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METHODS ARTICLE

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Steps into a Small World: First glimpses on everyday moment-to-moment decision making in an ecologically meaningful multi-choice system for assessing animal preferences

Fiona Puls[1,2] | Louisa-Mae Kosin[1] | Fiona Garbisch[1] | Chadi Touma[3] | Christa Thöne-Reineke[2] | Lorenz Gygax[1]

[1]Faculty of Life Sciences, Albrecht Daniel Thaer-Institute of Agricultural and Horticultural Sciences, Animal Husbandry & Ethology, Humboldt-Universität zu Berlin, Berlin, Germany

[2]Institute of Animal Welfare, Animal Behaviour and Laboratory Animal Science, School of Veterinary Medicine, Freie Universität Berlin, Berlin, Germany

[3]Department of Behavioural Biology, Osnabrück University, Osnabrück, Germany

Correspondence
Lorenz Gygax, Faculty of Life Sciences, Albrecht Daniel Thaer-Institute of Agricultural and Horticultural Sciences, Animal Husbandry & Ethology, Humboldt-Universität Zu Berlin, Berlin, Germany.
Email: lorenz.gygax@hu-berlin.de

Present address
Louisa-Mae Kosin, The Roslin Institute, The Royal (Dick) School of Veterinary Studies, The University of Edinburgh, Midlothian, UK

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Abstract

The behaviour shown by an animal at any one time is the consolidated output of its behavioural control mechanism. Moreover, what animals “want” is viewed as (the most) important component for individual welfare. Accordingly, studying the motivation of animals helps understanding basic mechanisms and welfare related needs. However, studying wants of animals is notoriously difficult and many previous studies on the preferences of animals have been restricted in the sense that only two choice options were presented in an artificial test environment. Here, an extended approach, the “Small World” is presented, in which the choices of animals between eight ecologically relevant resources can be observed in a long-term test to reach conclusions with respect to everyday moment-to-moment decisions. In this sense, the system offers a quasi-natural environment. The approach was tested in three experiments with observations of individual female rats, small groups of female rats (Long Evans, *Rattus norvegicus*) and small groups of female chickens (Lohmann Brown, *Gallus gallus domesticus*). The animals oriented themselves quickly in the system and it was possible to collect multifaceted data on the use of the resources. These data included the faecal and urinary markings in the Small World cages, the daily frequency and duration of visits to these cages, the sequential analyses of the choices for and decisions among the resources, and the synchrony of the animals in the groups. Given the richness of these data and the lack of a stress response in the tested animals, the use of the Small World approach seems to be highly promising as an extension to previously used procedures. To further improve the approach and more directly reflect the subjective value of the different resources from the animals' point of view, the distances between the resources in a quasi-natural landscape shall be manipulated in future studies.

KEYWORDS
faecal corticosterone metabolites, home-cage testing, positive welfare, proximate behavioural control mechanism, welfare assessment

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Louisa-Mae Kosin and Fiona Garbisch contributed equally to this work.

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1 | INTRODUCTION

Knowing and understanding what animals "want" is important for basic science concerned with proximate behavioural mechanisms ("animal psychology") as well as for improving animal welfare. The animals' decision-making and the resulting choices, i.e. the processes that manifest their wants, reflect the rules governing their behaviour (Hein et al., 2020) and, accordingly, open a window for understanding how behaviour is controlled. In this sense, understanding animal wants aims at answering directly the proximate why questions of behaviour (Tinbergen, 1963). Yet, these questions are of relevance to the ultimate why questions, too, because the behavioural mechanisms determine how optimal, i.e. with what relative fitness, an animal can make decisions (Bell, 2024).

For practical purposes, animal welfare can be ensured beyond health if an animal is allowed to do what it wants (Dawkins, 2004, 2008, 2015). It may even be the case that this is how far improvement of animal welfare is possible at all. Animals can then follow their motivations and reach their proximate aims, which is closely linked to potential positive affective states (Gygax, 2017). Finally and bridging fundamental and applied questions, "natural behaviour" can be thought of as the behaviour being performed when the proximate behavioural control mechanism can run freely (Gygax & Hillmann, 2018). Again, this coincides with animals being able to do what they want and reach what they aim for.

Apart from investigating animal preferences ("wanting"), many welfare scientists rely on behavioural indicator variables for affective states (measured in specific situations, e.g. Reefmann et al., 2009a, 2009b; Reefmann, Wechsler, et al., 2009) or asking animals about their affective state (e.g. based on a judgement bias test, Lagisz et al., 2020). In a recent paper, Paul et al. (2022) have measured animal preferences (what animals want), indicator variables of their (affective) welfare state, and judgement bias outcomes in the same hens in a single coherent study. They found that the preferences were the most stable response of the hens. Judgement bias changed in the course of the study, which is plausible because mood may be more sensitive to change than to chronic states (Eldar et al., 2016; Raoult et al., 2017). Moreover, indicator variables are likely to be influenced by many causes such that they are sensitive to affective reactions but not specific to them. Given these specific results, Paul et al. (2022) could not substantiate clear relationships between preferences, indicator variables of welfare, and judgement bias. They concluded that preferences provide the most reliable measure of the needs of the animals. In this sense, assessing what animals want based on the decisions they make seems likely to be reflecting those aspects in an animal's life at best that have the potential to improve its welfare.

Assessing what animals want is fraught with many hurdles (Franks, 2019). Therefore, a variety of approaches are needed to investigate what animals want, reflecting different perspectives on the same question. One such approach that builds on and extends previous set-ups is presented here: the Small World. In the Small World approach, a larger number of resources is presented simultaneously compared with classical choice-tests offering two options only (e.g. Bateson, 2004; Beeby & Alsop, 2017; Bruzzone & Corley, 2011; Elmore, Garner, Johnson, Kirkden, Patterson-Kane, et al., 2012a; Elmore, Garner, Johnson, Kirkden, Richert, et al., 2012b; Fernandez & Timberlake, 2019; Fuhrer & Gygax, 2017; Jensen et al., 2008; Kirkden & Pajor, 2006; Reijgwart et al., 2015). The idea of using several resources builds on prior experiments that used more than two choice options (three options: de Maia et al., 2019; Jensen et al., 2008; four options: de Jong et al., 2007; Seaman et al., 2008; five options: Li et al., 2018; seven options: Reijgwart et al., 2016). The dichotomous choice seems to be a rare situation in real life and several options are usually available that an animal can choose from at the same time (Juechems & Summerfield, 2019; Reijgwart et al., 2015; for humans, see Busemeyer et al., 2019). This has implications for what animals may learn based on the success and errors according to their choices (Molano-Mazón et al., 2023) and reduces the risk of providing the animals with an irrelevant small selection of options (Franks, 2019). Prior multi-choice studies usually focused on a selective context only by providing a variety of options of the same type, such as environmental enrichments (e.g. Hobbiesiefken et al., 2021, 2023). Here, the resources that were offered as the choice options were selected to be ecologically meaningful in respect to the animals' more complete niche (Rosenthal et al., 2017; Zilkha et al., 2016). Consequently, they are relevant in respect to the animals' behavioural control mechanisms (Mason et al., 1997, 1998; Patterson-Kane et al., 2008). In this sense, a (quasi-)natural environment was mimicked, in which animals can choose between several options (Houston, 2009; Sherwin & Nicol, 1996). Given the previous set-ups, one might ask for a direct comparison of our Small World approach with these more traditional approaches. This cannot be done directly because neither the previous set-ups nor the Small World system are approaches that are standardised to a large extent. Rather, they represent more general approaches to the question of animal decision-making that can be varied in each specific operationalisation (see also issues of validity addressed below and in Section 4). Moreover, we are not aware of any previous attempts addressing concurrent choices to such a wide range of resources and with respect to "common" decisions (see next paragraph).

In the Small World approach, our focus is on common decisions that animals would need to take on a daily basis and repeatedly in the course of a day (moment-to-moment everyday decisions). These decisions are highly relevant for basic research because the sum of these decisions will influence how successful an individual deals with its environment, which will be decisive for its ultimate fitness (Bell, 2024). These decisions are also relevant to animal welfare due to their sheer number (Rosenberg et al., 2021), i.e. the number of times an animal needs to deal with this type of decisions on a daily basis. In addition, they have a direct effect on the time budget and the invested physical effort (Bennie et al., 2014; Dunbar et al., 2009; Dunbar & Shi, 2013). The time and energy budget constraints the decision-making process, which reflects again the ecological importance of such decisions (Bell, 2024). This is reflected in the system such that costs in terms of constraints common to all the activities are imposed, i.e. all resources are at the same distance and the use of one resource implies not being able to use any of the other resources at the same time. Moreover, animals spend a long continuous time (several days) in the system. In doing so, re-scheduling of activities to other times and places outside the experiment is avoided (Asher et al., 2009; Cooper, 2004; Jensen & Pedersen, 2008; Ladewig et al., 2002; Mason et al., 1997, 1998; Reijgwart et al., 2015). In the end, animals may even perceive their own "agency" that may increase their welfare (Franks, 2019; Franks et al., 2016; Špinka, 2019).

Such common decisions have been little studied (Lawrence & Illius, 1997). This is in contrast to the number of studies on decision-making that focus on "difficult" or "ambiguous" choices. These studies focus on investigating the situations in which a seemingly rational choice may be limited or break down, i.e. becoming seemingly irrational (e.g. Hinnenkamp et al., 2017; Shimp et al., 2015; van den Bos et al., 2014). Yet, the focus on common and «relaxed» decisions (that are neither taken under temporal pressure nor have life-threatening consequences) seems highly ecologically relevant for animals, and we can assume that these kinds of decisions also play a role in welfare due to their sheer number.

Here, three initial experiments using the Small World approach with individual female rats, small groups of female rats (Kosin, 2022), and small groups of female hens (Garbisch, 2022) are presented. The animals continuously lived in the Small World system (in small groups) for an extended experimental period. This enabled us to take the social situation into account (Jensen, Pedersen, & Ladewig, 2004; Pedersen et al., 2002), choices occurred in different contexts throughout the study (Mason et al., 1997), and within the same subjects (Patterson-Kane et al., 2008). For social species, the choice situation in groups (Kirkden & Pajor, 2006) is less artificial compared with experiments where animals are put into a solitary testing environment (Albentosa & Cooper, 2005; Patterson-Kane et al., 2008) and for a short time (Fuhrer & Gygax, 2017; Jensen, Pedersen, & Ladewig, 2004). In short-term experimental choice tests, the problem can arise that animals are not motivated for the choice that they are tested for (e.g. Arvidsson et al., 2017; Elmore, Garner, Johnson, Kirkden, Patterson-Kane, et al., 2012a; Elmore, Garner, Johnson, Kirkden, Richert, et al., 2012b; Kirkden & Pajor, 2006; van Horik et al., 2017). When continuously living in the Small World system, animals can choose the option they are motivated for at any given moment. This is the case even without prior deprivation of the resources, which has been used to increase motivation (e.g. Jensen, Munksgaard, et al., 2004; Wichman & Keeling, 2008). Furthermore, the animals are not interrupted when interacting with the outcome of their decisions or when engaging with resources (Jensen, Munksgaard, et al., 2004; Jensen & Pedersen, 2008; Jensen, Pedersen, & Ladewig, 2004; Mason et al., 1997; Olsson et al., 2002; but see Patterson-Kane et al., 2008).

