than in the humidity of 77 % R.H. By this time the specimens were also very fatigued.
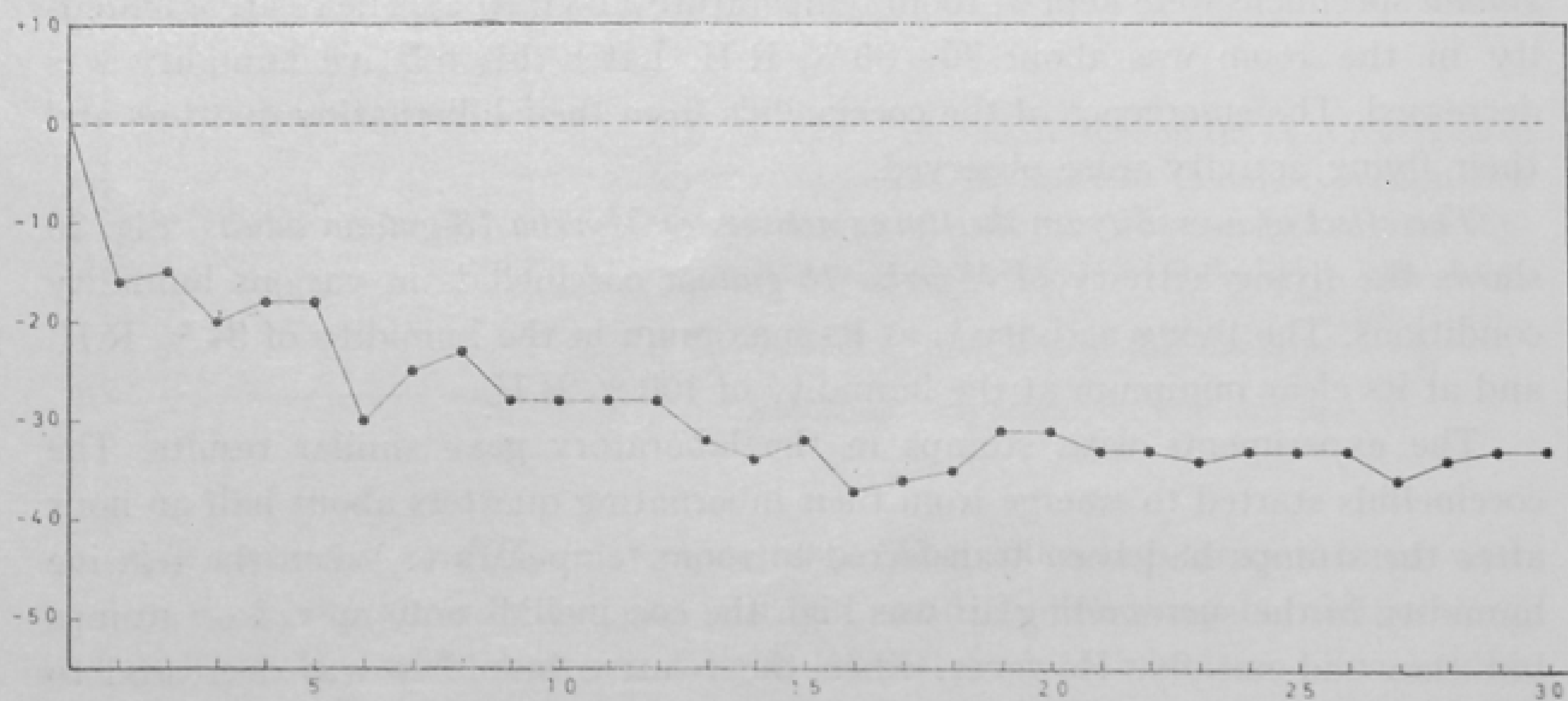