THE WATER RELATIONS OF SNAILS AND SLUGS

II. WEIGHT RHYTHMS IN *ARION ATER* L. AND *LIMAX FLAVUS* L.

By N. H. HOWES and G. P. WELLS.
(From the Department of Zoology, University College, London.)

(*Received 5th December*, 1933.)

(With Five Text-figures.)

In the first paper of this series (Howes and Wells, 1934), we showed that active specimens of the edible snail (*Helix pomatia*) continually undergo considerable fluctuations in weight, due to changes in their water content, even in environments which do not greatly vary in physical properties. The following experiments were performed in order to find out whether similar phenomena occur in slugs. Most of the experiments were done on *Arion ater*, but specimens of *Limax flavus* were also studied. The results obtained on the two species will be described separately and then discussed together.

I. EXPERIMENTS ON *ARION ATER* L.

Each animal was kept alone and weighed daily. The following simple vivarium was devised: its merits are that it is cheap and easy to make, easy to clean, and although well ventilated it does not allow the slugs to escape. The last advantage is by no means easy to secure. A cylinder of perforated zinc, about 6 in. across and 5 in. high, stands on one glass plate and is closed above by another (Fig. 1). On the lower glass plate are put a piece of cabbage, a slug and a glass Petri-dish of water. Both the food and the water are changed every day.

Ten animals were kept in this way. The weight curves of three representative specimens are shown in Fig. 2. Five of the animals, like the upper two records of Fig. 2, ate enormously and grew very fast; superposed on the growth curve are weight fluctuations of great amplitude. These animals were still growing and active at the end of the experiment. The other five lost weight and died, but even these showed weight fluctuations; the lower record in Fig. 2 is an example of this group. As a glance at the illustrations of our former communication will show, the weight records of *Arion* are very similar in type to those of snails.

In *Helix* we found that fluctuations occur in animals given water but no food, and not in animals given food but no water. They are therefore due primarily to changes in water content. In order to determine whether the same is true of *Arion*, we tried the effect of deprivation of food and of water on the slugs.

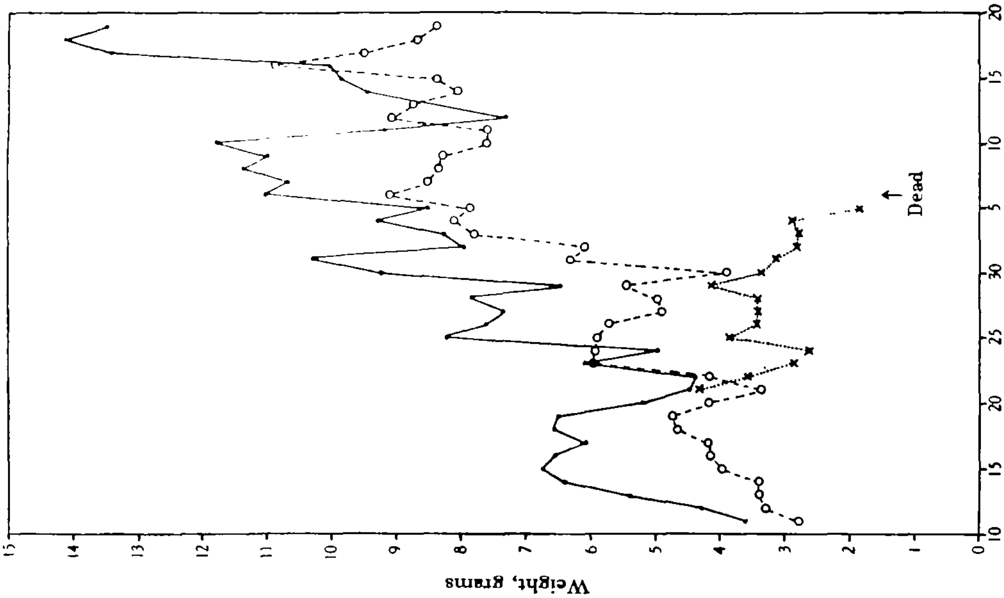

Fig. 2. *Arion ater*. Weight records of three slugs receiving food and water.

