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Natural Frequencies in Sexual Pelvic Thrusting

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Synopsis Seventy percent of mammals copulate using repeated pelvic thrusting, while the transfer of sperm requires just a single intromission. Why did thrusting evolve to be the dominant form of sexual intercourse? In this study, we investigate how the rate of sexual pelvic thrusting changes with body size. By analyzing films of copulating mammals, from mice *Mus musculus* to elephants *Elephantidae*, we find that bigger animals thrust slower. The rate of pelvic thrusting decreases from 6 Hz for the pocket mouse *Pergonathus* to 1.3–1.8 Hz for humans to an absence of thrusting for the rhino *Rhinocerotidae* and elephant *Elephantidae* families. To understand this dependence on body size, we consider the spring-like behavior of the legs, which is associated with the elasticity of the body's muscles, tendons, and ligaments. For both running and thrusting, greater displacment and energy savings can be achieved if the system is oscillated at its resonant or natural frequency. Resonant frequencies, as measured through previous studies of running in dogs *Canis familiaris* and horses *Equus ferus caballus*, show good agreement with sexual thrusting frequencies. Running and sexual thrusting have nothing in common from a behavioral perspective, but from a physical perspective, they are both constrained by the same musculoskeletal systems, and both take advantage of resonance. Our findings may provide improved treatments for human sexual dysfunction as well as improving breeding strategies for domestic mammals.

Introduction

Elvis Presley's hip gyration and pelvic thrusting were once considered so sexually suggestive that in August 1956, he was ordered to stop by a Florida Juvenile Court Judge (Jorgensen and Guralnick 1999). While sexual pelvic thrusting may have crossed the line for some, it is the dominant form of sexual intercourse for mammals (Dewsbury 1972). Much of the difficulty in studying copulation is its elusive nature; mammals often copulate hastily or secretly to escape predation or inter-species competition (Campbell 2006). Nevertheless, there has been much interest in the neural underpinnings of copulation (Georgiadis et al. 2012; Yin and Lin 2023), with the hopes of using this easily replicable behavior to understand the brain. Sexual dysfunction is highly prevalent in humans, affecting 43% of women and 31% of men, indicating the need for multiple approaches to understand sexual behavior (Rosen 2000). By studying sex in fellow mammals, we may shed light on our own species.

With a cornucopia of penis shapes and sizes, mammal species exhibit an equally dazzling array of copulation patterns. In 1972, Dewsbury identified four canonical copulatory patterns: locking, thrusting, multiple intromissions, and multiple ejaculations (Dewsbury 1972). Given the possibility of each of these four independent sexual patterns, Dewsbury stated that 2^4, or 16, unique patterns of copulation are possible. He proposed that the variety in patterns seen across species could serve to prevent closely related species from wasting their energy trying to mate. While homosexual mounting and thrusting is common among mammals (Dagg 1984; Leca et al. 2015), due to a lack of quantitative data on thrusting frequencies, we focus here on het-

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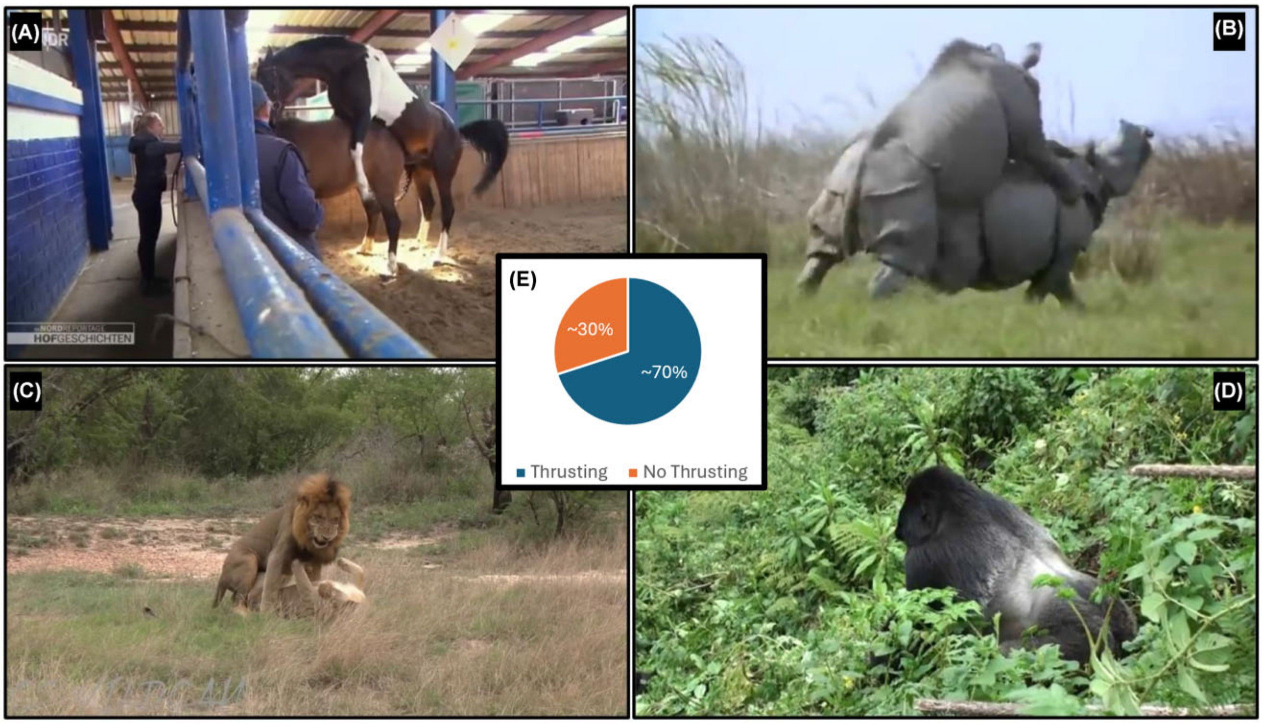