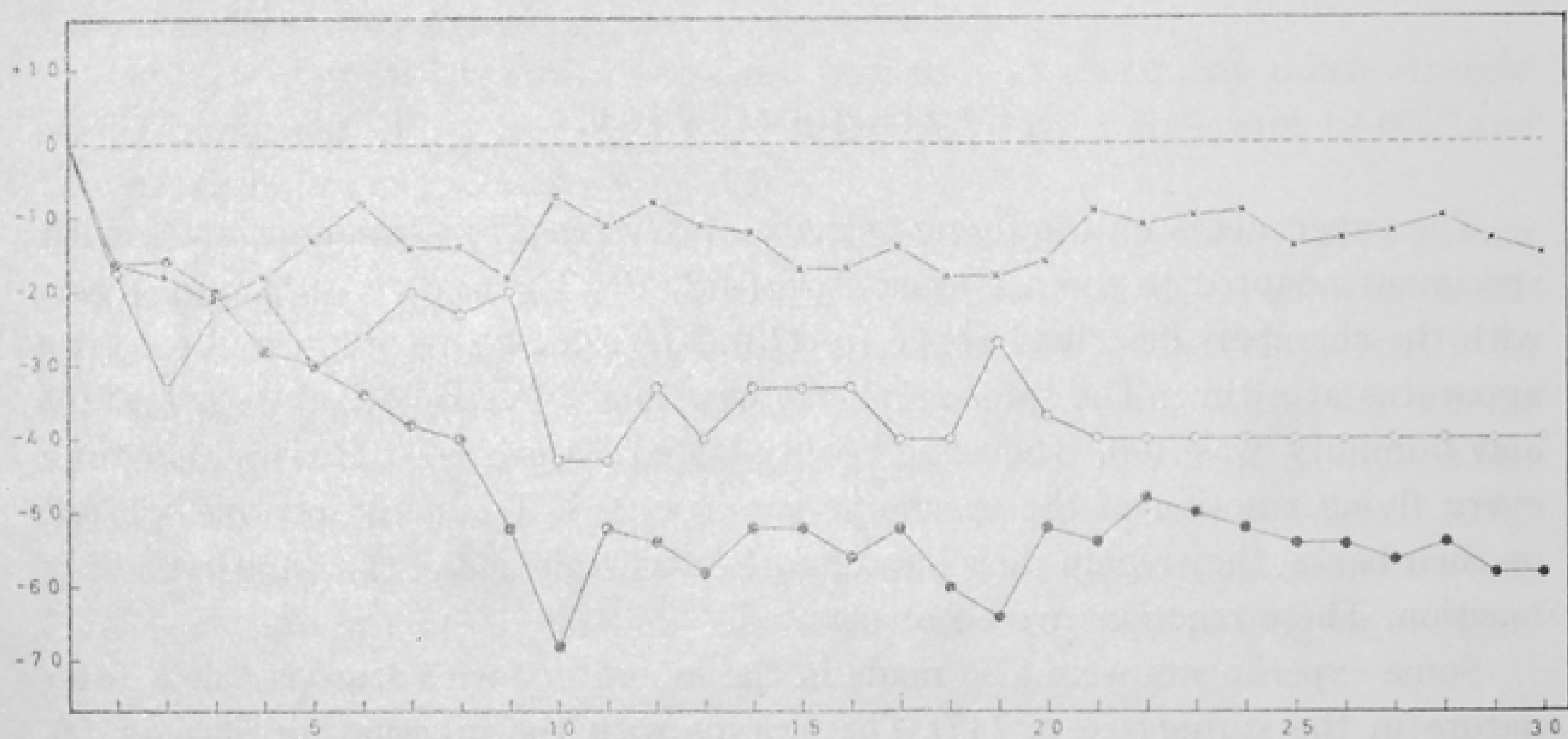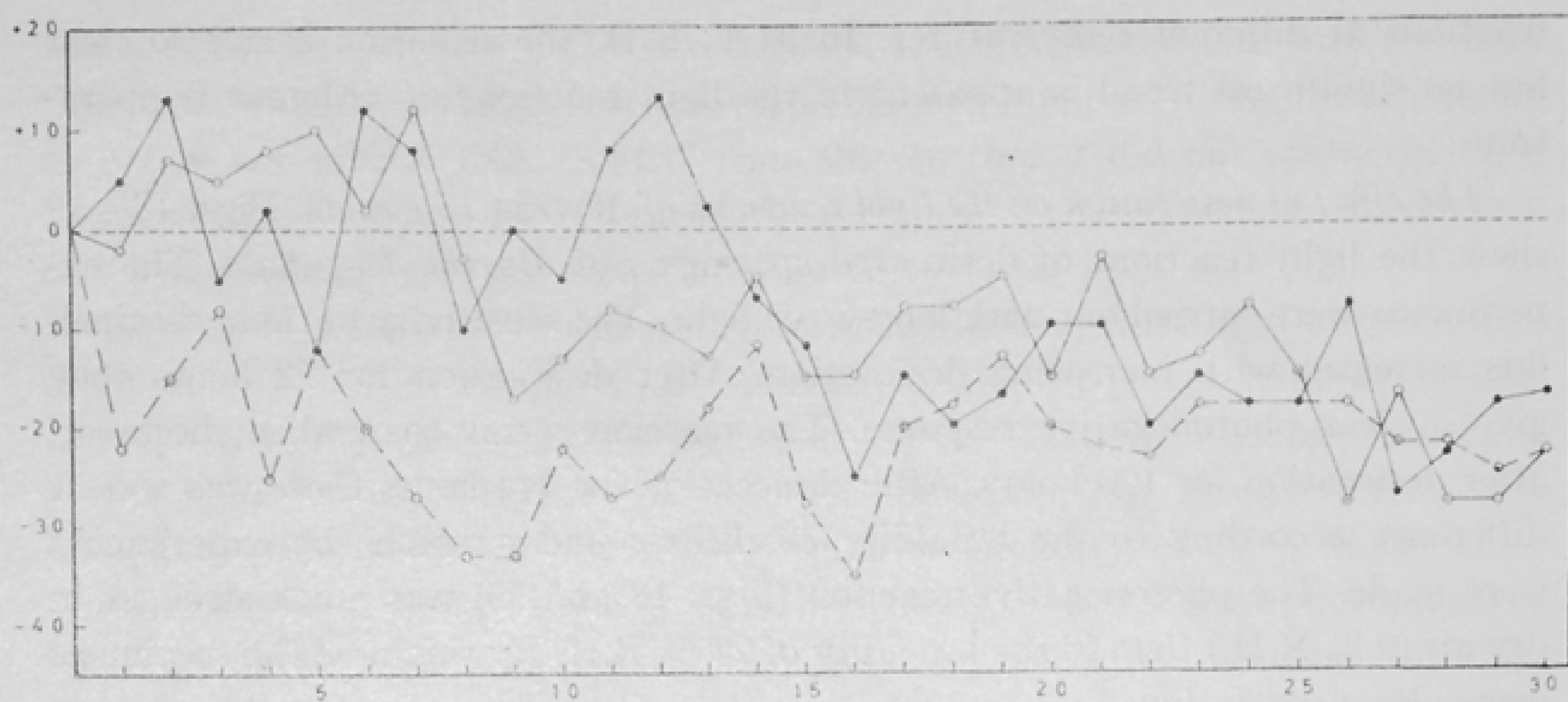
Flying activity.

