

this study, variations in pressure may also affect the color of squid luminescence in the ocean. The color of downwelling light is related to depth, and pressure is a more accurate depth indicator than temperature.

Abralia trigonura exhibited additional color shifts in response to increasing light intensity when temperature was held constant. The day emission band became broader (maximum between 468 and 492 nm; FWHM, about 56 nm) and the night band became narrower (maximum between 468 and 508 nm; FWHM, about 88 nm) (Fig. 3). Under bright light, the optimal color seems to be sacrificed in order to obtain maximum intensity.

The mechanisms that produce the color changes are obscure. However, in a brightly luminescing *A. trigonura* under night conditions, photophores of differing brightness can be seen, while under day conditions the photophores have uniform brightness. Apparently more than one type of photophore is involved in producing the bimodal emission spectrum displayed by this squid at night (8). A gradual shift of the day luminescence peak to longer wavelengths as night conditions are approached, however, suggests that the blue peak in the day and the green peak at night are produced by the same photophores. That is, individual photophores change the color of their light.

These squid can adjust the color of their luminescence to approximate the color of downwelling sunlight in deep cold waters or of moonlight in warm waters near the surface. The ability to match background color, however, does not imply that potential predators have color vision. Rather, the appropriate color ensures an intensity match between bioluminescence and background light in the eyes of different predators, even if they have different spectral sensitivities.

Because of the greater variability in downwelling light near the surface at night, effective counterillumination there requires a much more sophisticated system than is needed during the day. As we have shown, squid have considerable control over the color of the light they produce. If the animals have similar control over the angular distribution of their luminescence, their ability to conceal themselves in moonlit waters may be as effective as their daytime counterillumination.

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5. *Abraliopsis* sp. B (undescribed) is usually captured at depths of 500 to 600 m during the day and 50 to 100 m at night. It has been captured, however, in depths as shallow as 15 m. *Abralia trigonura* is usually captured between 450 and 550 m during the day and between 50 to 100 m at night. The shallowest capture was 30 m [R. E. Young, *Fish. Bull.* **76**, 583 (1978)].
6. The 488-nm filter (FWHM, 3 nm) was used for most experiments. The monochromator (Instruments SA model DH-10) contained holographic gratings (linear dispersion, 4 nm/mm, with slits 2 mm wide), and the PMT (RCA model 31034-02) had a gallium arsenide photocathode. A small computer operated the monochromator and analyzed the output from the photon counter (Princeton Applied Research model 1109). The system was calibrated with a standard lamp for spectral irradiance (Gamma Scientific model RS-10A). Methods of capture and maintaining squid were described by R. E. Young, C. F. E. Roper, and J. F. Walters [*Mar. Biol.* **51**, 371 (1979)].
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9. Moonlight curve from F. W. Munz and W. N. McFarland, in *The Visual System in Vertebrates*, F. Crescitelli, Ed. (Springer Verlag, Berlin, 1977), p. 193.
10. We thank the officers and crew of the Research Vessel *Kana Keoki* (University of Hawaii) and the members of the scientific party who participated in cruise FIDO XIII, for their assistance. We also thank F. Hochberg, G. Leisman, S. Maynard, K. Nelson, J. Morin, and C. F. E. Roper for reviewing the manuscript. We especially thank S. Maynard, who supervised the cruise. This report is based on research supported by NSF grant OCE 78-25342. This is Hawaii Institute of Geophysics Contribution 1047.

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Locomotion: The Cost of Gastropod Crawling

Abstract. *The power of locomotion of a terrestrial slug rises linearly with crawling speed. The metabolic cost of movement is 904 joules per kilogram per meter, considerably more than that reported for other forms of locomotion. This high cost is primarily attributable to the production of the pedal mucus by which the slug adheres to the substratum.*

The cost of locomotion of vertebrates has been extensively studied (1, 2). The energetics of invertebrate movement apart from studies on insect flight, have received far less attention.

In this study, the cost of one widespread form of invertebrate locomotion, the adhesive crawling of gastropods, has been examined with the use of the terrestrial pulmonate slug, *Ariolimax columbianus*, as an example. Gastropods crawl using a single appendage, the foot; and the power of locomotion is typically provided by a series of muscular waves on the foot's ventral surface (3). These movements are coupled to the substratum by a thin (10 to 20 μ m) layer of pedal mucus which allows the animal to adhere to the substratum. There are two consequent disadvantages: (i) The adhesiveness of the mucus must be overcome for the animal to move, and (ii) mucus must be produced to replace that expended during locomotion.

