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Reporting guidelines for terrestrial respirometry: Building openness, transparency of metabolic rate and evaporative water loss data

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A R T I C L E I N F O

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A B S T R A C T

Respirometry is an important tool for understanding whole-animal energy and water balance in relation to the environment. Consequently, the growing number of studies using respirometry over the last decade warrants reliable reporting and data sharing for effective dissemination and research synthesis. We provide a checklist guideline on five key sections to facilitate the transparency, reproducibility, and replicability of respirometry studies: 1) materials, set up, plumbing, 2) subject conditions/maintenance, 3) measurement conditions, 4) data processing, and 5) data reporting and statistics, each with explanations and example studies. Transparency in reporting and data availability has benefits on multiple fronts. Authors can use this checklist to design and report on their study, and reviewers and editors can use the checklist to assess the reporting quality of the manuscripts they review. Improved standards for reporting will enhance the value of primary studies and will greatly facilitate the ability to carry out higher quality research syntheses to address ecological and evolutionary theories.

1. Introduction

Measurements of energy and water exchanges date back to the 18th Century (Lavoisier and Seguin, 1789; Townson, 1799) and continue to be an important skill for evolutionary and ecological physiologists in the 21st Century. For example, the effects of temperature on energy and water budgets have been essential for predicting the impacts of rapid anthropogenic global heating on biodiversity, whether using species-specific empirical data (Bozinovic and Rosenmann, 1989; Swanson and Liknes, 2006; Mckechnie and Swanson, 2010; Seebacher et al., 2015; McKechnie et al., 2021; Alton and Kellermann, 2023) or for developing bioenergetic models (Kearney and Porter, 2009; Riddell et al., 2021; Briscoe et al., 2023). Alongside this, the field of ecotoxicology and disease ecology relies on measurements of energy use (e.g. metabolic rate, MR) and water balance to evaluate species risk to novel toxins and pollutants (Sokolova and Lannig, 2008; Baas and Kooijman,

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2015) and emerging infectious diseases (Agugliaro et al., 2020; Wu, 2023). The same applies to other growing fields such as conservation physiology (Wikelski and Cooke, 2006; Cooke et al., 2013) and macrophysiology (Chown et al., 2004; Ruf and Geiser, 2015; Chown and Gaston, 2016; Wu et al., 2024) in which, through the mechanistic lens of physiology, improve our understanding of ecological and evolutionary responses of different organisms to changes in their environment.

The most widespread approach to quantifying the amount of energy expended over a time in animals is indirect calorimetry (Depocas and Hart, 1957; Koteja, 1996; Withers, 2001; Lighton, 2019). This involves respirometric measurements of oxygen consumption ($\dot{V}_{O_2}$) and/or carbon dioxide production ($\dot{V}_{CO_2}$), from which MR can be estimated if the metabolic substrate can be inferred or reasonably assumed (Withers, 1977; Walsberg and Hoffman, 2006; Lighton, 2019), but see Walsberg and Hoffman (2005). Combined with simultaneous measurements of evaporative water loss (EWL; see Glossary) and body temperature (T_b), respirometry remains an essential tool for several disciplines in biology in the contemporary era, allowing us to advance knowledge in key aspects of ecological and evolutionary theories, including size-scaling relationships, environmental adaptation, and phenotypic plasticity (McNab, 1988; Lovegrove, 2000; Addo-Bediako et al., 2001; McNab, 2002; Chown and Nicolson, 2004; McKechnie and Wolf, 2004; Angilletta, 2009; Mckechnie and Swanson, 2010; Genoud et al., 2018; White et al., 2022).

The need for standardised reporting is well-timed because of the exponential rise in empirical and synthesis studies using respirometry data (Mathot et al., 2019; Arnold et al., 2021; Le Galliard et al., 2021; White et al., 2022; Wu and Seebacher, 2022). A Web of Science search for terrestrial respirometry studies in the field of ecology and evolution (23 November 2023) showed a 158% increase in whole-animal MR studies over the last 10 years (2012–2022; Fig. 1a) and 170% increase in whole-animal water loss studies (2012–2022; Fig. 1b), while the overall publication rate in science is doubling almost every decade (Bornmann and Mutz, 2015). In the aquatic world, reporting of intermittent-flow respirometry experiments were generally poor and inconsistent (Killen et al., 2021). This inconsistency likely applies to terrestrial respirometry, as we are aware with our own studies. For example, 22% of respirometry studies measuring avian MR do not provide the duration of the experiment (Downs and Brown, 2012). Inconsistent and incomplete reporting can hamper the value of primary studies for comparative analyses (Parker et al., 2016). Such studies may be excluded if key information is missing, such as acclimation time, body mass, sex, and measurement duration (example synthesis papers with exclusion criteria; Pottier et al., 2021; Downie et al., 2023).

To help facilitate the quality of reporting respirometry studies, we provide a checklist with five main sections to facilitate interpreting and replicating (see Glossary) empirical studies relating to measurements of whole-animal MR and EWL via flow-through respirometry for terrestrial air-breathing organisms (terrestrial respirometry). Note that many of the reporting descriptions in Table 1 also apply to close-system respirometry, intermittent-closed respirometry, and gravimetric measurements of EWL. We broadly followed Killen et al. (2021) with sections specific to terrestrial respirometry. The checklist comprises five main sections (Fig. 2) with specific reporting criteria and references that provide more detail, justification for the criteria, or example studies (Table 1). We do not intend to be overly prescriptive in how to design and undertake respirometry studies as there is already an extensive literature on respirometry designs, data processing, and calculations (Depocas and Hart, 1957; Bakken, 1991; Koteja, 1996; Withers, 2001; Arch et al., 2006; Lighton and Halsey, 2011; Malte et al., 2016; Schoffelen and Plasqui, 2018; Lighton, 2019), yet we draw attention to some common reporting issues. The checklist does not include all possible elements, but it is formulated to aid in the design and reporting of most studies to increase transparency (see Glossary). The checklist is available on GitHub (https://github.com/nicholaswunz/resp-commentary).

