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Voluntary wheel use across animal taxa: motivation, enrichment, stereotypy and ethological interpretation

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Abstract

Exercise wheels are simple devices for recording animal movement, but they elicit surprisingly complex behaviours. In laboratory rodents, running wheels are key for studying voluntary exercise, circadian rhythms, motivation, energy balance, stress physiology and brain plasticity. Outside rodents, wheel-like devices have also been provided to rabbits, cats, squirrels, reptiles and invertebrates. This wide use prompts a key ethological question: what does wheel running mean? This review investigates wheel use as a behavioural phenomenon, not just as a method for measuring activity. Historically, running wheels seem to have developed from captive-animal husbandry and display practices, especially squirrel cages. They were later adopted as scientific instruments in early twentieth-century rat research. Since then, wheel running has been interpreted in overlapping ways: as locomotor exercise, reward-seeking behaviour, exploration, play-like activity, coping behaviour, environmental enrichment or abnormal repetitive behaviour. These interpretations are not mutually exclusive. Their relevance depends on species, individual phenotype, housing, motivation, wheel design and available behavioural alternatives. The review argues that wheel running should not be treated as a unitary behaviour. In some animals, wheel access may provide behavioural agency and support motivated activity. In others, high or rigid use may signal constraint, stress, or limited environmental complexity. For non-traditional wheel-using species, video confirmation is important. Wheel revolutions may reflect climbing, pushing, manipulation, or other non-locomotive interactions. Further work should report animal characteristics, housing conditions, wheel dimensions, access schedule, sensor methods, behavioural context and welfare outcomes. Interpreting wheel running through an ethological framework helps distinguish voluntary locomotion, enrichment, play, coping and stereotypy. This can improve the use of wheels in behavioural research and animal care.

Keywords: *animal behaviour, animal welfare, enrichment, play, running wheel, stereotypy, voluntary exercise.*

1. Introduction

Running wheels occupy an unusual position in the study of animal behaviour. They are a familiar object in captive animal housing and a quantitative instrument in laboratory research (Sherwin, 1998; Novak et al., 2012). They also provide a behavioural opportunity that animals may use voluntarily (Meijer & Robbers, 2014). A wheel allows an animal to move continuously while staying in one spot. When connected to counters or sensors, it can provide measures of locomotory distance, speed, duration, timing and bout structure. As a result, running wheels have become one of the most widely used measures of spontaneous activity in laboratory rodents — especially mice, rats and hamsters — informing studies of energy balance, circadian rhythms, motivation and reward (Verwey et al., 2013).

The attraction of the wheel is both methodological and behavioural. Unlike forced exercise procedures such as treadmills or swimming, wheel running lets the animal start, control and stop the activity. This voluntary control — the animal choosing when to start, sustain and stop, rather than the exercise itself — is what has made the wheel so widely used, extending its applications to metabolism, stress physiology and neural plasticity (van Praag et al., 1999a,b; Allen et al., 2001; Rhodes et al., 2003; Novak et al., 2012). Yet this same feature also complicates interpretation. If the animal chooses to run, what is it choosing? Exercise, escape, stimulation, play, coping, or a rewarding motor pattern? The answer is unlikely to be the same in all species or conditions. Wheel running has been described as a strongly motivated behaviour in some rodents (Sherwin, 1998), a potential form of enrichment in hamsters and other captive animals (Gebhardt-Henrich et al., 2005) and a possible indicator of abnormal repetition when it is excessive or inflexible (Mason & Würbel, 2016). Field studies have shown that wild animals may use wheels placed outdoors, even in the absence of obvious food rewards (Meijer & Robbers, 2014), although subsequent work suggests that voluntary wheel use in wild mammals is variable rather than universal (van Lunteren et al., 2021). These data weaken the simple claim that wheel running is only an artefact of captivity, but they do not imply that all wheel use is benign.

This review, therefore, treats wheel running as an ethological problem: a behaviour best understood by considering its mechanism, development, function and evolutionary context, the four levels of explanation revisited in Section 12. It asks how wheel use has been studied, why animals may engage in it and when it should be interpreted as enrichment, reward, play-like behaviour, stress-related coping or stereotypy. The review is intentionally comparative. Rodents dominate the evidence base, but studies and observations from rabbits, cats, reptiles and invertebrates broaden the question from “how much do rodents run?” to “how should wheel-directed behaviour be interpreted across taxa?” This article is a narrative review rather than a systematic search or meta-analysis, it synthesises influential and illustrative work on running wheels across taxa.

2. Historical origins of running wheels

The running wheel did not begin as a modern laboratory instrument. Wheel-like devices appear to have been used in captive animal housing before they became part of experimental biology. Nineteenth-century squirrel cages included wheels and commercial cage catalogues show that such devices were sold before the term “hamster wheel” became common (Oxford English Dictionary, n.d.; Osborn Manufacturing Co., 1876; Smithsonian Libraries and Archives, 2014). These early wheels were probably used for husbandry, display, entertainment or exercise, rather than for measurement.

