

male (once after the escape of a female with which the male was trying to mate), but no audible sound could be detected.

It is extremely difficult to induce *S. maurus* to produce sound, but we succeeded in eliciting this response several times by the use of irritating stimuli. Once a scorpion has begun to respond in this manner, after either a natural or an artificial stimulus, it will often repeat the response a few times, running around and stopping every now and then in order to produce the sound. So far only males have been observed to perform this type of reaction, but the possibility that females too may be able to do so has not been excluded.

Stridulation is a very common method for sound production among insects (5) and crustaceans (crabs) (6), but cases of sounds produced by rapidly tapping any part of the body on the substrate (or "drumming," as the mechanism is often termed) also occur in both these classes. Thus Imms (5) lists cases among Anobiidae, pupae of Hesperidiidae and Lycaenidae, termite soldiers, and Psocoteria. Drumming in *Pimelia striata* is mentioned by Darwin (7) and in some Acrididae by McE-Kevan (8) and Pierce (9). Crane (10) describes drumming in some crabs of the genus *Uca* (Brachyura). However, to the best of our knowledge, drumming in scorpions has never been recorded before.

The body vibrations of *Scorpio maurus* during sound production recall in their tetanic nature the juddering of males of *Opisthophthalmus latimanus* (Scorpionidae) (11) and *N. hierochonticus* (Diplocentridae) (12) during courtship, except that in the latter case the pedipalps are outstretched and the motion is performed horizontally, so that the body does not hit the ground. The juddering of scorpions is not limited to sexual behavior and may occasionally be performed in the presence of other males, specimens of another species, and sometimes even in the presence of prey. However, emission of sound in *Scorpio maurus* does not constitute a part of the normal courtship behavior.

Scorpio maurus exhibits various types of threatening behavior and also repeated forward and backward jerks of the body with outstretched pedipalps and arched tail. This reaction is very common in both sexes. (An identical, or at least a very similar, reaction is almost invariably performed by the male at the beginning of courtship.) There may be some relation between this threatening behavior and sound production, since scorpions were observed several times to change such a threatening reaction into the sound-

producing one. The body jerks were quickened, the pedipalps were gradually flexed, and the tail was lowered over the body; the sound was at first very feeble, but soon acquired full volume.

It is not yet known whether the difference observed in the frequency of the sound by the two subspecies *S. maurus palmatus* and *S. maurus fuscus* is innate.

No response of one scorpion to the sound produced by another was noted. Alexander (2), who found no such response in the cases she investigated (stridulatory type), suggested after making a few experiments that the sound may have a defensive value against predators. The presence of a sense of hearing in scorpions is still doubtful, but considering that their sensitivity to vibrations of the substrate is apparent (13), the possibility that, in the case of *S. maurus*, sound may have also an interspecific role is not to be dismissed without further careful investigation.

Variations in the loudness of the sound, due to changes in intensity of reaction of one and the same specimen, were mentioned above. We realize, however, that the loudness of the sound may also depend, at least partially, on the hardness of the substrate against which the body hits, although slightly pressed soil suffices for the production of a clearly audible sound. It should also be noted that scorpions do not usually inhabit terrains of soft loose sand (14).

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References and Notes

1. F. Werner, "Scorpiones," *Bronn's Klassen und Ordnungen des Tierreichs* 4, no. 8 (1934).
2. A. J. Alexander, *Behaviour* 12, 339 (1958).
3. M. Vachon, B. Dumortier, R. G. Busnel, *Bull. soc. zool. France* 83, 253 (1958).
4. F. Werner, *Zool. Anz.* 109, 211 (1935); A. Shulov and P. Amitai, *Hateva vohaaretz* 2, 1 (1960).
5. A. D. Imms, *A General Textbook of Entomology* (Methuen, London, ed. 9, 1957).
6. D. Guinot-Dumortier and B. Dumortier, *Crustaceana* 1, 117 (1969).
7. C. Darwin, *The Descent of Man, and Selection in Relation to Sex* (London, ed. 2, 1874).
8. D. K. McE-Kevan, "Unorthodox" methods of sound production in Orthoptera," *Spec. Papers Univ. Nottingham School Agr. Zool. Sect. No. 2* (1954), pp. 1-22.
9. G. W. Pierce, *The Songs of Insects* (Harvard Univ. Press, Cambridge, Mass., 1948).
10. J. Crane, *Zoologica* 26, 145 (1941).
11. A. J. Alexander, *Proc. Zool. Soc. London* 128, 529 (1957).
12. A. Shulov and P. Amitai, *Arch. inst. Pasteur Algérie* 36, 351 (1958).
13. J. L. Claudsley-Thompson, *Ann. Mag. Nat. Hist.* 12, 556 (1955).
14. The senior author was the recipient of a grant (E-2960) from the National Institutes of Health, U.S. Public Health Service.