The rate at which energy is expended by the slug as it crawls is the total internal power, P_i , of locomotion expressed as watts per kilogram of body mass. This value can be estimated from measurements of the total rate of O_2 consumption. A large portion of P_i (62 to 73 percent) is used in the maintenance of the slug and is not directly related to loco-

motion. Consequently the value of interest is the net internal power of locomotion, P_{in} , which is estimated by measuring the increase in O_2 consumption above the resting rate as the animal moves. For many animals P_{in} is linearly related to speed (1, 2, 4), the slope of this line being a measure of the cost of movement, C_m , expressed as joules per kilogram of body mass per meter.

An apparatus was constructed to measure simultaneously O_2 consumption and crawling rate in *A. columbianus* (5). The slugs remained stationary during the day and moved at a varying rate for 3 to 4 hours at night. The resting and active metabolic rates were determined by continuously recording respiration rate and movement over a 24-hour period. The respiratory quotient for *A. columbianus* is 0.95 (6).

Measurements showed a substantial increase in O_2 consumption during and following movement (Fig. 1). The peak in O_2 consumption occurs 1 hour after the peak in crawling rate because (i) the slugs may respire anaerobically during locomotion, the resulting O_2 debt requiring considerable time to be realized as O_2 removed from the atmosphere; (ii) the initiation of mucus production, and therefore the metabolic cost of production, may lag behind the onset of crawl-

ing; and (iii) the absorption of CO_2 in the respirometer is not instantaneous; also the increased respiration rate due to movement continues for several hours after movement has ceased. Since it is difficult to correlate each peak in increased respiration with a specific speed, these data were analyzed as follows: For each period of movement the total distance moved, the total duration of movement, and thereby the average speed were determined. The area under the peak in increased respiration rate was taken as the net O_2 consumption required to move that distance (a measure of internal energy) and, when divided by the time of movement, yields P_{in} required to move at that speed. Similarly, the internal energy divided by the total distance moved gives the cost of movement, C_m .

Nine measurements on seven slugs (Fig. 2a) indicate that the power necessary for movement increased with speed (r , linear regression, was 0.879). The slope of the line through these points is the average C_m ($903.9 \pm 70.9 \text{ J/kg m}$). My method of calculating power and cost differs from others (7) in that it does not measure steady-state O_2 consumption. Since slugs could not be persuaded to walk at a constant rate, the measurement of steady-state O_2 consumption was not possible. The net O_2 consumption values used here, in that they include O_2 consumed after locomotion has ceased, are likely to be somewhat higher than if steady-state values could be measured. The cost of adhesive locomotion can be compared to the cost of other forms of locomotion (Fig. 2b), and it is apparent that the slug's crawling is 12 times as costly as that of a running animal [such as a mouse (3)] of equal size. While the apparent high cost of slug crawling is in part due to its measurement in a nonsteady state, it is unlikely that this factor alone can account for this cost.

To ascertain why crawling is so costly, the components of the energy expenditure of slugs were examined. A slug crawling on a level surface expends energy on its surrounding principally in overcoming the adhesive, viscoelastic properties of the pedal mucus. The rate of this external energy expenditure is the external power, P_e . Because of the nature of internal mechanisms of power production, P_e is always less than P_{in} . For example, all the work of muscular contraction during locomotion is not directly applied to movement; muscles must contract to maintain the slug's hydrostatic skeleton, and, in general, the locomotory

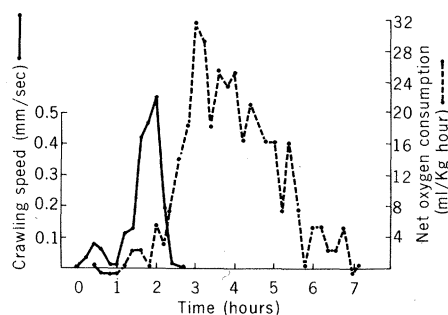


Fig. 1. A representative record of crawling speed and net oxygen consumption (increase above resting rate) for *A. columbianus*. The slug does not crawl at a uniform speed, and the oxygen consumption lags the peak in rate of movement and continues for several hours after movement ceases.

muscles do not contract directly along the line of movement.

