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TOWARDS AN ACTIVITY BUDGET FOR THE SANDY BEACH WHELK *BULLIA DIGITALIS* (DILLWYN)

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ABSTRACT

Measurements of the oxygen uptake of *Bullia digitalis* during its various activities are applied to field records of the length of time spent by adult female animals in each activity. Burrowing and crawling cost less than does crawling in slugs, while transport in the surf, though costly in terms of time, is cheap in terms of distance covered. The energetic cost of being active during the tidal cycle is low compared with maintenance costs.

INTRODUCTION

Bullia digitalis (Dillwyn) is a nassarid whelk whose ecology and behaviour have been studied by Brown (1961, 1964, 1971). The oxygen consumption of adult, female animals under a variety of controlled conditions, at fixed levels of activity, has also been reported (Brown *et al.*, 1978; Brown, 1979a,b,c; Brown & Da Silva, 1979). The results gained in this work have been used to assess the energy requirements of various activities, including transport in the surf (surfing), crawling, burrowing and emerging from the sand, as well as the cost of remaining buried (Brown, 1979b).

The present paper combines this data with field records of the length of time spent by adult female animals in each activity phase, so constructing an activity budget for them.

METHODS

On frequent occasions over the past 20 years, the following of single individuals of several species of *Bullia* from their time of emergence from the sand on a falling tide until their final burrowing as the tide rose has been attempted. Usually this proved impossible, resulting in several hundred incomplete records. However, 23 large, female individuals of *B. digitalis* have been successfully observed for a full cycle of activity, and the amount of time spent in each activity phase recorded. In 18 of these cases the animals did not feed during the cycle; the results discussed below are restricted to these individuals as the increased metabolic rate associated with feeding has not yet been measured accurately.

RESULTS AND DISCUSSION

The most obvious feature of the field data is the considerable variation in the amount of time spent by different individuals in different activities, as well as in the length of the total period spent above the sand. This period appears to vary from beach to beach, being shorter, for example, at Ou Skip, on the west coast, than at Muizenberg in False Bay. The results presented in Table 1 are thus limited to data gained at Ou Skip, this being the site from which animals were obtained for all the respiratory measurements already referred to.

Two categories of buried state are listed in Table 1; buried (observed) refers to timed periods of burial between crawling and/or surfing, while buried (residual) refers to the assumed state of the animal for the unobserved part of the tidal cycle, while the tide was in. The latter is by far the longest of the activity states listed and it is here that the greatest errors in calculation are likely to occur. Brown (1979a) reported a mean oxygen uptake of 560 $\mu g.h^{-1}$ for animals of 750 mg dry tissue mass buried in sand; however, this figure would seem to be too low as in the field buried animals respond to wave

TABLE 1. Average energy expenditure by 8 non-feeding female *Bullia digitalis* during single tidal cycles of activity, referred to a standard-sized animal of 750 mg dry tissue mass.

Activity	*O_2 uptake per minute (μg)	Actual time (mins)	O_2 uptake for period (μg)	Energetic equivalent (joules)
Transport in surf	20.8	14.5	302	4.31
Crawling	11.3	23.0	260	3.69
Burrowing	18.8	7.5	141	2.01
Emerging	18.8	3.8	72	1.05
Buried (observed)	9.3	42.0	391	5.57
Buried (residual)	10.6	653.2	6924	98.60
Total for tidal cycle		744.0	8090	115.23

*After Brown (1979b).

crash by taking a step down into the sand. A few seconds later they take a step towards the surface, regaining their previous positions. Thus to the oxygen uptake of buried animals in the laboratory has been added the uptake associated with two burrowing steps per minute, giving a total of 634 $\mu g.h^{-1}$.

Burrowing and emerging activities could not always be timed accurately. However, it is known that a complete burrowing event averages 10 digging cycles taking 45 seconds (Trueman & Brown, 1976), while emergence takes about half as long and involves half as many steps. These figures have been used in calculating the data presented in Table 1.

That animals in the most active state consume oxygen at approximately twice the rate of resting animals conforms well with observations on other molluscs and marine invertebrates (P. F. Newell, 1970; R. C. Newell, 1979). However, that the most active state should be transport in the surf, previously referred to as "passive transport," is surprising. During surfing the animal displays maximum turgour of the foot and waves it vigorously from side to side; presumably it is the combination of these actions which demands high energy expenditure. Nevertheless, in terms of distance travelled—up to ten or more meters in a few seconds—surf transport is far less costly than crawling. Burrowing is comparable with surfing as far as energy demand per unit time is concerned but is by far the most costly activity in terms of distance travelled.

