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Hydrodynamics of defecation†

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Animals discharge feces within a range of sizes and shapes. Such variation has long been used to track animals as well as to diagnose illnesses in both humans and animals. However, the physics by which feces are discharged remain poorly understood. In this combined experimental and theoretical study, we investigate the defecation of mammals from cats to elephants using the dimensions of large intestines and feces, videography at Zoo Atlanta, cone-on-plate rheological measurements of feces and mucus, and a mathematical model of defecation. The diameter of feces is comparable to that of the rectum, but the length is double that of the rectum, indicating that not only the rectum but also the colon is a storage facility for feces. Despite the length of rectum ranging from 4 to 40 cm, mammals from cats to elephants defecate within a nearly constant duration of 12 ± 7 seconds ($N = 23$). We rationalize this surprising trend by our mathematical model, which shows that feces slide along the large intestine by a layer of mucus, similar to a sled sliding down a chute. Larger animals have not only more feces but also thicker mucus layers, which facilitate their ejection. Our model accounts for the shorter and longer defecation times associated with diarrhea and constipation, respectively. This study may support clinicians use of non-invasive procedures such as defecation time in the diagnoses of ailments of the digestive system.

1 Introduction

Eat, defecate, repeat. Nearly all animals defecate, and in turn feces play a role in a number of industries. Manure is produced in large quantities by the dairy and pork industries, requiring devices for their transport and disposal.[1] In medicine, defecation, also known as a bowel movement, is one of the most common ways a physician gauges a patients health. Problems with the digestive system are quite common, and Americans spend billions of dollars annually treating conditions such as gastrointestinal infections,[2] inflammatory bowel disease,[3,4] irritable bowel syndrome,[5] and other gastrointestinal disorders, all of which cause severe changes in bowel habits. Despite years of veterinary and medical studies, defecation still does not have an agreed-upon physical basis. A 2011 overview of digestion states that "the process of defecation is subject to considerable controversy."[6] By understanding the physics of defecation, we will provide not only new ideas for medical diagnostics, diapers, and incontinence products but also transport methods for the feces of humans, pets, and agriculturally important animals.

Bowel movements are often judged qualitatively and subjectively by their frequencies and the appearance of feces such as the color, the shape, and the size. In 1997, physicians Stephen Lewis and Ken Heaton at the University of Bristol provided a typology of feces called the Bristol Stool Chart, which rates feces by their viscosities from Type 1, consisting of hard nuts that are hard to pass, to Type 7, constituting a watery-like liquid.[7] Udén used radioactive markers to show that feces solidify with time in the intestine.[8] For years, animal trackers have been recording the shapes and sizes of the feces of a range of animals,[9,10] yet there is no unified view of processes that generate feces.

By showing the influences of the intestinal shape on the form of feces and their discharge rates, this work provides a unified view of defecation. In Section 2, we report our measurements of feces, rectums, and the material properties of feces and mucus and present a mathematical model for defecation and compare its predictions to our observations. In Section 3, we discuss the implications of our work and suggest directions for future research. In Section 4, we summarize the contributions of our study. In Section 5, we provide the detailed methods.

2 Results

2.1 Filming defecation *in vivo*

We film elephants, giant pandas, and warthogs at Zoo Atlanta, as well as dogs in a local park, as shown in Fig. 1(A)–(D).

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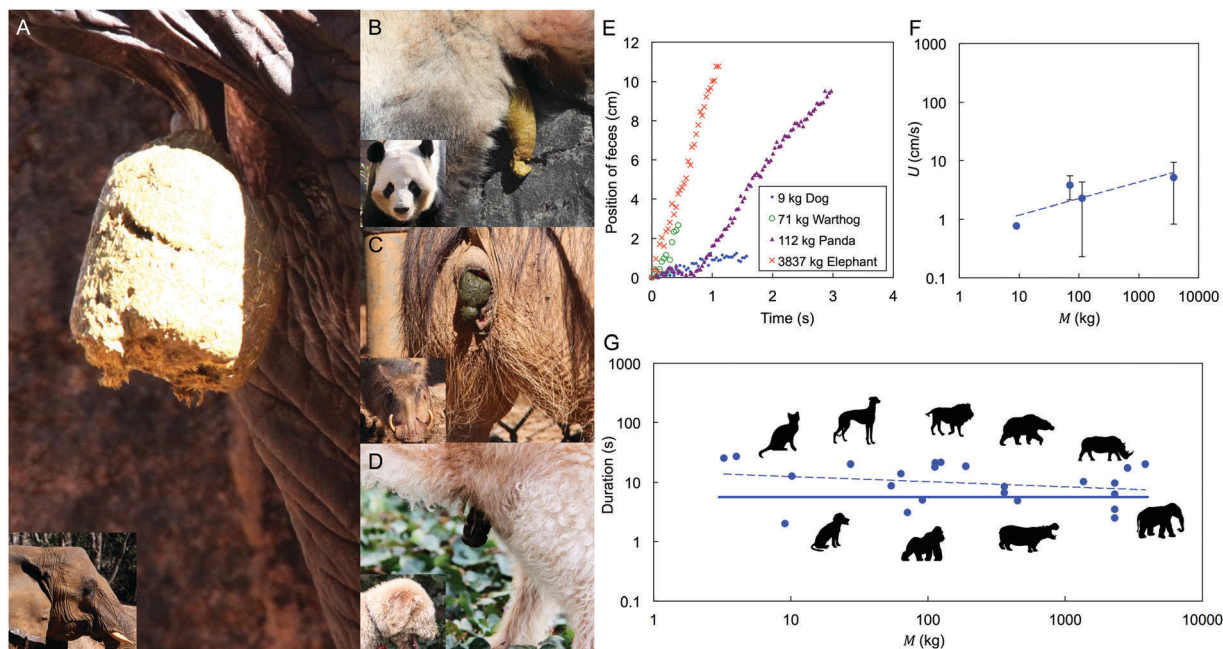
Fig. 1 Cylindrical feces from animals, including (A) an elephant, (B) a giant panda, (C) a warthog, and (D) a dog. (E) The time course of the position of feces. (F) The relationship between body mass M and the speed of feces U. (G) The relationship between body mass M and defecation time. Symbols represent experimental measurements, the dashed line represents best fit to the data, and the solid line represents the theoretical prediction.

We also obtain 19 videos of defecation from YouTube. Fig. 1(E) shows the time course of the positions of the discharged feces for each of four animals. We define the beginning of defecation, $t = 0$, when the tip of feces appears. In our videos, the duration of defecation at an initial transient state is less than one second. This transient time is much shorter than that time at a steady state, which is approximately ten seconds. Thus, we employ a steady-state model of defecation in Section 2.7 (Fig. 2). The defecation speed U of large animals is faster than that of small animals, which scales linearly with the body length of animals: $U \sim M^{0.28} \sim M^{1/3}$ ($N = 4$), where M is the body mass and $M^{1/3}$ is the body length of animals, as shown in Fig. 1(F). This scaling trend of the defecation speed is isometric, which describes a physical quantity that increases linearly with body length. Isometric scaling is a common feature of our findings in this investigation.