2. Materials, set up, and plumbing

The respirometry set up should be designed to answer your research question. Given the flexibility and modularity of respirometry set ups, many creative variations have been used. For example, masks have been fashioned from large buckets to fit over the trunk of an elephant (Langman et al., 1995; Langman et al., 2012), some made to resemble a flower to measure the MR of hovering hummingbirds (Bartholomew and Lighton, 1986; Welch Jr, 2011), or burrows constructed by the animal itself (White et al., 2008; Wu et al., 2015). Maximum metabolic rates (MMR; see Glossary) and EWL during exercise have been quantified in treadmills, exercise wheels, or wind tunnels (Fedak et al., 1974; Anderson and Prestwich, 1985; Norberg, 1996; Wiersma et al., 2007; Clemente et al., 2009). Tree cavities, with a single entrance as an inlet and a small outlet hole, have also been used as flow-through chambers to measure MR in wild primates (Dausmann et al., 2009), and bespoke 6 m^3 chambers have been constructed to measure the MR of estuarine crocodiles weighing up to 389 kg (Seymour et al., 2013). Test tubes have been used to test the influence of tree hollow shelter on EWL of casque-headed tree frogs (Navas et al., 2002). These creative set-ups can be summarised generally by the two ways air moves past an animal—pushing or pulling, each their associated advantage and disadvantage (Lighton and Halsey, 2011). Lighton (2019) provides comprehensive information on setting up push and pull systems which we highly recommend reviewing prior to designing respirometry experiments.

The more creative and elaborate the set-up, however, the more potential measurement errors can occur during the experiment. Every component such as the plumbing set up, materials used, the use of physical scrubbers, chamber size relative to flow rate can influence the

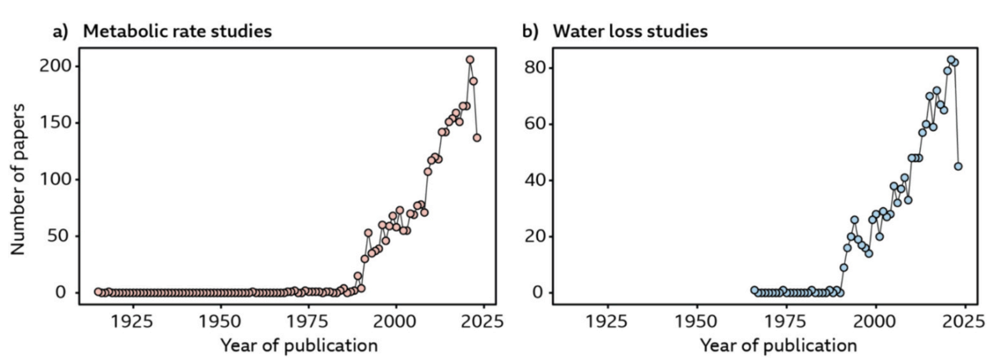

Fig. 1. Number of studies published in the field of ecology and evolution relating to **a**) whole-animal metabolic rate, and **b**) water loss (via gravimetric, respirometry-based approaches). Data obtained from the Web of Science on 25 November 2023 using the search terms (respirometry OR gas exchange OR open-flow OR flow-through) AND (metabolic rate OR MR OR metabolism OR energy budget OR heat production) for metabolic rate studies and (respirometry OR gas exchange OR open-flow OR flow-through) AND (water loss OR evaporative OR skin resistance OR water budget OR desiccation rate OR hydroregulation) for water loss studies.

Table 1
A checklist of criteria for reporting the methods and results from respirometry experiments for terrestrial animals. Example references are provided for each criterion. Endotherm-specific details are provided in **bold**. A printable checklist is also provided in the electronic supplementary attachment.