The experiments on the flying activity of *Myrrha 18-guttata* were made with specimens adapted to room temperature (+20°C). The experiments were made with the chambers described above (p. 118). 20 specimens were inserted into the apparatus at a time. The total number of specimens tested at each temperature and humidity was 100. The experiments lasted 15 minutes. During this time every flying reaction of the specimens was counted. When the coccinellids fall on their backs, they regain their former posture with the aid of the wing-spreading reaction. These reactions were not counted.

Some experiments were also made in the laboratory with stumps taken from nature in the spring (see p. 117). The stumps with the hibernating *Myrrha 18-guttata* specimens were kept at room temperature (about 20°C). The relative humidity in the room was about 70 – 80 % R.H. Later this relative humidity was decreased. The emergence of the coccinellids from their hibernating quarters and their flying activity were observed.

The effect of humidity on the flying activity of Myrrha 18-guttata adults. Fig. 20 shows the flying activity of *Myrrha 18-guttata* coccinellids in various humidity conditions. The flying activity is at its maximum in the humidity of 34 % R.H. and at its clear minimum at the humidity of 100 % R.H.

The experiments with stumps in the laboratory gave similar results. The coccinellids started to emerge from their hibernating quarters about half an hour after the stumps had been transferred to room temperature. When the relative humidity in the surrounding air was high the coccinellids only moved on stumps but they did not fly. However, when the relative humidity was decreased to 30 – 40 % R.H. the coccinellids started to fly. Then the relative humidity on the surface of the stumps was higher than in the surrounding air.

The effect of temperature on the flying activity of Myrrha 18-guttata adults. Fig. 21 shows the flying activity of *Myrrha 18-guttata* specimens in relation to temperature conditions. The flying activity really begins when the temperature rises above $+15°$C. It increases with increasing temperature to $35°$C. This is the maximum point, and at higher temperatures, the flying activity decreases rapidly.
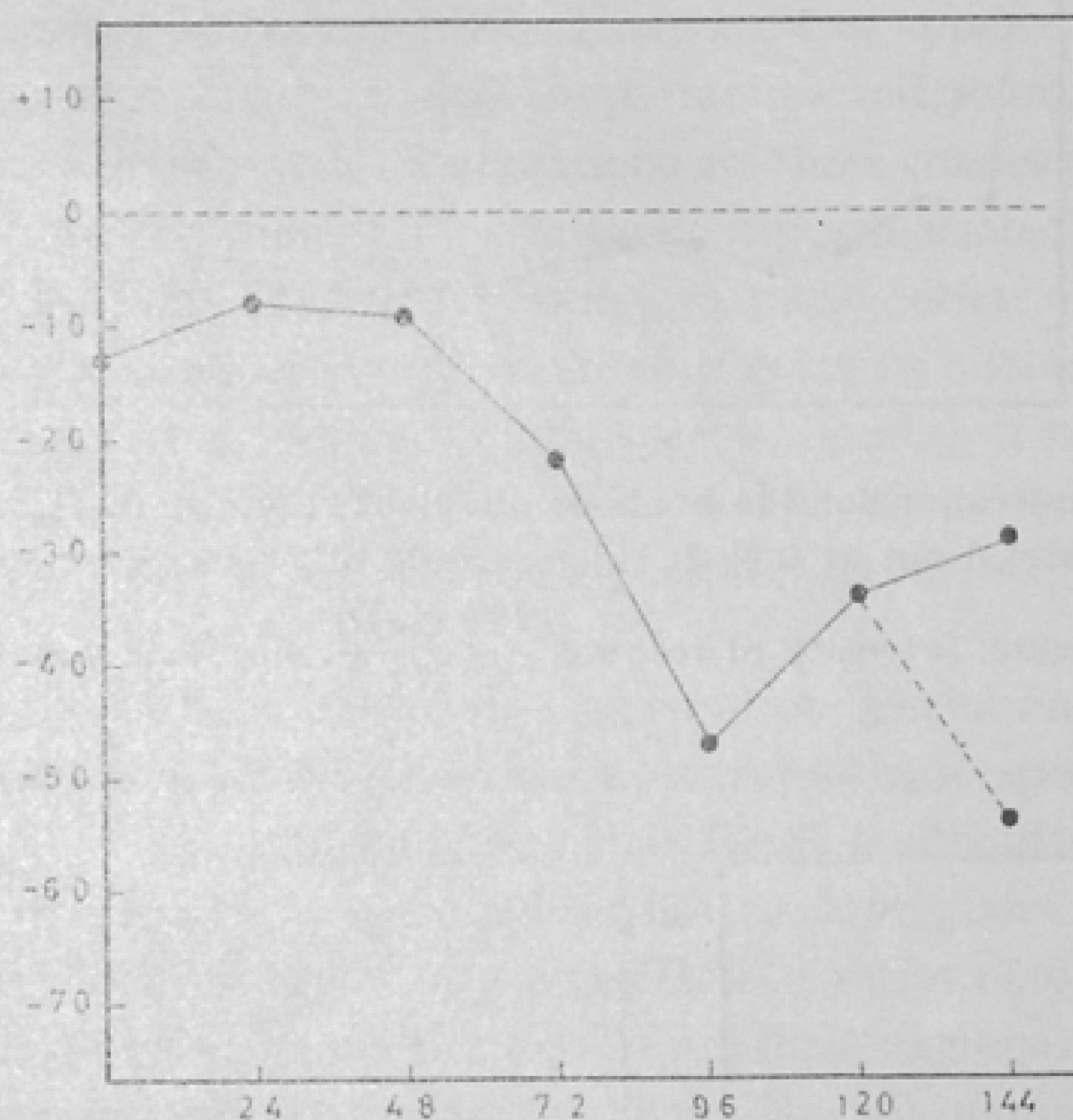