Fig. 1(G) shows the defecation time across three orders of magnitude of body mass from 4 kg to 4000 kg. Despite this wide range in mass, defecation time remains nearly constant within $T = 12 \pm 7$ s ($N = 23$). Using the method of least squares, we fit the time to the power law shown by a dashed line: $T \sim M^{-0.09}$. The power law indicates that as body mass increases by a factor of ten billion, defecation time decreases by only a factor of ten. This invariance in defecation time is surprising even though the rectum of an elephant of 40 cm in length is nearly ten times as long as that of a cat. How do animals defecate at a constant duration? To answer this question, we begin with measurements of feces.

2.2 Dimensions of feces

Animals can defecate several pieces of feces at once. For example, a dog can defecate four pieces of feces, as shown in Fig. 3(A). We use an animal tracking guide to compile 87 measurements of feces,[9] including the number of fecal pieces N_{piece}, the diameter of fecal pieces D, and the length of one fecal piece L_{piece}. We combine these measurements with anatomical dissection studies that report rectal length L_{rectal}[11–19] and rectal diameter D_{rectal},[13,15,16,20–22] as shown in Fig. 3(B). The rectal diameter is approximated as the outer diameter of the intestine, which has negligible thickness. However, we exclude mammals that defecate round feces. Such animals, including rodents, rabbits, and ruminants, eject either spherical pellets individually or appear to dump out a bag of pellets. Unlike human ejection of cylindrical feces, such defecation is not at steady state. From hereon, we limit our discussion to cylindrical feces.

By counting the number of fecal pieces in the animal tracking guide,[9] we discover that mammals defecate an average of two fecal pieces ($N_{piece} = 2.1 \pm 0.9$, $N = 35$), as shown in Fig. 3(C).
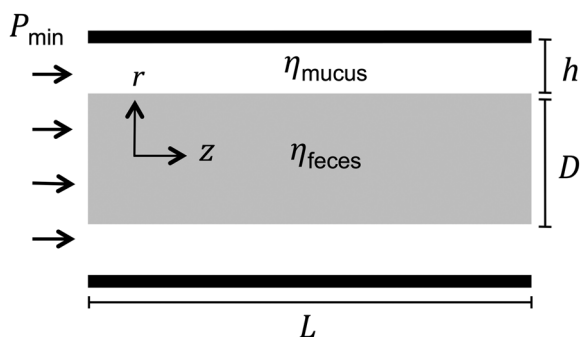

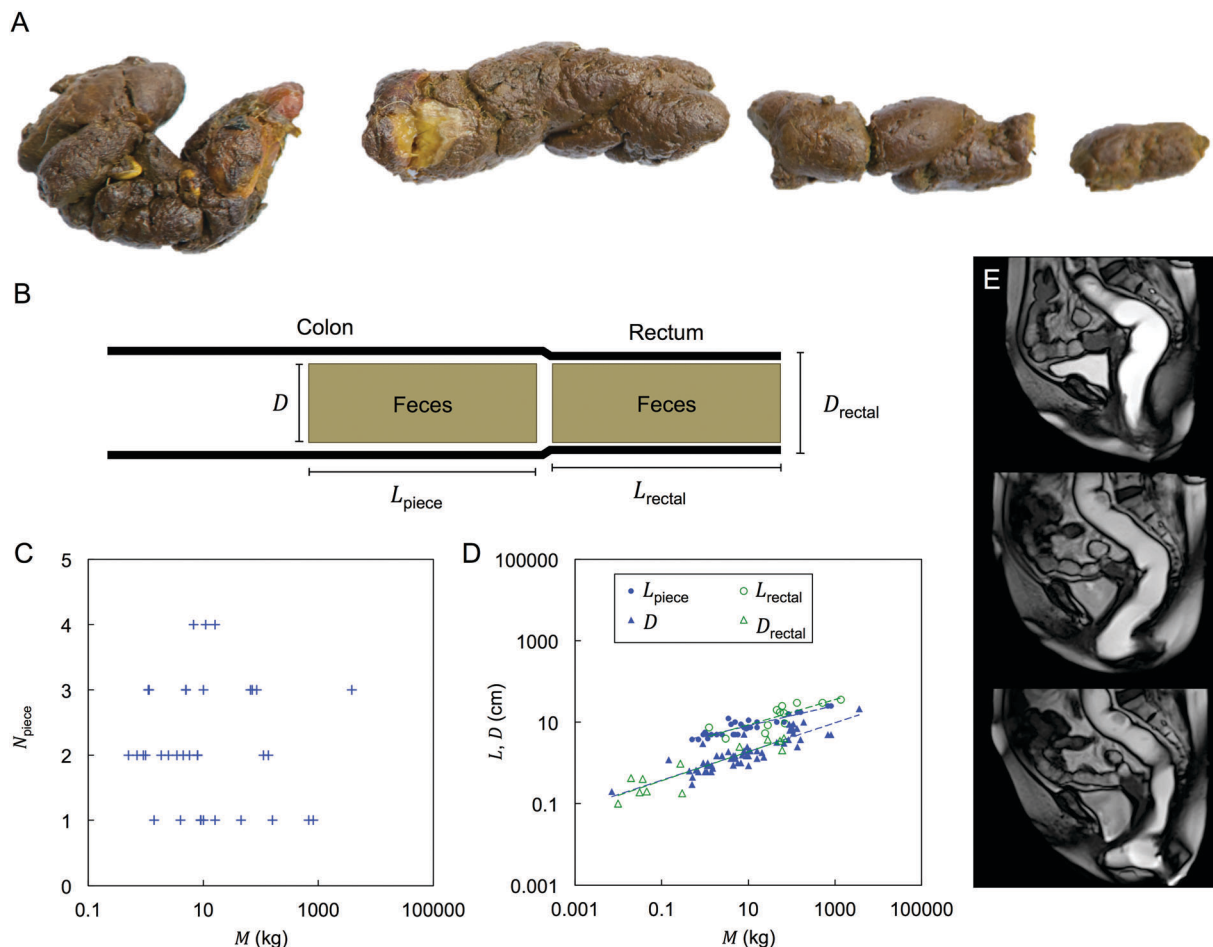Fig. 2 Schematic of the lubrication system in the large intestine.

Fig. 3 (A) A dog defecates four pieces of feces coated with remnants of yellow mucus. First piece is on the left and the feces proceed chronologically to the right. (B) Schematic of the dimensions of the rectum and fecal pieces. (C) The relationship between body mass M and the number of fecal pieces N_{piece}. (D) The relationship between body mass M and the dimensions of rectum and one fecal piece. Symbols represent experimental measurements, and dashed lines represent best fits to the data. (E) The MRI defecography shows the rectum and the anal canal of a human. Courtesy of Ashwin Porwal.

