

metabolic rate relative to the maximum O₂ delivery capacity of the respiratory system. Discontinuous ventilation is observed in some non-insect, tracheate arthropods (such as sun scorpions, solifugids and ticks)^{23–25}. We propose that these arthropods must also reduce gas exchange during periods of low metabolic activity to avoid the toxic effects of oxygen.

One can quite reasonably ask, given the capacity of evolutionary forces to refine and improve physiological systems, why the insect respiratory system is designed in a manner that subjects the insects to periodic bursts of toxic O₂ levels and complicates respiratory and pH homeostasis. The answer lies in the fact that the DGC is observed only in resting insects²⁶. The insect's respiratory system has been designed to function most efficiently at high levels of O₂ consumption. We argue that the insects' respiratory system is designed to provide a high delivery capacity, not to swamp the tissue with oxygen during periods of low aerobic demand but rather to supply abundant oxygen during periods of high oxygen demand. Extensive studies of the design of the vertebrate respiratory system have shown that its design is driven by demands during periods of maximum aerobic activity^{27,28}. The respiratory system of insects is similarly 'overdesigned' for providing oxygen to the tissues during non-exercise conditions. The respiratory pattern that we observe during low demand is the insect's attempt to use a high capacity system during periods of 'metabolic idling'.

Evidence in support of this notion is provided by the fact that the cycle disappears when insects increase their metabolic rate, for example in high temperatures or during exercise^{26,29}. Under these conditions the cells use O₂ at a much faster rate. We observe that the spiracles do not fully close under these conditions by the fact that the release of CO₂ never goes to zero. We propose that an O₂-sensing system is located somewhere in the animal and that under conditions of enhanced metabolic rate, this permits the spiracles to remain more fully open. Previously, physiologists have reasoned that the spiracles open during exercise to provide more oxygen. We would argue that they open because they are released from their need to close. □

Methods

To measure the hydrostatic pressure and the O₂ pressure within the tracheal system, two spiracles were intubated. A short length of polyethylene tubing (length 50 mm, outer diameter 0.9 mm; inner diameter 0.4 mm) was inserted past the spiracular valve into one spiracle in order to record the intratracheal pressure. The spiracle was then carefully sealed with wax. The tubing was fitted to a miniature differential pressure sensor (SenSym SDXL010D4, Sensortech) that was connected to a custom-made amplifier. The pressure range was 2,500 Pa, with an accuracy of about ±10 Pa. Abdominal movements were recorded optically with a miniature infrared light reflection switch (SFH900, Siemens). The light reflected from a reflecting sheet (23090, 3M) glued to the tip of the abdomen was used to record the distance between the sensor and the tip of the abdomen with a custom-made amplifier built to obtain a linear relation of output voltage versus distance. Tracheal p_{O₂} was measured with a custom-made Clark-type p_{O₂} electrode through a single spiracle as previously described³⁰. The O₂ sensor was calibrated before and after experiments using moistened air and pure nitrogen at 15 °C. The animal (with sensors) was housed in a flow-through, temperature-controlled respirometer at 15 °C and CO₂ release patterns were recorded using a differential infrared gas analyser (URAS 4, Hartmann & Braun). Ambient p_{O₂} was modified using a computer-controlled mass-flow controller (MKS 1259, 200 ml min⁻¹) that permitted the addition of nitrogen or oxygen to the ambient air. Accuracy of the mixtures was checked by means of a flow-through O₂ sensor (Ametek S-3A/II with Sensor N-37).

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Asymptotic prey profitability drives star-nosed moles to the foraging speed limit

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Foraging theory provides models for predicting predator diet choices assuming natural selection has favoured predators that maximize their rate of energy intake during foraging^{1–6}. Prey profitability (energy gained divided by prey handling time) is an essential variable for estimating the optimal diet. Time constraints of capturing and consuming prey generally result in

handling times ranging from minutes to seconds, yet profitability increases dramatically as handling time approaches zero, providing the potential for strong directional selection for increasing predator speed at high encounter rates (tiny increments in speed increase profitability markedly, allowing expanded diets of smaller prey). We provide evidence that the unusual anatomical and behavioural specializations characterizing star-nosed moles resulted from progressively stronger selection for speed, allowing the progressive addition of small prey to their diet. Here we report handling times as short as 120 ms (mean 227 ms) for moles identifying and eating prey. ‘Double takes’ during prey identification suggest that star-nosed moles have reached the speed limit for processing tactile information. The exceptional speed of star-nosed moles, coupled with unusual specializations for finding and eating tiny prey, provide new support for optimal foraging theory.