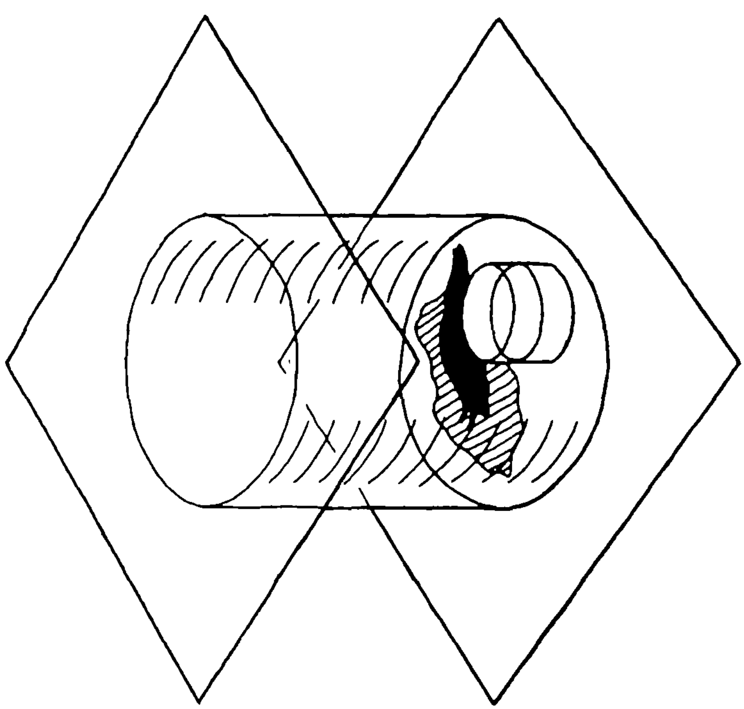

Fig. 1.

Fig. 3 shows the weight records of three individuals from a group of ten, which received water but no food. Only three of this group died during the experiment. The others were started at different times, and had lived for periods of from 19 to 31 days when the experiment was discontinued. In every case the weight curves showed considerable fluctuations which can only be due to changes in the water content of the animals. As in the case of *Helix*, the amplitude of the fluctuations is noticeably less in fasting than in fed animals.

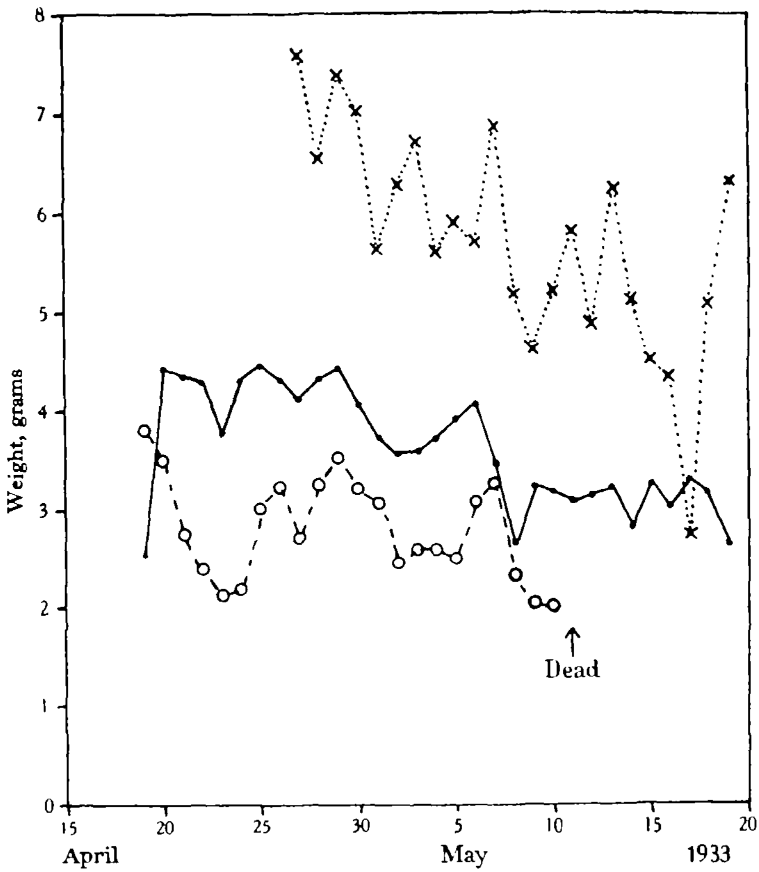

Fig. 3. *Arion ater*. Weight records of three slugs receiving water but no food.