Reporting criterion	Description	References
1. Materials, Set up, Plumbing		
Set up type	For MR measurements, report whether the system was closed, intermittent-closed, or flow-through. If flow-through, was it a push or pull system? For EWL measurements, report whether the system was designed to measure change in body mass, change in desiccant mass, flux chamber, or change in water vapour pressure.	(Kristín and Gvoždík, 2012; Lighton, 2019)
Air flow	Report the air flow as volume over time corrected to standard temperature and pressure (STP), and how the flow rate was achieved and maintained. Definitions for STP vary and so should be defined (in comparative physiology, it is usually defined as 273.15 K and 101.325 kPa). Air flow should refer to the flow experienced by the animal and not the flow through the analysers. See Subsampling below.	(Bakken et al., 1991; McNab, 2006)
Physical and chemical scrubbing	Report whether air was scrubbed of H_2O and/or CO_2 physically or mathematically. If physically scrubbed, what type of scrubbers were used (e.g., Drierite) and where in the plumbing set-up were they placed? If mathematically scrubbed, what equation was used?	(Elia et al., 1986; Koteja, 1996; White et al., 2006; Lighton, 2019)
Chamber design	Provide details on the chamber design including empty chamber size and volume, and what material(s) the chamber is made from. If objects were placed inside the chamber (e.g. mesh, platform, nest material), describe them. If a layer of mineral oil or similar is placed in the bottom of the chamber to prevent evaporation from excreta affecting EWL measurements, indicate the approximate depth of the layer.	(McNab, 2006; Wu et al., 2015; McGuire et al., 2017; Nowack et al., 2020; Rodgers and Franklin, 2021)
Incurrent air	State the source of the incurrent air (e.g. outdoor air, gas cylinders). If gas mixes were used, provide the gas composition (e.g., nitrogen-oxygen mix, helium-oxygen mix (helox), CO_2-free air).	(Cooper and Withers, 2014; Lighton, 2019)
Chamber mixing	Describe how chamber mixing was achieved. Important for the correct gas mixture, and also mediating washout times if animals are exercising/ active/shivering in the chamber.	(Frappell et al., 1989)
O_2 analyser	Report what type of analyser was used (e.g., paramagnetic, fuel-cell, zirconia-cell, infrared, oxygen-quenched fluorescence) and provide the model and manufacturer.	(Hill, 1972; Lighton, 2019)
CO_2 analyser	Report what type of analyser was used (e.g., infrared, nondispersive infrared) and provide the model and manufacturer.	(Lighton, 2019)
H_2O analyser	Report what type of analyser was used (e.g., chilled mirror, capacitive, infrared) and provide the model and manufacturer.	(Lighton, 2019)
Calibration	Describe how the flow meters, gas analysers, temperature probes, etc. were calibrated and how often. Include the concentrations of any span gases used.	(Withers, 2001)
Connectors	Provide details on the tubing material and connectors, as different materials can alter gas and humidity measurements due to potential leaking.	(Lighton, 2019)
Temperature recorder	Report how and where respirometer temperature was measured. **Endotherm**: Temperature should generally be measured inside the respirometer chamber due to heat production by the animal.	
Multiplexers	If multiplexers were used, describe how and where they were set up. Was a digital-to-analogue converter used for automation?	(Lighton, 2019)
Subsampling	If subsampling was used, provide the flow rate and explain how the flow rate was achieved and maintained.	(Lighton, 2019)
Visualisation	Ideally, a schematic diagram of the plumbing and position of the equipment relative to the respirometry chamber will help facilitate the description of the set-up.	(Bakken et al., 1989; Wilz and Heldmaier, 2000; Lighton, 2019)
2. Subject conditions/maintenance		
Study species	State the study species (and strain if relevant).	
Origin	State the origin of collection such as where (coordinates) and when (dates) the animals were collected. Provide the habitat characteristics if relevant to discussing the environmental context of the study. For laboratory raised subjects, provide the number of generations since caught from the wild and the source of the original population.	(Smit and McKechnie, 2010; Burton et al., 2011; Bovo et al., 2023)
Husbandry conditions	Describe the husbandry conditions relevant to the study including, but not limited to: enclosure, feeding schedule, maintenance duration, acclimation duration, treatment groups, etc.	(Terblanche et al., 2005; Alton et al., 2020; Dezetter et al., 2022; Weaver et al., 2023)

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Table 1 (*continued*)

Reporting criterion	Description	References
Age/life stage	Provide the life stage of the test subjects, and if known, provide the age.	(Gray, 2013; Medina-Báez et al., 2023)
Sex	Report the number of test subjects of each sex and state whether sex ratios were equal or similar across experimental groups	(Videlier et al., 2019; Pessato et al., 2023)
Reproductive condition	State the reproductive condition of the test subjects.	(Demarco and Guillette Jr, 1992; Angilletta and Sears, 2000; McLean and Speakman, 2000; Burton et al., 2011)
Biometrics	Measure biometrics for the test subjects (e.g., fresh mass, length, body condition) immediately before or after the respirometry trial. Biometrics collected upon arrival to the laboratory or at the time of capture may not reflect the animals physiological state at the time of experimentation Moreover, dry body mass, lipid-free dried mass, non-skeletal body mass is not recommended because live animals tightly control their hydration and lipid levels. Therefore, the total mass (water, fat and everything else) measured at the start or end, or both, should be reported.	(Kaiyala et al., 2010; Lighton, 2019)
3. Measurement conditions		
Blinding	If possible, data recorders should be blind to the experimental treatment imposed on the subjects when gathering data. Also, report whether or not blinding was implemented.	(Parker et al., 2018)
Baseline recording	Provide information on the background/baseline (empty chamber) recording including how often and how long the baseline was recorded for. For multiplexed systems, check whether each system is baselined with air before and after the experiment, or was a separate system relied on.	(Lighton and Halsey, 2011)
Time	State when the measurements were taken. MR fluctuates over the day and is affected by photoperiod.	(White et al., 2006; Page et al., 2011; Connolly and Cooper, 2014)
Lighting	Provide information on the lighting conditions during the experiment.	(Chew et al., 1965; Powers, 1991; Riccio and Goldman, 2000)
Duration and frequency	State the experiment and measurement duration and frequency. This is especially important for obtaining minimum MR and EWL. Reducing the frequency of sampling can underestimate BMR and EWL. Duration should include the total time the animal is in the respirometer and not just while the recording is happening.	(Cooper and Withers, 2010; Jacobs and McKechnie, 2014)
Test temperature	Provide the test air temperature (T_a) and how it was maintained. If a stepped temperature change was used, provide details on the duration and rate of change between each temperature setpoint.	(Short et al., 2022)
Test humidity	Provide the test humidity (incurrent and excurrent) and how it was maintained. Humidity should be reported as absolute values or partial pressures (g H_2O m^{-3} or kPa) rather than relative humidity (RH, %). If only RH values are available, it is critical that the corresponding T_a are provided. If converting to water vapour pressure and water vapour deficit from RH and T_a, provide the reference to the equations used.	(Gilson et al., 2021; Freeman et al., 2024)
Standard temperature and pressure	Given that definitions of standard temperature and pressure (STP) vary, it is important that a definition of STP should also be provided for transparency.	(Lighton, 2019)
Fasted	State whether the test subjects were fasted prior to the experiment and for how long.	(McCue, 2006)
Hydration	Hydration state affects MR and EWL measurements. How was the hydration level controlled prior to experimentation? If wet-skinned animal (e.g. amphibians), make sure to gently dry excessive water droplets over the surface (skin) exposed to evaporation. This effect is exaggerated in smaller test subjects.	(Preest and Pough, 1989; Senzano and Andrade, 2018)
Grouping	If more than one test subject was placed inside the chamber, provide the exact number of individuals.	(Rusli et al., 2016)
Measurements	State what measurements were obtained (see Glossary), when, and for long they were measured. If individuals were repeated, state the number of repeats per exposure. If multiplexors where used, providing the sampling period	(Jacobs and McKechnie, 2014)
Animal state	Describe the state of the animal when the measurement was taken [e.g., inactive, active, rest-phase, active-phase, post-exhaustion, digesting, torpid, aestivating, normothermic (for endotherms)]. - For resting states, state the recovery time from handling stress after being placed into the chamber. - If post-exhausted for MMR, how was this achieved? - Activity should be monitored visually or measured to confirm an animal is inactive or to account for variation in MR and EWL associated with variation in activity levels.	(Seymour et al., 1998; Duarte et al., 2010; Snelling et al., 2017; Wu et al., 2018; Videlier et al., 2019; Alton and Kellermann, 2023)
Multiple animals	When multiple animals are measured in sequence in one measurement period, provide	(Lighton and Halsey, 2011)