In the classical prey selection model for predicting predator diets³ the rate of energy intake (R) is equivalent to $E/T_s + T_h$, where E is the energy obtained from prey, T_s is the time spent searching for prey, and T_h is the time spent handling prey^{4–7}. Thus, minimizing T_s and T_h maximizes R . For most species there are numerous constraints on how short search and handling times can become. Yet the pay-offs for energy intake could rise dramatically if the denominator ($T_s + T_h$) is minimized, providing the potential for progressively stronger directional selection for increasing predator speed if short search and handling times can be achieved. The result would presumably be extreme sensory-motor specializations. Investigations of such species (that is, those species that have been pushed to the speed limits for foraging behaviours) may provide new insights into predator evolution. Star-nosed moles seem to have reached this extreme. Star-nosed moles have long been considered a biological enigma, exhibiting unusual anatomical and behavioural specializations that set them apart from other mammals⁸. Here we report that they are also the fastest of mammalian foragers, and suggest that their unusual anatomy and behaviour are the result of unusually strong directional selection for increasing predator speed,

allowing them to exploit small invertebrates in their wetland habitat⁹.

Using a high-speed video system we documented star-nosed moles detecting and eating small prey items as they foraged on a glass plate in a simulated tunnel. Moles searched using their mechanosensory star with a stereotyped behaviour that can be divided into a search phase and a feeding phase. During the search phase, the star was rapidly touched to different areas in the environment (Fig. 1). The average duration of the movements and touches was approximately 50 and 25 ms, respectively¹⁰. Thus a foraging mole typically contacted 13 different areas with the star every second. Contact of the star to prey constitutes the beginning of an ‘encounter’ and usually resulted in a foveation movement that brought the high-resolution 11th appendage pair—the tactile fovea⁸—into contact with the prey item, followed by capture of the prey with small, tweezer-like front teeth.

Figure 1a shows the relationship of the search phase to the feeding phase. Handling times were calculated to reflect the ‘principle of lost opportunity’⁶; that is, foraging time lost to consume prey. Thus, handling time began at the end of the first touch and lasted until the mole had eaten and began a star movement, resuming the search phase. Here we have considered handling times for the smallest prey that were detected and eaten (pieces of earthworm, 0.8–2.0 mm diameter, with an average energy value of approximately 10 J^{11}). The (weighted) average handling time for three moles was 227 ms for these prey sizes (mole 1: 228 ms, 85 trials; mole 2: 223 ms, 40 trials; mole 3: 230 ms, 24 trials). Figure 1 shows selected frames from high-speed video of moles encountering and eating prey (see also Supplementary Video 1). The handling time ranged from 120 to 440 ms.

Prey profitability (P)—the ratio of energy gained to handling time for each prey item (E/T_h)—provides a useful index of value for each item and is an important parameter for determining whether a prey type should be included in the optimal diet^{3–7}. The short handling times for star-nosed moles have a marked effect on profitability of small prey (Fig. 2a). Remarkably, tiny prey items