Fig. 1 Copulation in nature and in captivity. (A) Horse *Equus ferus caballus*, courtesy of NDR Hofgeschichten, (B) Rhino *Rhinocerotidae* courtesy of Nature Bites, (C) Lion *Panthera leo persica*, courtesy of CS-WILDCAM, (D) Gorilla *Gorilla beringei beringei*, courtesy of Ian Redmond. (E) Proportion of mammals that exhibit thrusting during copulation.

erosexual thrusting. In our work, we cannot tell if heterosexual thrusting is initiated or maintained by the female or the male. In any case, the penis enters the vagina in a repeated fashion. Approximately 70% of mammal species use pelvic thrusting during copulation (Dewsbury 1972) (Fig. 1). Why is thrusting so prevalent among mammals? Since thrusting is a clearly observable behavior, we use it as an entry point to begin unraveling the complex mechanics of copulation.

Depending on the duration and intensity, pelvic thrusting may incur significant metabolic cost. In a study of young healthy human adult couples having sex, men used 101 kCal or 4.2 kCal/min and women used 69.1 kCal or 3.1 kCal/min, a metabolic expenditure between walking and jogging (Frappier et al. 2013). Given that the average sexual activity lasted for 24 ± 12 min, the authors concluded that "sexual activity may potentially be considered, at times, as a significant exercise." In the extreme are mammals that perform suicidal sex, such as the marsupial mouse, *Antechinus* (Fisher et al. 2013). The male mouse seeks intercourse with females over a 3-week period, accumulating corticosteroids in his blood to such a high level that his immune systems shut down and most males die by the end of the mating period. Similarly, female lions are receptive to mating for 3–4 days during their reproductive cycle; during this time, they may mate every 20–30 min, with up to 50 copulations per day (Kays 2025). At least in these sex marathoners, we expect energetically efficient thrusting strategies to have evolved.

Thrusting may help create physiological changes in the female to increase the chance of pregnancy. Studies into cervical stimulation in rats found that artificial insemination without cervical stimulation did not produce any pregnancies, while the addition of cervical stimulation led to an 80% pregnancy rate (Terkel et al. 1990). Some mammals like cats and rabbits are induced ovulators, which means that physical contact such as thrusting is necessary for the females to induce ovulation (Wildt 1991). At least in mice *Mus musculus*, paternal behavior changes profoundly a few weeks after intercourse from feeding on pups to caring for pups (Lonstein and De Vries 2000). Thrusting may be the trigger for the paternal biological clock. Certainly, thrusting serves to generate the stimulation required for male ejaculation. Penile spines are keratinized structures that protrude from the penis tactile receptors (Dixson 1991). Dixson finds that the removal of these structures from the common marmoset *Callithrix jacchus*, inhibiting the ability of the male to feel friction, significantly increases the amount of time necessary to achieve ejaculation. Lastly, thrusting may play a similar role to multiple intromissions, to "prepare the females vagina for a deep penile insertion to produce a tight

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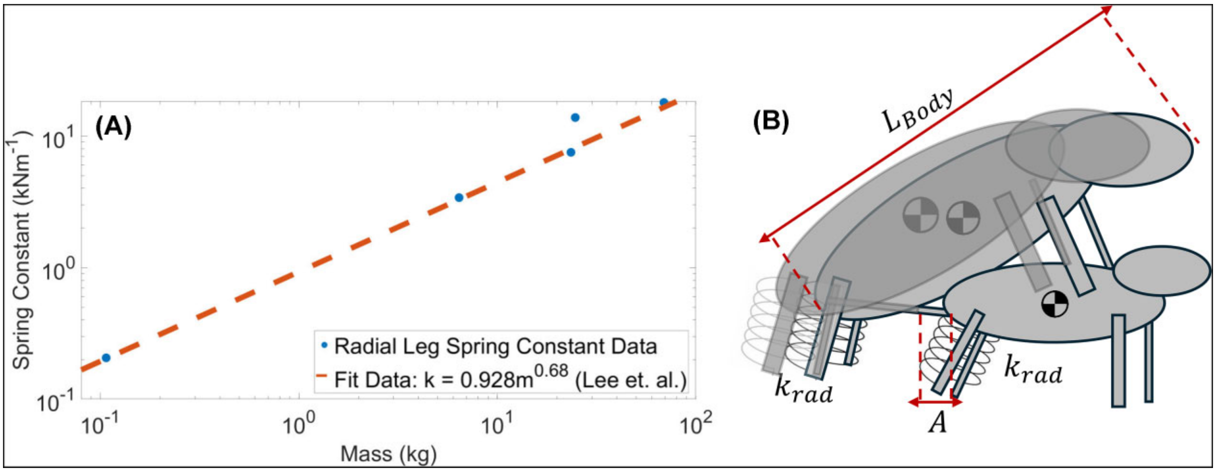

Fig. 2 (A) Relationship of radial leg spring constant k_{rad} with body mass. Data reprinted from Lee et. al. (Lee et al. 2014). (B) Schematic of mating animals, where k_{rad} represents the radial spring constant, A is the amplitude of thrusting, and L_{Body} is the body length of the male.

seminal plug against the cervix that will facilitate sperm transport to the uterus" (Paredes and Vazquez 1999).