Apart from these theoretical considerations, the experimental situation used in the Small World approach should improve what experimental animals are confronted with in comparison to short-term testing of individually separated animals in the sense of the third R, refinement (Russell & Burch, 1959). For example, the animals do not need to be transferred on a regular basis, for a short period, and by a human handler to an unknown testing situation. In this sense, the Small World approach is a form of home-cage based testing (Grieco et al., 2021; Habedank et al., 2022; Kahnau et al., 2023; Kim et al., 2019; Koot et al., 2009; Winter & Schaefers, 2011). Yet, and specifically in the case of our first experiment where individual rats were tested, the experiment may still be stressful for the tested individuals. The potential stressors that our rats encountered when tested as individually separated focal animals were restricted social contact (Arakawa, 2018; Boero et al., 2018; Peartree et al., 2012), exposure to a novel environment and stimuli (Kurumaji et al., 2011; Nikaido & Nakashima, 2009; Tanaś & Pisula, 2011), potentially threatening stimuli (Adamec et al., 2004; Apfelbach et al., 2005; Kliuchnikova et al., 2020), and a restricted variety of feed (Modlinska et al., 2015). When testing individual rats, two other rats served as the resource "social contact". These two rats experienced reduced space (Lee et al., 2018; Sharp et al., 2003), and a restriction in feed availability as potential stressors. These potential stressors may be alleviated, if the Small World system in itself was a form of environmental enrichment (Key, 2004) allowing for increased physical, sensory, cognitive and social stimuli relative to standard housing conditions (Ratuski & Weary, 2022) and ensuring that the animals are able to express more natural behaviour (Olsson & Dahlborn, 2002). To assess this, we used non-invasive assessment of faecal glucocorticoid metabolites in our experiment with single rats (Palme, 2019; Touma et al., 2004) to assess stress levels during approximately up to 15 h before taking the samples (DeVallance et al., 2017).

For our three initial experiments using the Small World approach, we used individual female rats, small groups of female rats, and small groups of female hens. We used two widely different species (mammals and birds) to illustrate how our approach can be set-up differently for different species. We chose female rats only for this initial experiment because we assumed that they would be more socially compatible specifically if the groups consisted of sisters. At the same time, the data may become more representative if variability arises throughout their hormonal cycle. Focusing on female hens was mostly for practical reasons because these animals could be reused at our facility and could be housed without the risk of serious aggression. Using single rats in our first experiment allowed a relatively easy automatic recording of their visits to the different resources and assessing the value of social contact. However, we have focussed on group-living species that are typical animals for laboratory research and livestock farming. For such species, being tested in partial isolation may involve reduced welfare and be unusual. Accordingly, the group experiments that followed can be viewed as reflecting a more common ("natural") situation of making decisions as they are made within a small group as well as a refinement because no (partial) isolation was necessary. All in all, the selection of our species and animals will not lead to high external validity but our aim was to illustrate our approach as a series of proof of concept experiments.

In the Small World system, "natural" decisions can be studied. We consider them "natural" because the decisions are made between ecologically relevant resources, among a continuously available set of options, under ecological constraints, and are common on a daily basis. Overall, these decisions reflect the proximate behavioural control mechanism as it could be observed in the wild but allowing experimental manipulations. These aspects extend previous choice test paradigms in a meaningful way.

These three experiments reflect first steps into the validation of our approach (e.g. Würbel, 2017). Construct validity, i.e. whether an approach can measure the phenomenon of interest is often the first question in respect to validation. As we observe directly the process of interest, i.e. motivation reflected by natural decisions, construct validity is assumed to be given on a theoretical level. Practically, we can start to assess construct validity if small changes in the Small World can be detected specifically by the measured variables. Internal validity is reflected by how an experiment is designed (see Section 2).

Here we show the principles of such experiments with a Small World system. Specifically, we wanted to demonstrate the richness of quantitative data that can be collected on resource use in a Small World approach (Cooper & Mason, 2001; Mason et al., 1997; Patterson-Kane et al., 2008) to allow for informed decisions in later applications. These data are largely based on the detailed sequence and durations of the visits to the different resources, allowing to model decision sequences quantitatively (Gygax et al., 2022). Finally, we do not consider our initial experiments as the basis for a highly standardised assessment but rather as a conceptual approach. Accordingly, future studies may adjust their set-up with respect to the species studied and the specific questions asked. Validation in such a system will take place over time if and when the results of continuous experimentation converge. Such a step-wise procedure may be slower but its external validity is likely to be better compared with a highly standardised approach (see also Section 4 and Voelkl et al., 2018).

2 | MATERIALS AND METHODS

The three single experiments took place from October 2020 to the beginning of April 2021 (rats, individual observations), from the end of April to mid of June 2021 (rats, small groups) and during the months of July and August 2021 (hens in small groups). All animals were kept at the Teaching and Research Station for Farm Animal Sciences (Humboldt-Universität zu Berlin, Faculty of Life Sciences, Albrecht Daniel Thaer-Institute of Agricultural and Horticultural Sciences, Berlin, Germany).

2.1 | Animals and housing

The same 12 female Long Evans – rats (*Rattus norvegicus*; Janviers Labs S.A.S., Le Genest-Saint-Isle, France) were used for the observations of single rats and the rats in small groups. We used female wild-type rats such that natural variability regarding the genotype and the hormonal cycle was represented in our data. One rat fell sick unrelated to our experiment at the time when her individual observation was to start and was anesthetised. Accordingly, only the data of 11 rats were available for evaluation. The rats were kept and tested in four groups of three sisters each (for the observations of the small groups, one group of rats consisted of two animals only). The rats were approximately 70 days and 235 days old at the start of the period when they were tested singly and in small groups, respectively. They could be identified by their individual fur patterns. Outside the experiment, the four groups of rats were each kept in a highly enriched cage measuring 99 × 71 × 85 cm [$W \times D \times H$] (Happy Home 99A for Rodents, Montana Cages, Geilenkirchen, Germany). The rats were kept on an automatic light schedule with a 12 h light-on period starting at 09:00 and were fed shortly after lights on at around 10:30 (for details of the housing, management and initial acclimatisation of the rats, see Methods S1). Temperature ranged usually between 20 and 24°C and relative humidity between 50% and 70%. Light-schedule, temperature, and relative humidity were identical in the housing and the experimental room.

From the point of view of the STRANGE framework (Webster & Rutz, 2020), our rats had a variable genetic background in that they were of the outbred Long Evans breed, although the variability depended on the (unknown) detailed breeding program of the provider. Also, we restricted ourselves to female animals such that results cannot automatically be generalised to males. Following selection at the breeder, no self-selection was involved in our approach, although the relatively small number of kin-related animals may have led to a non-representative sample due to chance. Animals lived in sister-groups and were raised in enriched conditions, such that results may not hold for groups formed by non-kin females nor animals raised under standard laboratory conditions. Changes with the hormonal cycle may have led to increased variability but, e.g. circadian patterns should not have had a systematic influence as the animals were tested and observed continuously throughout complete days. The habituation to the experimental set-up was part of our research question with both species tested.

For the third experiment, 12 laying hens of the Lohmann Brown breed (*Gallus gallus domesticus*) were used. The hens had been part of a feeding experiment before and were kept and tested in four groups of three hens. Each group of hen was housed in an aviary (380 × 140 × 210 cm). The aviaries were bedded with chopped miscanthus, and the hens were fed standard chicken feed (laying meal) and offered water via round feeders. In the back of the aviaries, there was a perch (70 × 3 × 5 cm), and the sidewalls of the aviaries were barred. In addition, there was a laying nest at the front of the cages (37 × 27 × 17 cm). The hens could see other groups of hens through the bars but could not interact physically. The hens of group 1, 2, 3, and 4 were 315, 327, 339, and 351 days old at the start of their experimental phases, respectively. To enable the identification of the individual hens, they were marked with a (non-toxic) blue colour mark on either the left or right side of the body (or left without marking). The colour marks were not visible at night. Accordingly, foot bands were also used on the left or the right leg (or none). The hens were not restricted in their movement by wearing the foot bands. The three groups of hens that remained in the aviaries during the experimental phase of the fourth group were fed standard feed, given water, and examined in respect to their well-being daily by the animal caretakers.

Our hens were from a typical layer breed but were raised in relatively non-intensive conditions (small groups and enriched housing) and may thus not be representative for hens raised in intensive and large housing systems for egg production (cp. STRANGE framework; Webster & Rutz, 2020). As with the rats, our results cannot automatically be generalised to male domestic fowl. No direct self-selection was involved in our approach. The small number of animals and groups may have led to a non-representative sample due to chance. Again, circadian patterns should not have had a systematic influence as the animals were tested and observed continuously throughout complete days.

2.2 | The Small World systems

The experiment took place in a so-called Small World system that was specifically designed for the investigated species. Both systems were set up such that each of the eight resources was located at the same distance from a central choice cage. The resources were accessible at all times, except for the daily period when the Small World system was cleaned and resources were replenished (see Section 2.3).

The Small World system for the rats (custom built by Phenosys, Berlin, Germany) consisted of eight resource cages arranged around a central cage, the *choice cage* (all cages were of the type 2154F, 482 × 267 × 210 mm; Tecniplast, Buguggiate, Italy). The eight resource cages were situated on two different height levels within two cage racks (Figure 1, left; for more details see Methods S2). This configuration was mainly chosen such that the system could be set-up using space effectively and be built with standard laboratory animal equipment. Moving between the two levels was not considered problematic for the rats.

The Small World system for the hens was located in a different barn than the aviaries. It consisted of an arrangement of eight resource cages around the central choice cage. Except for one cage offering perching opportunities (which was higher), the resource cages had the same dimensions ($W \times D \times H$: 70 × 70 × 80 cm). Thus, a floor space of about 49,000 cm^2 was available in each cage. The cages were made of metal. On the sides of each cage were closed metal walls. The floor, ceiling, and part of the entrance area consisted of bars. The rear part of the cage consisted of a frosted plexiglass pane. The eight resource cages were arranged in a radial pattern and the resulting central octagon (*choice cage*) allowed the hens to reach all resource cages via identical walkways (width × length × height: 45 × 110 × 50 cm; Figure 1, right). The walkways and the cages could be separated at the entry to the resource cages using sliding bars.

For these first validation studies, the *resources* were chosen such that they covered aspects necessary for basic survival, known behavioural needs, and needs that may be weaker (i.e. leading to problems in behavioural adaption only in the long run) and could be considered a form of enrichment. The list of resources was thought to be exemplary and non-exclusive. Depending on the exact question, future studies are likely to vary in their choice of resources. Needs directly relevant for survival were chosen here to be reflected by ad-libitum feed, ad-libitum water, and an opportunity for resting for both species (resting equalled to nesting material for the rats, and perching opportunity for the hens). These were complemented by resources covering more specific needs (foraging; special activities, i.e. running wheel for the rats and a sand bath for the hens). Finally, additional ecologically relevant stimuli were provided (novel objects; olfactory stimulus of a potential predator; restricted social contact for the rats tested individually, an empty control for the small groups of rats, and a laying nest for the hens). All further details of how these resources were provided in the cages are presented in Methods S2.