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Theory of Oxygen Transport through Hemoglobin Solutions

Abstract. A combination of equations describing diffusion, gas solubility, and mass conservation yields a general relation for oxygen transport in hemoglobin solutions. Total oxygen flux is shown to be the sum of the flux in the plasma and the flux due to transport by hemoglobin. The total flux depends not only on oxygen concentration gradient but also on absolute oxygen concentration.

Because of the recent interest in the transport of oxygen in hemoglobin solutions (1, 2), it seems desirable to attempt to understand this transport phenomenon in terms of simple physical-chemical principles.

The theory that one generally applies to transport phenomena is embodied in the statement of Fick's law (3). This law states that the mass transport per unit time per unit area, $\partial m/\partial t$, is directly proportional to the concentration gradient, $\partial c/\partial x$, where the constant of proportionality, D , is called the diffusion coefficient. That is

$$\frac{\partial m}{\partial t} = -D \frac{\partial c}{\partial x} \quad (1)$$

For the problem at hand we must consider the diffusion of three species, namely, oxygen dissolved in plasma or water, oxygenated hemoglobin, and hemoglobin. We choose a geometry of plane parallel boundaries so that the problem is one dimensional. Let A be the concentration of dissolved oxygen, B the concentration of hemoglobin, and E the concentration of oxygenated hemoglobin.

We may now write three simultaneous diffusion equations:

$$\begin{aligned} J_A &= \frac{\partial m_A}{\partial t} = -D_A \frac{\partial A}{\partial x} \\ J_B &= \frac{\partial m_B}{\partial t} = -D_B \frac{\partial B}{\partial x} \\ J_E &= \frac{\partial m_E}{\partial t} = -D_E \frac{\partial E}{\partial x} \end{aligned} \quad (2)$$

These equations are not independent and must satisfy certain boundary conditions. Since hemoglobin and oxygenated hemoglobin cannot spill over the boundary of the diffusion cell, we must require that

$$J_B + J_E = 0 = -D_B \frac{\partial B}{\partial x} - D_E \frac{\partial E}{\partial x} \quad (3)$$

A further constraint on the system is imposed by conserving the total amount of A and B and remembering that $A + B \rightleftharpoons E$. The material balance for oxygen (A) implies that

$$D_A \frac{d^2 A}{dx^2} + D_B \frac{d^2 E}{dx^2} = 0 \quad (4)$$

while the material balance of hemoglobin (B) similarly requires that

$$D_B \frac{d^2 B}{dx^2} + D_E \frac{d^2 E}{dx^2} = 0 \quad (5)$$

For the case assumed here, namely that D_A , D_B , and D_E are independent of concentration, the general solutions of Eqs. 4 and 5 may be written as

$$D_A A + D_B E = a_2 x + a_1 \quad (6)$$

$$\text{and } D_B B + D_E E = a_3 x + a_4 \quad (7)$$

where a_1 , a_2 , a_3 , and a_4 are constants to be determined by the boundary and subsidiary conditions. At the two boundaries, $x = 0$ and $x = x_f$, we require the following conditions:

$$\text{at } x = 0, \quad A = A_i, \quad (8)$$

the initial value of A

$$\text{at } x = x_f, \quad A = A_f, \quad (9)$$

the final value of A , and,

$$B = B_f,$$

the final value of B .

There is only one other condition needed to specify uniquely a solution to Eq. 2 and that is the relation between A and E . When one has a reaction of the form $A + B \rightleftharpoons E$, he is often tempted to describe the equilibrium situation as follows:

$$E/AB = K \quad (10)$$

where K is the equilibrium constant. This is not a good description in the case of the oxygen-hemoglobin equilibrium. The oxygen-hemoglobin dissociation curve, Fig. 1 (4), cannot be fit by an equilibrium expression of the form of Eq. 10. We therefore choose to write E as a function of A and use the curve of Fig. 1 to define the function. Therefore