Fig. 18. Effect of desiccation (0 % R.H., 25°C) on the light reactions of *Myrrha 18-guttata*. For experimental conditions, see legend to Figs. 15 – 17. – – – – the experiments with desiccated specimens were carried out at 0 % R.H., in other cases at 77 % R.H. Ordinate: intensity of reaction $\dfrac{100\,(L\text{-}D)}{N}$. Abscissa: time in hours.

Figs. 15 — 17. Effect of desiccation on the light reactions of *Myrrha 18-guttata*. Experiments were carried out at 20°C and 77 % R.H., with 1000 lux (long-wave) on the illuminated side of the chamber. Ordinate: intensity of reaction $\dfrac{100\,(L\text{-}D)}{N}$. Abscissa: time in minutes.

Fig. 15 (above). –●– reactions after desiccation for 24 hours, –○– reactions after desiccation for 48 hours, – –○– – reactions after desiccation for 72 hours.

Fig. 16 (in the middle). –×– reactions of undesiccated specimens, –●– reactions after desiccation for 96 hours, –○– reactions after desiccation for 120 hours.

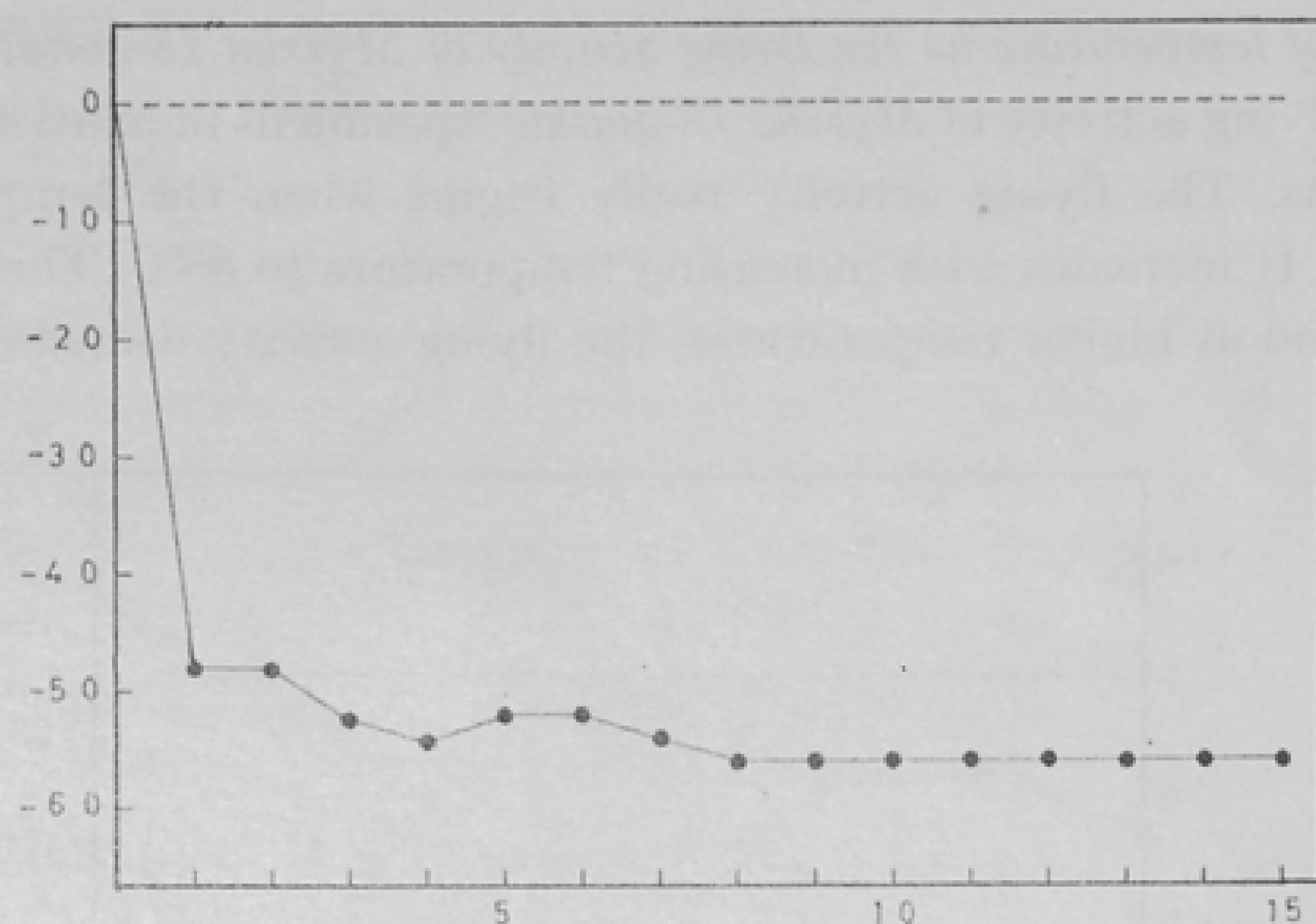Fig. 17 (below). Reactions after desiccation for 144 hours.