For both males and females, thrusting involves coordinated motion of the rear and hind appendages to generate the forward thrusting and the return phase. The muscles that drive thrusting also drive legged locomotion like walking and running. Thus, to understand the biomechanical constraints on thrusting, we turn to studies of legged locomotion. An important theme of studies of legged locomotion in the 1980′s was the analogy of running as a bouncing ball and thus representing the tendons and muscles of the legs as a single effective spring with spring constant k (Fig. 2). This analogy, called the "virtual pendulum" (Maus et al. 2010), was first proposed by tracking the center of mass of the body during walking and running. As animals walk or run, their center of mass bounces up and down. Walking occurs on stiff legs, in which the gravitational and kinetic energy peaks are out of phase. Walking can be modeled by an inverted pendulum with no spring. In contrast, running is compliant: low gravitational energy is in phase with low kinetic energy, similar to a ball bouncing against the ground (Cavagna et al. 1988). Thus, a running animal can be modeled as a single mass atop an effective spring representing the legs. Such a tuned mass spring system has an associated natural frequency,

$$f_n = \sqrt{k/m} \qquad (1)$$

Mass-spring systems that oscillate at their natural frequency are said to do so at resonance. Slow running gaits such as trotting have symmetric position profiles and a step frequency that matches the body's natural frequency. Fast running gaits such as hopping have asymmetric profiles and step frequencies lower than the natural frequency (Cavagna et al. 1988).

Since the advent of automated tracking and improved force platforms, the body's effective spring constant has been measured for dogs *Canis familiaris,* goats *Capra aegagrus hircus,* horses *Equus ferus caballus*, and red kangaroos *Osphranter rufus*. In 1993, Farley et al. created a model for the legs where bones are linkages and muscles, tendons, and ligaments are springs (Farley et al. 1993). Animals ran across force platforms with strain gauges attached to either the ground or the treadmill. The spring constant k for the leg was calculated using Hooke's Law: $F = k\Delta x$ where F is the peak force and Δx is the peak displacement of the leg-spring. Spring constants were found to be constant across animal speed: higher speeds resulted in greater deflection of the spring and thus greater force. Higher body masses result in lower stride frequencies. In 2014, Lee et al. studied the kangaroo rat *Dipodomys*, tammar wallaby *Notamacropus eugenii*, dog *Canis familiaris*, goat *Capra aegagrus hircus*, and human during bouncing gaits which include hopping, trotting, and running (Lee et al. 2014). While Farley et al.'s work modeled the entire body as an effective spring, Lee considered a more accurate radial spring constant k_{rad} associated with an extensible strut between the hip and the ground. Lee found the radial spring constant to be

$$k_{rad} = 0.928m^{0.68} \qquad (2)$$

where the spring constant k_{rad} is in N/m and body mass m is in kg (Fig. 2).

In this study, we hypothesize that sexual pelvic thrusting occurs at the same resonant frequencies as "bouncing gaits" such as running. We propose this hypothesis because saving energy may be important for many animals, including humans, whose copulation may be considered as "significant exercise" (Frappier et al. 2013) and animals with prolonged copulation or performing

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suicidal sex. Secondly, sexual pelvic thrusting involves the same leg muscles as used in running, so it makes sense that they may involve the same resonant frequencies. Our approach to determine thrusting frequencies involves both experiments with mice and literature review.

Methods

Video footage of mice *Mus musculus* copulation was gathered in a lab environment at NYU and Westlake University (Yin et al. 2022). For videos filmed from the sides of a cage, two mice *Mus musculus* were placed in an acrylic box together with bedding and allowed to move freely. Cameras (Basler acA640-120gc or Daheng Imaging MER-131-75GM-P NIR) recorded at 25 fps across time periods of 30 min to 1 h. The footage was shot in a semi-dark room with infrared lighting. For videos filmed from the bottom of the cage, lighting conditions were standard room light and all bedding was removed. The cage was then elevated 3 feet above the table, where a camera filmed from below.

Literature review was performed across the month of June in 2024. Literature was searched for using Google Scholar, while videos of animals were searched for directly in the YouTube search algorithm or through the Google search algorithm. Search terms used include but are not limited to thrusting, humping, sex, copulation, and reproduction, along with the common name of the animal being searched for. No filters were used while searching. For a video to be included in this study, the pelvic region had to be clearly visible for at least 10 s. This provided enough time to extract an averaged thrusting frequency. Sources were searched separately by two different researchers and screened independently. Data extracted included any quantity related to copulation that could be found, such as thrusting frequency and copulation duration. We used reported data from literature first. All other data extracted from videos was taken because the data for the specific animal in question did not exist or the methodology for the data was lacking, such as failing to specify whether the frequency reported was pre-intromission or post-intromission. Although this paper is not a systematic review, we include a PRISMA checklist and flowchart that follows the data extraction procedure.

Using the aggregated video dataset (Contreras and Agmo 1993; Angelica Lucio et al. 2022; Agmo and Morali 2022), we extracted the thrusting frequencies by importing them into the free motion analysis software, Tracker. Sequences were marked where the thrusting motion was visible for at least 10 consecutive thrusts. When possible, videos were analyzed to separate pre-intromission thrusting from post-intromission thrusting. Pre-intromission thrusting, characterized by rapid, shallow movements, was measured during the period before intromission. Post-intromission thrusting, which typically involves slower, deeper movements, was measured during the period following intromission. Using Tracker, each selected video was analyzed by hand, frame by frame, selecting a singular point of reference for each animal. The point of reference for the body motion was usually the tip of the buttocks for males and the top of the sternum for females.

In both the literature sources reviewed and the videos analyzed for thrusting frequency, explicit data on the mass of the animals involved was not consistently provided. To address this gap, average body mass values were obtained from literature sources. These mass values were assumed to represent typical adult body masses for each respective species (See Supplemental Fig. 1).

