imply that in aerobic conditions there is a partial aerobic fermentation. It was not, however, possible to sterilize worms in order to repeat this observation in the absence of antibiotics.

In anaerobic conditions, acetic, propionic and the C_5 fatty acid were formed (ratio 1 : 10 : 0·8) together with traces of butyric acid and branched C_6 fatty acid, both in the presence and absence of antibiotics. These acids accounted for almost 100 per cent of the glycogen broken down in anaerobic conditions. Traces of acetoin were present, but other chemical tests for possible end products, including lactic acid, were negative. Succinic acid was only found in the medium if the worms had begun to disintegrate.

The swamp worm thus has a type of metabolism that resembles most closely the metabolism of certain parasitic worms, for example *Ascaris lumbricoides*. This resemblance may represent a convergent biochemical evolution in animals that have become adapted to low oxygen levels or quite anaerobic conditions. Certain aquatic pulmonate snails produce acetic and propionic acids in anaerobic conditions[2] and it seems highly likely that other interesting metabolic pathways exist in free-living invertebrate animals that have become adapted to a scarcity, or complete absence, of oxygen.

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G. C. COLES

Department of Zoology,
Makerere University College,
Kampala, Uganda.

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Displacement and De-arousal

A RECENT communication by Delius[1] calls for some comment. Delius regards displacement behaviour as essentially made up of actions which are related to going to sleep. He therefore interprets displacement behaviour as a homeostatic mechanism in which "de-arousal" actions are called into play to counteract the excessive arousal occasioned by the conflict or thwarting situation to which the animal is exposed.

If this interpretation is correct, then clearly it must be applicable to displacement behaviour in general, and not only to a small number of selected cases. Displacement grooming in rats and cats are two of the cases cited by Delius in support of his views. Bolles[2] has shown that while rats may groom at almost any time, they are particularly prone to do so before going to rest and, to this rather limited extent, displacement grooming in *Rattus norvegicus* accords with Delius's views. I know of no study in cats comparable with that of Bolles, and while it is perfectly true that a cat does frequently groom before sleeping, grooming is also a normal accompaniment of waking up. In the absence of quantitative data, there is no justification for regarding grooming in cats as a de-arousal rather than an arousal action. In *Cricetomys gambianus*, however, grooming is an activity characteristic of arousal from the day's rest in preparation for the night's activity. It is therefore definitely not a de-arousal action and yet, in this species also, it is the predominant displacement activity[3]. In rats, cats and *Cricetomys* the factor which determines that grooming should be the chief displacement activity must therefore be sought elsewhere than in its relations to arousal or de-arousal. A comparison with two species in which grooming is not a very frequent activity is of some relevance. *Xerus erythropus* and *Suricata suricatta* are both burrowing animals with rather coarse fur which is groomed much less extensively than in any of the three species previously considered. Both, however, are enthusiastic excavators. In *Xerus*, digging is predominantly an activity connected with burrowing, but in *Suricata* its predominant function is in food finding. In both species digging is the commonest displacement activity and I have not seen displacement grooming in either. These facts all suggest that the factor which decides what action shall be performed in a displacement context relates to its importance in the life of the animal and the frequency with which it is performed in its normal context, rather than its relation to going to sleep. If Delius's interpretation were correct, one would expect turning round in a circle to be the common canine displacement behaviour, for this action so commonly precedes settling to rest. I cannot, however, recollect ever having seen displacement circling in a dog.

Tinbergen[4] long ago suggested that displacement behaviour has some therapeutic function, which serves to protect the central nervous system from over-activity and provides what in ourselves would be described as "relief of tension". Delius's view is, in a sense, an extension of this idea and an attempt to make it more precise. The attempt is laudable but I believe the interpretation put forward is mistaken. If we accept the disinhibition theory[5,6] as providing at least a partial explanation of displacement behaviour, then it is easy to see why the actions performed should so often be those which are of very frequent occurrence in the normal behavioural repertoire. The high frequency patterns are the ones which the animal is almost always ready to perform provided they are not inhibited by the activation of some other pattern with a higher urgency. They are therefore the ones most likely to appear if the currently activated patterns are suddenly switched off, with consequent cancellation of inhibitory effect on the high frequency pattern. Moreover, there is no need to invoke a necessary relation to de-arousal to account for the postulated tranquillizing effect of displacement behaviour. Once the latter is switched on, it is to be expected that it will, in its turn, inhibit the frustrated action and so bring about the required reduction in excitatory level. How beneficial this may be to the animal will, of course, depend on how extensive and how lasting is the effect produced. If it were very transitory, the *status quo* would merely be restored, but in a dynamic context even a fairly brief pause may permit changes in the external situation to occur and would at least allow the animal's central nervous system to re-assess the total situation from an altered "viewpoint"—that is, with a different excitatory/inhibitory balance in the relevant areas.

Clearly if the tranquillizing effect is indeed a reality and if a species is likely to show either of two displacement actions, one of which is a more effective tranquillizer than the other, then there will be selection in favour of the latter. If linkage with de-arousal were the basis for the greater tranquillization, then the situation postulated by Delius would result. The data available do not, of course, prove that this has never happened: the cases cited here, however, suggest that linkage with de-arousal has not been a factor of great importance in the evolutionary history of displacement behaviour.

R. F. EWER

Department of Zoology,
University of Ghana.

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