Fig. 19. Effect of desiccation for 144 hours on the light reactions of *Myrrha 18-guttata*. The experiments were carried out at 0 % R.H.; regarding other conditions, see legend to Figs. 15 – 17. Ordinate: intensity of reaction $\dfrac{100\,(L-D)}{N}$. Abscissa: time in minutes.

Fig. 20. The flying activity of *Myrrha 18-guttata* in different humidity conditions. For experimental methods, see text. Ordinate: number of flights of 100 specimens during 15 minutes at 25° C. Abscissa: experimental relative humidities.
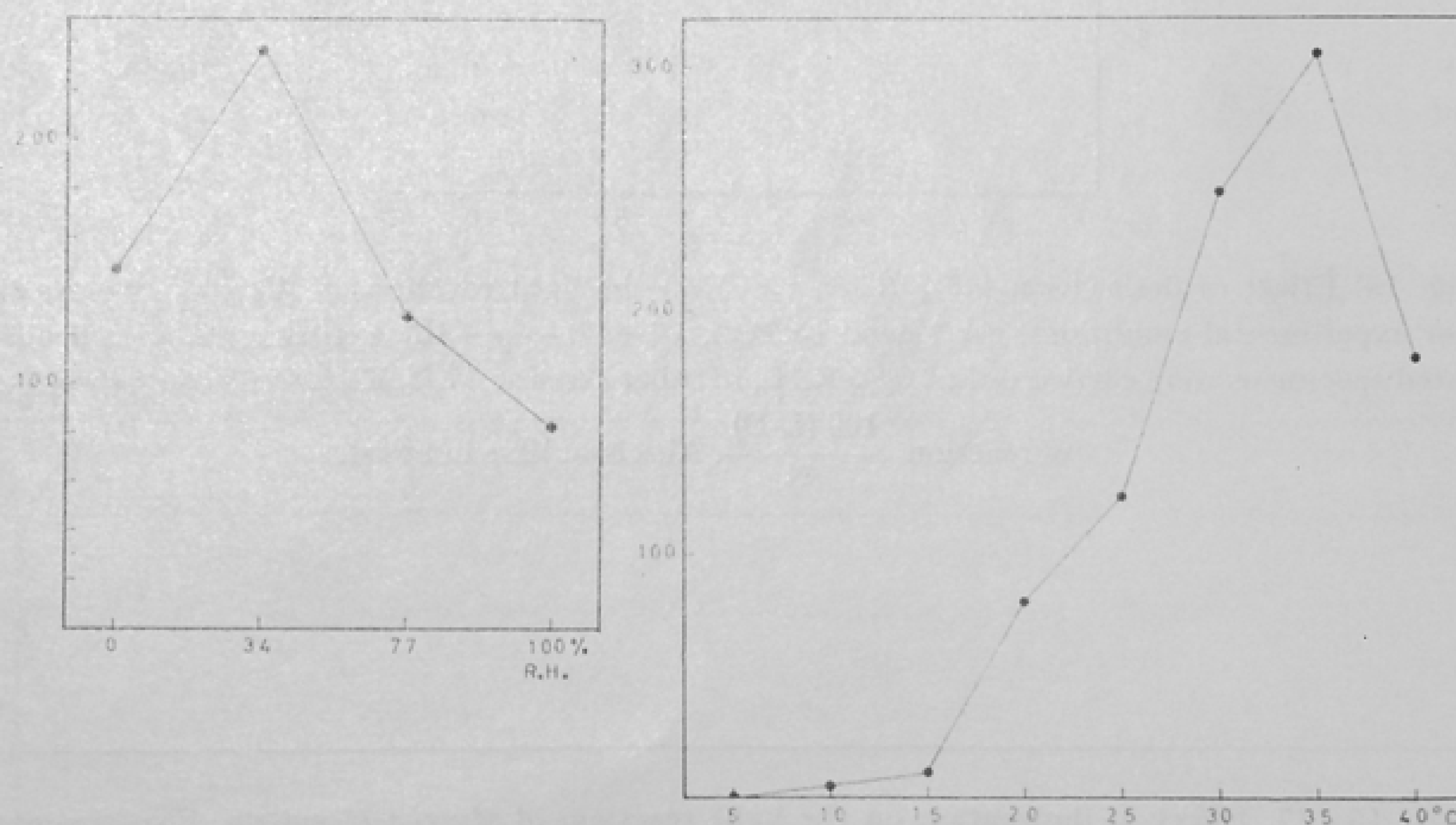
Fig. 21. The flying activity of *Myrrha 18-guttata* at different temperatures. For experimental methods, see text. Ordinate: number of flights of 100 specimens during 15 minutes at 77 % R.H. Abscissa: experimental temperatures °C.