We define the total length of feces as the product of the number of pieces and the average length of one piece,

$$L = 2.1\, L_{piece}. \qquad (1)$$

The average length of one piece ($L_{piece} = 4.65M^{0.25}$ cm, $N = 31$) is equal to that of the rectum ($L_{rectal} = 4.20M^{0.31}$ cm, $N = 12$). Thus, the total length of feces L is twice as long as that of the rectum L_{rectal}. This finding suggests that the colon also acts as a storage facility for defecation, a fact that was not stated in previous studies. In fact, many studies have claimed that the rectum is the only storage facility for feces.[23,24] We do not consider the physics of the fecal breakoff, which is likely related to the material properties of feces and the angle at which they are extruded. Instead, we focus on elucidating the physics leading to constant defecation time.

Table 1 shows the allometric relationships of fecal and rectal geometry. All power law fits of these relationships have exponents from 0.25 to 0.36, reasonably close to one-third. Therefore, we conclude that both feces and the rectum are isometric. Moreover, the length of fecal pieces is five times as long as the diameter, indicating the aspect ratio of fecal pieces does not change appreciably with body mass. Larger animals simply have more feces. Measurements of fecal and rectal diameters match, suggesting that defecation is a process of pushing pre-shaped feces through a tube, similar to a sled sliding down a chute. In later sections, we report the properties of the mucus lubricant that facilitates this motion.

This physical picture of feces sliding rather than being extruded is an important point. Extrusion is pushing paste from a large reservoir through an orifice, such as squeezing toothpaste out of a tube. Because toothpaste pellets are not pre-formed, this process requires substantial energy. As we show in Section 2.6, the high stiffness of feces indicates that the pressure that deforms them is much higher than the pressure that animals typically apply during defecation. Thus, feces are effectively rigid with respect to the pressure from large intestines. Now that we have the dimensions of feces, we turn to their material properties, which affect the discharge rate of feces.

2.3 Material properties of feces

We collect fecal samples from 34 species at Zoo Atlanta, seven species at local farms, and two species at our university's animal facilities. Each day, the Zoo Atlanta staff provide a

Table 1 Measured allometric relationships for the duration of defecation, the velocity of feces, the dimensions of the rectum and feces, rectal pressure, and the thickness of mucus on feces, and the mass flow rates of food intake and excreted feces

|	Variable	Unit	Best fit[a]	R^2	Isometric fit[a]	R^2	N
Duration of defecation	T	s	$15.13M^{-0.09}$	0.06			22
Velocity of feces	U	cm s^{-1}	$0.62M^{0.28}$	0.72			4
Average length of one fecal piece	L_{piece}	cm	$4.65M^{0.25}$	0.82	$3.16M^{1/3}$	0.80	31
Diameter of one fecal piece	D	cm	$0.85M^{0.35}$	0.76	$1.11M^{1/3}$	0.74	56
Rectal length	L_{rectal}	cm	$4.20M^{0.31}$	0.66			12
Rectal diameter	D_{rectal}	cm	$0.83M^{0.36}$	0.84			12
Rectal pressure	P_{min}	kPa	$0.57M^{0.06}$	0.51			5
Mucus thickness	h	μm	$13.75M^{0.27}$	0.51	$15.1M^{1/3}$	0.54	5
Mass flow rate of food intake	$\dot{M}_{food}$	kg day^{-1}	$0.08M^{0.91}$	0.78			23
Mass flow rate of excreted feces	$\dot{M}_{feces}$	kg day^{-1}	$0.01M^{0.83}$	0.86			22

[a] Body mass M is in kg.
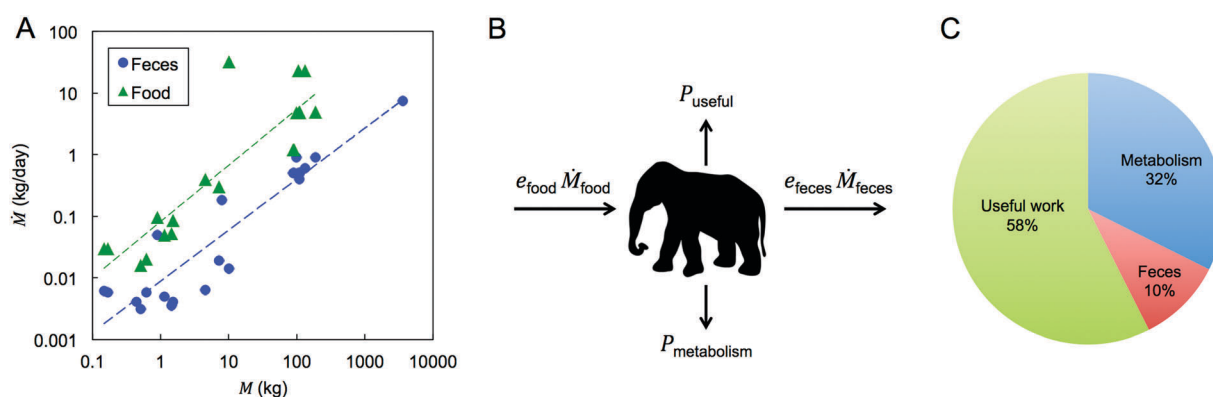
Fig. 4 (A) The relationship between body mass M and the mass flow rates of food intake and excreted feces. Symbols represent experimental measurements, and dashed lines represent best fits to the data. (B) Schematic of the flow rate of energy in mammals. (C) Pie chart of the distribution of energy intake.

specific amount of food to 14 species of animals. We combine their measurements with our measurements of fecal production to calculate the efficiency of energy conversion in mammals. Fig. 4(A) shows daily food intake, $\dot{M}_{food}$, and daily excreted feces, $\dot{M}_{feces}$, as functions of body mass. Table 1 shows the allometric relationships for food intake and excreted feces, which have exponents of 0.83 and 0.91. The exponents of near unity suggest that the amounts of food and feces are proportional to body mass. Specifically, daily food constitutes 8% of body mass, and daily fecal production constitutes 1% of body mass. These numbers differ because much of the water content in the food is absorbed and released as urine. Using previously reported energy densities of food and feces, we convert the flow rates of mass to the flow rates of energy. The average energy density of food is e_{food} = 11 kJ g^{-1} (2 to 20 kJ g^{-1})[25] and that for feces is e_{feces} = 9.2 kJ g^{-1} (3.5 to 14.9 kJ g^{-1}).[26] These energy densities already account for water content. Since the energy density of water is negligible,[27] we do not include drinking water or voided urine in our analysis. The energy flow rate in mammals is shown schematically in Fig. 4(B) and written as

$$e_{food}\dot{M}_{food} = P_{metabolism} + P_{useful} + e_{feces}\dot{M}_{feces}, \qquad (2)$$

which states that food intake is converted, in part, into the energy for useful work and metabolism, also known as the basal metabolic rate, which is the minimal energy expended at

rest for mammals. The remaining energy from food intake is lost in feces.

We use our measurements and others to compute the efficiency of digestion in producing useful work. Our zoo measurements show that the energy flow rate of feces is $e_{feces}\dot{M}_{feces}$ = $92M^{0.83}$ kJ day^{-1}, which is 10% of the average energy intake ($e_{food}\dot{M}_{food}$ = $902M^{0.91}$ kJ day^{-1}). Our calculated energy intake is comparable to $611M^{0.75}$ kJ day^{-1}, suggesting that our zoo measurements accurately represent the energy flow in mammals.[28] Kleiber has reported the energy for metabolism as $P_{metabolism}$ = $292M^{0.75}$ kJ day^{-1},[29] which is 32% of the energy intake. Thus, we infer that 58% of energy intake is available for useful work, as shown in Fig. 4(C).