Data on copulation duration was exclusively sourced from Brennan and Orbach (Brennan and Orbach 2020b). For each species, if a range of copulation duration was reported, the median value was taken as the representative copulation duration. Once again, average body mass was assumed to be representative for each species and was sourced from literature (See Supplemental Fig. 2).

Results

Mouse *Mus musculus* courtship lasts an hour, beginning with sniffing and chasing. When mounting was identified, we segmented 7-s video sequences where there were clear views from the side or underneath. Mice *Mus musculus* exhibited a faster thrusting pre-intromission of at least 12 Hz (measured by counting thrusts within a set time and neglecting aliasing) and a slower thrusting post- intromission of 1.49 Hz (measured by fast Fourier transformation [FFT]). Since pre-intromission thrusting could only be seen from the underside view, we henceforth focus on post-intromission thrusting.

Fig. 3 shows the time series of the male (red) and female (blue) horizontal position of the buttocks. Since we did not record the exact body lengths of the mice, we report distance values non-dimensionalized by the body length of the male (snout to vent). Despite initially chaotic regions of male and female movement, there were clearly durations where male and females are synchronized.

The thrusting observed was roughly periodic during the 20-s video interspersed by 2–3 s rest pauses (see Supplemental for a Zenodo link to all videos used). Such pausing is common across the entire period of intercourse. To determine the thrusting frequencies, we used an FFT taken across the entire 20-s period of thrusting.

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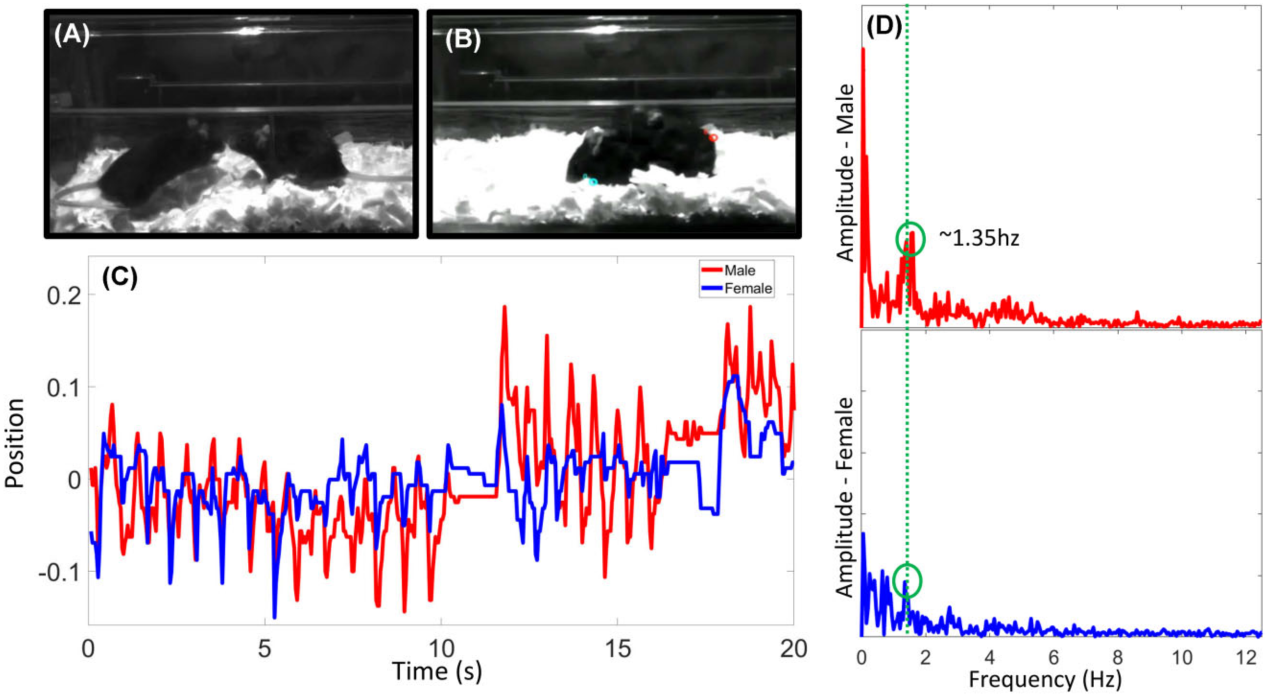

Fig. 3 Copulation of mice from the side view, filmed in the dark with an IR camera. (A) Mice sniffing each other before copulation. (B) Copulation. The blue and red dots highlight the female and male, respectively, to track their positions. (C) Time course of body position scaled by male body length with male in red and female in blue. Position is given in the y-axis or vertical. (D) Fast Fourier transformations for the male and female position from part B. Both tracks exhibit frequency peaks at approximately 1.35 Hz, indicating synchrony.

Since we were interested in periodic behavior, the FFT breaks down the body position of the mice into a sum of sinusoidal functions of arbitrary frequency. By analyzing the FFT for peaks, we looked past the noise to identify the dominant thrusting frequency. The frame rate of the video was 25 fps, indicating that the maximum frequency that could provide meaningful insight, the Nyquist frequency, was 12.5 Hz. Thus, we disregarded frequencies above this range. Frequencies below 0.2 Hz were also disregarded as they were influenced by periods of pausing and the duration of the video. Based on the FFT, the dominant thrusting frequency for males was 1.39 Hz and for females was 1.34 Hz. The closeness of these frequencies demonstrates synchrony between the pair.