2.3 | Experimental procedures

In the first experiment, during which rats were observed individually, each rat served as a focal animal once. For the experimental phase, the focal rat lived in the Small World system for 10 consecutive days (10 times 24 h in direct succession). In the week preceding the experimental phase of the first focal rat, each group as a whole was put into the system for 1 h, which allowed the animals to explore the system. While the focal rat could move freely in the Small World system during the experiment, the two sister rats served as social partners and the movement of these two animals was restricted to their cage (type 2154F, 482 × 267 × 210 mm). When tested in small groups, rats and hens were kept in their corresponding Small World system for 10 consecutive days, too. The rats had prior experience with the system from their individual observation. Rats were transported between the housing and the experimental room as a group either in a plastic cage with litter or on the shoulders of the experimenters, to where they would climb voluntarily from either the home cage or the Small World system. The hens were completely new to the system to avoid additional transports between the housing and the experimental room. They were transported as a group in a portable cage.

To avoid a systematic bias in the choice of particular resource cages due to their position in absolute space, the *location of the resource cages* varied between individuals and groups and care was taken not to repeat the positions of the cages (Tables S1–S3). For the observation of the individual rats, each animal in a group was assigned a different position of the cage for social contact (i.e. three different positions per group) and all four possible positions in the rack (related to an asymmetric connecting tube; see information on resting cage in Methods S2) were used three times across all animals. The remaining resources were sorted based on random numbers and assigned to the remaining positions for the first animal. This procedure was repeated for each focal rat with the side

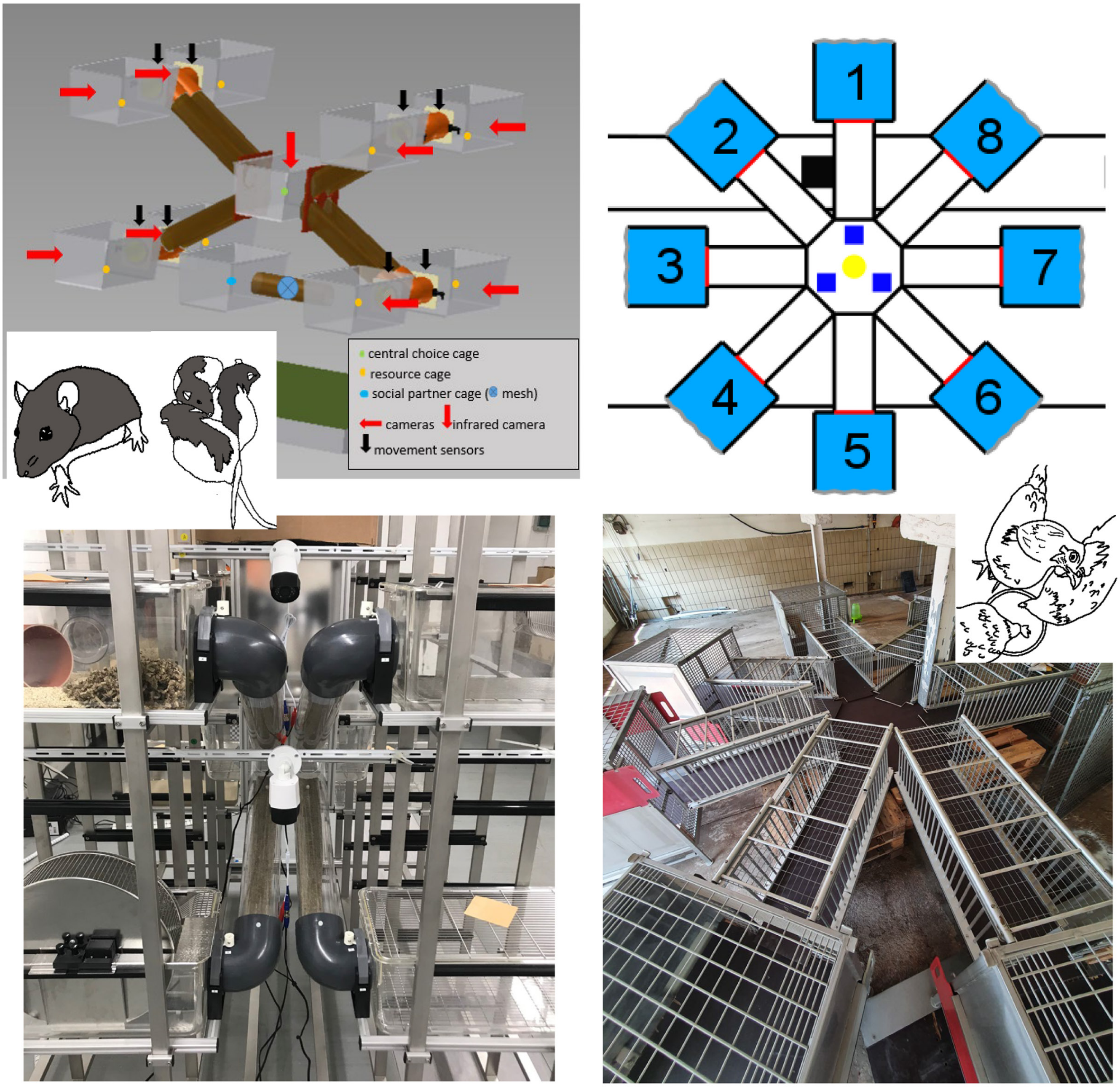

FIGURE 1 Small World Systems for rats (left) and hens (right), schematic drawings (top), and photograph (below). Rats: schematic drawing shows configuration for single rats, photograph for small groups of rats (specifically the position of the white video cameras). Hens: light blue rectangles: resource cages; dark blue squares: camera positions; yellow point: position of the light. See text for further descriptions.

condition that each resource was observed at least once and a maximum of two times in every position across all rats. For the small groups of rats, the four potential positions of the resting cage were assigned to each group first and the other cages were then chosen with the constraint that every group had a different arrangement of resource cages. In the hens, the perching cage was installed in one fixed location and could not be easily moved. All other resources were installed in the remaining cages specific to each group and placed in such a way that their location and their nearest neighbours varied across groups.

For the observations of individual rats, we rotated through groups 1 to 4 three times to use all rats as focal animals. Within a group, the testing sequence was chosen randomly by rolling a dice. This meant that rat 1 of group 1 was tested first, then the 1st rat of group 2, the 1st rat of group 3, the 1st rat of group 4 (first period), followed by the 2nd rat of group 1 (second period) and so on. This resulted in a total of 3 periods (each with one of the three rats per group) of 4 times 10 testing days each (covering the four groups). Accordingly, the individual rats had a minimum rest duration of 30 days in the housing cage between the different focal animals of that group (the time needed for the experiment for the other three groups) to keep stress levels as low as possible.

All animals and groups were observed for roughly 23 h a day. In the remaining approx. 1 h starting at 09:00 (rats) or 13:00 (hens), the animals were checked for health, the technical equipment was checked, rats were weighed, marking of the cages with faeces and urine was documented as well as cages cleaned and resources replenished when necessary. Rats were also handled for approximately 5–15 min. In the first experiment, the social partners also had a minimum of 1 h in a run so that they could move unrestrictedly on a daily basis (190 × 100 cm, situated in a corner of the experimental room and equipped with hiding opportunities). The focal rat was put in a separate cage (1354G Eurostandard Type IV S, Tecniplast, 598 × 380 × 200 mm) equipped with litter, sizzle nest and a plastic tube (diameter: 10 cm; length: 18 cm) and provided with basic feed and water ad libitum (on a raised mesh lid; -123, Tecniplast). The rats of the small groups spent approx. 1 h during the daily check in a separate cage of the type used for housing but with fewer objects and materials (two plastic tubes as hiding opportunities, a cup of basic feed, see description of feed during housing above, and water). Rats were put back into the Small World system between 10:00 and 11:00. Individual rats were put back into the Small World system into the social contact cage, while small groups of rats were put back into the cage with nesting material.

The hens were locked using a barslider in the cage where they were at the moment of the daily check and cleaning. They remained in the Small World system to avoid unnecessary stress by daily handling. Usually, the hens were locked as a complete group of three. Exceptions were in group 1 and group 3, where the hens split up on one day each (two and one hen), so that they could not be locked together in one cage. When the Small World system had been cleaned and all resources had been replenished, the slider was pushed back, and the hens were allowed again to move freely in the system (at approx. 14:00).

2.4 | Data collection

During the experimental period, rats were weighed daily (Etekcity EK6211-S, Vesync Co., Anaheim CA, USA) while the resource cages were checked and cleaned each day. In addition, all rats were weighed every 10 days when the group in the experimental system changed, to furthermore reflect the weight development during phases in the housing cages. Each hen was placed on a commercial scale and weighed on the first and final day of the 10-day experimental phase. The soiling by faeces and urine as a potential marking behaviour was documented daily for each cage (see Methods S3 for details) and eggs were counted for the hens, their number recorded, and then removed.

For the observations of individual rats, movements at the entries of the different resource cages, the paths through the central choice cage, and the use of the running wheel were recorded automatically and additional videos were recorded. The video recordings allowed for complementation of the automatic data when the technical equipment failed (see Methods S3 for details on the basic recording and data complementation). Both movement sensor and video recording data were missing for 10 days (two rats of one group with one missing day each, and one rat each from two more groups with three and five days missing, respectively). One rat fell sick with no relation to the experiment on her first day as a focal rat. Data of this rat were not considered for analysis. This resulted in a total of 100 (of a planned 120) rat-days stemming from 11 rats for evaluation.

To record data of the small groups of rats, four cameras (of the same type as above) were installed onto the rats Small World system above the transparent tubes leading to the resource cages. Each camera captured the entrances towards two resource cages each. Three cameras (of the same type) were attached on the ceiling above the Small World system of the hens. One camera captured two cage entrances/exits and two cameras surveyed three entrances each (Camera 1: cages 1, 2, and 8; camera 2: cages 3 and 4; and camera 3: 5, 6, and 7; Figure 1, right; Figure S1, right).

Based on the video recordings, entries to and exits from the resource cages were recorded including the exact time and the identity of the individuals. For the rats, entering and leaving a cage was defined in the same way as for replacement data of the individual rats (see Methods S3). To determine precisely when the hens had entered or left the cages, a white line with non-toxic varnish was drawn at the threshold of the resource cages. This line clearly stood out from the dark floor and could easily be identified on the video footage. If one foot of a hen was on or above the white line, the identity of the hen and an entry to the resource was recorded. The same criterion (one foot of a hen was on or above the white line) applied for leaving a resource. For the details of the video analysis using the software BORIS (Friard & Gamba, 2016), see Methods S3.

During the observations of individual rats, we collected faecal samples for the analysis of corticosteroid metabolites (FCM; Lepschy et al., 2007). Eight samples per experimental phase of each of 10 focal animals (80 faecal samples in total) were collected and analysed. The phases of two rats could not be evaluated: the very first rat, because we only started collecting faecal samples systematically from the second rat onwards and the rat that fell sick.

Each sample consisted of at least three fresh faecal boli of either the focal animal or the social partners. Samples were collected at the end of the 24 h period of days 1, 3, and 10 (i.e. in the mornings of days 2, 4, and 11; 2 types of animal x 3 sampling days = 6 samples/each focal rat). In addition, a collective sample for all three animals was taken from the housing cage on the morning of the first experimental day (before the rats were moved to the experimental system) as a baseline measure and 24 h after re-locating the animals of a group to their home cage (plus 2 samples/each focal rat, Figure S19). All samples were frozen immediately at −20°C (for their preparation and analysis, see Methods S3).

All samples were assayed in duplicates. This allowed us to separate the samples into two data-sets without re-using any individual data point (for details, see Figure S19). In one data set, we wanted to reflect the time course throughout the experimental phase from day 1 to day 3 and to day 10. In a second dataset, we wanted to reflect the change from the housing cage to the experimental system and back.