$$E = f(A) \quad (11)$$

Having enumerated all the assump-

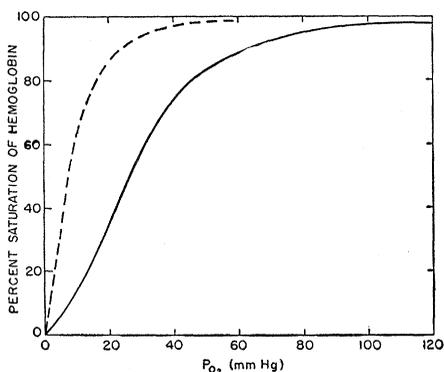


Fig. 1. Dissociation curve for oxyhemoglobin to oxygen and hemoglobin. Solid line is for hemoglobin at 38°C and pH 7.4 (after Comroe *et al.*, 4). Dashed line is for Hemmingsen and Scholander (2) hemoglobin solution at 23°C and pH 7.3.

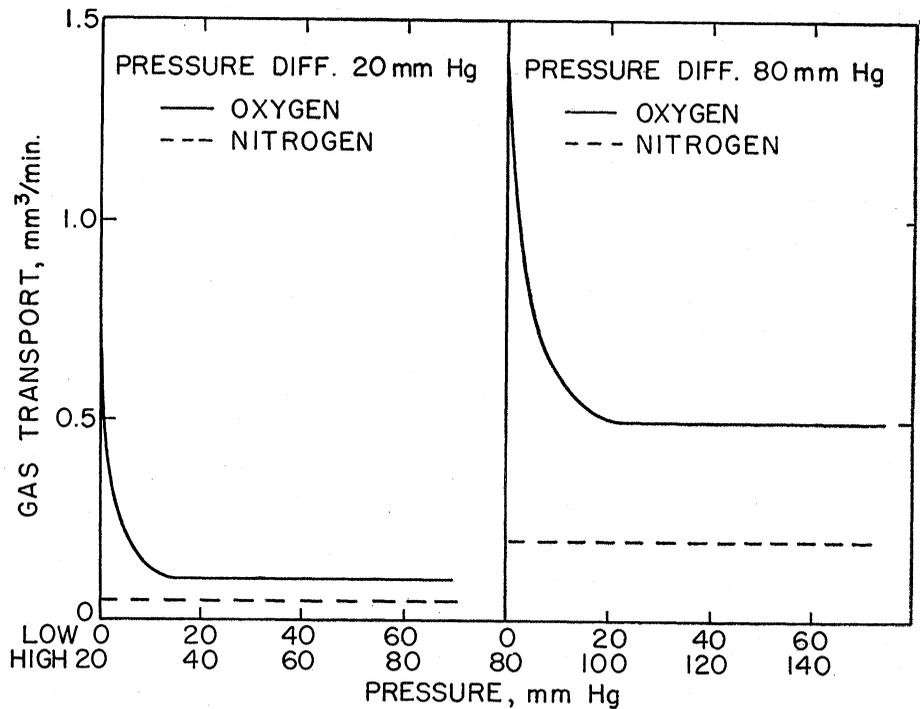


Fig. 2. Flux of oxygen and nitrogen through hemoglobin solution at constant pressure gradients but varying absolute pressure (after Hemmingsen and Scholander, 2).

tions, constraints, and boundary conditions, we now wish to calculate the total transport of oxygen whether it be as dissolved oxygen or as oxygenated hemoglobin. This means that we wish to find the sum of J_A and J_E .

$$J_A + J_E = D_A \frac{\partial A}{\partial x} - D_E \frac{\partial E}{\partial x} \quad (12)$$

By differentiating Eq. 6 with respect to x we obtain

$$J_A + J_E = -a_1;$$

the value a_2 may be evaluated from the boundary conditions if $x = 0$ is applied to Eq. 6

$$a_2 = D_A A_i + D_E f(A_i) \quad (13)$$

Substitutions from Eq. 13 for a_2 and solving for $-a_1$ gives us

$$J_{\text{total}} = -a_1 = \frac{D_A (A_i - A_f) + D_E [f(A_i) - f(A_f)]}{x_f} \quad (15)$$

The significance of this equation is that the transport of oxygen arises from two sources: direct diffusion of the dissolved gas, and transport as a complex with hemoglobin.

We can write Eq. 15 in terms of the initial and final partial pressures of oxygen by use of Henry's law which relates concentration to pressure as follows:

$$A = kP \quad (16)$$

Perhaps it should be stressed at this point that, although the concentration of oxygen dissolved in plasma or water

is related to the pressure by Henry's law, this is not true for the oxygen complexed by hemoglobin. The relation between the oxygen partial pressure and the fraction of hemoglobin complexed is given by Fig. 1.