For more accurate tracking of mice *Mus musculus* thrusting, we used films of the mice *Mus musculus* from below, as seen in Fig. 4c, and analyzed oscillatory motion, excluding long pauses. The time course of male body position over 3 s was shown by the blue points for pre-intromission in Fig. 4a and post-intromission in Fig. 4b. Pre-intromission movements were shallow, but the drift due to body movement precludes us performing an FFT. Moreover, pre-intromission frequencies, which we estimated by counting peaks in positional tracks to be around 18 Hz, appeared to be higher than the Nyquist frequency, and would require a higher-speed camera to measure.

Post-intromission thrusting was distinguished by slower, deeper and more methodical movements. From the bottom view, we observed 0.2-s pauses midway in the return phase, which were not apparent in the side views (see the blue points in the return phase in Fig. 4b). Fig. 4c compares the FFT from underside (blue) and side views (orange). Underside views show a male frequency 1.49 Hz close to that of the side view frequency 1.39 Hz. We note the underside view is more accurate because the body motion can be more clearly seen.

To demonstrate how periodic thrusting is, we compared the experimental position of males from below with that of simple harmonic motion, which is that associated with a mass-spring system. The position of the male body may be written

$$x = A \sin\left(2\pi f t\right) \tag{3}$$

where the frequency $f = 1.49$ Hz is taken from the underside view. The amplitude $A = 0.13$ was found by hand and is given in units of body length. The sinusoidal trend from Equation 3 is shown in yellow

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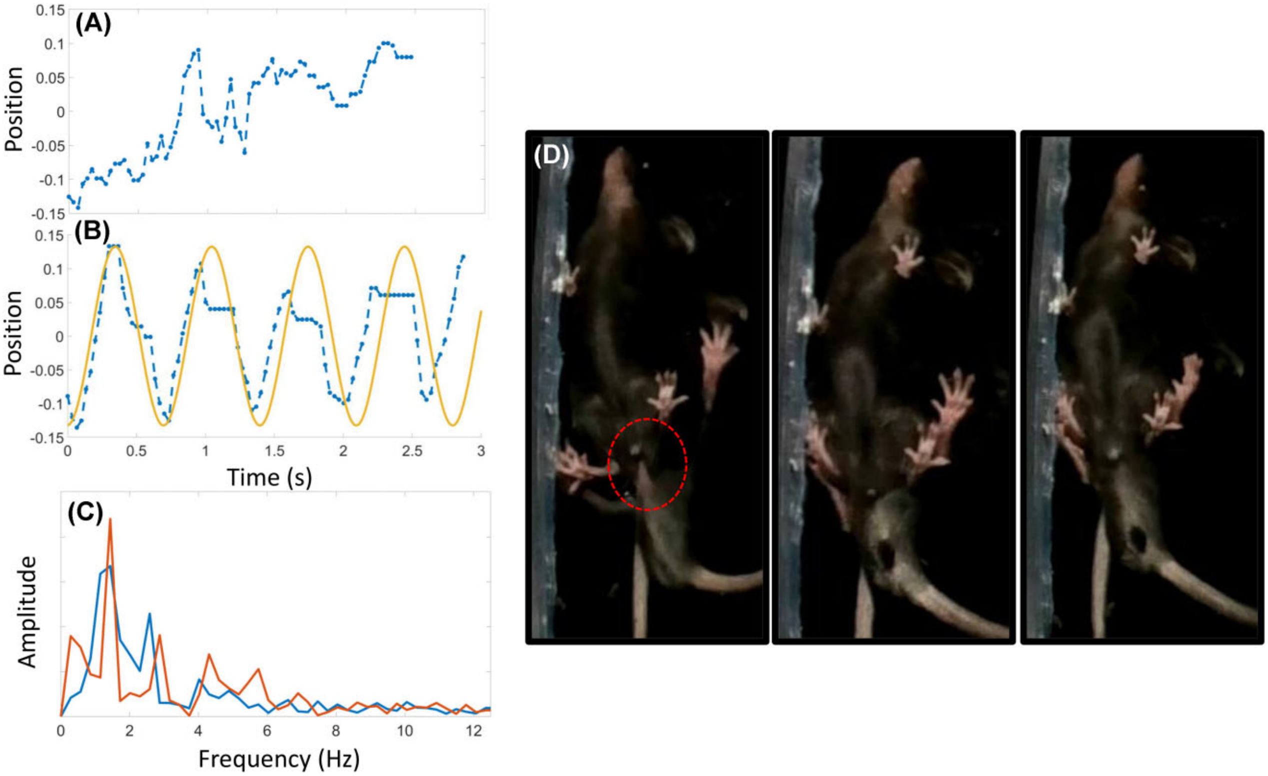

Fig. 4 Copulation of mice from the underside view. (A) Time course of the male position before intromission. (B) Time course of the male position post-intromission, shown in dotted blue. Sinusoidal fit shown in solid yellow. All positions are scaled by male body length. (C) Fast Fourier transformations of part B (blue) and the side view of the mouse (orange) from Fig. 3. (D) Video sequence of mouse copulation from beneath. The penis is highlighted with dashed circle.

in Fig. 4b. The trend fits the first two periods well. However, the next period is shorter, causing a constant phase difference between the fit and the experimental values.

Using our experiments on mice *Mus musculus,* YouTube, and previous literature (Contreras and Agmo 1993; Angelica Lucio et al. 2022; Agmo and Morali 2022), we gathered 12 male mammal thrusting frequencies, from mice *Mus musculus* to elephants *Elephantidae* (see Supplemental for a zenodo link to all videos used). Since videos involved either many thrusts or ended in ejaculation, we assumed the thrust was post-intromission. Fig. 5a shows the relationship between thrusting frequency and body mass. Bigger animals thrust slower. As body mass increased from 20 g to 5200 kg, thrusting frequencies ranged decreased from 6 Hz to 0.71 Hz to no thrusting at all. We noted that some frequencies were an order of magnitude higher than the trends found, and we suspect these data involved pre-intromission frequencies or errors in reporting units. Such data was not included in our analysis but is included in the Supplement.