Discussion.

It appears from the present investigation that in the adults of the coccinellid *Myrrha 18-guttata* the strong hygronegative reaction plays a very important rôle in the process of abandoning the hibernating quarters (see also PULLIAINEN 1963). This was verified by many different methods. The aggregation of coccinellids in hibernation and aestivation quarters is a very typical feature of these insects (see the review by HAGEN 1962). There are two apparently different types of aggregations, which can be called »hypsotactic» and »climatotactic» (HAGEN op.cit., p. 309). The »hypsotactic» aggregations are those connected with prominent isolated objects usually present in relatively dry situations, whereas the »climatotactic» aggregations are mostly found in moist situations in forest litter and are not usually associated with isolated objects or silhouettes. *Myrrha 18-guttata* can be regarded as a climatotactic species, because it hibernates in forest litter (SALMELA 1938, p. 25, 35) and in the crevices of the bark on the butts of pines (PULLIAINEN 1963; about the biology of the species see also SAALAS 1917, 1923, KANERVO 1940, 1946).

There are great differences in the aggregation mechanisms of hypsotactic and climatotactic coccinellids. As a rule most hypsotactic species congregate on or near the apex of a prominent object that forms a silhoutte on their horizon. (HAGEN 1962). Climatotactic aggregations are brought about by an even more complex mechanism than the above type. Here a series of physical factors interacts simultaneously to guide the beetles to their aggregation sites.

In their summer aggregations on the Sierra Nevada mountains *Hippodamia convergens* GUER. specimens settle down along the river banks in the litter and often in spots where the afternoon sun strikes the surface. The depth to which they penetrate the litter and the vertical movement up and down plants or other objects are apparently governed by moisture conditions (HAGEN 1962, p. 310).

HODSON (1937, pp. 284 – 286) exposed samples of leaf-covered soil of various degrees of moisture to *Coleomegilla maculata* DEG. and *H. convergens* adults taken from hibernation. Both species exhibited a marked preference for certain specific moisture conditions.

HAGEN (1962) has observed that the water balance of *H. convergens* beetles is maintained by imbibing water. He has also paid attention to a distinct water loss of these insects in dry air. Similar results were obtained in the present investigations with *M. 18-guttata*. Comparative morphological studies of the Malpighian tubule arrangement among different species that aggregate may permit the separation of hypsotactic aggregators from climatotactic ones. This is predicted on the finding of LANDIS (1936) with *C. maculata* and PRADHAM (1942) with *Coccinella septempunctata* and some other species, which revealed a difference between the species in the reassociation of the Malpighian tubules (HAGEN 1962).

The physiological requirement of free water may prove to be the basic difference between the hypsotactic and climatotactic aggregators. It appears from

the present investigation that in the adults of *M. 18-guttata* the normal hygro-negative reaction is reversed by sufficient desiccation. After desiccation for 72 and 86 hours there existed during the first minutes of the experiments a clear hygronegative reaction, which soon became indifferent, however. The fact that this kind of reversal in the humidity reaction was observable during the experiments is connected with the ability of these insects to extract water vapour from the surrounding air (during the experiments the air on the moist side of the chamber was saturated with moisture). Such an ability has been observed in *Ixodes ricinus* L. (LEES 1946, 1947), too. This ability could be confirmed by measurements of their weight increase after desiccation. Reversal of the humidity reaction on desiccation has been observed in a number of arthropods (see e.g. the reviews by SYRJÄMÄKI 1962, pp. 49 – 52, ROTH & WILLIS 1963, HENSON 1964).

The death rate pattern of the species on desiccation is very similar as that observed, for instance, in spiders (LAGERSPETZ & JÄYNÄS 1959, p. 219).

Moisture, however, is not the only factor involved in guiding the climatotactic species to aggregation sites and away from them, for temperature and light also play a part. *Coleomegilla maculata* moves from meadow grasses and forest foliage into the forest floor during the autumn, and stays in the deeper portions of the floor mould during the winter, moving back into the meadow and upper forest the following spring (PARK 1930). WEISS (1913), PARK (op.cit.) and HODSON (1937) observed a downward movement when the temperature dropped, and the first two authors concluded that a fall in temperature caused *C. maculata* to become negatively phototactic. Once having reached their place of hibernation the beetles also become positively thigmotactic, and with a rise of temperature the reverse occurs (WEISS 1913), but HODSON (1937) observed the same downward movement in complete darkness, thus indicating a geotactic response associated with temperature changes.

Hippodamia convergens also moves vertically during aggregation. Moisture appears to dominate as a stimulus; however, temperature may be involved, inasmuch as BEASER (1913) and HAWKES (1926) found that lowering of the temperature caused the beetles to aggregate. Light is also involved, since laboratory tests show this species to be positively phototactic over a wide range of temperatures (HAGEN 1962). MICHIELI (1959, 1963) has paid attention to »Schirmorientierung» in the behaviour of coccinellids.