2.5 | Data preparation

For the observation of individual rats and based on the automatic recording of the use of the running wheel, we calculated the variables average wheel use [sec/h] and average speed of the running wheel [No. turns/s] for each individual rat and day.

Still for the observations of individual rats, movement sensor data from the entries to each resource cage was automatically stored in a text-based file with a timestamp for each activation. From this and based on an R script, we calculated the frequency at which rats entered a resource cage (after having been in the central choice cage) as a general indicator of activity (number of entries divided by the duration of the observation day). We calculated further the frequency of resource use given by the average number of visits per hour per experimental day for each resource and focal rat. Similarly, we calculated the relative duration of resource use per experimental day for each resource and focal rat. To do so, we summed the durations of all single visits to each resource and divided this sum by the total duration of the observation for a given day (which was around 23 h, see Section 2.3).

Furthermore, we calculated the "choices" of the focal rats, which we defined as the durations between the first activation of the movement sensor of one resource cage until the first activation of the sensor at the following resource cage, independent of whether it was the same cage again or a different one. Additionally, the duration of "decisions" was defined in respect to three separate periods: First, the time between the last activation of the movement sensor at the exit of a resource cage until the first recording of the infrared camera in the central choice cage ("exit" from resource). Second, the time spent in the central choice cage ("stay"). Third, the last recording of the infrared camera in the central choice cage until the first activation of the movement sensor at the entry of the following cage ("entry" to resource).

In the central choice cage (period of stay), the paths of the rats were recorded in detail. Here, we visually categorised the paths for each rat and each possible transition (type of preceding and following resource) in respect to their convolutedness.

The following variables were additionally kept in the data sets: group identity (1–4), individual focal rat (1–11), and day number (1–10). Additionally, for choices and decisions, some more variables were necessary: current resource cage, subsequent resource cage, whether the observation was censored (see Methods S4), phase of experiment (early: days 1–3, intermediate: days 4–6, and late: days 7–10), and period of decision (exit, stay, entry). For all these measures, we had a total of 100 rat-days available for evaluation (see Section 2.4).

For the data of the small groups (of rats and hens), the raw data exported from BORIS was further processed using an R script. Data were exported from BORIS for the observations of each group, day and camera as a csv-file each. These files contained the start-time for the day (set in BORIS) and, in the columns, the time since the start time, the total length of the observation, the subjects (the individual animals), the behavioural categories (the resource cages captured by the respective cameras) and the status ("start" or "stop" reflecting entries to and exits from a resource cage).

BORIS transcribed the analysed video material with a frame rate that differed slightly from the actual rate achieved with our video equipment. Therefore, an elongation factor was determined as the ratio of the actual total time of each analysed group, day and camera divided by the total length of the observation as measured by BORIS. Accordingly, this elongation factor was specific to each csv-file and was either around 0.9 or 1.3 depending on the recorder. The times recorded by BORIS and subjected to this correction factor were very close to the time-stamps in the videos (differing a few seconds at the most) and were used for all further evaluations.

To correct mistakes that occurred while recording the cage visits, e.g. caused by the misidentification of an animal, the data of each day was checked for every other state being a "start" and every other state being "stop" (entering a resource cage had to be followed by exiting a resource cage). If such errors occurred, the videos were watched again, and the errors corrected.

Again, we calculated the overall frequency of visits to the resource cages, frequencies and durations per resource as well as choices and decisions (see Section 2.5 for the individual rats). For the small groups, decisions were defined as the duration between exiting one resource cage and entering the following resource cage. The following additional variables were kept in the data sets: group identity, subject identity, day number (1, 3, and 6), calendar date, an identifier for each observation day of a given animal, and, for choices and decisions, the current resource, and following resource.

In addition, we calculated the synchrony of visits to the different resources for the small groups. To do so, we first calculated to the nearest second how long one, two or all three animals visited each resource on each day. Based on the individual daily durations of the visits to the different resources, we calculated expected values for this usage (alone, two, or all three animals) based on the assumption that the animals moved independently. From this, we calculated a ratio of observed to expected durations of visits to the different resources either singly, in pairs, or with all three animals at the same time.

2.6 | Statistics

For these initial studies, we did not conduct any kind of formal sample size calculation but we expected to be able to reasonably estimate temporal effects within the 11/12 animals per species given the resulting error degrees of freedom in our models (as described below). Animal weights, soiling of the resources, laying activity and the number of changes between different resources were only evaluated descriptively.

Data from these experiments were analysed using generalised linear mixed-effects models in R versions 4.0.3 to 4.2.2 (R Core Team, 2021, 2022). We used package blme (Chung et al., 2013; extending package lme4, Bates et al., 2015) for the total activity, the daily frequencies and durations of visits to specific resource cages, as well as synchrony. Moreover, we used package brms (Bürkner, 2017, 2018) for analysing the durations of choices and decisions. For the details of the models set-up for the different outcome variables, see Methods S4.

We used sum-contrasts for all categorical fixed effects and normalised continuous fixed effects. *p*-Values for the blme models were calculated using parametric bootstrap (package pbkrtest, Halekoh & Højsgaard, 2014). Before calculating *p*-values for single fixed effects in the multivariate models, we also calculated a global test, comparing the maximum model with the null model (including an intercept only as the fixed effect and the identical random effects as in the maximum model). Confidence intervals were calculated also based on a bootstrap approach. Instead of using *p*-values for reflecting the uncertainty in the brms models, we relied our judgement on the credibility intervals resulting from these models.

In all models, assumptions were checked based on the approaches provided by package DHARMa (Hartig, 2022). Except for the models on synchrony, we did not detect any major deviations from the assumptions in the *blme* models. Even in the models on synchrony, the model fit followed closely the raw data. Accordingly, we did not develop these models further. In addition, there were some systematic patterns in the residuals in the *brms* models, which seemed to be related to the aspect of censoring in the data. Again, the model estimates seemed to follow the raw data well, such that we did not follow-up on these deviations in the residuals.

3 | RESULTS

In this section, we present some data readily available with the Small World system and their evaluation to indicate the richness of data that can be collected in such systems. This section can accordingly be considered as a template for more extensive studies using Small World systems. An outlook of additional potential data is given in Section 4.

The *total activity* as reflected by the average number of resource cages visited per hour, decreased from day one to day two and then remained on a similar level for individually tested rats (effect of day: $p=.001$; Figure 2, left-top). The duration of running wheel use remained constant throughout the experiment (effect of day: $p=.84$; Figure 2, left-middle). Running wheel speed increased markedly until day three and continued increasing until about day seven and then remained at this level until the end of the experimental phase (main effect day: $p=.001$; Figure 2, left-bottom). The total activity decreased in the groups of rats ($p=.07$) and was relatively constant with the groups of hens ($p=.86$; Figure 2, right).

The *daily frequency of resource use* by the individually tested rats, i.e. the number of visits per hour per day, was highest in all resource cages on the first day and relatively constant for the rest of the experimental phase (global test: $p=.001$, main effect observation day: $p=.001$; Figure 3 left). Rats visited each resource cage at least once a day throughout the experimental period. The frequency of resource use was relatively high in the resource cages running wheel, nesting material, social contact, intermediate in the resource cages feed and water and lower in the resource cages of predator odour, novel object and foraging (main effect resource type: $p=.001$). The resource cages running wheel, social contact, nesting material, water, and feed had a higher daily frequency at the first experimental day than at the following days compared to the resource cages predator odour, novel object, and foraging (interaction: $p=.001$). Additionally, the detailed development along the experimental days showed two peaks for the novel object on days 5 and 8, when the novel objects were indeed new. The daily visiting frequency to the single resources decreased in the small groups of rats (global tests: $p=.001$; main effect day: $p=.053$, interaction $p=.21$) but all resources were visited at least once on each day by all rats. The predator odour and the empty control were visited most rarely, the running wheel and nesting material most often (main effect type of resource: $p=.001$; Figure 3, middle). In the hens, there was no general pattern in the course of the experiment (global test: $p=.001$; main effect day: $p=.20$). The frequency of visits decreased for the laying nest, novel object, and predator odour, whereas it increased for water (interaction: $p=.001$). Overall, the resources novel object, predator odour, the laying nest and perching were visited most rarely, and feed most often (main effect type of resource: $p=.001$; Figure 3, right).

The *daily duration of resource use* in the individually tested rats averaged across all resources was relatively stable across experimental days (global test: $p=.001$, main effect observation day: $p=.99$). But the development of daily duration differed between the different resource cages (interaction: $p=.06$): e.g. nesting material had a constantly high duration, whereas predator odour, novel object and foraging had constantly low durations with peaks on the days when fresh predator odour, a new novel object, or treats in the foraging cage were available, respectively. Complementary to these peaks, we observed dips in the resource cage running wheel and social contact on the days with a new novel object as well as in the resource feed on the days when a treat was hidden in the foraging cage. The longest average daily duration of resource use was seen for the resource nesting material, the shortest ones for predator odour, novel object and foraging (main effect resource type: $p=.001$, Figure 4, right). The duration that rats in small groups spent with the nesting material was the longest – the shortest durations were spent with the empty control, the predator odour, foraging, and water (global test: $p=.001$; main effect type of resource: $p=.001$). Durations did not change consistently across days (main effect day: $p=.44$, interaction: $p=.23$; Figure 4, middle). The hens spent the longest durations with the feed and were observed for the shortest durations with novel object, predator odour, and sand bath (global test: $p=.001$, main effect type of resource: $p=.001$).