The results obtained by giving slugs food but no water are very striking; Fig. 4 includes the weight curves of the whole of a group of fourteen animals treated in this way. In every case, the weight falls rapidly, and in 3 or 4 days the slug is dead.

The experiments in deprivation of water were done in batches at various times. The air in the laboratory varied between 40 and 80 per cent. relative humidity, and between 15 and 19° C.

It occurred to us that the presence of a dish of water in the cages might perhaps affect the humidity of the air, in which case caution should be exercised in comparing

Fig. 4 with Figs. 2 and 3. To test this possibility, we tried the effect of keeping slugs with dishes of water of the type usually provided, but covered over with screens of perforated zinc, so that the animals could not reach the water although it could evaporate freely. Two of the curves in Fig. 4 were obtained in this way; it will be seen that there is no significant difference between these two and the others.

There are, broadly speaking, two ways in which this very abrupt weight loss might be caused—either by simple physical evaporation through the moist skin of the animal, or by excretion, respiration, slime secretion and other vital processes. In

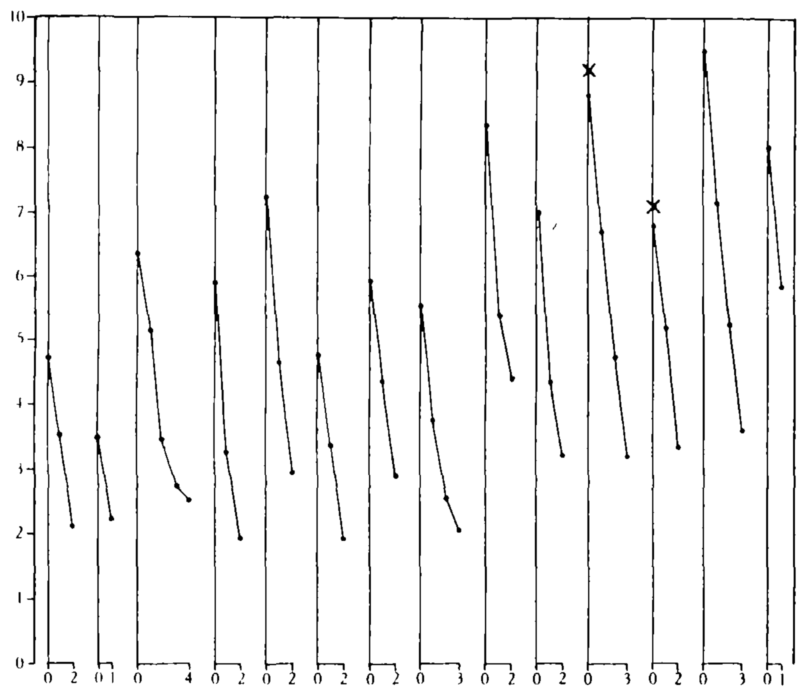

Fig. 4. *Arion ater*. Weight records of fourteen slugs receiving food but no water. Abscissae = days, ordinates = weight in grams. Points are only plotted for days on which the animals were alive; on the day following the end of each graph the animal was dead. In the case of the animals *X*, water was present in the cages but shielded so that the slugs could not touch it.

our experiments the first cause was by far the most important. In Fig. 5, the logarithms of the weights of two animals kept without water are plotted against time. We do not justify this procedure on theoretical grounds; it has the purely empirical advantage that it converts the weight curve into an approximately straight line. The weighings were continued after the death of the slugs. It will be seen that the line continues smoothly through both "living" and "dead" points. Even eating and defaecation produce no perceptible deviation. Evidently then water loss by evaporation is a factor of great importance in the life of these animals, at least in room air; in our experiments it predominates over all others in determining the shape of the strikingly steep drying curve.