This history matters because it reminds us that the wheel has always had two identities. It is both a technology of confinement and a possible outlet for movement within confinement. The same ambiguity remains central to modern interpretations of wheel running. A wheel may give an animal control over locomotor activity, but it may also exist because the surrounding environment restricts wider movement.

The wheel also belongs to a longer history of human-made devices that convert walking into rotation. Treadwheels and animal-powered wheels were familiar before laboratory activity wheels. Turnspit dogs, for example, ran inside wheels to power roasting spits (Bondeson, 2011). It is therefore unlikely that the animal running wheel was invented by direct imitation of a naturally occurring wild behaviour. More plausibly, humans adapted existing wheel technologies for housing small, active captive animals.

Table 1. Selected historical developments in running-wheel use.

Period	Development
Late 1800s	Wheel devices appear in captive squirrel cages and animal cages sold commercially.
1921–1922	Richter uses activity wheels to study spontaneous activity and rhythmicity in rats.
1930s–1980s	Wheels become common tools in rodent activity, feeding and circadian-rhythm research.
1990s–2000s	Wheel design, preference, enrichment value and welfare implications receive increasing attention.
2010s–2020s	Automated and open-source systems expand detailed recording of wheel-running behaviour.

The scientific transformation of the wheel took place in the early twentieth century. Curt Richter’s studies of spontaneous activity in rats helped establish the activity wheel as a recording instrument (Richter, 1922; Schulkin et al., 1994). A rotating wheel could be connected to counters or switches, allowing researchers to record when an animal was active and how activity

changed with light, feeding, reproductive state or physiology. This was especially important for chronobiology, where wheel-running rhythms became a standard behavioural output.

Over the twentieth century, wheel running moved into studies of circadian timing, food anticipation, metabolism, motivation, stress, addiction and brain plasticity. At the same time, researchers increasingly recognised that wheel design matters. Diameter, width, resistance, running surface and safety features can alter use and welfare value (Mrosovsky et al., 1998; Banjanin & Mrosovsky, 2000; Reebs & St-Onge, 2005). Flat rotating running discs (saucers) have also been used as an alternative to traditional wheels. A wheel is therefore not a neutral instrument. Table 1 summarises key historical developments. It shapes the behaviour it records, as shown by early work indicating that mice wheel preferences depended on wheel type and experience (Kavanau, 1966).

3. What wheels measure and what they do not measure

Exercise wheels are often treated as activity meters. They can indeed produce useful quantitative outputs: distance, speed, duration, number of bouts, bout length, timing of activity and, in some systems, direction of rotation. These measures are valuable because they can be collected continuously with relatively little disturbance (Verwey et al., 2013; Godfrey et al., 2022; Terstege & Epp, 2024). The main outputs and their interpretive limits are summarised in Table 2.

Table 2. Common outputs from wheel systems and their interpretive limits.

Measure	Behavioural meaning	Main limitation
Distance	Total wheel movement	May not equal biologically meaningful travel
Speed	Rate of wheel rotation	Depends on wheel size, resistance and posture
Duration	Time spent interacting with the wheel	Does not distinguish locomotion from manipulation
Frequency	Number of wheel-use events	Sensitive to bout definitions
Bout length	Structure of activity episodes	Requires consistent thresholds
Timing	Circadian or daily patterning	Influenced by light, feeding and disturbance
Direction	Direction of rotation	Rarely reported, may reflect apparatus or individual bias

However, wheel revolutions are not behaviourally self-explanatory. Each revolution records only that the animal moved the wheel, by itself it does not reveal how the wheel was moved or why.

In familiar rodent systems, wheel turns usually approximate running or walking, although speed and posture still depend on design. In less familiar species, revolutions may reflect attempts at climbing, pushing or bracing or manipulating from outside the wheel, or exploratory contacts. For this reason, sensor data should ideally be paired with direct observation or video, at least during validation.

The distinction is important. A high distance score (the total distance recorded by the wheel) may indicate sustained locomotion, but it may also reflect rigid, repetitive activity or a restricted environment in which the wheel is one of the few available outlets. In other words, the same total distance can arise from one prolonged, fluid run or from many short, repeated bouts, the latter pattern — especially if rigid and hard to interrupt — can signal restricted behavioural options or emerging stereotypy rather than healthy locomotion. This is why distance alone, without bout structure and context, can mislead. Conversely, low wheel use does not necessarily indicate poor welfare or low motivation for activity, it may reflect species-typical movement, an unsuitable wheel design, fear of the apparatus, age, sex, health status, social context, or the availability of more attractive alternatives. Several of these act in predictable directions: very young, aged, or unwell animals may run less because of reduced locomotor capacity or motivation and reproductive state raises or lowers activity mainly through the action of gonadal hormones. Oestrogen and testosterone are potent stimulators of rodent wheel running, so that intact females typically run farther than males, removal of the gonads (ovariectomy in females or castration in males) sharply reduces daily running and replacement of oestradiol or testosterone largely restores it (Lightfoot, 2008). By ‘social context’ we mean the presence, absence, or grouping of conspecifics, which can suppress or promote wheel use depending on species and housing (Sherwin, 1998; Novak et al., 2012).