In the experiments with long-wave light it appeared that *M. 18-guttata* specimens do not react to different light intensities. However, a photonegative reaction to a light intensity of 1000 lux could be observed in extreme dry conditions (0 % R.H.). A similar record was obtained with short-wave light. There were no differences in the strength of the light reactions with light intensities of 1000 and 10 000 lux. On the contrary, the coccinellids reacted differently to light of various wave lengths. They reacted photonegatively to short waves,

but indifferently (with the above-mentioned exception) to long waves. MADGE (1964) has recently studied the light reactions of the cutworm *Tryphaena pronuba* L. He observed an apparent bias towards yellow (5600 – 6100 Å) in a range of different colours. This was illusory, however, because yellow and black appeared the same to the larvae, which, being yellow-blind, aggregated equally in black and yellow. SCHLIEPER (1927, 1929), in his studies on the optomotor reactions of coccinellids, observed that they correspond to the human eye in its dark-adapted state. Further studies are needed to explain the exact mechanisms of the light reactions of coccinellids.

As regards the effect of humidity conditions on the light reactions of the species it is noteworthy that in the experiments with long-wave light the coccinellids showed a photonegative reaction in extremely dry conditions at the highest light intensity (1000 lux). By contrast they reacted indifferently in humidity conditions of 34 % R.H. with short-wave light (10 000 lux). In other (perhaps less favourable) humidity conditions they showed a photonegative reaction. PERTTUNEN & LAHERMAA (1963) and PERTTUNEN & PALOHEIMO (1963), in experiments on the light reactions of *Tenebrio molitor* L., have observed that there is a correlation between the intensity of the light and the intensity of the photonegative reaction. The insects, both larvae and adults, were more photonegative at a high than at a low intensity of light on the illuminated side of the chamber. In the adults of *T. molitor* the intensity of the photonegative reaction is considerably lower at 100 % R.H. than at lower uniform relative humidities. They normally have a hygronegative reaction (LECLERQ 1947, DODDS & EWER 1952) so that the photonegative reaction was weaker in unfavourable conditions.

The interference between the light and humidity reactions of the species was studied with the aid of long-wave light on the illuminated side of the chamber. The coccinellids orientated according to humidity conditions in spite of the light conditions. PERTTUNEN (1961) has made similar investigations with *Ligia italica* F. If the moist half (77 % R.H.) of the alternative chamber was illuminated and the dry half (34 % R.H.) was in darkness, the specimens chose the moist but illuminated side if the light intensity was 10 or 100 lux. If it was 1000 lux, they chose the dark but dry side in experiments of short duration. In prolonged experiments, the specimens first collected on the dry dark side. After half an hour, the reaction was indifferent, and after one hour the reaction was reversed and the majority of the specimens were found on the moist illuminated side. These isopods are normally hygropositive and photonegative.

I could observe no effect of temperature on the light reactions of *M. 18-guttata* over the temperature range 10° – 30°C. The same result was recorded by HAGEN (1962) with *H. convergens* and by CLOUDSLEY-THOMPSON (1963) with some desert Tenebrionidae. However, there are several references in the literature to reversal of the sign of phototaxis in insects by high temperatures (JACK & WILLIAMS 1937, DOLLEY & GOLDEN 1947, WELLINGTON 1948, DOLLEY & WHITE

1951, Wellington, Sullivan & Green 1951, Sullivan & Wellington 1953, Green 1954, Wellington, Sullivan & Henson 1954, Perttunen 1959,) and to similar effects of low temperatures (Dolley & Golden 1947, Perttunen 1958, 1960; cf. Weiss 1913, Park 1930).

Breitenbrecher (1918) reported that specimens of *Leptinotarsa decemlineata* L. taken from wet soil reacted positively to light, whereas specimens from dry soil reacted negatively. Perttunen (1963) has recently reviewed the literature concerning the effect of desiccation on the light reactions of arthropods. The reversal of a photonegative mean reaction to a photopositive one is found in *Ligia italica*, *Calandra granaria* L. and *C. oryzae* L., and the adult *Tenebrio molitor*. By contrast, a photopositive mean reaction is reversed to a photonegative one in *Drosophila melanogaster* Meig. In *Myrrha 18-guttata* an indifferent (long-wave) light reaction was reversed to a photonegative one by desiccation. Perttunen (1963) observed that desiccation alone was enough to reverse the light reaction of *Calandra*. There are many examples of the effect of starvation on the light reactions of certain lepidopterous and hymenopterous larvae and the beetle *Pissodes strobi* Peck (Wellington 1948, Sullivan & Wellington 1953, Green 1954, Wellington, Sullivan & Henson 1954, Sullivan 1959). Starvation did not change the light reaction of *M. 18-guttata*.