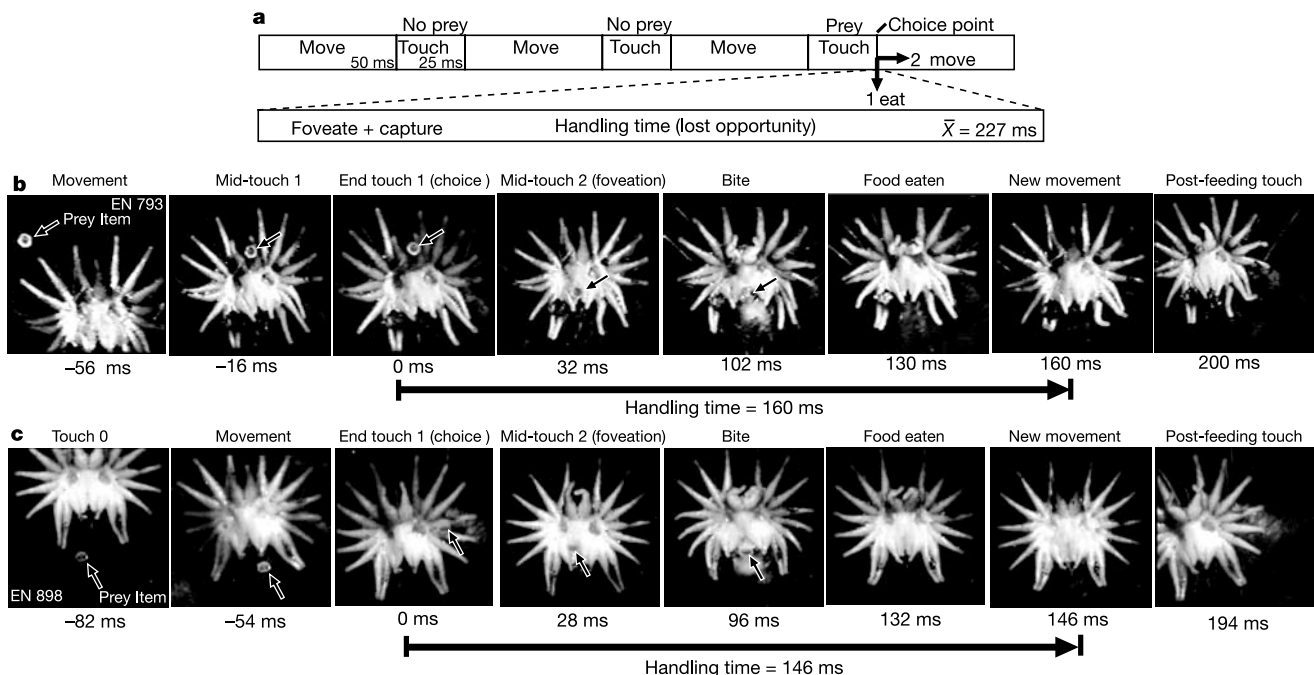


Figure 1 Star-nosed mole foraging. **a**, Search behaviour consisting of repeated cycles of star movements and touches lasting an average of 50 and 25 ms, respectively. When prey is encountered, moles feed (choice 1) or continue searching (choice 2). Feeding includes a foveation movement followed by grasping prey. **b, c**, Selected video frames illustrating

two feeding responses and the handling times. Handling time begins at the end of the first touch to prey and continues until searching is resumed. Arrows mark prey item (piece of earthworm).