Wheel data are therefore more informative when assessed alongside behavioural observations, body condition, food intake, health measures, housing details and environmental complexity. The wheel is not simply a measuring device. It is part of the animal’s environment.

4. Rodents

4.1. Mice

Mice are the most extensively studied wheel-running animals. Many laboratory strains run several kilometres per night during the dark phase when given wheel access and daily distance varies markedly and heritably among strains; in a survey of 13 inbred strains, C57L/J mice ran the farthest (Lightfoot et al., 2004). The widely used C57BL/6J line typically covers roughly 5–8 km per night, with females running farther than males (Lightfoot et al., 2004; Novak et al., 2012). Placing this figure in an ecological context is difficult. Free-living house mice range from small commensal territories to feral home ranges of several hectares (Chambers et al., 2000; Latham & Mason, 2004) and field studies of wild mice typically report net displacement or home-range area rather than cumulative path length — radio-tracked white-footed mice (Peromyscus leucopus), for example, moved only a few hundred metres over two nights yet used areas of up to 11 ha (Merriam & Lanoue, 1990). Because the quantity a wheel records is not the quantity these studies measure, it remains unclear whether several kilometres on a wheel exceeds or merely matches an animal’s natural locomotion.

This behaviour has been used to study energy balance and obesity (Novak et al., 2012), muscle adaptation (Allen et al., 2001), cardiac physiology (Konhilas et al., 2006), circadian rhythms (Verwey et al., 2013), neurogenesis (van Praag et al., 1999a,b), stress resilience (Greenwood & Fleshner, 2011) and disease models (Call et al., 2010).

Interpreting what mouse wheel running represents is nevertheless not straightforward, because wheel access also changes other aspects of behaviour. Wheel access increases energy expenditure, but it can also raise food intake to compensate and reduce other spontaneous home-cage activities, such as general ambulation and exploratory locomotion (Novak et al., 2012). Thus, wheel running should not be equated with total physical activity. It is a specific form of voluntary, repetitive, apparatus-directed locomotion.

In neuroscience, voluntary running has been influential because it promotes hippocampal neurogenesis and can improve learning-related measures (van Praag et al., 1999a, b). These effects have made the wheel an important tool in studies of brain plasticity, ageing and neurodegenerative disease. Expanding on the cardiac and muscular effects noted above, voluntary running can increase heart mass and shift skeletal muscle toward a more oxidative, fatigue-resistant phenotype and resisted wheels have been used to model progressive exercise loads (Allen et al., 2001; Konhilas et al., 2006; Call et al., 2010).

Wheel running is also a standard behavioural output in circadian biology. Mice usually run most during the dark phase and wheel records can reveal entrainment, free-running rhythms and food-anticipatory activity (Verwey et al., 2013; Flôres et al., 2016). Wheel access can also reshape behaviour in less benign ways. A striking example comes from activity-based anorexia models, food restriction combined with wheel access can lead to excessive activity and dangerous weight loss (Schalla & Stengel, 2019; Spadini et al., 2021). This demonstrates that voluntary access does not guarantee a welfare benefit.

4.2. Rats

Rats also use running wheels, although patterns vary with strain, sex, age, prior experience and wheel design (Sherwin, 1998). Rat wheel studies have contributed substantially to research on stress physiology and reward. Voluntary running has little effect on basal circadian corticosterone but facilitates habituation of the corticosterone response to repeated stressors (Fediuc et al., 2006; Sasse et al., 2008). It can also modulate drug reward and drug seeking, suggesting that wheel running engages motivational systems relevant to reinforcement (Smith & Pitts, 2012; Peterson et al., 2014).

The rat literature is especially useful because it shows that wheel running is not simply “exercise”. It can function as a reinforcer: animals may work to obtain access to the wheel (Belke & Wagner, 2005). This supports the view that wheel running has intrinsic motivational value in at least some contexts. However, reward value and welfare value are not identical. A highly reinforcing behaviour can still become excessive or maladaptive under certain environmental constraints.

4.3. Hamsters

Hamsters are among the most enthusiastic wheel users. Their strong, regular wheel-running has made them important in chronobiology and enrichment research. Wheel design is particularly important. Syrian hamsters prefer larger-diameter wheels (Reebs & St-Onge, 2005) and run more when the running surface provides good footing, such as a mesh floor rather than bare rods (Mrosovsky et al., 1998). Small wheels may force abnormal spinal curvature and should not be assumed suitable merely because the animal uses them (Manzanares et al., 2019).

For hamsters, wheel access may reduce some repetitive behaviours, including bar-mouthing and may improve behavioural opportunity in otherwise restricted housing (Gebhardt-Henrich et al., 2005). However, hamsters also exhibit metabolic responses to wheel access that may differ from those in mice and rats, including changes in food intake and body composition (Gattermann et al., 2004; Coutinho et al., 2006). These differences reinforce a central theme: wheel running is species-specific and context-specific.