Combining Eqs. 15 and 16 gives

$$J = \frac{D_A k (P_i - P_f)}{x_f} + \frac{D_E [f(kP_i) - f(kP_f)]}{x_f} \quad (17)$$

The first term in Eq. 17 is due to the direct diffusion of the dissolved gas, and as long as the pressure difference, $P_i - P_f$, remains constant it is independent of the value of P_i or P_f . The second term, however, is not only dependent on the pressure difference, but is also sensitive to the absolute value of P_i and P_f as may be clearly understood by an examination of Fig. 1. If P_i and P_f are each so large that the hemoglobin is saturated with oxygen at both boundaries of the transport path, then the second term in Eq. 17 will be negligible compared to the first.

In the light of these results let us consider the results of Hemmingsen and Scholander (2) on the transport of oxygen in hemoglobin solutions. One of their experiments was to keep the pressure difference, ΔP , across a diffusion cell constant but to vary P_i and P_f . That is to say they maintained the constraint

$$P_i = P_f + \Delta P$$

They observed a maximum transport for $P_f = 0$ followed by a sharp drop as

P_f was increased and finally a constant transport for large P_f . Their results are shown in Fig. 2. Their experimentally determined oxygen-hemoglobin dissociation curve is given as the dashed curve in Fig. 1. We readily see that these results are in qualitative agreement with Eq. 17. When P_f is zero $f(kP_i) - f(kP_f)$ takes its maximum value, and as P_f is increased to the point where the hemoglobin is largely saturated, $f(kP_i) - f(kP_f)$ decreases, monotonically approaching zero. As the second term in Eq. 17 becomes negligible, all the oxygen transport is due to dissolved gas and is therefore independent of P_f .

We feel that these considerations make it clear, by and large, how hemoglobin is effective in oxygen transport. That is, if the hemoglobin is under conditions such that it is saturated with oxygen at both ends of the transport path, it cannot be effective at all.

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References

1. P. F. Scholander, *Science* **131**, 585 (1960).
2. E. Hemmingsen and P. F. Scholander, *ibid.* **132**, 1379 (1960).
3. D. R. Olander, *A.I.Ch.E. Journal* **6**, 233 (1960).
4. J. H. Comroe, R. E. Forster, A. B. DuBois, W. A. Briscoe, E. Carlsen, *The Lung* (Year Book Publishers, Chicago, 1955), p. 98.

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Effects of Plant Nutrients on Uptake of Radiostrontium by Thatcher Wheat

Abstract. The effects of various dosages of ammonium dihydrogen phosphate, monocalcium phosphate, calcium chloride, and potassium chloride on the uptake of radiostrontium by Thatcher wheat grown in Saskatchewan Oxbow loam soil containing strontium-85 were studied. Monocalcium phosphate at a dose level of about 600 lb/acre of soil effected a statistically significant reduction of strontium-85 uptake in each of the four plant fractions of grain, chaff, stem, and leaf. At the very reasonable dosage of about 60 lb/acre, monocalcium phosphate gave a statistically significant reduction in strontium-85 uptake in the grain and chaff.

In 1958, Libby (1) reported that addition of solutions of potassium salts to a Washington garden soil containing Sr^{90} had a beneficial effect in reducing the uptake of the Sr^{90} by radish plants. His conclusions were criticized (2) because the soil was not fully characterized and the experiments lacked sufficient replication. There is no dispute, however, on the need for more research on methods of soil treatment which may lead to a reduction in plant uptake of Sr^{90} (3). Recently, Fowler and

Table 1. Uptake of strontium-85 by Thatcher wheat grown in Saskatchewan Oxbow loam soil. Each value for uptake is the mean of 18 replications.