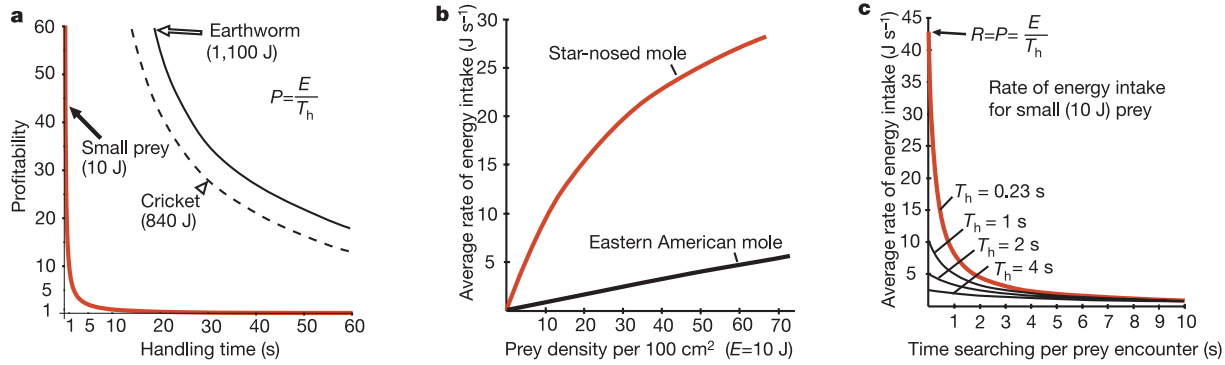


Figure 2 Prey profitability and energy intake for different handling times and prey densities. **a**, Red line represents small prey profitability. Short handling times (230 ms) make small prey profitable (filled arrow). Short-tailed shrews (dotted line) took 30 s to eat 840-J crickets (open arrowhead) that star-nosed moles avoid. Larger earthworm segments (1,100 J) were more profitable to star-nosed moles ($T_h = 19$ s), but their expected lower density suggests that moles would include small prey in their diet⁶. **b**,

Predicted effect of search speed on average energy intake for star-nosed moles and slower eastern moles with smaller receptor arrays, assuming equal T_h and small prey (10 J) (see text). **c**, The effect of T_h on average energy intake for different lengths of search between small prey encounters. Red line indicates star-nosed moles. Note that the maximum possible energy intake (arrow) is equivalent to prey profitability³ (43 J s^{-1} for star-nosed moles).

may be more profitable to star-nosed moles than large insects (open arrowhead, Fig. 2a) are to other, competing species (Supplementary Video 2). Even large earthworm segments have only a slightly greater profitability to star-nosed moles than the tiny prey items (Fig. 2a; see also Supplementary Video 3). These considerations suggest that small prey should be included in the star-nosed mole's diet, as large prey would have to be common (encountered once every 10 s in this simplified example, see ref. 6 for calculating diet breadth) for small prey to be rejected. In fact, the star-nosed mole's unusual dentition provides evidence for a long history of selective pressure for ingesting tiny prey (Fig. 3a, b). The unique incisors function like a pair of tweezers that are coordinated with the final movements of the star to rapidly grasp tiny prey (Fig. 1b, c frame 5; see also Supplementary Videos). This observation is consistent with gut content analysis of star-nosed moles, which indicates that they consume large numbers of small invertebrates⁹.

Clearly star-nosed moles are specialized to minimize handling time (T_h) for small prey. However, to maximize energy intake the encounter rate with prey must also be maximized (thus minimizing T_s). Habitat choice has an obvious role in the type and number of prey that are encountered, and the star-nosed mole's unique (for moles) wetland habitat contains high densities of invertebrates^{9,12}. In addition, encounter rates can be increased by searching quickly and increasing the size of the sensory receptor sheet. Both of these specializations are apparent in star-nosed moles. Although nearly all moles have an array of mechanosensory organs on the nose, the expanded star configuration greatly increases the surface area of the receptors relative to other moles (Fig. 3c, d). The star covers 0.92 cm^2 per touch, whereas the snout of their close relative, the eastern mole (*Scalopus aquaticus*), covers only 0.11 cm^2 per touch. Star-nosed moles touch the substrate 13 times per second whereas eastern moles touch eight times per second. Thus, for equivalent small prey densities, star-nosed moles would be expected to encounter roughly 14 times more prey items per unit search time than eastern moles. Figure 2b illustrates the effect of these sensory specializations on R for the two species encountering prey at different densities (assuming equal handling times). However, this comparison remains theoretical because eastern moles do not eat the small prey items eaten by star-nosed moles (see Supplementary Video 4).