4.4. Squirrels

Squirrels are historically important because early running wheels were associated with captive squirrel cages. Scientifically, they are less frequently studied than mice, rats and hamsters, but available work shows that wheel-directed behaviour can be diverse. Palm squirrels (Funambulus pennantii) and red squirrels (Tamiasciurus hudsonicus) have been used in studies of daily activity, light, temperature and photoperiod (Bahnak & Kramm, 1977; Kumar et al., 2020). In these studies, wheel-running served mainly as a readout of circadian and seasonal activity rhythms, showing how day length and ambient temperature shift the timing and amount of locomotor activity. White-tailed antelope ground squirrels (Ammospermophilus leucurus) interact with wheels in variable ways: alongside running, individuals may grip, climb on, or push the wheel, so that recorded revolutions need not correspond to locomotion (Refinetti, 2020).

Squirrel studies are valuable because they challenge the assumption that wheel turns are always equivalent to locomotion. For agile, climbing species, video observation is therefore not optional, it is essential for behavioural interpretation.

4.5. Degus and Nile grass rats

Most wheel-running research concerns nocturnal rodents, but two diurnal species, the degu (Octodon degus) and the Nile grass rat (Arvicanthis niloticus), have become valuable models precisely because their day-active habits allow wheel use to be interpreted against a natural activity profile. Both are diurnal in the field and in standard laboratory housing, yet both reveal a striking sensitivity to the wheel itself. When given free access to a running wheel, a proportion of degus and grass rats switch from a day-active to a night-active pattern and this inversion reverses once the wheel is removed (Blanchong et al., 1999; Kas & Edgar, 1999). In these species the wheel does not simply record pre-existing activity, it can reorganise the timing of the behaviour it measures.

In the degu, this phase switch appears to be shaped by thermoregulation as much as by the circadian clock. Vigorous wheel running raises body temperature and the shift toward nocturnal activity is promoted by higher ambient temperatures and constrained at lower ones, consistent

with an animal moving its exercise to the cooler part of the day (Vivanco et al., 2010; Baño-Otálora et al., 2021). Under a light–dark cycle the degu's wheel running is otherwise crepuscular, concentrated around dawn and dusk (Baño-Otálora et al., 2021).

The Nile grass rat shows comparable plasticity with additional sources of individual variation. Wheel-running patterns differ markedly among individuals, are influenced by parentage and sex and range from clearly diurnal to relatively nocturnal (Katona & Smale, 1997; Blanchong et al., 1999). Part of the increased night-time activity in wheel-running animals reflects a direct (masking) response to light rather than a true shift of the underlying clock (Redlin & Mrosovsky, 2004) and the expression of wheel running is further modulated by ambient temperature and light intensity, with warmth and dim light both reducing overall wheel use and dim light able to trigger a switch in temporal niche (Fogo et al., 2019).

These two species reinforce a central theme of this review. In diurnal rodents, wheel revolutions cannot be read as a simple quantity of exercise: the same apparatus interacts with the circadian system, thermoregulation and the light environment and can change an animal's temporal niche rather than merely sampling it. As with the squirrels, the wheel is best understood as part of the animal's environment, not as a neutral instrument placed within it.

5. Rabbits

Rabbits provide an instructive case because their locomotion differs from that of small rodents. A standard rodent wheel is inappropriate for a rabbit because rabbits primarily move by hopping and require a much larger, wider and more stable apparatus. Nevertheless, adapted wheels have been used to study circadian wheel-running activity in domestic rabbits (Kennedy et al., 1994).

For rabbits, the main issue is not whether wheel movement can be recorded, but whether the apparatus permits safe, species-typical movement. Wheel diameter, width, traction, entrance design and stability are central. A wheel that bends the spine, restricts hopping, or risks slipping may produce activity while compromising welfare. Rabbit wheel studies should therefore be interpreted as apparatus-specific rather than as evidence that "wheels" in general are suitable for rabbits.

6. Domestic cats and other felids

Domestic cats have recently emerged as a prominent example of non-rodent wheel use. Cat wheels are marketed for indoor enrichment and exercise, especially for obesity prevention. Scientific evidence remains limited, but one study found that adult cats could be habituated to a running wheel and that activity patterns differed by sex, with females showing clearer increases in activity after habituation (Detweiler et al., 2017).

Cat wheel use is behaviourally distinct from rodent wheel running. Many cats require gradual introduction, play-based encouragement or positive reinforcement. Use may occur in short bouts and is likely to vary with personality, age, sex, body condition, prior experience and household environment, although to date only sex has been examined empirically (Detweiler et al., 2017). A wheel should not be viewed as a stand-alone solution for feline inactivity or obesity.

It is one possible enrichment device among many, alongside diet management, veterinary care, play, climbing structures, hiding places and social context.

The felid literature raises a wider question relevant to animal behaviour: when does wheel use become play-like? This question is especially relevant for cats because of the character of feline play. Cats continue to play well into adulthood and their play is conventionally divided into social, locomotor, object and predatory forms (Delgado & Hecht, 2019). Adult object and predatory play is assembled from hunting motor patterns — stalking, chasing, pouncing and batting — and is readily released by small, moving, prey-like stimuli (Biben, 1979; Hall & Bradshaw, 1998). Because cats will also use running wheels (Detweiler et al., 2017), wheel running in a cat may express this chase-and-locomotor-play motivation. The persistence of predatory and locomotor play into adulthood is what makes the play interpretation especially natural for cats. It is this persistence of adult predatory and locomotor play, which has no clear parallel in the rodent wheel-running literature, that makes the play interpretation more natural for cats and gives the felid case its particular bearing on when wheel use becomes play-like.