P_e was measured by inducing slugs to crawl across a small force transducer incorporated into a horizontal surface (8). At a typical speed of 0.2 mm/sec, P_e needed to overcome mucus resistance is $3.2 \times 10^{-3} \text{ W/kg}$, for a C_m of 16 J/kg m. When P_e is compared to P_{in} at this speed, the locomotory mechanism is seen to have an efficiency (P_e/P_{in}) (9) of 1.8 percent. This value, while similar to that for a slowly running human (2 percent) (9) is considerably less than that for other forms of locomotion, such as flying (20 percent) (9).

How much of the apparent inefficiency of adhesive locomotion can be attributed to the production of pedal mucus? At present, this question cannot be answered with great precision, but reasonable assumptions can be made to arrive at an estimate. A typical (15 g) slug with a foot 1 cm wide and a mucus

layer 10 μm thick expends 0.1 ml of mucus for each meter it crawls. Pedal mucus is a hydrated glycoprotein composed such that 10 μg of protein and 6.3 μg of carbohydrate are expended per meter crawled (8). If it is assumed that the cost of producing the carbohydrate is similar to the cost of producing glycogen from pyruvate, and that the protein is assembled from free amino acids, the cost of producing the glycoprotein to replace that lost as the slug crawls can be estimated at 313 J/kg m (10). This value is equal to 34.6 percent of C_m , or 9.5 to 13.3 percent of the slug's overall energetic cost, and is similar to values measured by calorimetric means for other pulmonates (11). Thus, when compared to the external cost of locomotion (1.8 percent of C_m) the cost of mucus production is the dominant factor. If the intrinsic maximum efficiency of slug muscle is similar to that of vertebrates (~ 20 percent), the minimum internal cost of muscular contraction directly leading to external work can be calculated by multiplying the cost of external work by five. Thus the minimum internal cost of effective muscular contraction during locomotion is 8.9 percent of C_m . This muscular cost added to that of mucus production accounts for an estimated 43.5 percent of the internal cost of locomotion. The remaining 56.5 percent must be accounted for by the combined inefficiencies of internal mechanisms such as that described above. The individual contributions of each of these mechanisms is difficult to estimate, and a complete energy budget awaits further study.

In conclusion, the cost of adhesive locomotion has been shown to be very high, and its efficiency relatively low.

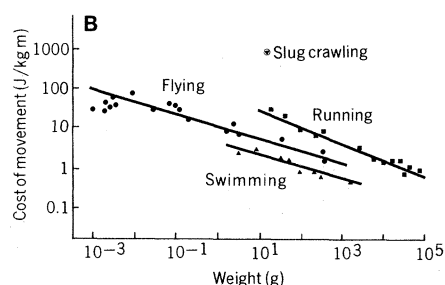
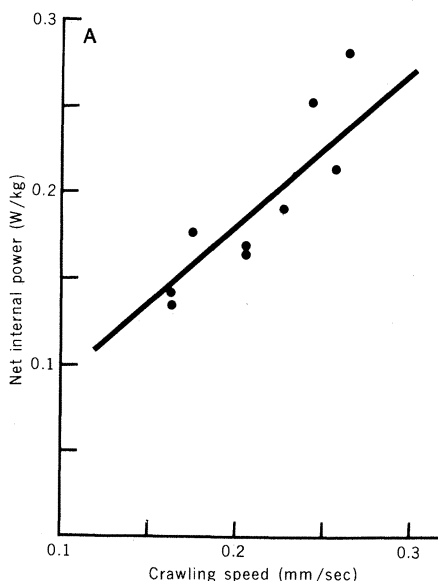


Fig. 2. (A) The net internal power of locomotion, P_{in} , as a function of average crawling speed for *A. columbianus*; nine measurements from seven slugs. The slope of the line is the average cost of movement, 903.9 J/kg m. (B) The cost of locomotion. For any given weight it is more costly to fly than swim, and more costly to run than fly. The cost of locomotion measured for slugs is considerably greater than any value previously measured. [Redrawn from (7); after Schmidt-Nielsen (2); courtesy of Chapman and Hall].

The high cost is primarily due to the cost of mucus production, which alone is greater than the total cost of movement for a mammal or reptile of similar weight, a fact which may be useful in examining the evolutionary ecology of slugs and other animals with similar locomotory systems. It seems likely that the high cost of movement has affected the "lifestyle" of these animals, for example, by limiting the distance over which it is profitable to crawl in search of mates or food.

