Incline running in the blue hedgehog (*Erinaceus celeritas*)

Hayao Naka[a] **and Naoto Yasuhara**[a]

[a]Laboratory of Biomechanics, South Island Research Institute

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We report the results of a study of the movement of the blue hedgehog (*Erinaceus celeritas*) in an natural setting. We obtained measurements of its speed using high-quality cameras and automatic video analysis software. We show that the blue hedgehog is the fastest of all animals of its size and is capable of incline running as well as full loops.

blue hedgehog | mammalian biomechanics | running speed | field work

Introduction

The blue hedgehog (*Erinaceus celeritas*) is a species of small diurnal insectivores in the *Erinaceidae* family (Order: Eulypotyphla). Originally endemic to Japan, the species is now found in all continents (1).

In most habitats where it is found, the blue hedgehog is a favoured prey for carnivores or birds of prey. Its distinct blue color is known to play a role in sexual selection (2), but makes it an easily findable target against the background of most natural environments.

Many defining traits of the blue hedgehog are understood as evolutionary responses to the intense predation (3). Defense mechanisms starts with its aposematic coloration, but can also be seen in its characteristic spikes, as well as in the ability to roll into a ball when threatened or alarmed - behaviors shared by most hedgehogs. What makes *E. celeritas* special are its evasive movements.

It has been widely known from field observations that the blue hedgehog can achieve high speeds when running, especially when rolling as a ball (4), which allows it to avoid most predators it detects. In fact, due to its quickness and evasiveness, the species was only described in 1991 (5).

Here we report measures of the speed of the blue hedgehog in an natural setting for the first time. We strategically placed cameras to be able to capture the movement of the hedgehog in video, which we later processed at the laboratory.

Methods

Study Area. The present work is based on three separate periods of fieldwork between March and September, 2019, in Green Hill Zone, South Island, Japan (**Figure 1A**). The study area of about 20 km^2 consists primarily of woodland. The zone is characterized by lush fields of evergreen grass, with patches of droopy palm trees reaching 4-5 m. Crumbling cliffs and tunnels complement the environment, which is full of sudden changes in elevation. It serves as a habitat for a number of woodland species such as echidnas (*Tachyglossus aculeatus*), two-tailed foxes (*Vulpes bicauda*) and other rare species of hedgehogs, such as the black hedgehog (*Erinaceus umbra*).

Camera Setup. We set up 8 high-speed high-resolution cameras around the environment (iCapture Series 5 X2; **Figure 1B**). To save batteries and storage space, the cameras were modified to add motion sensors that would start the capture and programmed to function only during day hours. Cameras were left for up to 4 weeks. About once every month, we replaced the memory cards in the cameras with empty ones and brought the videos back for processing.

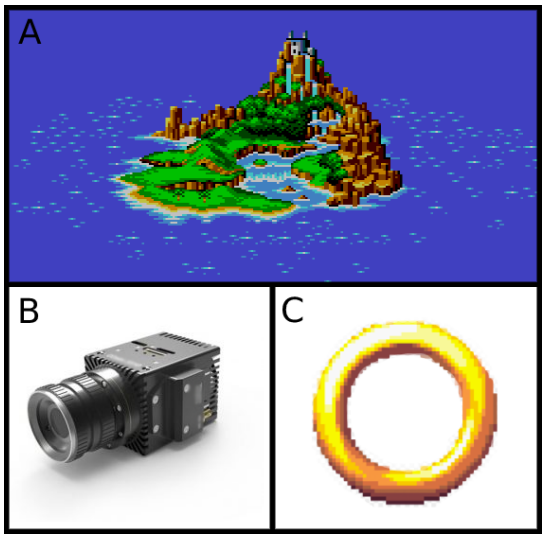

Fig. 1. (A) A photograph of the South Island, where the study was conducted. The Green Hill Zone is seen in the front of the island, (B) The iCapture Series 5 X2 high-speed camera used for image capture and (C) a close up of the golden rings used to attract and induce movement in the blue hedgehogs.

Cameras were placed strategically after scouting the zone. We place them near the entrances of hedgehog burrows and tunnels. To increase the chances that the hedgehogs would be captured on camera, we spread custom-made gold rings on trees that were within the camera's field of view (see **Figure 1C**). We took advantage of the well-documented field observations that blue hedgehogs will collect golden objects (6). We replenished the golden rings once every month during the study.

Video Analysis. We first watched the hours of video sped up, to identify the timestamps where a blue hedgehog was visible and moving on the frame. At this step, we filtered out most of the material, including failures of the hardware and of the video itself - e.g. when some object blocked the view or the camera was moved or lost focus. Snippets of these moments were then cut and divided into separate files. Two other

HN and NY designed the study, analyzed the data, collected the data and wrote manuscript.