In zoo and sanctuary contexts, large wheel-like devices might provide behavioural opportunities for some small or medium-sized felids, but this remains speculative and would require careful safety and welfare assessment.

7. Reptiles

Reptiles have often been underrepresented in enrichment and behavioural-choice research, but recent observations suggest that some reptiles may voluntarily use wheel devices. A leopard gecko (Eublepharis macularius) was reported to use a running wheel spontaneously and this behaviour was interpreted as possible locomotor play (Digirolamo, 2024). A later 12-month report described voluntary wheel use by a captive leopard gecko and estimated a daily distance of approximately 161 metres (Digirolamo, 2026).

These observations are intriguing but preliminary. The available evidence is based on very small samples and reptile activity is strongly influenced by temperature, light, enclosure design and individual temperament. Because reptiles are ectotherms, wheel use cannot be interpreted without environmental context. A gecko may interact with a wheel differently across thermal gradients, seasons or feeding states and each of these generates testable predictions grounded in ectotherm physiology. Because metabolic rate and locomotor capacity in ectotherms depend strongly on body temperature — rising toward a thermal optimum and falling outside it — voluntary wheel use should track body temperature, with little running when the animal is below its preferred activity range and more as it warms toward that range (Huey & Stevenson, 1979). For a nocturnal, crepuscular species such as the leopard gecko this optimum may lie at moderate rather than peak temperatures, since sprint performance in nocturnal geckos can be maximal at relatively low body temperatures (Huey et al., 1989), wheel use might therefore be greatest at intermediate nocturnal temperatures rather than the warmest conditions available. The same temperature dependence predicts a seasonal pattern, with more running in warmer months and less as temperatures fall and the animal becomes generally less active. Feeding state should matter too: digestion is metabolically costly (specific dynamic action) and reptiles commonly reduce locomotion and instead seek warmth to process a meal (postprandial thermophily), so wheel use might decline for a period after feeding and resume once digestion is

complete (Regal, 1966; Secor, 2009). Testing these predictions would require logging wheel use alongside body or substrate temperature, photoperiod and feeding schedule.

The reptile case is important because it questions assumptions about behavioural complexity in taxa sometimes regarded as relatively inactive. Leopard geckos actively engage with enrichment: Bashaw et al. (2016) found that captive geckos interacted with all five enrichment types they were offered — thermal, feeding, olfactory, object and visual — with all but a visual (mirror) stimulus increasing exploration, species-typical behaviour and behavioural diversity. A running wheel may represent one further enrichment of this kind. If some reptiles voluntarily engage with locomotor devices, future work should ask whether such devices provide stimulation, exploration, play-like opportunities or are merely novel objects. Larger samples and controlled preference tests are needed.

8. Invertebrates

Wheel-like devices have also been adapted for invertebrates, although these systems are usually specialised apparatuses rather than standard exercise wheels.

8.1. Earthworms

Earthworms are too light and slow to operate a conventional rodent wheel, but a low-friction wheel system has been developed to measure earthworm locomotion (Wilson & Johnson, 2016). Such devices show that the principle of wheel-based movement recording can be expanded well beyond mammals, provided the apparatus is designed around the animal's body plan and movement mechanics.

8.2. Land crabs

A running-wheel apparatus has been used to monitor locomotor rhythms in the land crab Gecarcinus lateralis (Darnell et al., 2008). Most tested individuals showed circadian rhythmicity under constant conditions. This example illustrates that wheel-like systems can reveal the temporal organisation of behaviour in animals with very different morphologies from rodents. It additionally reinforces the need to avoid assuming that a "wheel" is a single standard device across taxa.

9. Why do animals use wheels?

9.1. Reward and reinforcement

One of the strongest explanations for wheel running is that it can be rewarding. Rats will work for wheel access and wheel running can produce reinforcing after-effects (Belke & Wagner, 2005). In mice, variation in voluntary running is associated with activity in brain regions involved in reward and motivation (Rhodes et al., 2003). These findings support the view that wheel running is not simply an expression of surplus energy. It may be an activity animals are motivated to perform.

Reward, however, should not be interpreted simplistically. A behaviour can be rewarding because it satisfies locomotor motivation (Sherwin, 1998; Belke & Wagner, 2005), provides sensory feedback (such as vestibular and proprioceptive input from movement), which can be intrinsically stimulating (Kish, 1966), modulates arousal toward a preferred level (Berlyne, 1960), produces predictable, contingent stimulation, or allows behavioural control — the ability to start, sustain and stop the activity at will, which is itself reinforcing in many species (Kavanau, 1967; Leotti et al., 2010). The same motor pattern may be rewarding for different reasons in different species or environments. Each of these is a distinct candidate reason an animal might be motivated to use a wheel and they need not be mutually exclusive.