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Table 1 (*continued*)

Reporting criterion	Description	References
	the timing of switching between channels. Describe how the washout times for the respirometry system and multiplexed sampling period was matched.	
4. Data processing		
Data acquisition	Provide information on the data acquisition systems/ software.	(Lighton, 2019)
Baseline drift	Baseline measurements will fluctuate, especially for O_2 concentrations. State whether and how baseline drift was corrected.	(Lighton and Halsey, 2011)
Time lag	The position of the equipment and length of plumbing (and if physical scrubbers were used post-respirometer chamber) will influence the time of the recording. State whether and how time lag was corrected.	(Lighton and Halsey, 2011)
Mathematical scrubbing	If physical scrubbers were not used, provide details on how gas concentrations were mathematically scrubbed. Report whether it is appropriate for the type of O_2 analyser used and how this was determined e.g. paramagnetic?	(Lighton, 2019; Lighton, 2023)
Sampling	Describe and justify sample selection (mean, time period) as well as exclusion criteria (activity, posture, excretion etc). **Endotherm**: Some mammals will lick their fur or the chamber during respirometry trials which will produce relatively high EWL. The use of video surveillance is recommended to monitor such activities.	(Pough et al., 1983; Frappell et al., 1989; Withers, 2001; Cooper and Withers, 2009; Cooper and Withers, 2010)
Boundary layer	For calculating skin resistance from EWL, state how the boundary layer was accounted for, either mathematically or empirically (e.g. from agar models) estimated.	(Riddell et al., 2017; Senzano et al., 2022)
Equations	Show the equations for all calculations in addition to citing their sources.	(Depocas and Hart, 1957; Koteja, 1996; Withers, 2001; Malte et al., 2016; Schoffelen and Plasqui, 2018; Lighton, 2019)
Calculations	State how MR and EWL values were calculated (e.g., lowest value, lowest 10% of average, first hour slope, residuals around a linear regression). Differences in metabolic sampling can cause small but significant effects on minimum MR measurements. - For maximal or forced locomotion, define method of extraction e.g., MR at fastest speed, highest value, immediately post-exhaustion?	(Nickerson et al., 1989; Withers, 2001; Cooper and Withers, 2010)
Data exclusion	If data were excluded from the study due to experiment/ measurement/animal issues, provide such information for transparency. Indicate the criterion e.g. extreme values, outlier statistics.	
5. Data reporting and statistics		
Aims and hypotheses	In the Introduction, clearly state the aims and/or hypothesis for which the study was conducted and data were gathered.	(Parker et al., 2018)
Units	Always report units in the paper. Use only International System of Units (SI) or SI-derived units.	
Raw data	Supply raw data on the rate of O_2 consumption, CO_2 production or EWL in addition to converted values used in the paper. E.g. translating to energy equivalents, mass-corrected or mass-specific values, surface-specific values. And when presenting mass- or surface-specific values, remember that such data remove the effect of mass only in very specific (and usually not realistic) situations.	(Packard and Boardman, 1988, 1999; Arch et al., 2006; White and Kearney, 2011; Lighton, 2019)
Sample size	Report sample sizes for all data, including subsets of data (e.g., each treatment group, other subsets), and sample size used for all statistical analyses.	(Parker et al., 2018)
Pseudoreplication	Report pesudoreplication if used. E.g. the number of tanks, rooms, chambers used, and the number of animals in each. Also report how pesudoreplication was statistically accounted for (e.g. random effect).	
Statistics	List each statistical test and analysis conducted in sufficient detail such that they can be replicated and fully understood by those experienced in those methods. Fully report outcomes from each statistical analysis. For most analyses, this includes, but is not limited to, basic parameter estimates of central tendency (e.g., means) or other basic estimates (regression coefficients, correlation) and variability (e.g., standard deviation) or associated estimates of uncertainty (e.g., confidence/ credible intervals). Thorough and transparent reporting will involve additional information that differs depending on the type of analyses conducted. · For null hypothesis tests, this also should at minimum include test statistic, degrees of freedom, and *p*-value. · For Bayesian analyses, this also should at a minimum include information on choice of priors and MCMC (Markov chain Monte Carlo) settings (e.g. burn-in, the number of iterations, and thinning intervals).	(Parker et al., 2018)