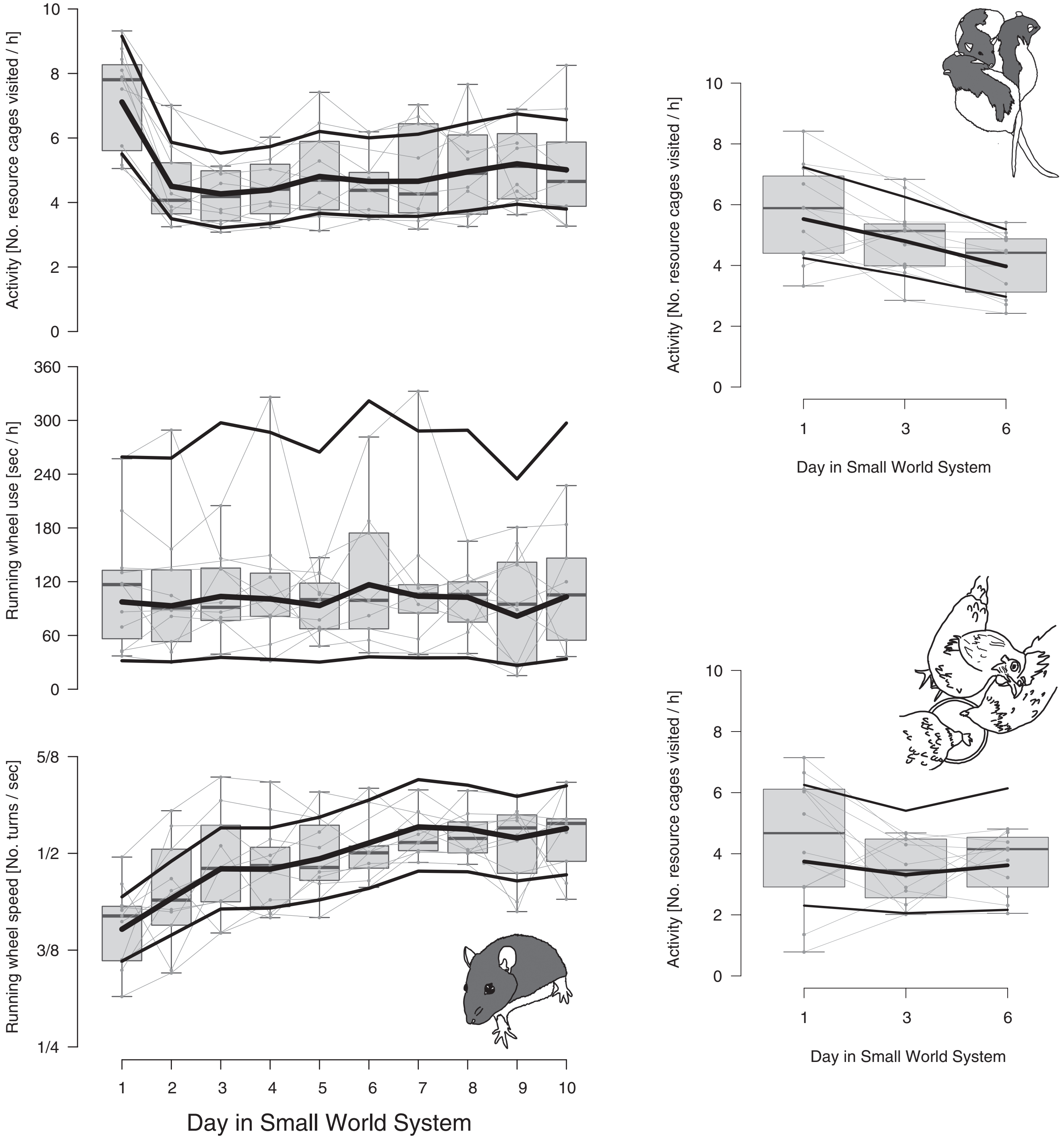

FIGURE 2 Development of general activity as expressed by the number of resource cages visited on average per hour (top), duration of running wheel use (middle) and running wheel speed (bottom) of the single rats throughout the 10-day experimental phase (left). General activity for days 1, 3, and 6 in small groups of rats (top, right) and hens (bottom, right). Raw data are shown as boxplots indicating the median, the quartiles, and the data range. Thin lines: individual data. Bold line: model estimates; bold, thin lines: 95% confidence intervals.

The durations with feed, water, and foraging increased across days, whereas the durations of visits to the other resources did not show a systematic pattern (main effect day: $p = .78$, interaction: $p = .005$; Figure 4, right).

So far, all results were described from the point of view of the single animals. Yet in the 2nd and 3rd experiments, the animals lived in small groups of three animals (one group of two in the rats) throughout the experiment. Accordingly, we also looked at the *synchrony* among the animals of each group. The rats showed diverse patterns in their synchrony across days and resources (global test: $p = .001$; three-way interaction: $p = .037$). Feed and foraging were visited with high synchrony. Water and running wheels were initially visited with high synchrony but high synchrony was avoided on day 6. Predator odour and the empty control were visited more often

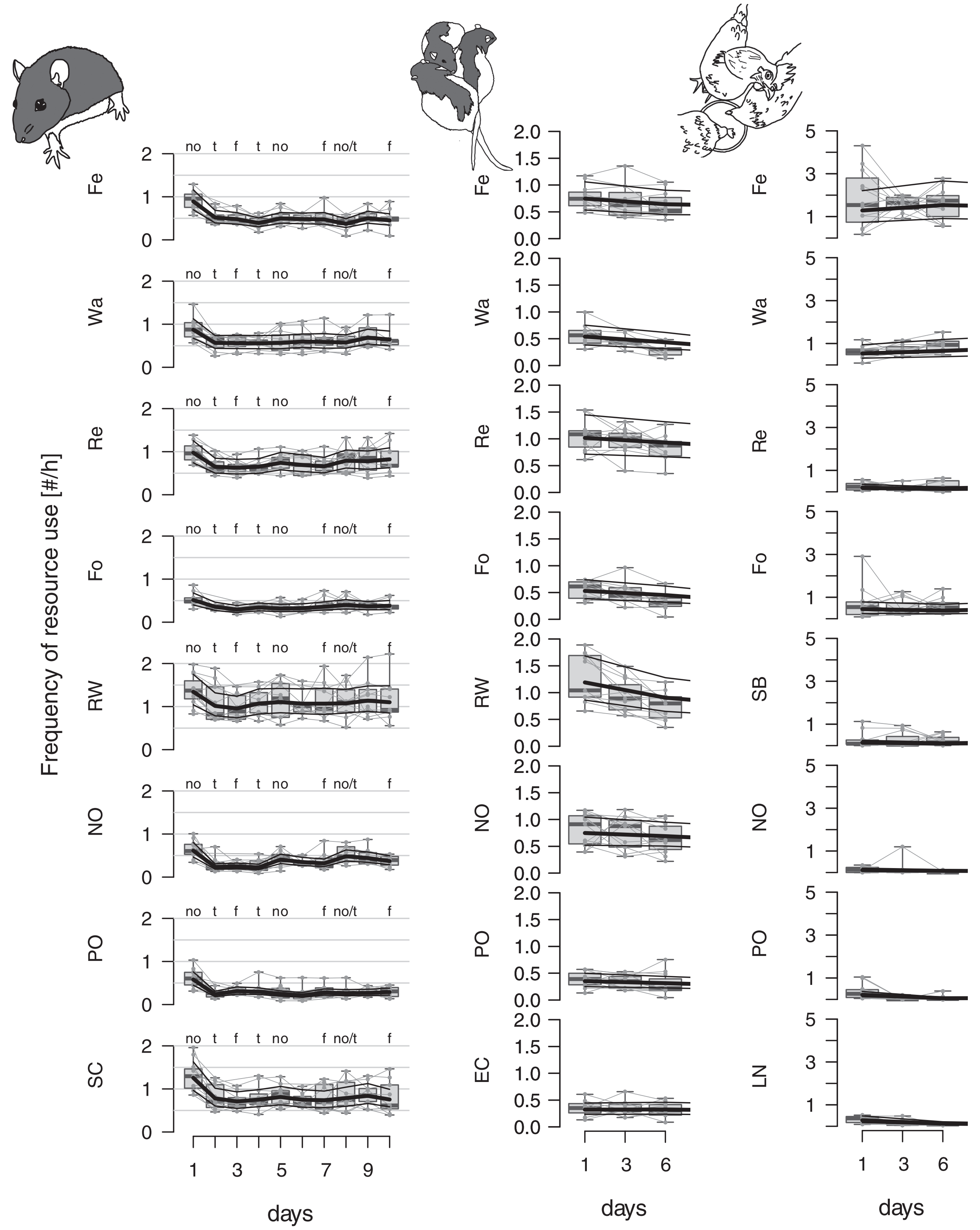

FIGURE 3 Frequency of visits to the different resources for days 1 to 10 in single rats (left) and days 1, 3, and 6 in small groups of rats (middle) and hens (right). The frequency is indicated as the average number of visits to different resource cages per hour for each day. For the single rats, the presentation of new novel objects (no), the provision of treats in the sand (t), and the olfactory presentation of fox urine (fo) is shown for specific days. Please note the different scales of the *Y*-axes. Resource cages: feed (Fe), water (Wa), resting (Re), foraging (Fo), special activity (RW: running wheel, SB: sand bath), novel object (NO), predator odour (PO), remaining cage (EC, empty control; LN, laying nest; SC, social contact). Raw data are shown as boxplots indicating the median, the quartiles, and the data range. Thin grey lines: individual data. Bold line: model estimates; bold, thin lines: 95% confidence intervals.

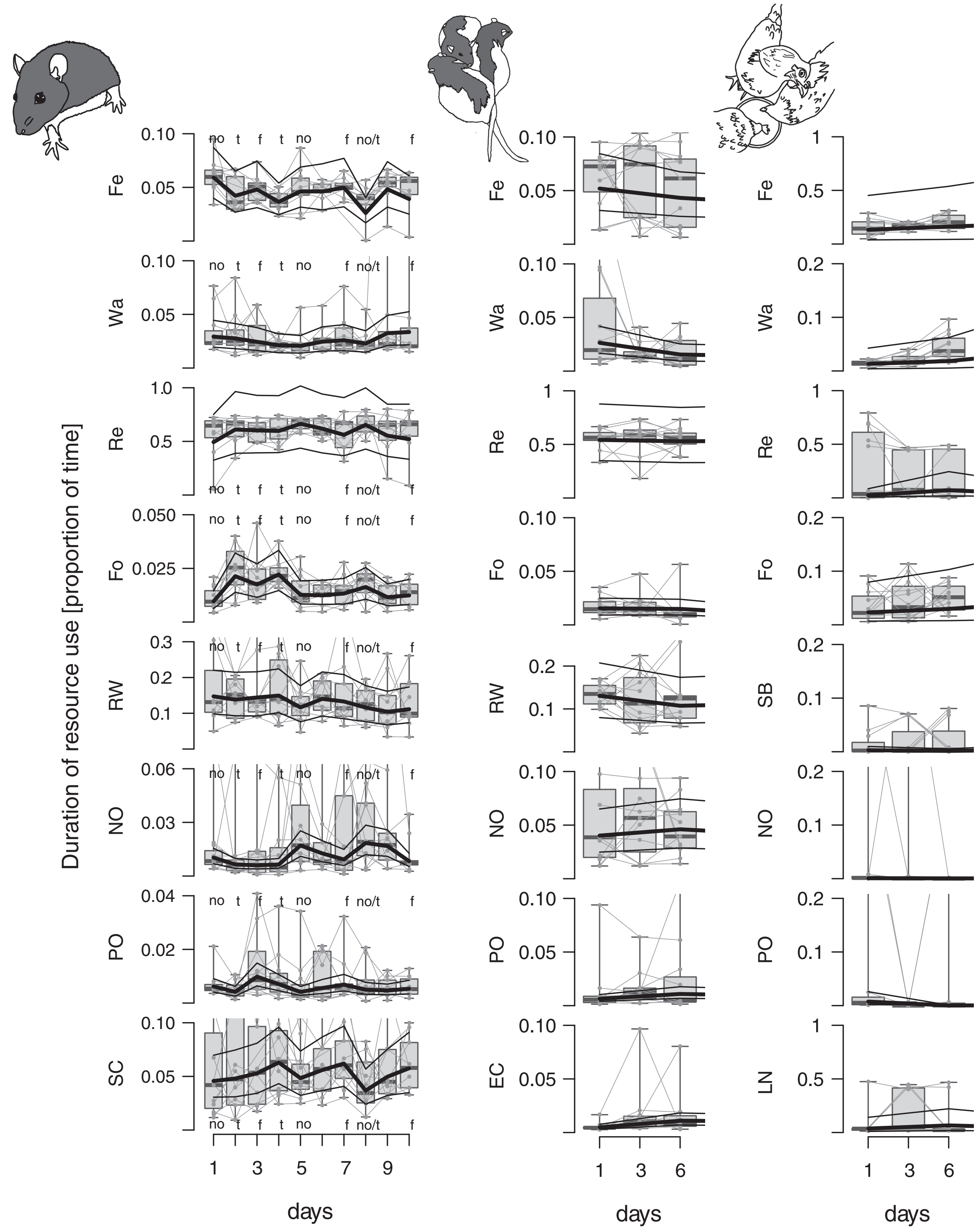

FIGURE 4 Duration of visits to the different resources for days 1 to 10 in single rats (left) and days 1, 3, and 6 in small groups of rats (middle) and hens (right). The duration is indicated as the proportion of the total observation time spent in the different resource cages for each day. For the single rats, the presentation of new novel objects (no), the provision of treats in the sand (t), and the olfactory presentation of fox urine (fo) is shown for specific days. Please note the different scales of the *Y*-axes in the subplots. Resource cages: feed (Fe), water (Wa), resting (Re), foraging (Fo), special activity (RW, running wheel; SB, sand bath), novel object (NO), predator odour (PO), remaining cage (EC, empty control; LN, laying nest; SC, social contact). Raw data are shown as boxplots indicating the median, the quartiles, and the data range. Thin grey lines: individual data. Bold line: model estimates; bold, thin lines: 95% confidence intervals.

as pairs than expected but more rarely than expected when alone or as triplets (Figure 5). In the hens, the pattern of synchrony was less complex (global test: $p=.001$; all two-way interactions except the interaction between day and usage [degree of coordination]: $p=.001$; three-way interaction: $p=.74$). In the hens, too, there were resources visited with a high degree of synchrony (water, feed, foraging, and sand bath), resources, where a high degree of synchrony was avoided (laying nest), resources, which were visited at random (perching), or which were visited more rarely than expected overall (novel object, predator odour).