To estimate the gravitational force on feces, we measure fecal densities, which range from 0.2 to 1.5 g mL^{-1} across species, shown in Fig. 5(A). These feces are split into two broad classes, sinkers or floaters, depending on their densities relative to water. Most large carnivores at Zoo Atlanta, such as fossa, bears, tigers, and lions, defecate ''sinkers'' with an average fecal density of 1.4 ± 0.1 g mL^{-1} (N = 7). Fig. 5(B) shows feces from a cat, which is also denser than water. Such feces sink because carnivores eat indigestible ingredients, including fur and bone.[30] The density of powdered bone is twice as dense as water.[31] Besides carnivores at Zoo Atlanta, skeletal constituents have even been found in dinosaur feces, known as coprolites.[32] Conversely, pandas and herbivores, such as hoofstock, elephants, and
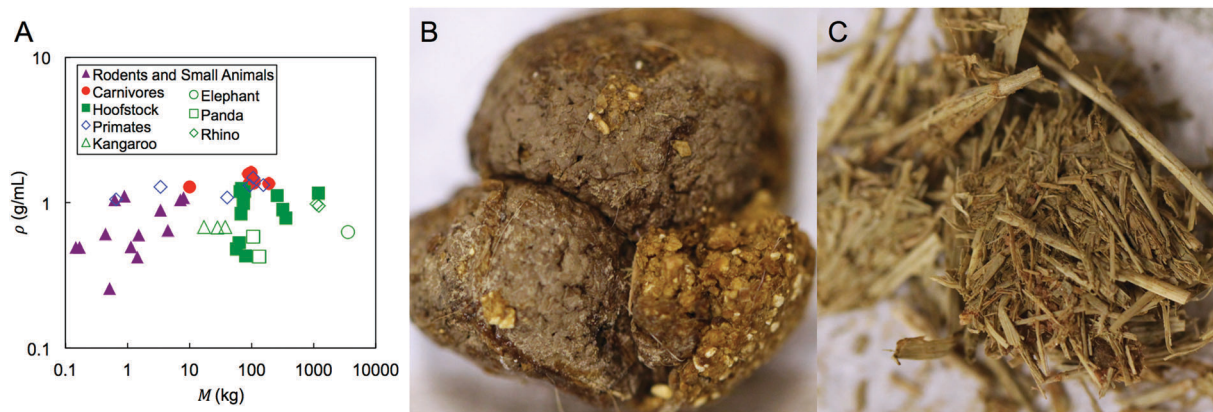
Fig. 5 (A) The relationship between body mass M and density of feces ρ. (B) Feces from a cat. (C) Feces from an elephant.
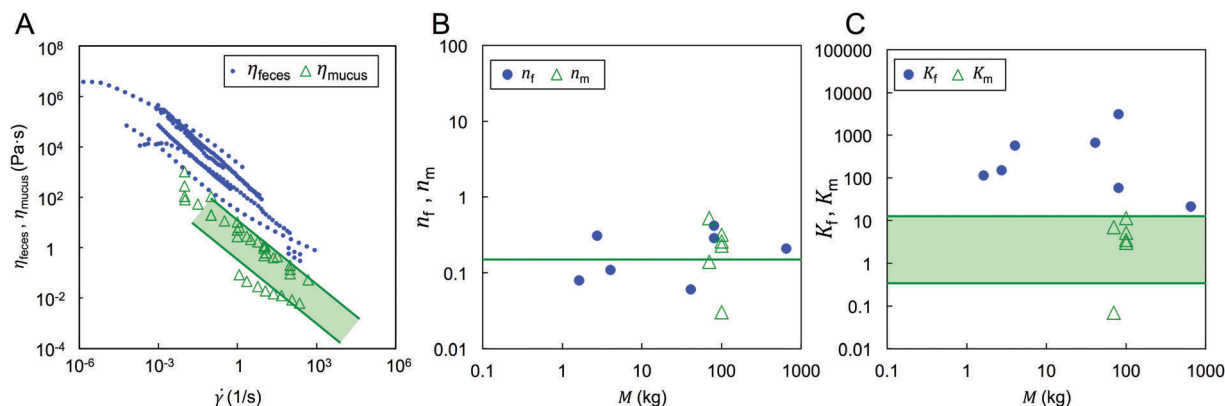

Fig. 6 (A) The relationship between the viscosities of feces η_{feces} and mucus η_{mucus} and the shear rate $\dot{\gamma}$. (B) The relationship between body mass M and the flow behavior indices of feces n_f and mucus n_m. (C) The relationship between body mass M and the flow consistency indices of feces K_f and mucus K_m. Symbols represent experimental measurements. The shaded area and solid lines represent the viscosity of mucus from various glands across a number of species.[44]

kangaroos, defecate "floaters" with an average density of ρ = 0.83 ± 0.3 g mL^{-1} (N = 20). These animals eat low-nutrition food and defecate much of it in undigested form,[33] as shown in Fig. 5(C). From hereon, we represent the density of feces by its maximum.

We measure the rheology of feces using a cone-on-plate rheometer. However, most of the feces we collect are untestable because they are either too dry or they contain too many rocks and plant stems to fit in the testing region of the rheometer. We successfully obtain rheological measurements of the feces from rabbits, cats, and dogs. We also collect the rheology of feces from a number of animals, including possums,[34] humans,[35] and cows.[36] Fig. 6(A) shows the relationship between the viscosities of feces and the applied shear rate, which indicates a power-law fluid behavior characterized by

$$\eta_{feces} = K_f\,\dot{\gamma}^{n_f-1}, \qquad (3)$$

where η_{feces} is the apparent viscosity of feces, exponent n_f is the flow behavior index of feces, pre-factor K_f is the flow consistency index of feces, and $\dot{\gamma}$ is the shear rate. The flow behavior index is constant across species, n_f = 0.21 ± 0.14 (N = 7), as shown in Fig. 6(B). The value of the flow index indicates

that feces are shear-thinning, exhibiting lower resistance when deformed faster. The shear-thinning property explains why dog feces feel slippery when stepped on. As the amount of water greatly affects the magnitude of viscosity,[35] flow consistency index K_f varies from 20 to 3000, as shown in Fig. 6(C).

2.4 Thickness of mucus

A thin layer of mucus coats the inner walls of both the esophagus and the rectum, providing lubrication for objects passing through. In the digestive tract, the thickness of mucus increases as it approaches the rectum.[37] In the rectum of fasted animals, the thickness of mucus ranges from 30 to 100 μm,[38–43] as shown in Fig. 7(B). Since fasting might affect the thickness of mucus, we introduce a new method of estimating its thickness in non-fasted animals.