As pointed out previously³, at high encounter rates a predator's energy intake (R) approaches a theoretical maximum equivalent to the prey's profitability (E/T_h); that is, T_s approaches zero (arrow Fig. 2c). Star-nosed moles live in wetlands with a high density of invertebrates, and it is likely that they encounter periodic patches of

dense prey. Is it possible for them to achieve the theoretical maximum rate of energy intake of E/T_h when T_s is zero? Our preliminary data from a mole encountering multiple prey items strongly suggest that this is the case. In an astounding flurry of star movements and prey captures, a mole presented with eight separate prey items located and ate them in 1.8 s during the first trial (see Supplementary Video 5). In the second small prey trial, ten separate prey items were located and eaten in 2.3 s. The average handling times for each of the multiple prey items were 229 ms and 233 ms respectively, for each trial—equivalent to the single-prey-item handling times and resulting in a profitability of 43 J s^{-1} for these prey; essentially identical to the single-prey-item profitability average of 44 J s^{-1} . Thus, star-nosed moles can achieve the theoretical

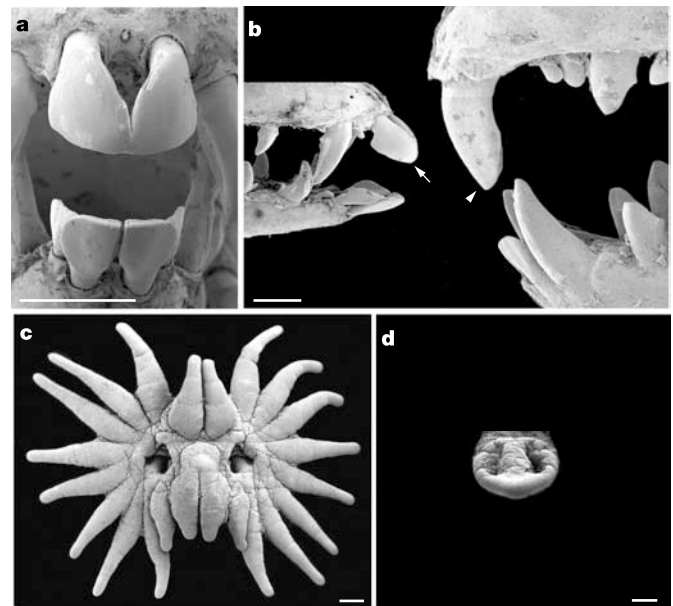


Figure 3 The unusual dentition and nose of star-nosed moles. **a**, **b**, The specialized incisors (arrow) are greatly reduced and modified into a tweezer-like form used to precisely grasp small prey. Compare to eastern mole incisors (arrowhead in **b**). **c**, **d**, The star (**c**) is many times larger than the nose of other moles (**d**), contains twice the density of receptor organs found in other moles, and is divided into a high-resolution central fovea and low-resolution periphery (paralleling trends in high-resolution visual and auditory systems)²⁰. Scale bars, 1 mm.

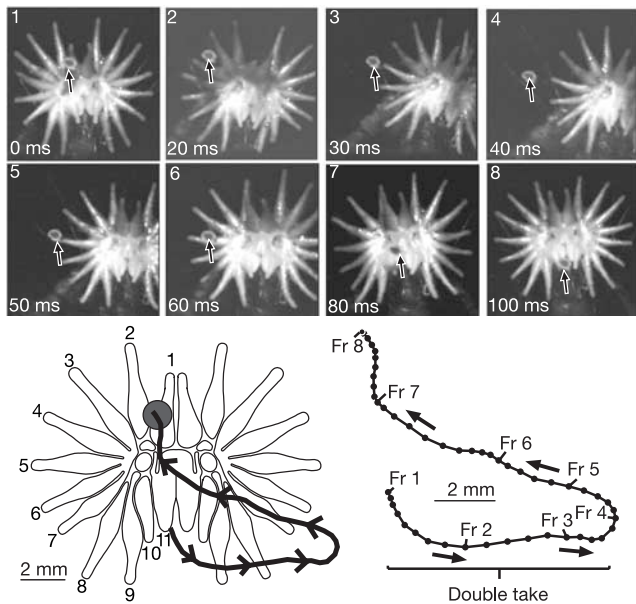


Figure 4 A double take illustrating initial movement in the wrong direction, followed by a sudden correction that brings the foveal region into contact with the prey. Arrows in the top panels (1–8) mark the prey item. The substrate is not contacted during the double take. The lower-left panel shows the track of the nose relative to the prey item (dark sphere). The lower-right panel shows the relative position of the nose every 2 ms (small dots) joined by a line showing the track. Each video frame is indicated (Fr).