The *number of changes* between the different resources was consistent across individuals, groups, and days within each of the experiments (Figure 6, Figures S2–S4). The most frequent transitions were observed for the individually tested rats between the resource cages running wheel, water, feed, and social contact. Repeated visits of resource cages were noted for the social contact, running wheel, feed, water, and nesting material. Rats in small groups showed the highest number of changes between running wheel, feed, nesting material, and novel object. Hens changed most often between feed, foraging, and water, often re-visiting these resources directly after having left the corresponding cages.

These changes between resources were visualised in the course of time (Figures S5–S7), and this time course was evaluated based on the multi-state parametric survival analysis. Basically, these models estimated (differences between) the specific durations of how long animals stayed with a given resource until they went to another resource (*choices*, defined as the time between entering one until entering the following resource cage). This estimate was translated into survival curves based on the chosen parametrisation (indicating the fit of the model; diagonal in Figure 7) and into relative hazards, indicating how much more probable a change from a given resource to a follow-up resource was in comparison to a change from the same resource to another follow-up resource (off-diagonals in Figure 7). Relative hazards are of specific interest when one transition was clearly more (relative hazard >1) or less likely (relative hazard <1) than another (cp. the thick black lines at $Y=1$ in Figure 4). In Figure 7, an example is given for the transitions from one resource, resting cage, to all other resources for the individual rats in the early phase (for the complete set of transitions, see Figures S8 and S9). It is visible in this example that hazards for the transition from the resting cage to any other resource was more likely than the transition from the resting cage to visiting the resting cage again (column Re in Figure 7; and vice-versa as seen in row Re in Figure 7). Overall, the relative hazards changed only little between the early, intermediate and late phases. In addition, many of the relative hazards were close to 1, as seen in all other relative hazards in Figure 7. In the small groups of rats, this analysis showed mainly that they rarely re-visited the resource(s) that they had just left and were less likely to visit novel objects, empty control and predator odour after each other (hazards <1). The hens' relative hazards showed that they were very likely overall to visit feed and water (often re-visiting them directly after leaving), and were unlikely to visit novel objects, predator odour, sand bath, and the laying nest.

As described above, multistate parametric survival analyses evaluate the durations in certain states. This means that instead of survival curves and relative hazards, these durations can be shown directly. We used this alternative for presenting the results for the *decisions*. In the individual rats, the "stay" part of the decisions, i.e. the duration that the rats spent in the central choice cage, was evaluated in dependence of the resource where the rats were coming from and the resource where they went to next (Figure S10). After all resource cages except running wheel re-entering that same cage again happened only rarely. We could not see any systematic differences in the duration of stay in the central choice cage depending on which transition was made. Mainly, censored observations led to long estimated durations in the central choice cage. We evaluated the "exit" part (last activation at a resource cage to first activation of the movement sensor in the central choice cage) and the "entry" part (last activation in the central choice cage until first activation in the following resource cage) of the decisions in the same way (Figures S11 and S12). Overall the exits and entries were short and there seemed to be little consistent differences between the duration of exits and entries dependent on which resource cage the rats were coming from and going to. When testing the small groups, the durations of stay with the different resources (choices) showed highly similar patterns as the *decisions* (time spent between resource visits; not shown). Accordingly, the decisions were also rather undifferentiated (Figure S13). Specifically, rare (censored) transitions showed long decision times and re-visits to the same resource in the hens showed short decision times spent in the choice cage.

For the choices in individual rats, the estimated general variability between subjects was 1.49-times higher than within the subjects (95% credibility interval: 0.49–5.85). For the decisions, the exit, stay, and entry between- to within-subject variability was 0.66 (0.19–2.43), 1.97 (0.69–7.43), and 1.16 (0.38–4.16), respectively. For the choices in the small groups, the estimated general variability between subjects in rats and hens was 74-times (95% credibility interval: 5–26,380) and 1.69-times (0.07–12) higher, respectively, than within the subjects. For the decisions the estimated overall variability between the subjects for rats and hens was 8-times (1–199) and 1.67-times higher (0.04–25), respectively, than the variability within the subjects.

For the individual rats, we processed the *paths of each decision* in the central choice cage graphically in dependence of the preceding and following resource (Figure S14). We observed different levels of convolutedness for the decision pathways (Figure S15): the most direct paths were observed from feed to water and to novel object, from water to predator odour and novel object and from digging area to novel object. The most convoluted paths were detected from novel object to running wheel, from running wheel to predator odour, from social contact to nesting material and to running wheel.

Overall, there were no strong differences regarding the intensity of marking of the resource cages between the 11 focal rats tested individually (Figure S16). The resource cage running wheel showed a consistently high level of faecal and urinary marking. The resource cages social contact and the central choice cage had a high grade of

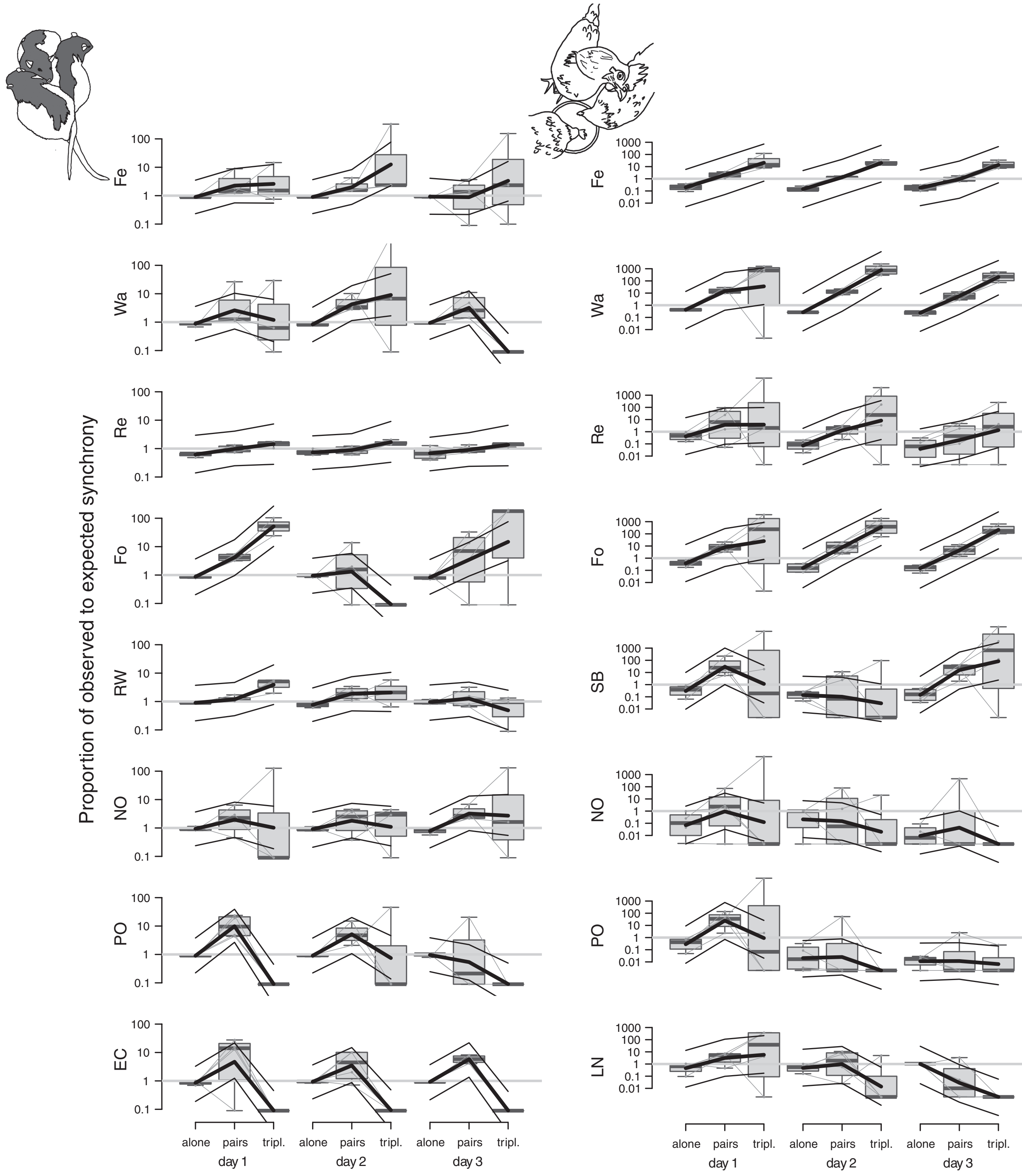

FIGURE 5 Synchrony of the visits to the different resources for days 1, 3, and 6 in small groups of rats (left) and hens (right). Synchrony is expressed as the ratio between the observed proportions of time that one, two, or three animals visited a specific resource and the expected duration based on the assumption that the animals moved independently. Please note the different scales of the Y-axes for rats and hens. Resource cages: feed (Fe), water (Wa), resting (Re), foraging (Fo), special activity (RW, running wheel; SB, sand bath), novel object (NO), predator odour (PO), remaining cage (EC, empty control; LN, laying nest). Data are shown as box plots indicating the median, the quartiles, and the data range. Thin grey lines: data of individual groups. Bold line: model estimates; bold, thin lines: 95% confidence intervals.