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Table 1 (*continued*)

Reporting criterion	Description	References
	· For hierarchical and other more complex experimental designs, full information on the design and analysis, including identification of the appropriate level for tests (e.g. identifying the denominator used for split-plot experiments) and full reporting of outcomes (e.g. including blocking in the analysis if it was used in the design). Relevant information will differ among other types of analyses but in all cases should include enough information to fully evaluate the design and analysis.	
Covariates	Provide a description of all covariates tested.	
Non-independence	State if the data presents sources of non-independence (e.g., group effect, repeated measures, spatial and temporal effects such as autocorrelations) and how they were accounted for in the analyses (e.g., random effects).	(Legendre, 1993; Noble et al., 2017; Cinar et al., 2022)
Softwares and packages	Cite all softwares and packages used in the data processing and analysis. If open-source programming languages were used (e.g. R, Python, Julia), provide the source code for data processing and analysis.	
Data	Include the data upon which analyses are based (as well as raw data) as supplementary materials with submission and archived in a permanently supported, publicly accessible database. Include a METADATA to describe what the naming conventions and abbreviations mean. If additional data was obtained from other sources for comparison (e.g., database, publication), list and cite the sources.	(Tedersoo et al., 2021; Gomes et al., 2022)

reliability of the data collected (Table 1). For example, tubing material (e.g., Tygon, Silicone, PharMed, Teflon, Bev-a-Line) and size are often not reported but can influence gas permeability, water vapour, and pressure resistance (Bloom et al., 1980; Dixon and Grace, 1982; Lighton, 2019). The same applies for the chamber/mask size, shape (cylinder, sub, rectangle), and material (plastic, acrylic, glass, metal). Chamber size is of particular importance because it influences the comfortability for the animal (size and behaviour) and flow rate which, in turn, influences washout characteristics (Kendeigh, 1944; Lasiewski et al., 1966; Withers, 2001; McNab, 2006). This delicate balance between chamber design and the flow rate is highly subjective and context dependent, but reporting these features can increase the replicability of the experiments. Lighton and Halsey (2011) provide calculations for optimising the chamber size and flow rates to minimise lag-time for analysers. Lastly, drawing the set-up plumbing and equipment position is of great help for researchers designing their experiments and for reviewers when assessing the quality of the setup.

3. Subject conditions/maintenance

Reporting where the test subjects were collected, their biological metrics (e.g., species, sex, reproductive status, age) and housing/maintenance condition (e.g., lighting, temperature, water access, food quality and quantity) are important because these factors can influence comparisons of MR and EWL measurements (Table 1; Fig. 2). For instance, MR shows substantial variation between individuals, populations, and species, and understanding this variation is an active research area (McNab, 2002; White and Kearney, 2013; Norin and Metcalfe, 2019; Koch et al., 2021; Glazier, 2022). Even when measurement errors are accounted for (Konarzewski et al., 2005; Konarzewski and Książek, 2013), variation in MR within species may still exist that can be explained by selection (Auer et al., 2018; Pettersen et al., 2018). This is the case when test subjects from different populations and/or localities may exhibit different physiology due to local adaptation to their environment (Angilletta and Michael, 2001; Kurbalija Novičić et al., 2015; Bovo et al., 2023). Therefore, comparative studies require such information from primary studies to formally deal with intraspecific variation, spatial autocorrelation, and environmental predictors.

Once the subjects are collected and housed, an important consideration is how long the test subjects are acclimated to their experimental condition before measurements of MR and/or EWL. Whether it is pollutant, pathogen, temperature exposure, food or water ration, it is important to report the magnitude and length of the different treatments (and whether a step process was used) for understanding the effects of acclimation within the study and allowing meaningful comparisons between studies (Harri, 1973; Sandblom et al., 2014). For example, the BMR of sparrows can reach back to pre-acclimation levels after 8 weeks acclimated from 15 to 30 °C (Barceló et al., 2009). If measurements were taken at 4 weeks, MR would be reported as significantly higher than pre-acclimation MR (Barceló et al., 2009).

4. Measurement conditions

Reporting what data were collected, how it was collected, and the conditions the animals were subjected to during the experiment is important for the replicability of the experimental procedure (Table 1; Fig. 2). Insufficient time for measurements is a common issue in studies measuring energy expenditure and water loss under standardised conditions (Benedict, 1938; Hayes et al., 1992; Cooper and Withers, 2009; Page et al., 2011), including standard metabolic rate (SMR; see Glossary) in ectotherms, basal metabolic rate (BMR; see Glossary) in endotherms (Londono et al., 2015; Chabot et al., 2016), and EWL rate (Senzano and Andrade, 2018). Many animals experience handling stress and require a substantial amount of time (e.g. up to 30 min for a 30 g mouse) for MR and EWL to drop back down to resting levels (Duarte et al., 2010). This time can depend on both temperament of the animal, as well as their mass and the temperature exposure (Winwood-Smith and White, 2018). Similarly, resting MR can differ significantly depending on the time of day, particularly in species with pronounced circadian activity patterns (Aschoff and Pohl, 1970). It is therefore important to ensure that the length of time for the measurement, as well as the time that the data are collected, match what is attempted to be measured (Jacobs and McKechnie, 2014).