The existence of an adult diapause in *Coccinella septempunctata* L. has been confirmed by Dobzhansky (1922), Hodek (1958 a and b, 1960), Hodek & Cerkasov (1960, 1961 a and b) (cf. also *Leptinotarsa decemlineata*, de Wilde, Duintjer & Mook 1959). Their investigations into the physiology of the diapause revealed that, besides fat, glycogen is also accumulated in both sexes, mainly in the fat body, before the beetles migrate toward their winter quarters. Hodek & Cerkasov (1960, 1961 a and b) also studied the artificial induction of an imaginal diapause in *C. septempunctata*. They observed that the proportion of glycogen was practically the same in beetles naturally and artificially induced to enter diapause. The fat content was one-fifth lower in the laboratory-reared beetles. Active females contained half the quantity of glycogen and less than half (43.9 %) the quantity of fat present in females in diapause. Hence the physiological state of the adults in diapause, whether taken in the field or reared in the laboratory, can be considered equivalent in this respect. The increase of the fat and glycogen content of the coccinellid body when entering diapause means a decrease of their relative water content. Whether this change in the relative water content produces a photonegative reaction is not yet known. Weiss (1913) and Park (1930) concluded that *C. maculata* specimens became negatively phototactic in the autumn on entering hibernation quarters. In my experiments, *M. 18-guttata* specimens became negatively phototactic when their water content was decreased by desiccation. We can consider this water balance mechanism from the ecological point of view, too. These coccinellids are normally hygronegative and they react indifferently to long-wave light and photonegatively to short-wave light. The

present studies on the effects of desiccation on the humidity and light reactions of *M. 18-guttata* suggest that the reversal of the indifferent light reaction to a photonegative one must play an important role in the ecology of the species, as also does the reversal of the humidity reaction. The beetles can avoid unfavourable conditions with the help of these mechanisms. We can thus class them with similar mechanisms of diapause, dormancy (hibernation and aestivation) and aggregation.

In the experiments concerning the flying activity of the species effects of both humidity and temperature could be observed. The flying activity was at its maximum at +35°C and 34 % R.H. The various kinds of effects of natural conditions on the flying activity of insects have been reviewed by HENSON (1962), TAYLOR (1963) and PULLIAINEN (1964). Temperature is as a rule one of the key-factors in the activity of insects. HAGEN (1962) has studied the migrational flights of *H. convergens*. The temperature at which the beetles were trapped during their migration back to the mountains ranged between 13° to 18°C (mostly between 13° to 15°C). HAGEN (op.cit.) has observed that the flight behaviour of *H. convergens* on leaving the aggregational sites is remarkably different from the behaviour of these beetles when they are reproductively active or are shifting aggregational sites locally in the mountains. The migratory flight take-off is directly vertical, occurring when there is no wind or only lulls in very gentle winds, and when the temperature is above 17°C. Beetles which were taken from hibernating sites in mountains and released in the valley took off with the wind, when the temperature in the shade was about 20°C, and dispersed widely (DAVIDSON 1919, 1924). *H. convergens* beetles continue to fly during migratory flights as long as the temperature permits. Air temperatures of 11° to 13°C (dry bulb) on clear bright days form a temperature ceiling which arrests active flying (HAGEN 1962). In general my investigations support the results of earlier studies on the threshold at which the flying activity of coccinellids begins. I have found no reports concerning the upper limit of the flying activity of the species. In this respect it is remarkable at what a high temperature (+35°C) the flying activity reached its peak. According to HENSON (1962), adults of *Conopthorus coniperda* SCHWARZ undertake spontaneous flight most frequently at temperatures between 27.5° and 35°C. The light, humidity and flying activity experiments showed that the optimal humidity of *M. 18-guttata* specimens which have left their hibernating quarters is about 30 – 40 % R.H. (cf. PULLIAINEN 1963).

Summary.

1. The undesiccated specimens of *M. 18-guttata* showed a preference for the drier side of the chamber when different humidity alternatives were offered.

2. This humidity reaction is based on very strong klinotactic and orthokinetic types of orientation.

3. The beetles lost 26 per cent of their weight during the first 24 hours of desiccation. Besides desiccation, »reflex bleeding» decreased their weight. During 144 hours of desiccation these coccinellids lost 50 per cent of their weight.

4. After 192 hours of starvation and desiccation (0 % R.H., +25°C) 97 per cent of the individuals were dead.

5. The hygronegative reaction of the species was reversed to indifference after desiccation for 24 hours. After desiccation for 72 and 96 hours there was a clear hygropositive reaction during the first minutes of the experiments, which soon became indifferent. The desiccated specimens could extract water vapour from the surrounding air.

6. As a rule *M. 18-guttata* specimens reacted indifferently to long-wave light and photonegatively to short-wave light. Light intensity did not affect the intensity of the reaction. Humidity conditions had a certain effects on the light reactions. In extremely dry conditions (0 % R.H.) these insects were negatively phototactic at the long-wave light intensity of 1000 lux. When using short-wave light the beetles reacted indifferently in humidity conditions of 34 % R.H.

7. In long-wave light (1000 lux) the beetles reacted to the humidity conditions in spite of the light conditions.

8. Temperature (range 10° to 30°C) did not change the light reactions.

9. After desiccation for 72 hours the beetles became strongly photonegative (long-wave light).

10. The flying activity of the species begins when the temperature rises above +15°C, and reaches its maximum when the temperature is +35°C.

11. The flying activity is at its maximum in humidity conditions of 34 % R.H.

12. The humidity, light and flying activity experiments showed that the optimal humidity for *M. 18-guttata* specimens which have left their hibernating quarters is about 30 – 40 % R.H.

13. The physiological and ecological basis and significance of the above-mentioned reactions is discussed. *M. 18-guttata* is regarded as a »climatotactic» species.

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