When feces pass through the large intestine, they shear the mucus lining along the walls and create a slippage plane. While mucus above the plane remains adhered to the walls, the remaining mucus coats the feces,[44] shown in Fig. 7(A). We estimate thickness h of the mucus on feces by observing its evaporation from fresh feces and measuring the associated mass change ΔM with an analytical balance. Visually,
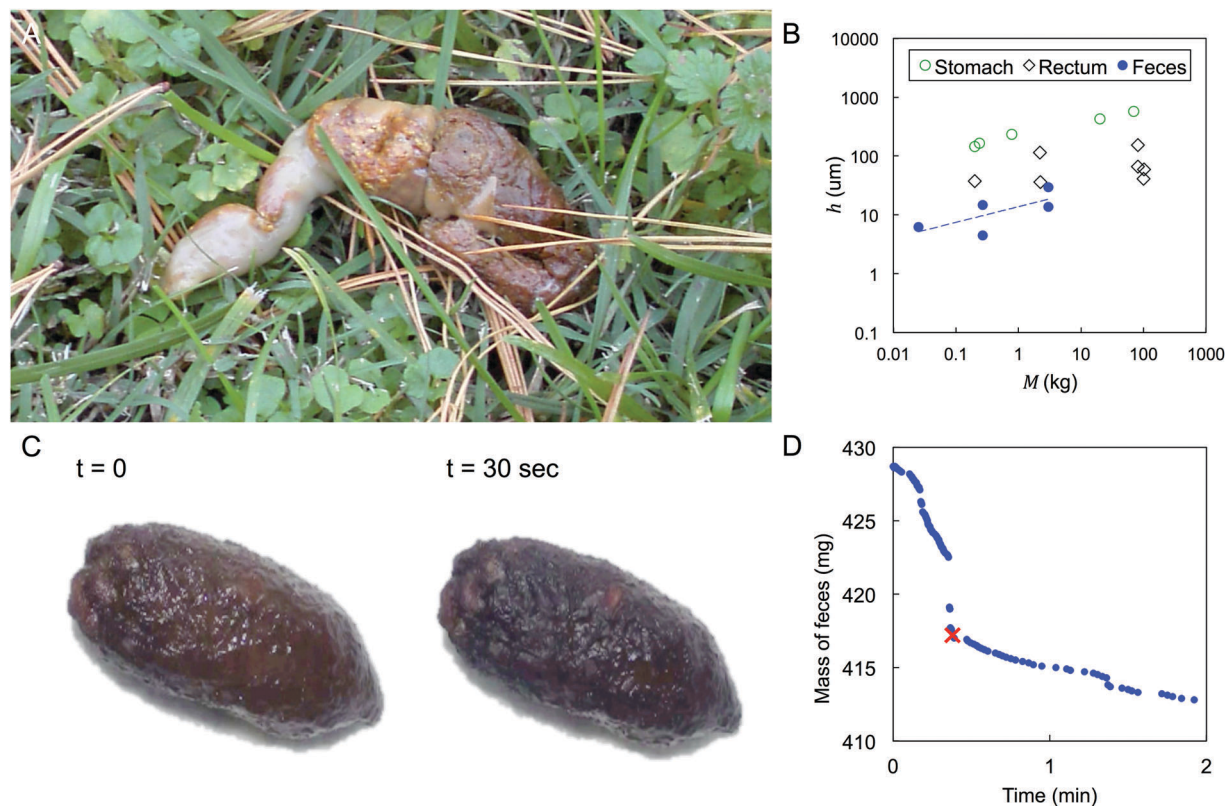
Fig. 7 (A) The surface of dog feces features patches of white mucus. Courtesy of Pamela Myers. (B) The relationship between body mass M and the thickness of mucus h. Symbols represent experimental measurements, and dashed lines represent best fits to the data. (C) The mucus on the surface of feces from rats shines at $t = 0$ and evaporates in less than 30 seconds. (D) The mucus on the surface of feces from rabbits evaporates faster than the water in the feces. The red cross represents the inflection point.

shiny mucus coats the fresh feces from rats, shown in Fig. 7(C). Since the mucus coats the feces, it must evaporate first before the water in the feces evaporates. We record the inflection point of the mass change at which the evaporation rate changes, which indicates that the mucus has disappeared. This inflection point is marked in Fig. 7(D), showing the time course of the mass of feces from rabbits. At this point, feces lose their sheen, consistent with the loss of mucus. Assuming a cylinder of feces of diameter D and length L_{piece}, the surface area of feces is $A = \pi D L_{piece} + \pi D^2/2$. We also assume that the mucus has the density ρ of water. Thus, thickness h is written as $h = \Delta M/\rho A$, where ΔM is the mass evaporated at the inflection point.

Fig. 7(B) shows the relationship between body size and mucus thickness, measured by our evaporation method. From mice and rats to rabbits, mucus thickness remains isometric with body size: $h = 13.75 M^{0.27}$ μm ($N = 5$). The isometric thickness of mucus appears to be a universal feature in the body, as shown by the exponent of near one-third. Pleural liquid,[45] which lubricates the space between visceral and parietal lung tissues, has nearly isometric thickness: $12.6 M^{0.2}$ μm. For comparison, we also provide previous measurements of mucus thickness in the stomach and the rectum. Gastric mucus has a thickness of $233.6 M^{0.21}$ μm, which is 17 times as thick as fecal mucus, but it follows the same isometric trend.[46,47]

2.5 Viscosity of mucus

We report the previously measured rheology of gastrointestinal mucus from pigs and humans.[48–52] Mucus is a shear-thinning power-law fluid with viscosity comparable to that of water (10^{-3} Pa s) at high shear rates.[44] Its viscosity changes with the shear rate according to

$$\eta_{mucus} = K_m \dot{\gamma}^{n_m - 1}, \tag{4}$$

where η_{mucus} is the apparent viscosity of mucus, exponent n_m is the flow behavior index of mucus, pre-factor K_m is the flow consistency index of mucus, and $\dot{\gamma}$ is the shear rate. The apparent viscosity of mucus is independent of the tested species, including humans and pigs, as shown by the low variation in the flow behavior index and the flow consistency index ($n_m = 0.25 \pm 0.25$ and $K_m = 5.06 \pm 3.88$, $N = 5$). Even measurements from the various glands show that both flow behavior index n_m and flow consistency index K_m vary only slightly.[44] The reported gastrointestinal mucus falls within these ranges, shown in Fig. 6(A)–(C). Therefore, we use values $n_m = 0.25$ and $K_m = 5.06$ Pa s$^{0.25}$ for our calculations.

Defecation involves feces and mucus, which are both shear-thinning. However, mucus is one-third as viscous as feces. Since this inequality holds for all shear rates, we safely neglect the flow of feces during defecation. In other words, feces act

like a solid plug, and the only flowing liquid is mucus. The solidity of the flowing mucus during applied forces is shown rigorously in the Methods section, in which we calculate the velocity profile in a two-layer concentric flow composed of power-law fluids. Based on the values of dimensionless groups, we conclude that flow of feces is negligible. Now that we have characterized the geometry of the rectum and the material properties of mucus and feces, we determine the forces that occur between feces and the wall of the large intestine.