9.2. Locomotor opportunity and energy expenditure

A wheel permits sustained locomotion in a confined space. For small, active animals, this may partly compensate for limited enclosure size. Wheel access can increase energy expenditure, alter body composition and affect physiological systems (Allen et al., 2001; Novak et al., 2012). Yet wheel running is not equivalent to natural ranging, foraging or exploration. It is repetitive locomotion in a fixed place. Its value depends on whether it provides a meaningful behavioural opportunity or merely substitutes one restricted pattern for another.

9.3. Exploration and agency

Wheel use may also reflect exploration and agency, the latter referring to an animal's capacity to influence its own activity and surroundings. Animals frequently interact with novel objects and a wheel provides immediate sensory consequences: movement, rotation, vestibular feedback and proprioceptive change. Free-living mice have been observed using wheels set up in the wild and several features of this behaviour argue against a purely novelty-driven, exploratory account (Meijer & Robbers, 2014). The mice ran even when no food reward was offered, their wheel-running bouts were as long as those of captive mice, rather than the brief, sporadic contacts expected of simple investigation and use recurred throughout the multi-year recording rather than appearing only at first encounter. Had wheel use merely reflected exploration of a novel object, one would expect short contacts that decline once the object becomes familiar, not sustained, repeated running. However, wheel use is far from universal across wild taxa. Even in that study, mice were the main runners, whereas other animals — including shrews, frogs and even slugs — only occasionally moved the wheels and rarely sustained "running" (Meijer & Robbers, 2014). The difference is more dramatic across settings: when van Lunteren et al. (2021) repeated the experiment in a genuinely wild Neotropical site in Paraguay, wheel running was almost entirely absent. Of 1857 small-mammal visits — predominantly rats, together with New World (cricetid) mice and opossums — only two brief episodes qualified as wheel running (one rat and one opossum, each about nine seconds and covering no more than two metres), more than 100-fold less frequent than in the Netherlands and far shorter and slower than the bouts recorded there (which reached up to 18 min and 5.7 km/h). The authors attributed this contrast to the different species pool and, especially, to urbanisation, suggesting that wheel running in the wild may depend on prior exposure to human-made objects rather than being a general trait of wild mammals. Species differences are therefore substantial: some rodents, particularly in human-influenced habitats, perform repeated, sustained wheel running, whereas

truly wild animals may only briefly investigate a wheel or not use it for locomotion at all (Meijer & Robbers, 2014; van Lunteren et al., 2021).

Agency may be central. A wheel offers control over the onset, intensity and termination of movement and the opportunity to produce immediate, predictable and controllable consequences appears to be motivating in itself — not the circular claim that an animal runs simply because it can, but the proposal that control is itself a source of reward (Kavanau, 1967; Leotti et al., 2010). This is testable rather than merely descriptive: if control contributes to the motivation, animals should prefer, or work harder for, wheel access they initiate themselves over wheel movement that is externally imposed, such as a motorised wheel. Agency is unlikely to be the whole answer — the locomotor drive and the rewarding consequences of running described above are also needed to explain why an animal begins to run — but it helps explain why a wheel that animals can choose to use, ignore or leave may differ markedly from forced exercise or from environments with no locomotor outlet.

9.4. Stress coping

Voluntary running can buffer some physiological and behavioural effects of stress, particularly in rodents (Fediuc et al., 2006; Sasse et al., 2008; Greenwood & Fleshner, 2011). At the same time, stress or environmental restriction may increase wheel use. Thus, wheel running may be both a coping response and a welfare concern, depending on context. The key question is not whether wheel running occurs, but whether it co-occurs with signs of improved behavioural diversity, health and affective state, or with rigidity, weight loss, injury or other abnormal behaviour.

9.5. Play-like behaviour

Some wheel use may be play-like. Using Burghardt's five-criterion framework, wheel use should be considered play-like only when it is incompletely functional in the immediate context, voluntary or self-rewarding, flexible or modified relative to functional locomotion, repeated without becoming rigidly stereotyped and expressed under relatively relaxed, low-stress conditions (Burghardt, 2005). The leopard gecko case report explicitly raised the possibility of locomotor play (Digirolamo, 2024). Some rodent and cat wheel use may also include play-like elements, especially when use is flexible, brief, self-initiated and integrated with other activities. Mapping the five criteria onto these cases gives a mixed picture. The voluntary or self-rewarding criterion is the most clearly met, since animals run without external reward and will work to obtain wheel access (Belke & Wagner, 2005; Meijer & Robbers, 2014). The relaxed, low-stress criterion is met only conditionally: it fits wheel use in enriched housing but not the same behaviour in barren or stressful cages, where running may instead reflect coping or stereotypy. The requirement that the behaviour be repeated without becoming rigidly stereotyped is the crux rather than an easy case, because wheel running is inherently repetitive and separating flexible play from rigid stereotypy is exactly what must be established. The two remaining criteria are the hardest to satisfy: running expends energy and so is not obviously non-functional — though, because a captive wheel produces no actual displacement, the locomotion arguably lacks its usual function — and it is unclear whether wheel-running gait and patterning are structurally modified relative to ordinary locomotion. Wheel use therefore satisfies the voluntary criterion well, the relaxed-context criterion conditionally and leaves the non-stereotypy,

incomplete-function and modification criteria unresolved. Cat wheel use may satisfy the flexibility and structural-modification criteria more readily than rodent wheel use, given the strong object- and predatory-play repertoire of cats, whereas the sustained, endurance-like character of rodent wheel running makes it harder to distinguish from non-play locomotion.