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Development of Contrast Sensitivity in Infant *Macaca nemestrina* Monkeys

Abstract. During an infant monkey's first 28 postnatal weeks, the visual contrast sensitivity function develops its characteristic adult form. Contrast sensitivity is depressed relative to that of the adult for all spatial frequencies during the early postnatal weeks. Absolute sensitivity to frequencies below 5 cycles per degree approaches adult levels by 20 weeks after birth, whereas sensitivity to fine spatial detail continues to develop through 28 weeks. The results imply that the development of primate spatial vision is more complex than just an improvement in the ability to resolve acuity gratings.

Primate visual acuity is immature at birth. Acuity improves gradually during the first six or more months after birth in human infants and during the first six or more weeks in macaque monkey infants. If the monkey time axis is expanded by about a factor of 4, the two species coincide closely over the early postnatal weeks (1). This developmental similarity, in combination with the established similarity of visual capacities of adults of the two species (2), supports the conclusion that the macaque monkey provides a good animal model for the development of human spatial vision.

Visual acuity provides information only about sensitivity to very fine, high-contrast spatial detail. The spatial contrast sensitivity function (CSF) provides information about visual sensitivity over the entire spatial frequency spectrum, including the acuity point (3). Thus, the study of CSF's during development provides a more complete description of the emergence of spatial vision. Through the

use of nonoperant techniques (4), CSF's have been obtained from human infants between 1 and 3 months after birth. To our knowledge, operant testing methods, used extensively with nonhuman primates in other contexts, have not been used to obtain CSF's from infants.

We have studied two infant *Macaca nemestrina* monkeys longitudinally by means of a specialized operant testing method. We found that contrast sensitivity increased with age at all spatial frequencies, but sensitivities to different spatial frequencies improved according to different time-courses. Sensitivity to low spatial frequencies reached an asymptote near adult levels first, whereas sensitivity to higher frequencies continued to improve over a longer postnatal period. This resulted in changes with age in the peak spatial frequency as well as in the high-frequency cutoff of the CSF.

We obtained contrast sensitivity measures from our infant monkeys in a two-alternative forced-choice psychophysical experiment. A spatial sinusoidal grating was generated on one of two cathode-ray tube (CRT) screens. The sinusoidal nature of the grating, its spatial frequency and contrast, and the position of the grating (on the left or on the right CRT) were controlled by computer (5). The spatial frequencies ranged from 0.8 to 25 cycle/deg, with each display containing six or more cycles of the grating.

The infant monkeys entered a strict shaping routine about 1 week after birth, during which they were eventually trained to discriminate between a sinusoidal grating displayed on one CRT and a homogeneous field of matched space-averaged luminance displayed on the other. The mean luminance was 27 candles per square meter. The monkeys were trained and tested in their home cages according to a face mask technique (6). The face mask consisted of a piece of plastic molded into the shape of a monkey's face, with eye holes for viewing the stimuli and a mouth hole for receiving reinforcement. Two grab bars, right and left, were located within easy reach through an armhole below the mask.

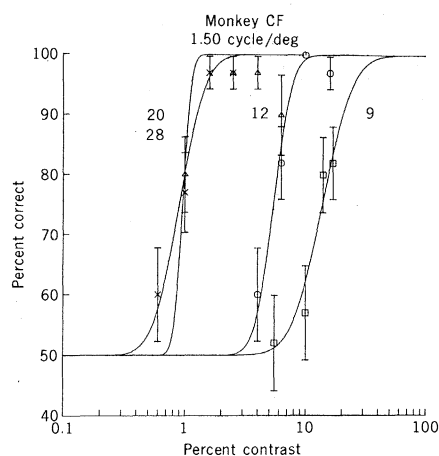


Fig. 1. Psychometric functions generated by infant CF 9 (□), 12 (○), 20 (Δ) and 28 (×) weeks after birth. Each data point was determined from a total of 40 trials with one contrast of a 1.5 cycle/deg grating. The error bars plotted around each point are ± 1 standard error of the mean of the binomial distribution. A cumulative normal curve has been fit to each data set using a least-squares criterion. Each point was weighted according to its binomial statistics. The contrast value where the best-fit curve crosses the 75 percent correct level is used as an estimate of threshold contrast.