2.6 Rectal pressure

Like a tugboat pushing a barge, muscles apply rectal pressure that pushes feces through large intestine. During normal defecation, the minimum rectal pressure, which is estimated in two ways. One is to collect the pressure–volume profile of the large intestine measured by balloons. Researchers insert a balloon into the large intestine and then measure the rectal pressure while inflating the balloon. The measurement provides the pressure–volume profile that illustrates the rectal pressure as a function of the balloon volume. The minimum rectal pressure is the corresponding pressure for the balloon volume equal to one fecal piece $V = \pi D^2 L_{\text{piece}}/4$ from the reported pressure–volume profiles.[53,54] We also estimate the minimum rectal pressure from the minimal distending pressure, which is the minimal pressure that animals can perceive.[55–57] Fig. 8 shows the relationship between body mass and minimum rectal pressure P_{min}. The minimum rectal pressure, given by the blue points, remains relatively constant across two orders of magnitude in body mass: $P_{\text{min}} = 0.64 \pm 0.3$ kPa ($N = 5$). The magnitude of minimum rectal pressure is less than the elastic modulus of feces from possums (2 kPa)[34] and sheep (10 kPa).[58] Thus, rectal pressure during normal defecation is insufficient to deform feces. The constancy of minimum rectal pressure (0.64 kPa) is consistent with other systems in the body such as the urinary system with a constant pressure of 5.2 kPa for mammals from a

mouse to a human[59] and the respiratory system with a pressure of 10 kPa for animals from a mosquito to an elephant.[60]

For comparison, we also plot the maximum rectal pressure P_{max} from previous studies.[61–75] The maximum rectal pressure is about seven times as high as the minimum. The body likely employs such pressure when feces are dry or when the mucus layer is either absent or thin. For our mathematical model, we assume our defecation videos represent normal behavior and thus use minimum rectal pressure.

2.7 Mathematical model of defecation

We present a mathematical model for defecation. Our system consists of a pipe whose length consists of the rectum and the colon, illustrated in Fig. 2. We model cylindrical feces of diameter D and total length L, consisting of several pieces joined like sausages. The walls of the cylinder are coated with a mucus layer of thickness h, which is considerably less than D. We parameterize the motion of feces and mucus using cylindrical coordinates (r,θ,z), in which z represents the horizontal direction along the cylinder and r the radial direction from the center of the feces to the walls. Since our system is axisymmetric, we neglect azimuthal coordinate θ. Our observations of steady-state defecation indicate that the flow is fully developed in the z direction.

We first discuss the possibility of gravitational force as the driving force. Rectal pressure across mammals is equivalent to the height of water $H_{\text{rectal}} = P_{\text{min}}/\rho g$, which is about 6.5 cm. Unlike humans, most animals defecate horizontally. Thus, animals with a rectal diameter comparable to the height experience gravitational force on feces. Since the density of carnivore feces can exceed that of water by 1.5, the equivalent diameter at which gravitational force becomes the driving force is 4.3 cm, which corresponds to a 100 kg animal such as a lion. However, since gravitational forces depend on the body posture during defecation, we do not include gravity in our model.

Defecation begins when the smooth muscles of the intestine apply pressure P_{min} to the end of feces. The shear stress at the wall is the ratio of the driving force on the cylinder, $\pi D^2 P_{\text{min}}/4$, to the wall surface area, πDL. The resulting shear stress is

$$\tau = \frac{DP_{\text{min}}}{4L}. \tag{5}$$

Since the mucus is thin, we assume that the stress remains constant across the thickness of the mucus. In the mucus layer, we derive the velocity field as Couette flow by assuming a no-slip boundary condition on both feces and the wall of the intestine. The shear rate in the mucus layer is

$$\dot{\gamma} \approx U/h, \tag{6}$$

where U is the steady velocity of fecal flow. Using the definition of apparent viscosity, $\tau = \eta_{\text{mucus}} \dot{\gamma}^{-1}$, and the rheology of mucus from eqn (4), $\eta_{\text{mucus}} = K_m \dot{\gamma}^{n_m-1}$, we combine eqn (5) and (6) to derive the fecal velocity in terms of the rectal pressure,

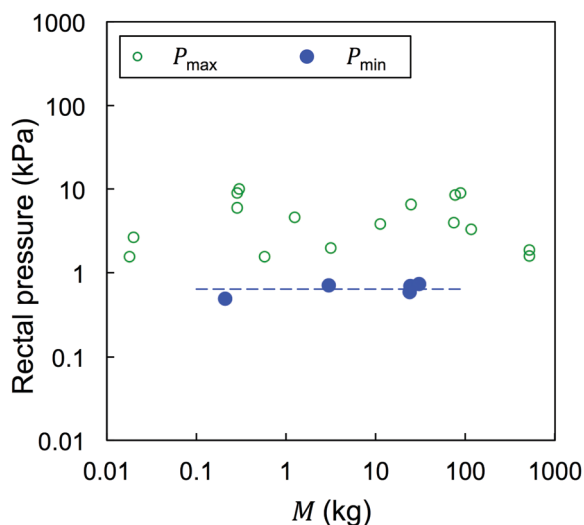$$U = h\left(\frac{DP_{\text{min}}}{4LK_m}\right)^{\frac{1}{n_m}}. \tag{7}$$

Fig. 8 The relationship between body mass M and rectal pressures, including minimum rectal pressure P_{min} and maximum rectal pressure P_{max}.

Defecation time is determined by the ratio of the fecal length to the fecal velocity, $T \sim L/U$:

$$T = \frac{L}{h}\left(\frac{4LK_m}{DP_{min}}\right)^{\frac{1}{n_m}}. \qquad (8)$$

Eqn (8) provides the time of defecation as a function of the geometry of the feces, applied pressure, and the non-Newtonian properties of the mucus layer. Our measurements in the previous sections indicate the isometry of the system; that is, the total length of feces L, the diameter of feces D, and the thickness of mucus h each scale with $M^{1/3}$. Moreover, rectal pressure, P_{min}, and the properties of mucus, n_m and K_m, are independent of body mass. Isometric scaling in eqn (7) yields fecal velocity $U \sim M^{1/3}$, consistent with our experiments. Moreover, eqn (8) shows that defecation time T is invariant with body size: $T \sim M^0$. The predicted and measured scaling exponents closely agree (0 and −0.09, respectively). Therefore, we conclude that our scaling has captured the observed invariance in the defecation time.

We go beyond simple scaling by substituting eqn (1) and the measured allometric relationships into eqn (8). From Sections 2.5 and 2.6, rectal pressure is $P_{min} = 0.64$ kPa, and the properties of mucus are $n_m = 0.25$ and $K_m = 5.06$ Pa s$^{0.25}$. With the best fits of the variables, including L_{piece}, D, and h from Table 1, the prediction of duration is $123.7M^{-0.4}$ s, which does not match the time invariance of 12 seconds from the experiment. Instead of best fits, we apply isometric fits to the geometric variables ($L_{piece} = 3.16M^{1/3}$ cm, $D = 1.11M^{1/3}$ cm, and $h = 15.1M^{1/3}$ μm) and determine that the predicted numerical defecation time is 5.6 seconds. This prediction captures the general trend as represented by a solid line in Fig. 1(G).