It is also important to consider in endotherms how the conditions mentioned above (mass, circadian phase, and resting state) influence body temperature and, thus, the interpretation of MR measurements. Body temperature can fluctuate by a few degrees, or up to 30 °C or more over the course of a 24-h period, depending on the species studied (Aschoff and Pohl, 1970; Boyles et al., 2013). This includes both non-steady state changes such as torpor (Willis, 2007; Geiser, 2021) or steady-state circadian rhythms (Aschoff, 1963; Aschoff, 1981; Refinetti and Menaker, 1992). Where possible we recommend the measurement of body temperature alongside MR, which is now made easier with relatively non-invasive measurement devices such as temperature-

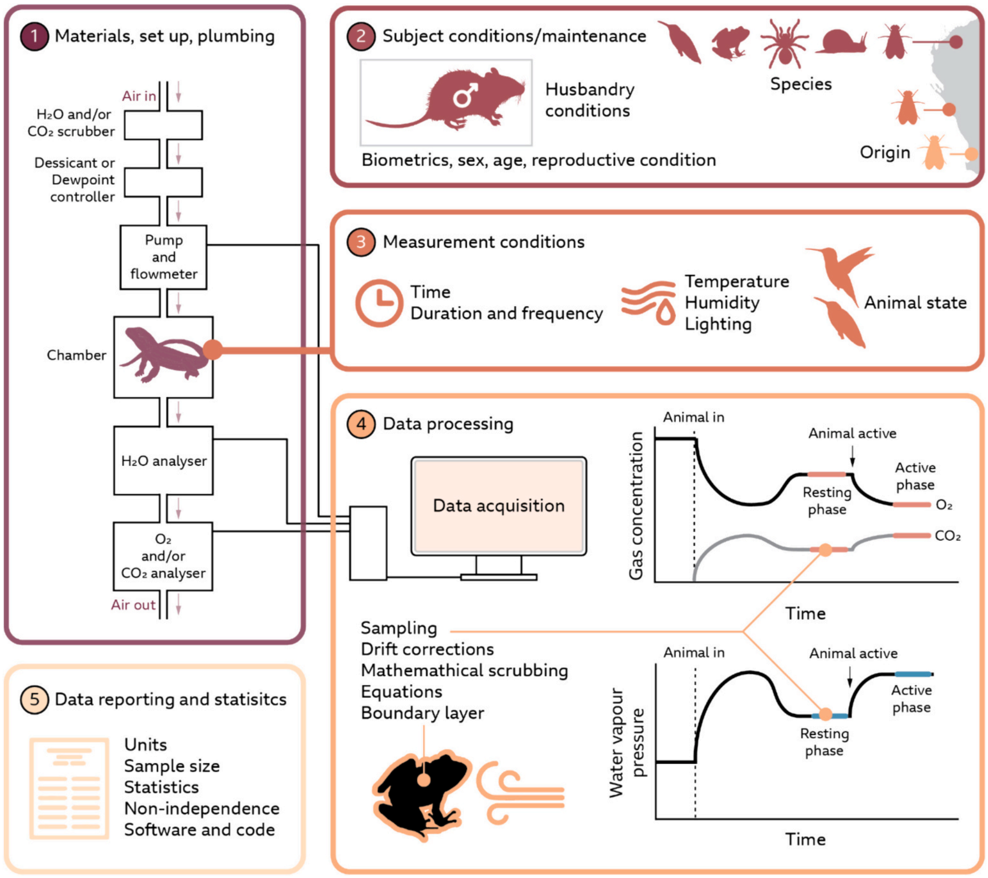

Fig. 2. Visualisation of the five checklist sections with example reporting information. 1) Materials, set-up, plumbing shows an example schematic diagram of a "push" flow-through system. 2) Subject conditions/maintenance focus on the test subjects in question, their origin, and how they are housed/acclimated prior to experimentation. This may include the species, their origin, sex, age, and reproductive condition, as well as the husbandry conditions they are kept in. 3) Measurement conditions focus on reporting the raw data collected, how long and often the measurements were taken, the experiment conditions, and the state of the animals during the measurements. 4) Data processing focuses on reporting how the data were recorded, what mathematical corrections were used, how the data were converted, and the equations to calculate meaningful values from raw data. The highlighted sections of the raw gas and water vapour pressure trace represent where values are extracted, typically periods of stable rate of O_2 consumption, CO_2 production or water vapour pressure. 5) Data reporting and statistics focus on reporting how the data were analysed, the statistics and program used, and sharing data and code.

sensitive passive integrated transponders and temperature-sensitive transmitters (Toussaint and McKechnie, 2012; Nord et al., 2016). This will enable distinctions to be made between metabolic states and ensure that the most accurate/relevant data are included in analyses, and can even enable detection of novel mechanisms of energy budgeting (Reher and Dausmann, 2021; Levesque et al., 2023).

The humidity and convective environment experienced by animals in metabolic chambers is another important consideration for measurements of gas exchange, as rates of EWL vary with humidity and wind speed (Lasiewski et al., 1966; Foley and Spotila, 1978; Waldschmidt and Porter, 1987). Depending on the mixing characteristics of chambers, authors either assume animals experience incurrent humidity (Young et al., 2005; Rolandi et al., 2014; Cooper et al., 2020) or excurrent humidity (Weathers, 1997; Gerson et al., 2014; Freeman et al., 2024). Lasiewski et al. (1966) provided empirical evidence that, in well-mixed systems, birds experience humidities equivalent to that of excurrent air. The existence of gradients of humidity within chambers, for instance along the length of cylindrical chambers with inlet and outlet ports opposite each other, remains little explored and requires further investigation. Similarly, wind speed within chambers is seldom measured other than in wind tunnels (Foley and Spotila, 1978; Wolf and Walsberg, 1996), despite the influence of this variable on the properties of boundary layers, a consideration particularly important when quantifying cutaneous resistance (Spotila and Berman, 1976; Riddell et al., 2017). Even for studies in which EWL is not quantified, chamber humidity is an important consideration when measurements are conducted at air temperatures approaching or exceeding body temperature, especially in endotherms, as evaporative heat dissipation is impeded by high ambient humidity (Lasiewski et al., 1966).