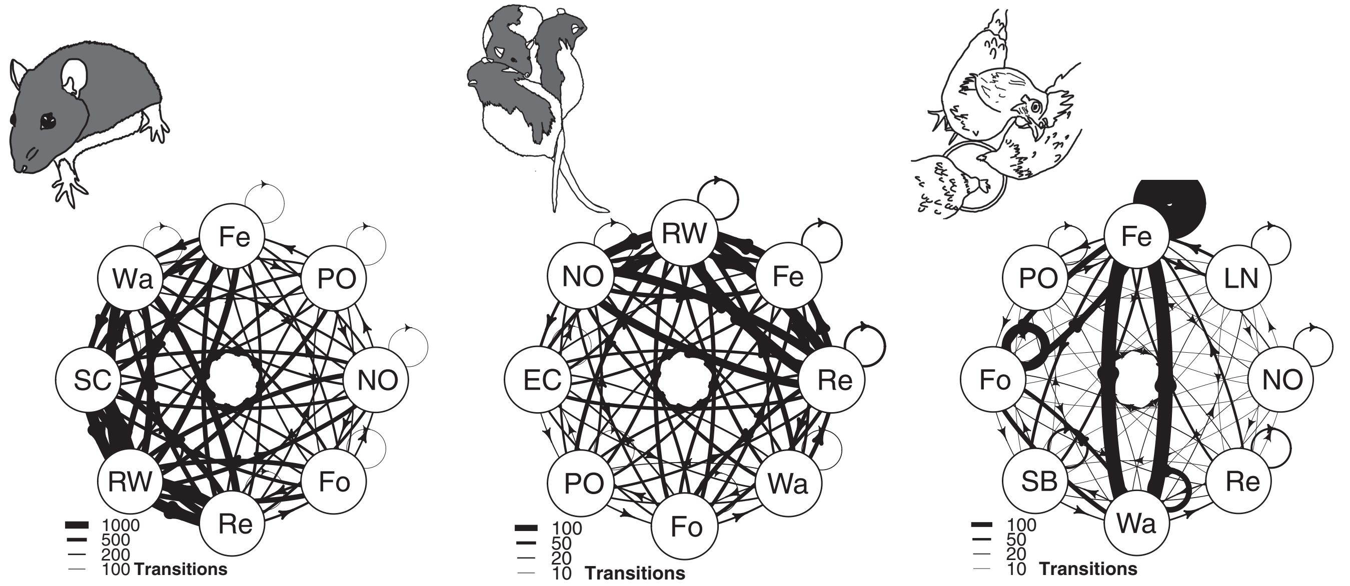

FIGURE 6 Number of transitions pooled for the complete experiments with single rats, groups of rats, and hens (from left to right). Resource cages: feed (Fe), water (Wa), resting (Re), foraging (Fo), special activity (RW, running wheel; SB, sand bath), novel object (NO), predator odour (PO), remaining cage (EC, empty control; LN, laying nest; SC, social contact). For the transitions of each animal and day, see Figures S2–S4.

urinary marking, but only a medium grade of faecal marking. Medium marking of faeces was also found in the nesting material and feed cage. The lowest faecal marking was observed in the resource cages predator odour, novel object and foraging. The lowest urinary marking was seen in the resource cage nesting material and water. With the rats tested in small groups, the marking was strongest in the cage with the running wheel (faeces and urine), with the nesting material (faeces) and in the central choice cage (urine). The central choice cage, the cage with feed and with the perches were most strongly soiled in the hens (Figures S17 and S18). The variation of the cage marking was small between groups for the rats as well as the hens. With few exceptions, each hen laid an *egg* daily and all eggs were laid in the nest.

None of the changes in *faecal corticosteroid metabolite* (FCM) concentration related to the move from the housing cage to the experimental system and back could be supported statistically (global test: $p = .69$). On average, the concentration decreased when rats were moved from the housing cage to the experimental system and increased slightly when moved back independent of whether they served as focal rats or social partners (Figure 8). The FCM concentration decreased slightly from days 1 to 3 and increased again until day 10 but this change could not be supported statistically (global test: $p = .68$; Figure S20).

While testing the individual rats, the average weight in the housing cage increased and levelled off towards the end of our study (global test: $p = .001$; main linear effect of age: $p = .001$; main quadratic effect of age: $p = .031$; grey lines in Figures S21 and S22). When the rats were in the experimental system, their weight was on average slightly lower (main effect of role: $p = .003$). This lower weight was found towards the end of our study, whereas the weight was even somewhat higher during the experiment than in the home cage at the beginning of the study (interaction between role and age: $p = .15$). Finally, the second focal animals tested showed a stronger decrease in their weight towards the end of the corresponding period of the experiment (interaction of squared age, role, and the indicator for the second period: $p = .001$; all other interactions: $p \geq .15$). Almost all rats maintained their weight when tested in the small groups or got increasingly heavier, whereas the hens lost 2% of their weight in the median across the experimental time (see Figure S23).

4 | DISCUSSION

We aimed at complementing current approaches to investigate decision-making in animals with our Small World approach. In this approach, we provided animals with a quasi-natural environment in that a variety of ecologically relevant resources were presented simultaneously in a long-term test. We focused on everyday moment-to-moment decisions that need to be taken frequently by animals in such a nature-like setting while conditions can be easily manipulated at the same time. With these aspects, we could solve many of the issues regarding the study of animals' decision-making process as discussed by Franks (2019), e.g. the dependence of decisions on the momentary motivation of the animals, a narrow selection of choices (possibly hiding some wants; see also Bell, 2024), or variation between individuals (by incorporating this aspect in the analysis). We do not claim that our approach is perfect but we see it as a valuable extension to the tool-box of studying animal decisions.

Overall, our Small World approach seemed promising: the animals habituated to the system within a few days as seen, e.g. in the general activity as well as the frequency and duration of the visits to the single resource cages. Accordingly, experiments with multiple

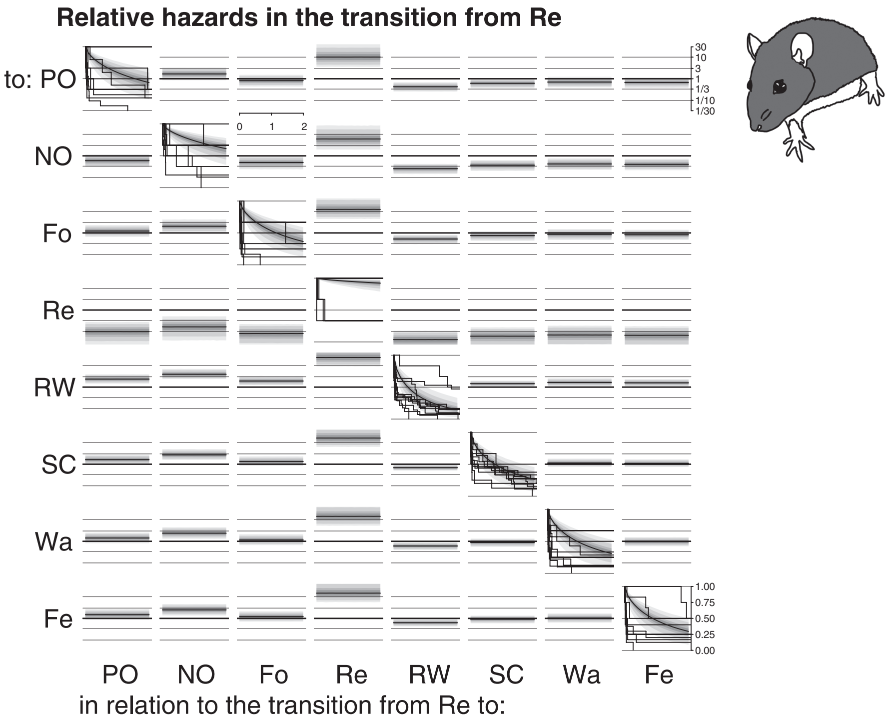

FIGURE 7 Exemplary plot of the relative hazards of choices for the subsequent resource when single rats were in the cage with nesting material in the intermediate phase (days 4–7). All *x*-axis represent time (0–2 h as indicated as an example in the top row). On the diagonal, survival curves are given per individual rat (black lines) for the durations of stay in the resource cage nesting material if the following resource was the one mentioned in the row (or column). For example, the top left subplot shows the survival curve for the durations of stay in the cage with nesting material when this visit was followed by a visit to the predator odour (the respective *Y*-axis scale is shown at the bottom right). On the off-diagonal, relative hazards are shown on the *Y*-axis (the axis range is from 1/30 to 30 times as indicated at the right of the top row; the horizontal black line indicates a neutral relative hazard = 1). The relative hazards are shown between the transition from the nesting material to the resources given in the rows and the transition from the nesting material to the resources given in the columns. For example, the second subplot in the top row indicates the relative hazard Re → PO versus Re → NO. Accordingly, the values above the diagonal correspond to the reciprocal value of the values below the diagonal. Given the model used, relative hazards are constant over time. Model estimates are given in grey shading: the darkest grey line in the middle represents the model estimates, the darkest grey shading corresponds to the 50% quantiles. Further quantile ranges (75%, 95%, and 99%) are given by ever lighter grey shades. Resource cages: feed (Fe), water (Wa), resting (Re), foraging (Fo), special activity (RW, running wheel), novel object (NO), predator odour (PO), remaining cage (SC, social contact). For the complete set of figures for all three experiments, see Figures S8 and S9.

phases varying the conditions between phases should be easy to implement. Throughout the experiment, we observed highly consistent behavioural patterns across animals, groups, and time in both species, which implied that the patterns observed are non-random. In addition, short-term detailed manipulations (introducing novel objects, providing treats in a digging area, and providing stimuli of a potential predator) lead to detailed and detectable changes in the behaviour of the animals indicating how sensitive our approach is. Finally, we could collect data on multifaceted aspects of the use of a variety of resources. These aspects – soiling as a form of marking, frequency of visits, duration of visits, synchrony, and sequential changes – combined with the simultaneous offer of eight resources allowed for an effective assessment of the resources from different points of view.

Another positive aspect in respect to our approach was the fact that we did not find any indication that the individually tested rats showed physiological signs of stress, as reflected by the lack of drastic changes in both, FCM and body weight. We cannot currently substantiate whether this absence of a stress response was due to the experimental conditions (restricted social contact, space, and choice of feed, exposure to a novel environment, novel stimuli, and potentially threatening stimuli) being less stressful than suspected given the way the animals were confronted with them here. Alternatively, the housing conditions provided to the rats outside the experiment may have been enriched sufficiently to make the rats resilient to our experimental conditions (Crofton et al., 2015; Kocahan et al., 2012). Accordingly, it can be stated that the Small World approach (in rats) does not lead to a physical stress response if the rats are housed in an enriched environment as provided here. We did not observe, on average, a clear decelerated growth of or even a clear loss in body weight as another indicator of stress (e.g. Retana-Márquez et al., 2003). The slight reduction in weight (gain) observed in our experiments may well have been due to the increased activity of the animals in the Small World systems compared with their housing conditions. It is advisable though to monitor weight of experimental animals such that the energy provided with the feed can be adjusted if necessary.

Different measures collected in respect to resource use may have indicated the importance of the different resources in the rats. For example, the running wheel, the feed, and the water cage were visited at a high frequency by the rats and the running wheel and nesting material cage also for long durations. For less frequently visited cages, such as the novel object and predator odour, the fact that the rats visited these cages at least once daily throughout the observation days may point towards an importance of collecting information for the rats. Finally, the high synchrony of the visits to the foraging cage indicated the social importance of this cage. In the hens, the different measures contained more similar information in that the feed and the water cages were often visited and for a relatively long duration. The latter was true also for the foraging cage. All these cages were also visited more synchronously than expected. Consistent visits over time, high frequencies of visits, or visits of long durations could each be taken to indicate the importance of resources. By providing such resources, the welfare of the animals could be increased. Yet, these current experiments did not aim at and could not conclusively assess the importance of the resources tested here from the point of view of the rats and hens (see Section 4.1). Moreover, the STRANGEness (Webster & Rutz, 2020) of our selected animals precludes widely applicable conclusions for the time being (see explanations on the selection of our sample in the introduction and the summary statement on the STRANGEness in Section 2.1).