II. EXPERIMENTS ON *LIMAX FLAVUS* L.

Two specimens only were studied. They were kept separately, in containers of the same type as those used for *Arion* (Fig. 1). At first they received food and water, then water only, then neither food nor water. The weight records for the first two periods show fluctuations similar to those of *Arion* and *Helix*. In the absence of water there is the same catastrophic loss of weight as was observed in *Arion*. On the second day after removal of water both the *Limax* were dead and hard. One was dead, but not hard, at the end of the first day.

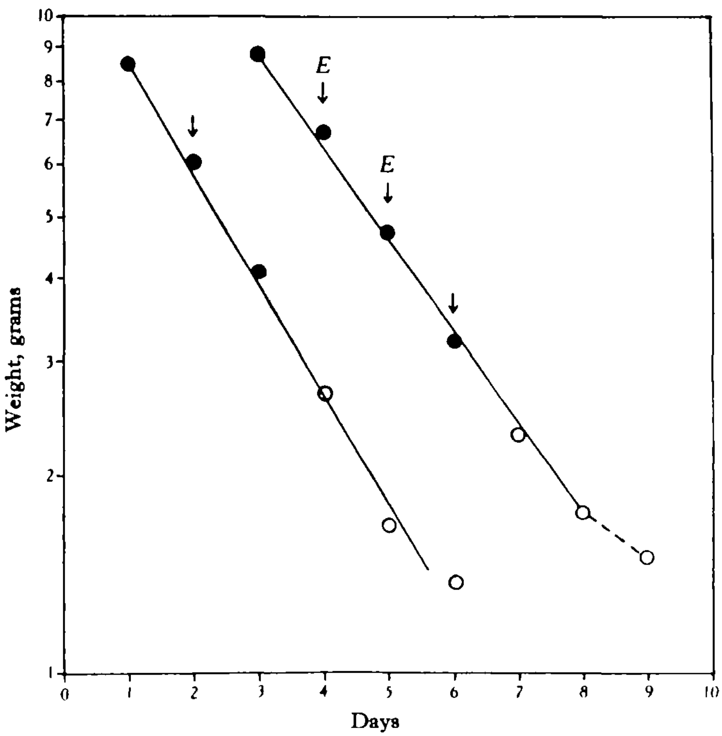

Fig. 5. *Arion ater*. Weight records of two slugs receiving food but no water, the weight being plotted logarithmically. ● = animal alive, ○ = animal dead, *E* = animal ate, ↓ = animal defaecated.

III. DISCUSSION.

Since weight fluctuations of considerable amplitude, due to changes in water content, appear in *Helix pomatia*, *Arion ater* and *Limax flavus*, it is likely that they occur very widely, perhaps universally, among terrestrial gastropods.

Apart from the resemblance between snails and slugs, the most striking fact which emerges from this investigation is the very rapid loss of weight by evaporation shown in Fig. 4. This confirms the results of Künkel (1916), who made a prolonged study of the weight loss of snails and slugs deprived of water. He found, working on a specimen of *Limax variegatus*, that if the animal was sitting motionless on a balance pan it lost weight at the rate of about 2·4 per cent. of its initial weight per hour. This works out at 57·6 per cent. in 24 hours. If, on the other hand, he compelled it by mechanical stimulation to creep continuously, it lost 16 per cent. of its weight in an hour, a performance which, if it could be kept up, would mean a loss in 24 hours of 384 per cent. of the initial weight of the slug. This difference in rate of weight loss is attributed by Künkel mainly to the secretion of slime during creeping. Our own animals were not stimulated to excessive physical exertion but left alone; we found that *Arion* deprived of water lost rather less than one-third of its weight per day, while *Limax* lost about two-thirds. As we have shown, this loss was due, at least in the case of *Arion*, almost entirely to evaporation. To judge by Künkel's figures, our slugs spent most of their time resting, and an actively creeping *Arion* probably loses weight at an even greater rate than the animals of Fig. 4.

The weight curves of *Helix pomatia* kept without water (Howes and Wells, 1934, Fig. 6) contrasts very strikingly with those of slugs. The snail retires into its shell, and loses weight extremely slowly. Künkel found that *Helix pomatia* could be kept alive without water for over 10 months. Other snails could resist dry conditions very much longer than slugs, except *Succinea putris*, which has a wide-mouthed shell into which it cannot completely retire, and which dried out rapidly like a slug. But although most species of snails can delay evaporation by retiring into their shells, we may safely guess that an active snail, creeping with its foot well out of the shell, has water relations similar to those of a slug, and will lose large amounts of water partly by evaporation and partly as slime.