The term “play” ought to be used cautiously. Wheel running should not be labelled as play simply because it appears voluntary or vigorous. Stronger evidence would include flexibility, positive affective indicators, a low stress context, persistence when alternatives are available and behavioural features similar to locomotor-rotational play in other settings.

9.6. Stereotypy and abnormal repetition

Stereotypies are repetitive, invariant behaviours with no obvious goal or function, often associated with barren or restrictive environments. Wheel running can resemble stereotypy when it becomes excessive, rigid, difficult to interrupt or associated with other signs of poor welfare (Sherwin, 1998; Richter et al., 2014; Mason & Würbel, 2016).

It would be a mistake, however, to classify all wheel running as stereotypic. Many animals use wheels in temporally structured, flexible and apparently motivated ways. The more useful method is to ask when wheel use crosses from a behavioural opportunity into pathological repetition. Warning signs include extreme use, weight loss and physical deterioration from excessive running (Schalla & Stengel, 2019; Spadini et al., 2021), reduced engagement with other available enrichment (Novak et al., 2012), behavioural inflexibility and perseveration, including running that intensifies after stressors (Mason & Würbel, 2016) and use concentrated in environments that lack other meaningful activities (Mason & Würbel, 2016).

10. Comparative interpretation throughout taxa

A comparative view shows that wheel use is not one behaviour but a cluster of related behaviours — sustained running, brief or intermittent running, climbing or gripping, pushing and manipulating the wheel from outside, play-like use and stereotypy-like running — shaped by interactions among animal morphology, motivation, environment and apparatus design.

The central implication is methodological and conceptual: wheel use must be interpreted at the level of species, individual and context. Table 3 summarises these interpretive issues across taxa. A mouse wheel is not a hamster wheel, a rabbit wheel, a cat wheel or a gecko wheel. Apparatus design is part of the behavioural phenotype being measured.

Table 3. Behavioural interpretation of wheel use across animal groups.

Animal group	Typical pattern	Main interpretation issues
Mice	High nocturnal running	Strain, sex, age and wheel design strongly affect results
Rats	Nocturnal running, reward effects	Exercise, reinforcement and stress systems interact

Hamsters	High motivation for wheel use	Wheel diameter and surface are welfare-critical
Squirrels	Variable wheel-directed behaviour	Wheel revolutions may not equal running
Rabbits	Possible with large adapted wheels	Standard rodent wheels are inappropriate
Cats	Short bouts after habituation	Training, sex, personality and household context matter
Leopard geckos	Voluntary use reported, possible play/play-like behaviour	Evidence is preliminary, thermal context is essential
Earthworms	Movement in low-friction devices	Requires specialised apparatus
Land crabs	Rhythmic locomotion in adapted wheels	Apparatus must match crab morphology and gait

11. Welfare and ethical implications

Wheel access can improve welfare when it provides safe, voluntary and meaningful behavioural opportunities. In hamsters, appropriate wheels may reduce some repetitive behaviours and support motivated activity (Gebhardt-Henrich et al., 2005; Reebs & St-Onge, 2005). In cats, wheels may increase activity for some individuals after habituation (Detweiler et al., 2017). In rodents, voluntary running can produce physiological and neural benefits in many experimental contexts (van Praag et al., 1999a,b; Allen et al., 2001).

However, wheel provision is not automatically beneficial. Poorly designed wheels can cause abnormal posture, slipping, foot or tail injury, overexertion or frustration. A wheel may also mask environmental inadequacy if it is used as a substitute for space, social contact, hiding places, foraging opportunities or species-specific enrichment. In some circumstances, especially food restriction or stress models, wheel access can contribute to harmful outcomes such as excessive running and severe weight loss, as seen in activity-based anorexia models (Schalla & Stengel, 2019; Spadini et al., 2021).

Welfare assessment should therefore ask several questions. Does the animal choose the wheel when alternatives are available? (e.g., Reebs & Maillet, 2003; Fischer et al., 2007) Does the use appear flexible or rigid? Is the apparatus safe for the animal's body size and movement style? Does wheel access increase or decrease behavioural diversity? Are there signs of injury, fatigue, weight loss or stress? Does the animal continue to engage with other environmental features? These questions are more informative than total distance alone.

12. Recommendations and future directions

Future studies should move beyond reporting wheel revolutions as though they were self-evident. At minimum, studies should report species, strain or breed, sex, age, body mass, health status, housing, social conditions, light–dark cycle, enrichment, wheel diameter, width, surface, material, resistance, access schedule, habituation procedures and recording methods. If distance is calculated, the formula and wheel circumference should be stated, if speed or bout structure is analysed, thresholds should be defined. Recommended reporting items are listed in Table 4.

Table 4. Recommended reporting items for wheel-use studies.