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Corresponding author: naka.hayao@siri.com

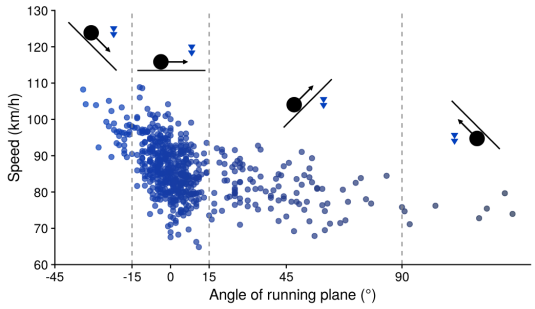

Fig. 2. Speed as a function of the angle of running. Diagrams on top exemplify the type of terrain and direction of movement in each section. Blue double arrows indicate the direction of gravity.

researchers then coded each snippet as walking, running or incline running. If necessary, files were divided again, such that each snippet contained only one type of movement.

Each snippet of video was then analyzed on the EasyMovePlus software (EMP; version 3.2 - Light Speed Software). Using EMP, we automatically tracked the blue hedgehogs captured in the frame. This was facilitated by the high contrast between the blue animal and the mostly green background, as well as the good lighting, since the blue hedgehog is diurnal. Using EMP, we also determined the speed of the tracked animal on the videos, which we calibrated with objects of known size we positioned in front of each camera when the memory cards were removed. We also estimated the angle of the inclination. We discarded the videos when we could not determine the speed or angle (e.g. due to the position of the animal or it disappearing behind obstacles on the frame).

Results

We obtained a total of 672 hours of video from all cameras, from which we could identify, code and record the speed for 826 events of blue hedgehogs in movement. Of these, 228 were coded as walking, 457 as running and 149 as incline running (angles above 15°, upwards).

Our findings show that blue hedgehogs can easily reach speeds upwards of 90 km/h and commonly do so in natural settings (**Figure 2**). Notice that this speed is comparable to that of mammals such as cheetahs (*Acinonyx jubatus*), which can reach over 100 km/h (7). Surprisingly, these speeds are achieved despite its small body size - for comparison, hares (*Lepus europaeus*) can reach 80 km/h (8).

We note two distinct modes of running, which we call here *Mode 1* and *Mode 2*. *Mode 1* is slower, not unlike what you see in other insectivores and small mammals and is the predominant mode. The noteworthy aspect of *Mode 1* is that at high speeds the hedgehogs take on a bipedal posture. In *Mode 2*, however, the animal seems to roll into a ball for running, which somehow helps it reach even higher speeds - and is particularly common when running on a slope. Curling into a ball is usually considered a defense mechanism, but here we report that it is also a speed aid.

We also find that the blue hedgehog does not lose much speed as it runs up steeper planes. They keep very high speeds even on high angles (**Figure 2**, last section). We recorded a few blue hedgehog doing a "loop", i.e. seemingly maintaining sufficient speed to run over surfaces which were inclined more than 90° in relation to the ground (see Supplementary Video 1).

Discussion

Our present data on this population of wild blue hedgehogs indicates that they are among the fastest extant species of mammal, specially considering the speed that would be expected for its body size (1 kg; see (5)). Moreover, we show that blue hedgehogs are able to perform incline running on leg strength alone, a behavior previously believed to require wing-like appendages (9).

Until further independent study, it remains a possibility that these movements are specific to the strain of blue hedgehogs endemic to the Green Hill Zone. Our exploratory analyses of the behavior of black hedgehogs suggest the opposite, that incline running is not even limited to the species (data not shown). Another possibility is that the movements are facilitated by the terrain. Again, we do not believe that to be the case. Although a more systematic investigation is lacking, field reports have documented the impressive speeds of the blue hedgehog in other terrains, such as jungles, underground tunnels near lava and even in urban environments (Brad Kurzawa, *personal communication*).

While it is not the focus of the present article, our videos capture other interesting behaviors of the blue hedgehog. In particular, we found evidence of biological interactions with other mammal species, in particular, with two tailed foxes (mutualistic) and black hedgehogs (competitive; manuscript in preparation).

Beyond providing important data on hedgehog movement and speed, this research raises many new questions. Are there special mechanisms that allow the hedgehogs legs to contract with such speed and strength? Similarly, some studies have shown the advantages of bipedal posture for endurance running (10), as well as the advantages of rolling to gain speed in downward slopes (4). In this study, however, we report the use of both strategies in other contexts, where the advantages are not so clear. The maintenance of high speeds on incline running suggests some biomechanical or tissue specializations that compensate for the steep angle. We hope this is a first step towards a better understanding of the biology of virtual animals.

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