Further considerations for studies where EWL is measured via flow-through methods include a) the requirement to exclude evaporation from excreta, usually achieved by placing the subject on a mesh platform elevated above a layer of mineral oil or liquid paraffin deep enough to cover any excreta that falls into it (McGuire et al., 2017), b) the need to use chambers constructed from material that does not adsorb water vapour (Whitfield et al., 2015), and c) the need to report the subject's posture (Pough et al., 1983) and position (Riddell et al., 2017), as the subject surface exposed to evaporation may alter measured EWL. Humidity should also be reported in absolute terms (g H_2O m^{-3} air or partial pressures in kPA). If RH values are reported, it is essential that it is accompanied by the corresponding air temperature to permit the calculation of absolute humidity, water vapour deficits and related variables. Finally, in studies involving high air temperatures and experimental humidity levels, condensation in tubing and analysers must be avoided at all costs as, per most manufacturers, liquid water can permanently damage the sensors. Freeman et al. (2024) for instance, placed their respirometry setup in a room within which air temperature was maintained at 35 °C to accommodate excurrent dew points of up to ~30 °C. Particular care should be taken when tubing is in contact with the floor or in the proximity of heat exchangers.

5. Data processing

Accurate descriptions of how the raw data were treated, what transformations were used, and details on the sampling procedure and data processing are important in both standardizing the findings as well as allowing for replicability (Fig. 2). These include data acquisition (what software and at what sampling intervals and if multiplexing how long on each chamber), measurement of and corrections for baseline drift, measurements of time lags between the parameters, sample selection, equations and calculations, as well as any data exclusion procedures (Table 1). How data are transformed, what time intervals are selected, and what criteria are used to exclude data (e.g., activity during resting measurements; Duarte et al., 2010) can impact the findings and are therefore important to report. Hayes et al. (1992) and Jacobs and McKechnie (2014) provide concrete examples of the effects of sample length on estimates of metabolic rate. In both cases estimates for BMR were 12–30% higher when calculated using 10–15 min intervals compared to 60 min intervals, while 30 min intervals were equivalent (Jacobs and McKechnie, 2014). Similarly, correcting for analyser drift or lag-time between analysers can impact the results and should be calculated or accounted for (Withers, 2001; Lighton and Halsey, 2011), particularly when instantaneous measurements are of interest (Bartholomew et al., 1981). Lastly, if the equations for calculating $\dot{V}_{O_2}$, $\dot{V}_{CO_2}$, and EWL are formulised instead of providing references to existing equations (Depocas and Hart, 1957; Koteja, 1996; Withers, 2001; Malte et al., 2016; Schoffelen and Plasqui, 2018; Lighton, 2019), we recommend mathematical notations following Edwards and Auger-Méthé (2019).

6. Data reporting and statistics

Describing how the data were analysed and presented is important for the interpretation and the reproducibility (see Glossary) of the study (Table 1). There are excellent resources available specially focusing on reporting statistics in experiment biology and more broadly in life sciences (Curran-Everett and Benos, 2004; Nakagawa and Cuthill, 2007; Gerstner et al., 2017; Harrison et al., 2018). Here, we highlight advantages of sharing data and code to understand how the data were analysed and interpreted, as well as giving the data new light for synthesis studies. Open research is not just a theoretical ideal but a practical necessity to assess, replicate, and compile research findings (Fraser et al., 2018; O'Dea et al., 2021; Bertram et al., 2023). Central to comparative physiology is the synthesis of original data, which should be made available along with the analytical methods. The encouragement of data and code sharing by journals, with some mandating data sharing, has been a welcome improvement in science (Parr and Cummings, 2005; Moore et al., 2010; Roche et al., 2022). The establishment of stable platforms for publishing data and code such as Dryad (https://www.datadryad.org), Zenodo (https://www.zenodo.org), Figshare (https://figshare.com), or the Open Science Framework (https://osf.io/) has also been instrumental in promoting data availability. Sharing data in such repositories has been shown to offer numerous advantages, including enhanced citation counts (Piwowar et al., 2007; Piwowar and Vision, 2013; Vines et al., 2013; Gomes et al., 2022).

Although data sharing has become more accepted, how the data is shared can vary in quality. A particular challenge in compiling data for comparative studies is the inconsistency in units and terminology in the measurement and reporting of data. Differences in data presentation, such as reporting absolute rates versus mass-specific or rates normalized to temperature, can impede meaningful comparisons. Similarly, water loss is sometimes reported either as the rate of water loss or as integument resistance to water loss (r; see Glossary), but not both (Tracy et al., 2007; Tracy et al., 2008; Riddell et al., 2017). Converting between the two units is difficult if conversion parameters are not provided in the methods section or raw data (e.g., vapour density gradient). Addressing these challenges necessitates clear and standardised metadata guidelines (Sansone et al., 2019). In addition, following best practices for sharing data, which include providing the raw data, metadata detailing each column, code detailing all data processing steps, and a README file describing how to navigate materials in the repository is typically needed for reproducibility (Reichman et al., 2011; Whitlock, 2011; Wilson et al., 2021).