We underpredict the defecation time by a factor of two. The difference likely results from the sensitivity of eqn (8) to the thickness of the mucus layer. Specifically, we may have underestimated the mucus thickness using our experimental method since mucus remains attached to the walls during defecation. Previous studies indicate that the thickness of mucus in the rectums of fasted animals is at least triple that of mucus on the surface of the feces we measured. However, the thicker layer of mucus decreases the predicted defecation time from 5.6 to 1.9 seconds, which is even faster than the observed time of 12 seconds.

Eqn (8) also shows the inherent difficulties of predicting defecation time because of the non-Newtonian nature of the mucus. Specifically, if a small fractional error, ε, occurs in each of the geometric variables and material properties, the resulting error in defecation time ε_T is amplified by error propagation. We show details of this calculation in the Methods section. According to eqn (19), amplified error ε_T depends on the flow behavior index of mucus n_m. With $n_m = 0.25$, the error in defecation time is 8.7 times as great as that in each variable, $|\varepsilon_T| = 8.7|\varepsilon|$. Such variability in time is also consistent with the defecation time observed in experiments, in which the standard deviation is equal to half of the average.

2.8 Diarrhea and constipation

We use our model to predict defecation times for various problems with the digestive system, such as diarrhea and constipation. Diarrhea occurs so quickly that steady state is not reached. Newton's first law indicates that rectal pressure drives feces of mass $\rho \pi D^2 L/4$ at acceleration a, $\pi D^2 P_{min}/4 = \rho a \pi D^2 L/4$, where D is the diameter of feces. We assume that the density of diarrhea, ρ, is the same as that of water. The diarrhea accelerates with zero initial velocity and travels a distance of L before exiting from the body. Writing the acceleration as $a = L/2T_{diarrhea}^2$, the duration of diarrheal defecation is

$$T_{diarrhea} = \sqrt{\frac{2\rho}{P_{min}}}L \qquad (9)$$

We substitute the variables in the above equation, including rectal pressure (0.64 kPa), the isometric fits of L_{piece} from Table 1, the density of water (1 g mL^{-1}), and those from eqn (1) into eqn (9). The time of diarrheal defecation is $0.16M^{0.25}$ s, and for a 70 kg human, it is 0.5 seconds, or nearly instantaneous. Since gravity alone can expel the diarrhea, applied pressure is optional.

In constipation, feces are hard and dry, and we assume that feces absorb the mucus layer onto the intestinal wall. Mucus is also severely altered and reduced in the inflammatory states of the colon and during active infections from the bacteria *Clostridium difficile*, an increasingly common intestinal disease in health care.[76,77] If a mucus layer is absent during constipation, the large intestine applies shear throughout the entire feces: $\dot{\gamma} \approx U/D$. Similar to the time mentioned in Section 2.7, the $\dot{\gamma}$ of defecation is

$$T_{constipation} = C\frac{L}{D}\left(\frac{4LK_f}{DP_{min}}\right)^{\frac{1}{n_f}}, \qquad (10)$$

where $C = 6/n_f + 2/n_f^2$, a constant derived in the Methods section. We substitute the properties of the stiffest feces from humans,[35] $(n_f, K_f) = (0.42, 3117)$, rectal pressure (0.64 kPa), the isometric fits of L_{piece} and D from Table 1, and those from eqn (1) into eqn (10). The defecation time for the stiffest feces without mucus is 10^7 seconds, or 524 days. If a human applies maximum rectal pressure (4.7 kPa) to squeeze the stiffest feces without mucus, the defecation time decreases to six hours. Because these times do not account for the deformation of the intestinal wall, they are likely overestimated. Nevertheless, our results show that mucus is critical for lubricating the large intestine so that feces are released in a timely manner.

3 Discussion

We provide two reasons to explain why defecation time remains constant around 12 seconds. One is the constancy of pressure across animals, and the other the consistency of the aspect ratio of fecal pieces, which is about five. This consistency of applied pressure, geometry, and properties of the mucus leads to a relative constancy in defecation time. The main thrust of our work is eqn (8), which yields the time for defecation. As shown by the structure of the equation and the underlying physics, the time of defecation is highly sensitive to the thickness and the properties of the mucus layer as well as small variations in the size of the system. Our results suggest that a

short defecation time plays a crucial role in the evolution of the dimensions of the digestive tract and the excretion of mucus.

4 Conclusion

We conduct a fluid mechanics study of feces that unifies 29 studies pertaining to feces and the anatomy of the digestive tract. We discover that feces are stored in not only the rectum but also the colon. We also conduct defecation experiments on 43 species. Results of experiments show that although the amount of feces is proportional to body size, all mammals defecate within a constant duration because of mucus coating the walls of the large intestine. Large animals have thicker layers of mucus, which facilitates defecation and contributes to a faster speed of defecation. This mechanism is the basis of our mathematical model, which incorporates the non-Newtonian properties of both feces and mucus. We hope that this work inspires further quantitative investigation into physiological processes in the body.

5 Methods

5.1 Animal preparation, fecal sample collection, and filming

We use a Canon 50D, a Canon SX160, and an iPhone 6 to film animals defecating at Zoo Atlanta and a local park. The number of animals and their locations appear in the ESI.† We use Tracker, an open-source software that measures the time course of the tip of each fecal piece before it detaches from the animal. We collect feces at Zoo Atlanta, local farms, and animal facilities at Georgia Tech.

5.2 Density and viscosity measurements

We store feces in a freezer. To measure their densities, we defrost them to room temperature, measure their mass M in a spoon with volume V of 5 mL. The density is calculated by $\rho = M/V$. We measure the viscosity of feces using a cone-on-plate rheometer (Anton Paar MCR 501), a high-precision device for measuring material properties. The Zoo Atlanta staff measure the body mass of animals using an analytical balance or recall it from the most recent annual veterinary exam.

5.3 Generalized mathematical model of defecation

We present a generalized mathematical model of defecation, incorporating the viscosity of both mucus and feces. Fig. 2 illustrates a cylindrical plug of feces surrounded by mucus. The velocity profile of the two layer flow is $\vec{V} = V_z(r)\hat{z}$. Feces have viscosity $\eta_{\text{feces}} = K_f(dV_z/dr)^{n_f-1}$ and fill the large intestine from $r = 0$ to $r = D/2$. In the outer layer, the mucus gel has a thickness of h with viscosity $\eta_{\text{mucus}} = K_m(dV_z/dr)^{n_m-1}$ in the region $r = D/2$ to $r = h + D/2$. We apply the Cauchy momentum equation, which represents the balance of linear momentum in the flow. Each term in eqn (11) represents a force per unit volume at a given location,

$$\rho \frac{D\vec{V}}{Dt} = \rho\vec{g} - \nabla p + \nabla \cdot \vec{\tau}. \tag{11}$$