The orange line shows the power law best fit, f_{fit} and the green line f_{theory} shows the leg's natural frequency from Equation 1 based on virtual spring measurements from Equation 2. All together, the two lines shown in the graph include:

$$f_{fit} = 2.4m^{-0.088}(R^2 = 0.2426) \tag{4}$$

$$f_{theory} = 0.85m^{-0.167}(R^2 = -0.3361) \tag{5}$$

where f is in Hz and m is in kg. While we have no free parameters in our "theory," our theoretical model is based upon empirically measured spring constants from Lee et al., shown in Equation 2, and then substituted to the equation for natural frequency, Equation 1. We proceed by highlighting a few mammals of interest.

Elephants *Elephantidae* performed intromission without repeated thrusting. According to Equation 3, a frequency of $f = 0$ corresponds to the male remaining stationary post-intromission. Other larger animals such as rhinos *Rhinocerotidae* do not thrust consistently across videos. One rhino *Rhinocerotidae* thrust with lateral side-to-side motions rather than anterior-posterior motion most commonly observed in mammals. Thus, we assigned elephants *Elephantidae* and rhinos *Rhinocerotidae* a frequency $f = 0$.

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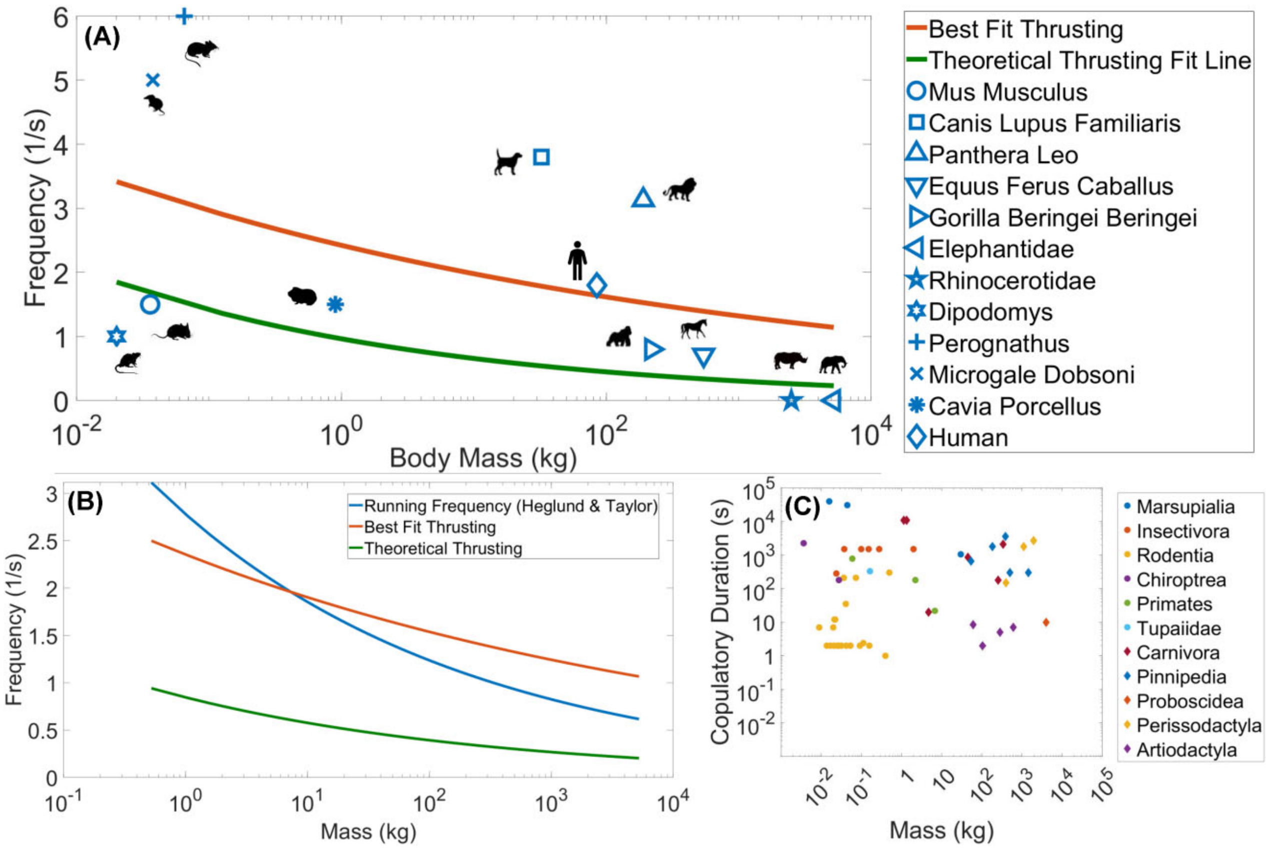

Fig. 5 (A) Relationship between thrusting frequency and body mass. Experimental data points (blue symbols), best fit Equation 4 (solid orange), and theoretical model Equation 5 (solid green). (B) Relationship between body mass and various frequencies, including running step frequency (Heglund and Taylor 1988), given by Equation 6 (blue), experimental thrusting frequency best fit (orange), and theoretical thrusting model (green). (C) Relationship between copulation duration and body mass, reprinted from Brennan and Orbach (Brennan and Orbach 2020b).