In recent years, open-source packages for processing respirometry and analysing data have become available, which allow the sharing of reproducible and succinct code detailing the processing methods. The adoption of such open-source packages, especially with command line code, is highly recommended, as they can streamline the analysis of respirometry data, provide standardised ways to perform common but complex tasks (e.g. applying adjustments from blank controls, unit conversions, standardizing rates by mass or area, etc.), and provide a transparent and standardised workflow. Given that the analysis of respirometry data often involves onerous manual processing, such open-source code minimizes manual data transformations and ensures reproducibility (Harianto et al., 2019; Powers and Hampton, 2019). Several packages are available for processing and analysis of respirometry data, from those aimed chiefly towards aquatic respirometry such as *respR* (Harianto et al., 2019), to time series analysis tools such as *LoLinR* (Olito et al., 2017). Unique aspects of terrestrial flow-through respirometry however, such as the irregular nature of discontinuous gas exchange data (see section 3 Measurement Conditions and 4 Data Processing), highlights the need to develop tools tailored specifically towards these data.

7. Conclusion

Standardised reporting can 1) provide important teaching opportunities for students/researchers new to respirometry on best practices in reporting and interpreting metabolic and water loss data, 2) increase the transparency of data curation for comparative studies and meta-analysis to reduce sampling bias and incorrect interpretation (Gerstner et al., 2017; Genoud et al., 2018; Schwanz et al., 2022), and 3) assist the efficiency of peer-review process by providing a clear checklist for reviewing studies with respirometry experiments (Parker et al., 2018). Overall, the goal of our checklist is to provide a comprehensive guide that will help both new and experienced researchers design, execute, and report respirometry experiments with consistency.

8. Checklist

Table 1

Glossary

Basal metabolic rate (BMR): The metabolic rate (see MR) of a non-reproductive, inactive, unstressed, postprandial adult endotherm that is thermoregulating in a thermoneutral environment during the inactive phase of its circadian cycle (but not sleeping, or in torpor–equivalent to SMR for ectotherms).

Evaporative water loss (EWL): The rate of water loss via evaporation, typically expressed in absolute terms as mass of water lost per unit time (e.g. g H_2O h^{-1}), in relative terms as mass of water lost per mass of animal per unit time (e.g. g H_2O g^{-1} h^{-1}), or the mass of water lost per exposed surface area per unit time (e.g. g H_2O cm^{-2} h^{-1}). EWL is often represented as total evaporative water loss (TEWL*), which is the sum of the rate of evaporative water loss through the cutaneous surface (cutaneous evaporative water loss; CEWL) and the rate of evaporative water loss through respiration (respiratory evaporative water loss; REWL[†]). For moist-skinned organisms such as amphibians, CEWL is the main mode of water loss, whereas in many endotherms respiratory evaporation predominates (REWL).

* TEWL is sometimes used in the literature to refer to transepithelial

(an equivalent of cutaneous) evaporative water loss.

† REWL is sometimes used in the literature to refer to resistance to evaporative water loss, but is now referred to as "r". Total resistance to EWL (r_t) is the sum of the boundary layer resistance (r_b) and the resistance provided by the animal integument (r_i), expressed as s cm^{-1}. r_b is resistance of the moist air surrounding the animal empirically taken from an equivalent biophysical (e.g. agar, plaster, foam, etc.) model with the same size/shape of the animal. As there is no epithelial barrier (skin) in biophysical models to create resistance to water loss through the evaporating surface, thus r_i = zero, and $r_b = r_t$. r_i is the resistance provided by the animal integument, estimated after subtracting the amount of water lost by the animal (r_t) from its biophysical ("no cutaneous") model (r_b), thus $r_i = r_t - r_b$.

Maximal metabolic rate (MMR): When induced by exercise, the energy expenditure (usually rate of oxygen consumption) during the maximum sustainable rate of exercise. When induced by cold for endotherms, the maximum rate of oxygen consumption during the maximum sustainable cold stress (often induced in a He—O_2 atmosphere at temperatures above 0 °C to avoid freezing injury to tissues).

Metabolic rate (MR): The rate of energy expenditure per unit time. Typically represented as the rate of O_2 consumption (ml h^{-1}), CO_2 production (ml h^{-1}), or converted to an energy equivalent such as Watts, or Joules or calories per unit time.

Replicability: Obtaining consistent results across studies aimed at answering the same scientific question, each of which has obtained its own data (National Academies of Sciences, 2019).

Reproducibility: Obtaining consistent results using the same input data, computational methods, and conditions of analysis (National Academies of Sciences, 2019).

Resting metabolic rate (RMR): The metabolic rate of an inactive animal when one or more of conditions required for measuring BMR or SMR cannot be met.

*Note that the abbreviation RMR is sometimes used in the literature to refer to routine metabolic rate, which is the MR averaged over a specified time interval, of an animal exhibiting spontaneous 'routine' behaviours, or a specified behaviour. Here, RMR refers to resting metabolic rate.

Standard metabolic rate (SMR): The metabolic rate of an inactive, unstressed, postprandial adult ectotherm measured under normothermic conditions during the inactive phase of its circadian cycle (but not sleeping, or in diapause, or brumating, or aestivating).

Transparency: The practice of openly and systematically sharing all aspects of the research process, including methodology, data, code, results, and interpretations. Importantly, transparency increases the replicability and credibility of the research.

Author contribution

NCW and DLL conceived the idea, and all authors contributed to the development and write up of the manuscript. Co-authors were listed in alphabetical order by last name.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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