The hydrostatic pressure is negligible. The external pressure gradient from the large intestine, ∇p, drives the flow, which viscous dissipation $\nabla \cdot \vec{\tau}$ resists. We write all terms in cylindrical coordinates and simplify eqn (11) in the z direction by assuming steady-state flow,

$$\frac{dP}{dz} = \frac{1}{r}\frac{d}{dr}(r\tau). \tag{12}$$

Shear stress in a power-law fluid is defined as $\tau = K(dV_z/dr)^n$, where K is the flow consistency index, and n is the flow behavior index. We apply a no-slip boundary condition on the wall, $V_z(h + D/2) = 0$, and at the interface, $V_z(D/2)|_{\text{inner}} = V_z(D/2)|_{\text{outer}}$. The shear stress is continuous at the interface, $\tau(D/2)|_{\text{inner}} = \tau(D/2)|_{\text{outer}}$, and symmetric at the center of the flow, $\tau(0) = 0$. We solve the velocity profile of the flow in both layers. The velocity profile in the inner layer is

$$V_z(0 < r < D/2) = \left(\frac{1}{2K_f}\frac{dP}{dz}\right)^{\frac{1}{n_f}}\frac{n_f}{1 + n_f}\left(r^{\frac{1+n_f}{n_f}} - \left(\frac{D}{2}\right)^{\frac{1+n_f}{n_f}}\right)$$
$$+ V_z(D/2). \tag{13}$$

The velocity profile in the outer layer is

$$V_z(D/2 \leq r < h + D/2)$$
$$= \left(\frac{1}{2K_m}\frac{dP}{dz}\right)^{\frac{1}{n_m}}\frac{n_m}{1 + n_m}\left(r^{\frac{1+n_m}{n_m}} - \left(h + \frac{D}{2}\right)^{\frac{1+n_m}{n_m}}\right). \tag{14}$$

The thickness of mucus is considerably less than the diameter of feces, $h/D \ll 1$. Thus, the flow rate is mainly determined by the inner fecal flow, $Q \approx \int_{r=0}^{r=D/2} V_z \cdot 2\pi r dr$. The average speed of the flow U is written as the ratio of the flow rate to the cross-sectional area: $U \approx 4Q/\pi D^2$. We approximate the pressure gradient as the total pressure drop among the cylinder, $-dP/dz \approx P_{\min}/L$. Thus,

$$U = \frac{n_f}{2 + 6n_f}D\left(\frac{P_{\min}D}{4LK_f}\right)^{\frac{1}{n_f}} + h\left(\frac{P_{\min}D}{4LK_m}\right)^{\frac{1}{n_m}}. \tag{15}$$

To determine the relative magnitude of the two terms in eqn (15), we perform dimensionless analysis. The six dimensionless groups are flow behavior indices n_f and n_m, consistency index ratio Co, pressure ratio Pr, the aspect ratio of feces As $= L/D$, and the thickness ratio of mucus Mu $= h/D$. Consistency index ratio Co and pressure ratio Pr are defined as

$$\text{Co} = \frac{K_f}{K_m}\left(\frac{U}{D}\right)^{n_f - n_m}, \quad \text{Pr} = \frac{P_{\min}}{K_m}\left(\frac{U}{D}\right)^{-n_m}. \tag{16}$$

Using the dimensionless groups, we non-dimensionalize eqn (15) to

$$1 = \frac{n_f}{2 + 6n_f}\left(\frac{\text{Pr}}{4\text{AsCo}}\right)^{\frac{1}{n_f}} + \text{Mu}\left(\frac{\text{Pr}}{4\text{As}}\right)^{\frac{1}{n_m}}. \tag{17}$$

Fig. 9 shows the values of the dimensionless groups based on both the geometry of the large intestine and feces and the
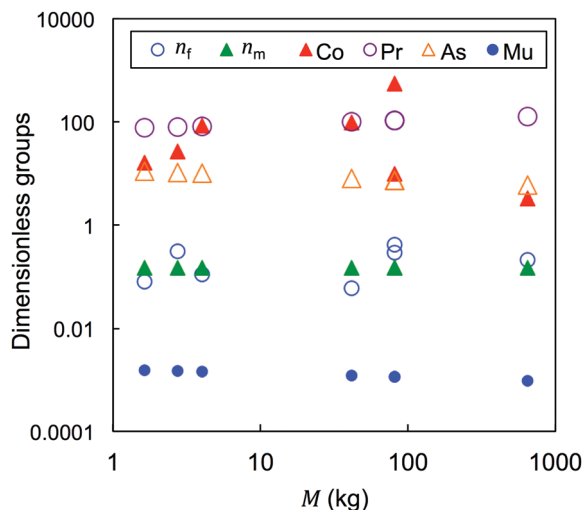
Fig. 9 The relationship between body mass M and the dimensionless groups n_f, n_m, Co, Pr, As, and Mu.

rheology of feces and mucus. Five of the six dimensionless groups remain consistent with body mass across three orders of magnitude, including $n_f \sim 10^{-1}$, $n_m \sim 10^{-1}$, $\text{Pr} \sim 10^2$, $\text{As} \sim 10$, and $\text{Mu} \sim 10^3$. The consistency index ratio, Co, is within the range of 1 to 10^3. As a result, the second term determined in eqn (17) dominates, and therefore, the velocity of feces is determined by the fluid properties of mucus. This equation can be simplified to obtain the same expression of fecal velocity in eqn (7), as derived previously.

5.4 Error propagation of defecation time

We calculate the propagating error in defecation time T given in eqn (8). Defecation time is a function of six variables, including the total length of feces L, the diameter of feces D, the thickness of mucus h, rectal pressure P_{min}, the flow behavior index of mucus n_m, and the flow consistency index of mucus K_m. We assume that the variables are uncorrelated. The error for variable X is written as σ_X. We apply the Gaussian error propagation rule on the error in defecation time as follows:[78]

$$\sigma_T^2 = \sigma_L^2 \left(\frac{\partial T}{\partial L}\right)^2 + \sigma_h^2 \left(\frac{\partial T}{\partial h}\right)^2 + \sigma_{K_m}^2 \left(\frac{\partial T}{\partial K_m}\right)^2 + \sigma_D^2 \left(\frac{\partial T}{\partial D}\right)^2$$
$$+ \sigma_{P_{min}}^2 \left(\frac{\partial T}{\partial P_{min}}\right)^2 + \sigma_{n_m}^2 \left(\frac{\partial T}{\partial n_m}\right)^2. \tag{18}$$

We convert all errors σ into fractional errors, $\varepsilon_X = \sigma_X/X$,

$$\varepsilon_T^2 = \left(\frac{n_m + 1}{n_m}\right)^2 \varepsilon_L^2 + \varepsilon_h^2 + \frac{1}{n_m^2}\left(\varepsilon_{K_m}^2 + \varepsilon_D^2 + \varepsilon_{P_{min}}^2\right)$$
$$+ (\ln n_m)^2 \varepsilon_{n_m}^2. \tag{19}$$

We assume that all fractional errors are the same, $\varepsilon_L = \varepsilon_h = \varepsilon_{K_m} = \varepsilon_D = \varepsilon_P = \varepsilon_{n_m} = \varepsilon$. With the flow behavior index of mucus in the Results section ($n_m = 0.25$), the fractional error in the duration of defecation propagates 8.7 times, $|\varepsilon_T| = 8.7|\varepsilon|$.

Acknowledgements

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