Human thrusting frequency has been measured in the context of reducing back pain and injury during intercourse (Sidorkewicz and McGill 2014). Sidorkewicz and McGill performed 3D-tracking of five human sexual postures, including sidelying, missionary 1 and 2 (in which male is propped on straight arms or elbows, respectively) and rear-entry, also known as quadruped 1 and 2 (in which females support themselves on elbows or straight arms, respectively). We neglected sidelying because it was not observed among other mammals. To add to our data set, we consider missionary 1 and quadruped 2 in which are most similar to other mammals. For these postures, the thrusting frequency, or as the authors call it "penetration cycle speed" was 1.4 and 1.8 Hz, respectively, for adult human males of body mass 85 kg. As shown in Fig. 5a, human thrusting frequencies are in the expected values for mammals of the same body mass.

The height of data points above the trendlines indicates animals thrusting abnormally quickly for their body mass. Certain animals like Madagascar's Dobson's shrew tenrec *Nesogale dobsoni*, pocket mouse *Perognathus*, and African lions *Panthera leo* have larger thrusting frequencies than expected. Further research into their mating strategies and their particular spring constants may lead to an understanding for why these animals are so much more energetic than others. Goats for example have abnormally high spring constants for their body size, but the effect on thrusting frequency is unknown (Lee et al. 2014). If the body moves at its natural frequency, less extra energy is expended per unit time. Thus, we expect animals that have thrusting frequencies comparable to the theoretical frequency, to conserve the most energy per unit time. We surmise that animals that thrust faster ($f > 2$ Hz) or slower ($f < 0.2$ Hz) than natural frequencies would expend more energy per unit time, in analogy with the U-shaped curves for power use for walking and running quadrupeds outside their natural pace.

In Fig. 5b, we compared the frequency scalings for pelvic thrusting experiments (orange), thrusting theory (green), and running frequencies (blue). Both thrusting and running use similar muscular groups, and thus should have comparable frequencies at resonance.

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Heglund and Taylor (Heglund and Taylor 1988) found step frequency of running scales with body mass according to

$$f_{run} = 2.78m^{-0.176} \quad (6)$$

The frequencies for running, thrusting theory, and thrusting experiments all scale with similar power law exponents (-0.176, -0.167, -0.088). Comparing running and thrusting experiments, running frequency decreased faster with increasing body size. Thus, some smaller animals thrust slower than they run: in mice *Mus musculus,* the thrusting frequency is 1.49 Hz and running frequency is 5.9 Hz (Bellardita and Kiehn 2015). A slower thrusting than running is also the case for humans (thrust at 1.3–1.8 Hz and run at 2.6–2.8 Hz) (Cavagna et al. 1997) and horses *Equus ferus caballus* (thrust at 0.71 Hz and run at 2.7 Hz) (Yamanobe et al. 1993). For some larger animals such as the lion *Panthera leo*, the thrusting frequency of 3.1 Hz exceeds running (trotting) frequency of 1.7–2 Hz (Chassin et al. 1976).

We have until now considered the frequency of thrusting, which is the short-time scale characterizing intercourse. We proceed by considering the whole duration of copulation which should be proportional to energy expenditure. Fig. 5 shows the relationship between copulation duration and body mass, where data is aggregated from Brennan and Orbach (Brennan and Orbach 2020a) and plotted. Unlike thrusting frequency which fits a narrow frequency range of 1 to 6 Hz, copulatory duration ranges across five orders of magnitude, from 1 s to 11 h. Although we analyzed with respect to phylogenetics or copulation style, we noticed no discernible trends. We conclude that copulation duration does not share the same relationship with body mass as thrusting frequency.

Lastly, we conducted an analysis of information transfer during mice *Mus musculus* copulation using the Shannon–Hartley theory of capacity, which indicates how much information a signal can reliably transmit on a noisy line. Shannon–Hartley's law states

$$C = B\log_2(1 + S/N) \quad (7)$$

where C represents the capacity, B represents the bandwidth of the channel, S represents the signal power, and N represents the noise power. We estimated bandwidth B as the product of frequency of thrusting, 2 Hz, and the number of degrees of freedom, which we assume to be 8, consisting of x, y, z, θ and their time derivatives. Thus, bandwidth B is 16 Hz. The signal to noise ratio is harder to estimate given that our methods for measuring signal are noisy themselves. Nevertheless, given the time course of calcium spikes in Yin et al. (Yin et al. 2022) and the time course of position, we assumed that the signal was the thrusting dominant frequency and that noise is the smallest frequency we observe. We estimated the signal to noise ratio S/N to be 100 to 1, which in decibels is 20 dB.

Using equation 7, we found the information capacity to be 120 bps. This was comparable to speeds that humans can read tactile information. Reading Braille at 200 words per minute yields an information capacity of 50 bps. By comparison, a hotel phone line transmits at 30 kbps, much more than thrusting information transfer. However, this preliminary analysis did not take into account ridges or bumps along the genitalia that may facilitate faster information transfer. Ribbed condoms too may give the female a sensation of thrusting higher than the motion of the body. In fact, the human finger is sensitive up to 30 Hz, meaning information transfer could theoretically function at 1500 bps (Mountcastle et al. 1972).

Discussion

In this section, we summarize our main findings and speculate for the differences between our theoretical model and the observed trends.

We showed that the largest animal that uses thrusting is the horse *Equus ferus caballus* (500 kg). We suspect there is a cutoff between horses *Equus ferus caballus* and rhinos *Rhinocerotidae* (2400 kg), for which thrusting is no longer used. Physical safety may be a consideration at those sizes, with most unsafe being the elephants *Elephantidae*, precariously balanced on hind legs during intercourse. Perhaps the elephant's *Elephantidae* lack of thrusting is associated with its ability to recover from a fall. It may have to do with muscular force to body weight ratio, which decreases with body size (Alexander 1985). The inability to thrust at large sizes may be influenced by their grip. The horse *Equus ferus caballus* thrusts mostly by walking back and forth with its legs. Male horses *Equus ferus caballus*, rhinos *Rhinocerotidae*, and elephants *Elephantidae* are all digitigrades: they balance their front legs on the female's back without the ability to grip. On the other hand, male mice *Mus Musculus* use their paws to grip the back of the female to avoid falling off.