The cost of crawling and burrowing in *Bullia* may be compared with crawling in the terrestrial slugs studied recently by Denny (1980). The metabolic cost of crawling in these slugs is given as 904 joules $kg^{-1}m^{-1}$, considerably more than that reported for other forms of locomotion in other animals. In contrast, the cost of burrowing in *Bullia* is only approximately 250 joules $kg^{-1}m^{-1}$, and the cost of crawling 150 joules $kg^{-1}m^{-1}$, a cost comparable with that of running in terrestrial animals (Schmidt-Nielsen, 1972). This difference between a slug's crawling and *Bullia*'s crawling is most probably to be attributed to the fact that the slug progresses by adhesive crawling, and expends much energy in producing the mucus by which it adheres to the substratum, while *Bullia* crawls in a series of "breast-strokes," without producing adhesive mucus (Trueman & Brown, 1976).

Table 1 lists averages. The most active of these animals expended some 133 joules during the arbitrary 744-minute tidal cycle. An animal of 750 mg dry tissue mass which remains buried during the same period is calculated to expend about 108 joules. Thus one of the points to emerge from this study is the relatively low cost to the animal of being active during the tidal cycle. Nevertheless, this low cost may well be critical for an animal whose life revolves around the erratic nature of the food supply, so that in fact only about 12% of the adult population becomes fully active during any one tidal cycle, unless an abundance of food is present on the beach (Brown, 1971).

From the above figures it is possible to estimate the average cost of free existence of adult animals, though this calculation is not as straightforward as it may at first appear. An attempt at such an estimate is presented elsewhere (Brown, 1981).

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REFERENCES CITED

BROWN, A. C., 1961, Physiological-ecological studies on two sandy-beach Gastropoda from South Africa. *Zeitschrift für Morphologie und Ökologie der Tiere,* 49: 629–657.

BROWN, A. C., 1964, Food relationships on the intertidal sandy beaches of the Cape Peninsula. *South African Journal of Science,* 60: 35–41.

BROWN, A. C., 1971, The ecology of the sandy beaches of the Cape Peninsula, South Africa. Part 2: the mode of life of *Bullia* (Gastropoda: Prosobranchiata). *Transactions of the Royal Society of South Africa,* 39: 281–319.

BROWN, A. C., 1979a, Oxygen consumption of the sandy-beach whelk *Bullia digitalis* Meuschen at different levels of activity. *Comparative Biochemistry and Physiology,* 62A: 673–675.

BROWN, A. C., 1979b, Respiration and activity in *Bullia digitalis* (Dillwyn). *South African Journal of Science,* 75: 451–452.

BROWN, A. C., 1979c, The energy cost and efficiency of burrowing in the sandy-beach whelk *Bullia digitalis* (Dillwyn). *Journal of experimental marine Biology and Ecology,* 40: 149–154.

BROWN, A. C., 1981, An estimate of the cost of free existence in the sandy-beach whelk *Bullia digitalis* (Dillwyn) on the west coast of South Africa. *Journal of experimental marine Biology and Ecology,* 49: 51–56.

BROWN, A. C., ANSELL, A. D. & TREVALLION, A., 1978, Oxygen consumption by *Bullia (Dorsanum) melanoides)* (Deshayes) and *Bullia digitalis* Meuschen (Gastropoda; Prosobranchiata)—an example of non-acclimation. *Comparative Biochemistry and Physiology,* 61A: 123–125.

BROWN, A. C. & DA SILVA, F. M., 1979, The effects of temperature on oxygen consumption in *Bullia digitalis* Meuschen (Gastropoda, Nassaridae). *Comparative Biochemistry and Physiology,* 62A: 573–576.

DENNY, M., 1980, Locomotion: the cost of gastropod crawling. *Science,* 208: 1208–1212.

NEWELL, P. F., 1970, Molluscs: methods for estimating production and energy flow. In *Methods of study in soil ecology:* 285–291. UNESCO, Paris.

NEWELL, R. C., 1979, *Biology of intertidal animals* (3rd edition), Marine Ecological Surveys, Faversham, Kent. 781 pages.

SCHMIDT-NIELSEN, K., 1972, Locomotion: energy cost of swimming, flying and running. *Science,* 177: 222–228.

TRUEMAN, E. R. & BROWN, A. C., 1976, Locomotion, pedal retraction and extension, and the hydraulic systems of *Bullia* (Gastropoda: Nassaridae). *Journal of Zoology,* London, 178: 365–384.