Rapid water loss seems then to be a necessary condition of active life in terrestrial gastropods. This results in part from their moist, permeable skin and in part from their method of locomotion, which depends on the continuous secretion of copious, watery slime.

Two points emerging from these considerations may profitably be discussed. The first is that in respect of water turnover, the land gastropods occupy a position which is apparently unique among the major land groups. The higher vertebrates, for instance, have a thick stratified epithelium which reduces evaporation through the skin very considerably. Kudo (1921) found that albino rats given dry food but no water developed serious symptoms in periods up to 16 days, after losing weight at the rate of about 3·4 per cent. of their initial weight per day. A rat given neither water nor food lived for 11 days, losing 4·8 per cent. of its weight per day. Adolph (1930) quotes as the average daily turnover of water in man, 3·4 per cent. of the body weight. Subsisting on food with a minimal water content and taking no water, the same authority (1921) lost about 4·3 per cent. of his weight in 4 days. It is evident that the water losses of mammals in normal atmospheres are very much less than those of gastropods. During strenuous thermoregulation in a hot, damp environment the figures for man rise considerably. Adolph (1921) was able by immersing himself in a hot bath at 39° C. to lose 1·0 per cent. of his weight in an hour; similarly placed, a colleague of his lost 2·1 per cent. per hour. These figures work out at 24 and 50 per cent. per day. In a "sweating chamber" (34° C. wet bulb) the same investigators lost water at only about half these rates. It will be seen that by very laborious sweating a man can approach the normal molluscan water output. Indeed, to judge by the figures of Hunt (1912), there is a close agreement between the percentage water losses of an *Arion* resting in room air and of a man dehydrating himself for experimental purposes in a Turkish bath.

Many insects, again, are protected against evaporation by their chitinous cuticle. The bug *Rhodnius prolixus*, fasting in atmospheres of various humidities, loses about 2–3 per cent. of its weight per day, and a fasting mealworm (*Tenebrio molitor*) loses up to 2 per cent. per day (Buxton, 1930, 1932). These figures resemble those given by mammals and are far below those given by molluscs. On the other hand, some insects lose water more rapidly. According to Davis (1928) certain *Collembola* can live only for a few hours in unsaturated air. Gunn (1933), working on cockroaches (*Blatta orientalis*), found weight losses in dry air at 30° C. which varied in different individuals from 5·5 to 32·2 per cent. per day, the latter figure (which seems to be exceptionally high, judging by his averaged results) equalling those given by our *Arion*. He found no explanation of these variations.

It is perhaps more interesting to compare snails and slugs with other land forms in which the skin is moist. Graphs published by Gray (1928) show a weight loss by a newt (*Triton cristatus*) of about 28 per cent. of the body weight per day; the same animal lost weight somewhat faster after death. A lizard (*Lacerta viridis*) lost only about 4·7 per cent. of its weight per day, alive or dead, as long as its skin was intact. After removal of the skin the weight loss approximated very closely to that of a newt. Durig (1901) kept frogs in a cage without water; their daily loss was about 10 per cent. of their weight. It seems then that amphibians lose water, mainly by evaporation, at rates which greatly exceed those obtained with dry-skinned vertebrates, and come near to the lower values recorded for resting slugs.

Phenomena resembling more closely those seen in slugs have been recorded for earthworms (*Lumbricus terrestris*). This animal, if it is first "saturated" with water by immersion for some days and then exposed on dry filter paper, loses water at the rate of about 10 per cent. per hour (Jackson, 1926). This enormous rate approaches, but does not equal, that of Künkel's continuously creeping *Limax*. The skin of earthworms would appear to be as freely permeable to water as that of snails and slugs, but it may be questioned whether *Lumbricus*, living most of the time in the soil, would usually suffer such extensive hydration changes as a land gastropod. As far as the data go, it seems that gastropods can survive much greater changes in water content than earthworms. Jackson's earthworms, after hydration by immersion, survived a water loss of 42–43 per cent. but not a loss of 50–60 per cent. Künkel, on the other hand, describes a highly hydrated *Limax tenellus* which survived a loss of 80 per cent. of its weight.