Some issues of interpretation may arise because we qualitatively observed that some resources were used differently than intended at some times. For example, rats rested in the cage with the running wheel or a group of hens stayed in the cage with the novel object overnight. In this respect, care should be taken in designing the resource cages such that resource use is restricted to the specific resource offered as much as possible. This will not always be easily achieved. Alternatively, cages could be monitored by video to observe the detailed behaviour of the animals in the cages. Yet, the time effort to do so would likely be prohibitive as was seen already in respect to recording each entry and exit "only" in the current study. This means that detailed behavioural observations would possibly need to be restricted to some sampling scheme or will be possible more extensively when automated (DeepLabCut, Mathis et al., 2018; incl. DLC2Action, https://github.com/amathislab/DLC2action). Recordings of the entry and exit to the different resources can (and should) be automated in future, e.g. based on RFID identification technology. Even the actual use of certain resources could be automated in similar ways using RFID, accelerometers (at the resources), or light barriers for specific areas in a cage.

In this experiment, we increased the number of available choice alternatives way beyond the classical tests for preferences between two options. Still, the options were finite, and accordingly, a (subjective) selection of options needed to be made in advance. Such a selection may in itself shape the preferences of the animals (Franks, 2019). Still, the eight resources provided were a clear extension of traditional approaches, could cover a much wider range of relevant environmental aspects, and could be provided with a realistic effort and sensible spatial arrangement. Moreover, the exact choice of options can be adjusted or changed from one experiment to another opening further avenues of research.

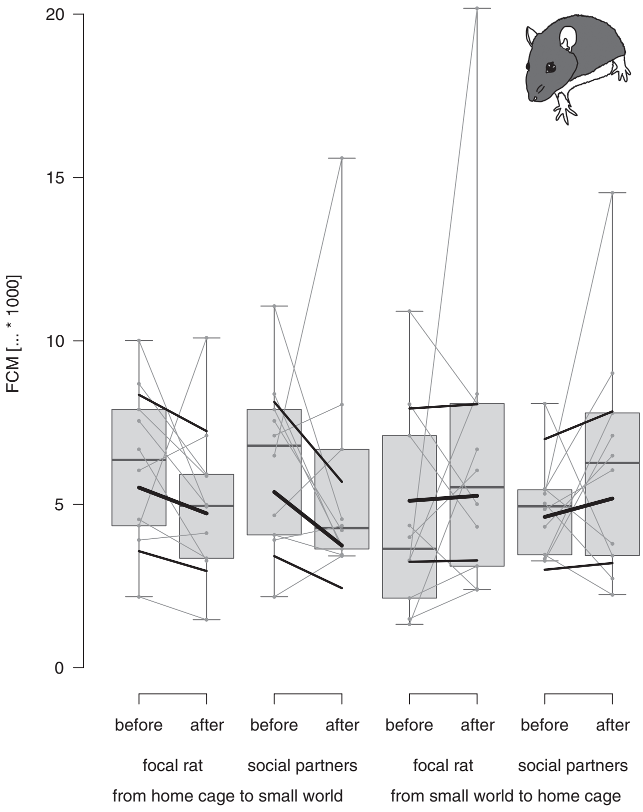

FIGURE 8 Changes in faecal corticosteroid metabolite (FCM) concentrations (ng/g) when focal rats and social partners were either transferred from the home cage to the Small World system or vice versa. Data are shown as box plots indicating the median, the quartiles, and the data range. Thin grey lines: individual data. Bold line: model estimates; bold, thin lines: 95% confidence intervals. For the development of FCM concentrations in focal rats and social partners from days 1 to 3 and 10 of the experimental phase, see Figure S20.

For the analysis of consecutive sequences, multi-state parametric survival analysis was used (Gygax et al., 2022). We applied this method to evaluate the choices as defined by the continuous non-interrupted sequences of visits to the different resource cages. These sequences were reflected by the duration of the entry to one resource until the entry to the next resource cage. Given that the overall pattern of choices and decisions (the duration between exit of one and entry to the next resource) were similar, future studies may be well advised to define choices and decisions independently. This could be achieved if the durations of the choices were taken as the time between an entry to one resource until the exit from the same resource. Yet, the application of such sequential analyses may even need to be questioned more fundamentally. The models included a high number of estimated parameters. The number corresponds to at least the number of potential transitions between states (here between the resource cages) and, accordingly, amounted to 8×8 resources = 64 transitions here. This provided a potentially differentiated picture of the transitions, but presenting this picture is a challenge (cp. Figure 7). In addition and for a stable model estimate, a high number of observations (a high density of the data) is necessary. Ideally, all the potential transitions should be shown several times by each animal on each day. The common call for "more data" is not productive here because all the data shown by the animals is used already. The only option would be to pool data across several days as was done here. Not even this approach leads to automatic success. Even with the pooled data, the models were difficult to estimate and potential day-to-day changes were blurred. Moreover, a central issue, how the decisions vary between individuals could not be addressed due to the necessary complexity of such a statistical model. Due to all these reasons, such a detailed analysis must perhaps be viewed as a good conceptual idea, which is, however, difficult to implement in praxis.

4.1 | Outlook

The (outcome) variables presented here resulted directly from the proposed observations of the continuous visits to the different resources. A multitude of further and more elaborate measures can be conceived. For example, it can be studied with our approach how (efficiently) animals explore the Small World system based on the sequence of the first visits to the different resource cages (in a similar way as in Rosenberg et al., 2021). If such an aspect is of interest, the location of the different resources can be changed repeatedly in the course of an experiment and the exploration and adjustment in behaviour to the new spatial arrangements can be studied. Similarly, circadian behavioural patterns can be addressed, or the paths in the choice cage can be studied more quantitatively (Choi et al., 2021). In addition, the social context of decision making can potentially be studied in more detail in, e.g. asking whether specific animals may often "lead" the way or "follow" in visiting the different resources. When animals are tested in groups, competition for access to the resources could potentially occur although such competition may have been low in our experiments due to the use of sister animals (in the rats) and long-term stable groups (in the rats and hens). Our data showed that the individuals seemed to avoid each other for some resources. This could have been the result of a voluntary decision as we did not have any obvious indication in our experiments that single animals would limit the access to the resources for other animals. Yet, such aspects of competition could be studied in detail by, e.g. providing the same resource in one cage only or, alternatively, in several cages allowing access to the same resource by several animals at the same time.

In respect to welfare, questions going beyond the value of resources such as whether the ability to express preferences ("agency", e.g. Špinka, 2019) in itself is a positive contribution to welfare are important. The Small World system may also provide a framework for such questions in that, e.g. animals living in the Small World can be compared to some sort of yoked controls in respect to changes in their affective state (e.g. by applying a cognitive judgement bias paradigm, Lagisz et al., 2020).

The Small World approach will become specifically interesting, too, if different phases in an experiment are included in order to evaluate, e.g. the choices among different sets of resources or changes in the behavioural budget if different types of resources (such as resources directly relevant for survival or those addressing further needs) are increasingly costly to be accessed (see the last paragraph of this section). Moreover, we have concentrated on the "wanting" aspect so far. If the resources offered in the cages were varied in an experiment, "liking" (Gygax, 2017), i.e. the animals' reactions to reaching (or even surpassing) their expectations or not reaching what they have become used to ("reward loss"; e.g. Burman et al., 2008) may extend the approach as described here.

Patterns observed can be substantiated in respect to external validity by testing also males and/or animals of different ages. In addition, the cage size for the resources could be varied, such that, e.g. different instances of novel objects, food types, nesting materials, or predator odours could be presented simultaneously in one cage (M. Gygax, personal communication). Furthermore, our approach can be easily adapted for a large selection of different species and is, accordingly, easily open for comparative research on animal decision making.

Although the multifaceted aspects of the collected data shed a differentiated light on the use of the resources provided and allowed for a correspondingly detailed interpretation, they showed also once again the challenge of a large number of indicator variables. In this sense, each resource was a special case and one of the indicator variables may have indicated the importance of any of the resources (see Section 4). In the end, this means that depending on the ecological function, different variables reflecting resource use implicate the importance of the resources from the animals' point of view. The actual value of the resources from the animal's view is, accordingly, not directly reflected by any single measure in the current implementation of the Small World approach.

In the future, we would like to impose a cost for access to the resources in Small World approaches, such that the animals can show how much they "value" each of the resources (Dawkins, 1983; Kirkden & Pajor, 2006; Olsson et al., 2002; Patterson-Kane et al., 2008). In the past, different types of cost such as pressing panels (e.g. Elmore, Garner, Johnson, Kirkden, Patterson-Kane, et al., 2012a; Elmore, Garner, Johnson, Kirkden, Richert, et al., 2012b; Holm et al., 2002; Sherwin, 2007), or exerting a force (e.g. lifting or pushing through heavy doors; mink: Borland et al., 2017; Reijgwart et al., 2016; Wenker et al., 2020) have been used often. Such operant responses need to be trained and the time and effort of training as well as the training itself may influence choices. Moreover, it is not always clear whether the experimental subjects easily understand such a cost and whether they can, accordingly, deal meaningfully with it (Cooper, 2004; Patterson-Kane et al., 2008). A meaningful currency should include relevant ecological constraints such as a physical effort as well as a time investment with an effect on the energy and time budget, respectively (Bell, 2024; Bennie et al., 2014; Dunbar et al., 2009; Dunbar & Shi, 2013). This could be implemented in having animals covering a distance between resources, e.g. using a treadmill. This reflects the situation, in which resources are available at different locations in space and should be easily understood by many animal species (as seen in pigs: Eulert, personal communication; Kosin, 2019; Kosin & Gygax, 2019; Krusch, 2024). Using such treadmills would allow to set-up semi-virtual landscapes with defined and, at the same time, freely variable distances between resources.

5 | CONCLUSIONS

We consider our initial experiments not so much as the basis of a standardised assessment but rather as a conceptual approach and see its merit in applying the ideas in ways adjusted to the specific species and question under study. The basic data collected from the Small World system – individual entry and exit times to the resources – are simple and are accordingly likely to be reliably collected. Validation of such a system will be possible only over time and the course of repeated experiments. This may be slower compared with a standardised approach, but likely to yield results that are externally more valid (e.g. Voelkl et al., 2018).

AUTHOR CONTRIBUTIONS

Fiona Puls: Conceptualization; data curation; formal analysis; investigation; methodology; visualization; writing – original draft; writing – review and editing. **Louisa-Mae Kosin:** Conceptualization; data curation; formal analysis; investigation; methodology; visualization; writing – original draft; writing – review and editing. **Fiona Garbisch:** Conceptualization; investigation; writing – original draft; methodology; visualization; writing – review and editing; formal analysis; data curation. **Chadi Touma:** Methodology; resources; writing – review and editing. **Christa Thöne-Reineke:** Project administration; supervision; writing – review and editing. **Lorenz Gygax:** Conceptualization; data curation; formal analysis; funding acquisition; methodology; project administration; resources; software; supervision; visualization; writing – original draft; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

All authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

The datasets generated and analysed during the current study and the code used for analysing the data are available in the OSF repository, https://doi.org/10.17605/OSF.IO/6TJRN.

ETHICS STATEMENT

The different parts of this project were approved by the university's animal welfare officers and by the responsible veterinary office (LAGeSo Landesamt für Gesundheit und Soziales, Berlin: rats, individual testing, permit no. G003/20; rats, small groups, StN 002/21; hens, small groups, StN 0012/21). The veterinary authority assessed the group studies as animal experiments that are not regulated under the animal protection law because no pain, suffering, or injury of the tested animals was expected in the course of the study.

ORCID

Lorenz Gygax https://orcid.org/0000-0001-8546-2930

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