| Nutrient treatment | Dosage (meq/100 g of soil) | Uptake (%) per gram of dried tissue | | | |
|--------------------|----------------------------|-------------------------------------|-------|-------|-------|
| | | Grain | Chaff | Stem | Leaf |
| None (control) | | 0.0106 | 0.026 | 0.071 | 0.376 |
| $NH_4H_2PO_4$ | 0.08 PO_4^* | .0116 | .027 | .071 | .378 |
| | 0.16 PO_4 | .0100 | .026 | .065 | .323† |
| | 0.80 PO_4 | .0101 | .031† | .066 | .338 |
| $Ca(H_2PO_4)_2$ | 0.08 PO_4 , 0.027 Ca* | .0088† | .021† | .070 | .399 |
| | 0.016 PO_4 , 0.054 Ca | .0089† | .026 | .073 | .390 |
| | 0.80 PO_4 , 0.27 Ca | .0078† | .023† | .061‡ | .324† |
| CaCl ₂ | 0.027 Ca | .0090† | .025 | .068 | .349 |
| | 0.27 Ca | .0097 | .025 | .062 | .343 |
| KCl | 1.9 K§ | .0092 | .021† | .059 | .351 |
| | 3.8 K | .0103 | .023† | .065 | .386 |
| L.S.D. | | .0016 | .002 | .009 | .047 |

* This dosage is equal to a treatment of about 60 lb. of nutrient per acre of soil, assuming the weight of 1 acre of soil to be 2×10^6 lb. † Significant at the 1 percent level. ‡ Significant at the 5 percent level. § This dosage is equal to the amount of exchangeable potassium already present in the soil. || Least significant difference.

Christenson (4) described a study on the effect of soil nutrients on plant uptake of fallout, and reported that increasing the concentration of soil calcium has a depressing effect on the concentration of Sr^{90} per milligram of calcium in lettuce, grass, and alfalfa. In an investigation with bean plants on the relative availability of a number of Sr^{90} compounds in soil, Uhler and Hungate (5) noted the low availability of strontium phosphate, especially in calcareous soils, thus suggesting the possibility of the use of phosphate fertilizers as a means of reducing Sr^{90} uptake. However, it was stated by these authors (5) that, although their results indicated that uptake of Sr^{90} might potentially be reduced through precipitation reactions, initial experiments with phosphate fertilizers did not permit much optimism on this point.

As an extension of our earlier work on the uptake and distribution of Sr^{90} in Thatcher wheat (6), the effects of a number of plant nutrients on the uptake of Sr^{85} by Thatcher wheat were investigated (7). The plants were grown, three per pot, in the greenhouse. Each pot contained 400 g of Saskatchewan Oxbow loam soil which had a pH of 7.2, and 19.2, 6.5, 1.9, and 0.1 meq of exchangeable Ca, Mg, K, and Na, respectively, per 100 g of soil. Before the seeds were sown, each pot of soil was first mixed thoroughly with 50 ml of Sr^{85} (8) solution ($1 \mu C/ml$) and then with 50 ml of nutrient solution or with 50 ml of distilled water as a control. The plant nutrients, used at various dose levels as given in Table 1, were ammonium dihydrogen phosphate, monocalcium phosphate, calcium chloride, and potassium chloride. Each treatment was repeated in six pots. The seeds were germinated, and the plants were grown to maturity. The soil moisture was kept at field capacity by daily watering. After harvest, individual plants were separated into grain, chaff, stem, and leaf and analyzed for radio-

activity. Since three plants were grown per pot and each treatment was repeated in six pots, analyses from 18 replications were obtained.

The separated plant tissues were ashed in a muffle furnace. Each sample of ash was dissolved in 1 ml of hot aqua regia, and when necessary, as in the case of the ash from leaves, a few drops of hydrofluoric acid were added to bring any siliceous residue into solution. Each dissolved sample was rinsed into a plastic tube and made up to a standard volume of 5.0 ml with an aqueous solution containing 1 mg of $SrCl_2$ per milliliter. The Sr^{85} activity was then determined in a well-type liquid scintillation counter. The data were analyzed statistically (9). The results are summarized in Table 1.

Inspection of Table 1 shows that ammonium dihydrogen phosphate, calcium chloride, and potassium chloride, when applied at dose levels used in these experiments, did not give any consistent pattern in reducing Sr^{85} uptake. It may be pointed out that as a means of expressing the data in a uniform way, the accumulations of strontium are given in Table 1 as the percentage uptake per gram of dried tissues instead of total uptake in various parts of the plant. With only one exception, the various nutrient treatments did not influence average yields by more than a few percent as judged by the weights of the grain. The exception was the treatment with the highest dose of ammonium dihydrogen phosphate, where an increase in average yield of about 30 percent was noted. This may bring in a carbohydrate dilution factor when the uptake of strontium per gram of dried tissue was calculated. However, statistical analysis of the data expressed as the percentage of total uptake also showed that treatments with ammonium dihydrogen phosphate did not cause any statistically significant difference from total uptakes in the control. Of the ten nutrient treatments given in Table 1,