In slugs, then, and probably in active snails, the permeability of the skin causes a continuous and rapid evaporation of water from the animal, at least in ordinary room air. When slime secretion is added to this, for instance during locomotion, the animals have a rate of total water loss which may sometimes be approached, but is probably never surpassed, by land animals of other groups. A loss of the velocity indicated by the available data on slugs would evidently be a serious obstacle to the maintenance of a constant water content. If constancy were necessary, an active slug in unsaturated air would have to be drinking all the time at a rate of somewhere about 2 or 3 per cent. of its weight per hour, and could never venture far from a supply of water. Instead of being thus enslaved, it seems that the animals have the power of enduring great changes in their water content, undergoing alternate phases of hydration and dehydration.

The second point emerges from the consideration of Fig. 4. Many of the graphs in our previous paper show a very striking cycle, having a period of several days, in the water content of snails. A similar cycle is apparently visible in the case of slugs, especially in the animals kept with water and no food (Fig. 3 of this paper). But on comparing Figs. 3 and 4 it will be seen that the slugs in Fig. 3 must have taken water every day, for the gradient of the downward parts of the curve is less in Fig. 3 than in Fig. 4. It seems therefore that the water cycle in slugs must be of shorter period than Fig. 3 would indicate. It is possible that by making daily weighings of an animal which undergoes rapid weight cycles one would get an impression of a slow cycle by a process somewhat analogous to that employed in the stroboscopic analysis of ciliary movement. We are at present devising methods for obtaining a more exact picture of the weight cycles than daily weighing can give. It may, however, be pointed out that, as regards *Helix pomatia*, the relations discussed in our previous communication between activity and feeding and the weight cycle suggest that the graphs give a fairly true picture of the curve of the animal's weight, and are not chance points on a rapidly oscillating curve[1].

[1] Since the above was written, one of us (N. H. H.) has built an apparatus in which the weight of *Helix pomatia* is continuously recorded on a drum and drinking and eating are also recorded. The animal is only disturbed once a week, and not daily as in the experiments above described. Preliminary results show that the animals undergo, in ordinary room air, weight cycles having a period of several days, and that our curves obtained by daily weighing indicate fairly exactly the true weight curves of the snails. Slugs have not yet been studied on the apparatus.

IV. SUMMARY.

1. Weight fluctuations, like those previously recorded for *Helix pomatia*, are shown by *Arion ater* and *Limax flavus*.

2. The fluctuations are shown by slugs receiving water but no food.

3. Slugs receiving food but no water lose weight very rapidly and die in a few days. The loss of weight is due mainly to evaporation of water through the skin.

The authors wish to thank Mr R. S. A. Beauchamp, of the Laboratory of the Freshwater Biological Association, Wray Castle, who was good enough to send a supply of Arion.

REFERENCES.

Adolph, E. F. (1921). *Journ. Physiol.* **55**, 114.
—— (1930). *Quart. Rev. Biol.* **5**, 51.
Buxton, P. A. (1930). *Proc. Roy. Soc.* B, **106**, 560.
—— (1932). *Parasitology*, **24**, 434.
Davis, W. M. (1928). *Brit. Journ. Exp. Biol.* **6**, 79.
Durig, A. (1901). *Arch. ges. Physiol.* **85**, 401.
Gray, J. (1928). *Brit. Journ. Exp. Biol.* **6**, 26.
Gunn, D. L. (1933). *Journ. Exp. Biol.* **10**, 274.
Howes, N. H. and Wells, G. P. (1934). *Journ. Exp. Biol.* **11**, 327.
Hunt, E. H. (1912). *Journ. Hyg.* **12**, 479.
Jackson, C. M. (1926). *Proc. Soc. Exp. Biol. Med.* **23**.
Kudo, T. (1921). *Amer. Journ. Anat.* **28**, 399.
Künkel, K. (1916). *Zur Biologie der Lungenschnecken.* Heidelberg: Carl Winter.