In this study, our hypothesis was that animals thrust at resonant frequencies to save energy per unit time. But why do some animals thrust faster than the resonant time scale? The observed thrusting frequency may be due to a tradeoff: resonant thrusting conserves energy per unit time while thrusting faster increase stimulation which may in turn reduce the duration of copulation and the total energy expended during copulation. Future work may consider measuring how thrusting's effect on stimulation and whether it indeed reduces the duration of copulation. We did not measure tactile stim-

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ulation in our study, but clearly it is an important part of the pleasure of sex. To understand the influence of thrusting on stimulation, careful measurements would have to be done across body size. In humans, the clitoris has approximately 6 times more nerve density than the male counterpart (Tunçkol et al. 2024), while a similar trend is observed in mice (Qi et al. 2024). Is faster thrusting aimed at stimulating the male, the female, or both?

While the genitals are notable for their high nerve density, there are many other factors that make them a uniquely specialized region of the body. Their stimulation leads to structural changes to the brain, early puberty development, and a cascade of irreversible changes to the body (Lima 2019). Brain scans of humans who are sexually abused as children showed thinning of the genital cortex as well as other parts of the brain (Brecht et al. 2018). Tactile cues to the genitals seem adequate to elicit these changes. Mice *Mus musculus* that are touched on the genitals by a lubricated brush experience expansion of their genital cortex (Lenschow et al. 2017). Female rodents receiving intromission in their vaginas with a vibrograver at certain species-specific patterns, called the “vaginal code,” will develop pseudopregnancy, which is the presentation of the symptoms of pregnancy without a fetus developing (Diamond 1970). Given the monumental changes that genital touch has on the brain and body, we were surprised that considerations, such as springiness of the legs, made good predictions of the thrusting frequency.

Its possible thrusting frequency and duration may be influenced by other factors, such as ecology or scaling effects. For example, we expect apex predators with an abundance of food and lack of predators to thrust at whatever frequency provides ideal stimulation. Smaller animals may be forced to thrust quicker due to the threat of predators. Behaviors such as burrowing could impact thrusting frequency. Species that burrow may have more time to safely copulate because they do not thrust out in the open. Showing that there is an effect of predator/prey relationships would require careful analysis and clever experiments. Lastly, thrusting may be faster for smaller animals simply because nearly all motion in smaller animals (chewing [Virot et al. 2017], walking, running, heart rates) occurs faster due to their greater muscular force to body mass ratio and shorter lifespan (Schmidt-Nielsen 1984).

By reducing sexual intercourse to a single variable, the thrusting frequency, we were able to make broad predictions across mammals. In the future, higher quality videos and force platform work would enable the study of the many repositioning and other micromovements that occur during intercourse. We now speculate how mating pairs communicate during the pauses and throughout thrusting to stay synchronized. In humans, pelvic floor muscles have been found to correlate with higher sexual desire, excitement, lubrication and orgasm (Sacomori et al. 2015); its possible female mice may also be contracting their pelvic floor during intercourse. Additionally, during thrusting, there were some thrusts where the female mouse appeared to move forward significantly more than the male by jolting forward as if rebounding from a hard impact. Here, the male seemingly exudes control over copulation. However, during these high-impact thrusts, the male was forced to readjust and pause thrusting, thereby giving the female mouse time to also readjust and control copulation.

Our cameras were unable to record high-frequency motion above 12.5 Hz, but it is quite possible that the many degrees of freedom of mammals make this motion a possibility during thrusting. Here we review the high frequencies that have been sought out by humans for sexual satisfaction. Over 50% of American women have used an electromechanical vibrator (Herbenick et al. 2009), a device that was invented a decade before both the electric iron and the vacuum cleaner (Maines and Maines 2001). Human sexual vibrators run at over 43–150 Hz (Prause et al. 2012), which is four times higher than our recording equipment could observe. However, this frequency may be possible for the muscles to achieve, as wet-dog shaking of mice can exceed 30 Hz. Vibrators can decrease rates of perceived bothersome pelvic organ prolapse and lichen sclerosus (Dubinskaya et al. 2024). Vibration of the genitals may provide some other health benefits, as shown by research with motorized massage tools. Exposure to high frequencies can increase strength gains across both sexes (Gondin et al. 2011). Thus, future work should seek to understand how higher frequency stimulation plays a role in thrusting and copulation.

Conclusions

In this study, we showed how sexual thrusting varies with body size. Mice *Mus Musculus* thrust in a sinusoidal motion, in which male and female are at times synchronized. Pre- and post-intromission thrusting differs in speed and depth. We proposed a theoretical model for “sexual harmonic motion” in which frequency is dictated by the spring-like behavior of leg muscles and tendons and frequency decreases in proportion to mass to the one-sixth power. Thrusting and running showed comparable trends due to their use of the same leg muscles to generate motion. We also found that thrusting frequency is more amenable to analysis than duration, which has no discernible trends. Future

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studies should look to understand outliers to the thrusting model and discrepancies across species.

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Supplementary data

Supplementary data available at *ICB* online.

Conflict of interest

This study has not been published elsewhere. It reflects original research conducted by its authors. None of the authors have any conflicts of interest to disclose concerning this study.

Data availability

The data underlying this article are available in Zenodo at https://doi.org/10.5281/zenodo.15569694 and in its online supplementary material.

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