maximal R for high densities of small prey—at least in bursts. This may represent the upper limit of energy intake for star-nosed moles consuming the smallest prey items, as details of their behaviour suggest that they have reached the limit of the mammalian sensory system for processing tactile information. For example, star-nosed moles have roughly 25 ms (average touch duration) to make their initial decisions about potential food items before they begin to move the star to the next area of the substrate (Fig. 1a). It takes 12 ms for neurons in the mole’s somatosensory cortex to respond to tactile stimulation of the star¹³, and we estimate that it takes roughly 5 ms for a motor command to be conducted to the periphery¹⁴. This leaves little time for central processing and may explain the relatively frequent occurrence of double takes. In over one-third of the trials the star was initially moved in the wrong direction (away from the contacted prey item) before a sudden reversal brought the fovea area into contact with the prey (Fig. 4; see also Supplementary Video 6). This inefficient behaviour lengthens handling times and suggests that star-nosed moles are at, or near, the speed limit for central processing of tactile information.

Supplementary Fig. 1 summarizes our results and their implications for the evolution of sensory-motor systems and foraging strategies. At long handling times there is a low cost to increasing speed because few adaptations are needed to reduce handling time from, for example, 30 to 29 s. However, there is also little to be gained in prey profitability. In contrast, at very short handling times there is a large pay-off in prey profitability in moving from a handling time of 1.5 s to 0.5 s. There are also likely to be great costs in the form of adaptations for speed and, as a corollary, adaptations for detecting smaller prey. Here we suggest that the many sensory-motor specializations characterizing star-nosed moles are the result (and cost) of selective pressure for exploiting high densities of small prey at high speed. The pay-off is not the profitability of individual prey *per se*, but rather the ability to add the resource of small invertebrates, present in the star-nosed mole’s wetland habitat⁹, to the diet while maintaining a high average rate of energy intake. But there are limits to how short handling times,

which include pursuit and capture of prey, can become. The ancestor to star-nosed moles probably had characteristics that might be considered exaptations¹⁵ for increasing speed. Specifically, the use of a touch organ near the mouth to detect prey allows for progressive reduction in handling time, whereas distance detection (sight, sound, or smell) limits reduction in handling time because of the need to approach prey. In addition, visual information takes longer to transduce as exemplified by the 200 ms reaction time for a human eye movement¹⁶, longer than the entire handling time for many star-nosed mole trials. Thus, despite potentially high pay-offs, a number of constraints may prevent the evolution of very short handling times in most species. □

Methods

Three star-nosed moles (*Condylura cristata*), two short-tailed shrews (*Blarina brevicauda*) and three eastern moles were collected under the authorization of scientific collecting permits. Moles and shrews were housed separately in 38 × 55 cm containers filled to a depth of 20 cm with moist peat moss. Mole home cages were connected to a separate water container by plastic tubing. The moles captive diet consisted of commercially raised earthworms. Shrews were fed crickets and mealworms. Small pieces of earthworm were used as prey items for star-nosed moles during behaviour trials. Average size of earthworm pieces for all trials was 1.4 mm, corresponding to a dry weight of approximately 0.5 mg and an energy value of 10 J¹¹. Crickets were used for prey of short-tailed shrews and had an average dry mass of 63 mg, equivalent to approximately 1,400 J¹¹; however, the energy content was reduced by 40% to estimate non-digestible chitin^{17–18}. Behaviour was filmed in a rectangular Plexiglas tunnel system with a removable glass bottom using an S-Series Motionscope (Redlake Imaging Corporation) at a sampling rate of 500 frames per second. Video was stored in a digital buffer and then transferred to VHS tape for scoring. Mole dentition and skin were examined under a Cambridge 360 scanning electron microscope after dehydration and sputter coating with gold. The cortex was fixed in 4% paraformaldehyde, cut tangentially at 60 μm and processed for the metabolic enzyme cytochrome oxidase¹⁹. Mole nose surface area contacts were determined from close-up, videotaped behaviour trials.

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