Category	Items to report
Animal information	Species, strain or breed, sex, age, body weight, health status
Housing	Enclosure size, bedding, enrichment, social housing, light-dark cycle
Wheel design	Diameter, width, material, surface, resistance, open or closed sides
Access	Continuous or limited access, number of days, habituation period
Recording	Sensor type, sampling rate, distance calculation, video validation
Behavioural context	Timing, bout structure, co-occurring behaviours, interaction style
Welfare monitoring	Injuries, body weight, food intake, abnormal behaviour, stress indicators

For non-traditional wheel-using species, video validation is essential: researchers should confirm whether the animal is running, walking, hopping, climbing, pushing, manipulating or merely contacting the wheel and should record the behavioural context (whether wheel use follows feeding, disturbance, social interaction, exploration, stressors or play). More broadly, integrating wheel sensors with video and automated behavioural tracking would allow revolutions to be linked to posture, gait, transitions between behaviours and signs of fatigue or frustration.

Preference and motivation tests would be especially valuable. Animals should be offered choices between wheels and other enrichment types, or between wheels of different dimensions and resistance and tested for whether preference changes with age, season, reproductive state, health or social conditions, such tests can distinguish mere use from strong motivation. Comparative work should also extend to more species, especially animals with contrasting locomotor systems such as hopping mammals, climbing mammals, reptiles, birds and invertebrates and studies

should incorporate welfare-sensitive endpoints rather than activity measures alone. Long-term studies are needed to assess body condition, behavioural diversity, injury risk and the persistence of wheel use over time and wider adoption and further development of open-source wheel systems could improve reproducibility and availability (Terstege & Epp, 2024).

Finally and most importantly, wheel running should be interpreted within a Tinbergen-style framework (Tinbergen, 1963). Mechanistic questions ask what motivates and regulates wheel use, developmental questions ask how experience, age and habituation shape it, functional questions ask what immediate benefits, if any, the behaviour provides and evolutionary questions ask why certain taxa or phenotypes are more likely to engage with such devices. Above all, the step that matters most is interpretive: wheel running should be analysed as a behaviour in its own right — not merely a number of rotations, but an interaction between an animal and an artefact, shaped by motivation, morphology, context and opportunity. This scheme can prevent premature conclusions and encourage more precise behavioural hypotheses.

13. Limitations of current evidence

The evidence base is uneven. Rodent studies are abundant, but many other taxa are represented by small samples, case reports or apparatus-specific studies. This limits broad generalisation. In addition, many studies report total distance but provide limited information on wheel design, bout structure, behavioural context and welfare outcomes. Comparisons among studies are therefore difficult.

Another limitation is conceptual. Wheel running is often treated as a proxy for activity, exercise or enrichment, but these are not identical. Activity is movement, exercise is physiologically consequential movement, enrichment is a welfare-oriented environmental provision and play is a behavioural category with specific criteria. Wheel running may overlap with all of these, but it should not be automatically assigned to any one of them.

The historical literature is also incomplete. Although squirrel wheels and activity wheels can be traced through catalogues and early laboratory work, the transition from husbandry object to scientific instrument deserves further historical study. Understanding that history may help explain why the wheel remains culturally associated with both confinement and agency.

14. Conclusion

Exercise wheels are simple devices that expose complex behaviour. Their history begins in captive animal housing and display, but their scientific importance developed through laboratory studies of spontaneous activity and biological rhythms. In modern research, wheels are used to study voluntary exercise, circadian timing, metabolism, motivation, stress, reward, brain plasticity and welfare.

Mice often exhibit high nocturnal activity and are useful for studies of metabolism, brain plasticity and circadian rhythms. Rats provide strong evidence for interactions between reinforcement and stress. Hamsters show high motivation and clear wheel preferences, making design especially important. Squirrels may interact with wheels in varied ways that require direct observation. Rabbits require large, adapted wheels that accommodate hopping. Cats may

use wheels after habituation, often in short bouts influenced by training and individual preference. Leopard geckos provide preliminary evidence that voluntary wheel use occurs in reptiles, but the evidence remains sparse. Earthworms and land crabs show that wheel-like principles can be adapted to very different body plans.

The central conclusion of this review is that wheel running has no single meaning. It may be voluntary locomotion, reward-seeking, exploration, enrichment, play-like behaviour, stress-coping, or stereotypy. Which interpretation is most appropriate depends on the animal, the environment and the apparatus. High use is not automatically good welfare, low use is not automatically poor motivation. A well-designed wheel can provide a behavioural opportunity, but a poorly designed or poorly interpreted wheel can mislead researchers and caretakers.

Beyond reaffirming that wheel running is multiply determined (cf. Sherwin, 1998), this review makes two specific contributions: it extends the analysis across taxa — from invertebrates to reptiles, cats and rabbits — and it treats the apparatus itself as part of the behavioural phenotype, so that wheel design is analysed alongside the animal rather than as a neutral measuring instrument. A comparative ethological approach can improve the study of wheel use. By asking how animals engage with wheels, why they do so and under what conditions wheel use is beneficial or detrimental, researchers can move beyond revolutions as a simple activity score. The wheel should be understood not only as a tool for measuring behaviour, but also as an object that affects behaviour.

Conflict of interests

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