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DATA ARTICLE

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A worldwide and annotated database of evaporative water loss rates in squamate reptiles

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Abstract

Motivation: The understanding of physiological adaptations, of evolutionary radiations and of ecological responses to global change urges for global, comprehensive databases of the functional traits of extant organisms. The ability to maintain an adequate water balance is a critical functional property influencing the resilience of animal species to climate variation. In terrestrial or semi-terrestrial organisms, total water loss includes a significant contribution from evaporative water loss (EWL). The analysis of geographic and phylogenetic variation in EWL rates must however account for differences in methods and potential confounding factors, which influence standard measures of whole-organism water loss. We compiled the global and standardized SquamEWL database of total, respiratory and cutaneous EWL for 325 species and subspecies of squamate reptiles (793 samples and 2,536 estimates) from across the globe. An extensive set of companion data and annotations associated with the EWL measurements of potential value for future investigation, including metabolic rate data, is provided. We present preliminary descriptive statistics for the compiled data, discuss gaps and biases, and identify promising avenues to update, expand and explore this database.

Main types of variables contained: Standard water loss rates, geographic data, metabolic rates.

Spatial location: Global.

Time period: Data were obtained from extant species and were collected between 1945 and 2020.

Major taxa: Reptilia, Squamata including lizards, snakes and amphisbaenians.

Level of measurements: Individual samples of animals from the same species, locality, age class and sex category.

Software format: csv.

KEYWORDS

ectotherms, evaporative water loss, functional traits, homeostasis, hydroregulation, macrophysiology

1 | BACKGROUND AND SUMMARY

The ecological niche of a species is an important concept in correlative species distribution modelling and describes the multivariate environmental space of abiotic and biotic factors that determine the boundaries of a species range (Chase & Leibold, 2003). In mechanistic species distribution models, however, the ecological niche of a species is not inferred from its realized niche but derived from a calculation of the fundamental niche of the organism, defined as the full range of conditions and resources suitable for survival and reproduction (Kearney & Porter, 2009). In the last decade, mechanistic models have become central to uncovering the potential effects of global climatic change on species viability and distribution (Boyle et al., 2020; Sinervo et al., 2010). Since properties of the fundamental niche are determined by organismal traits, current research aims to better understand how morphological, physiological and behavioural properties of organisms constrain their fundamental niche and ultimately define their ecological niche and distribution.

The compilation of databases of functional traits, defined as the morphological, physiological, phenological or behavioural traits that determine the performance of individuals (Kearney et al., 2021; Violle et al., 2007), is a fundamental step in this research programme (Schneider et al., 2019). Furthermore, global databases of functional traits can be used to investigate universal scaling rules and advance our understanding of evolutionary processes (Díaz et al., 2016; Etard et al., 2020). Research on the climatic tolerances of ectothermic animals over the last decade has focused on the study of functional traits characterizing their thermal biology, including thermal limits (Bennett et al., 2018; Sunday et al., 2012), thermal performance curves and metabolism (Dillon et al., 2010), thermoregulation behaviour (Kearney et al., 2009), or thermal sensitivity of development (Noble et al., 2018). However, studies have shown that traits associated with water balance in ectotherms are also critical in setting their climatic niche, their sensitivity to global changes, and their macroevolutionary radiation patterns (Brischoux et al., 2012; Garcia-Porta et al., 2019; Gouveia et al., 2019; Kearney et al., 2018; Lertzman-Lepofsky et al., 2020; Rozen-Rechels et al., 2019).

In animals, water balance is dynamically regulated by the constant adjustments of water loss and water intake processes (Figure 1a), which depend on morphological features and physiological and behavioural mechanisms (e.g., behavioural hydroregulation, skin resistance to water loss or respiration, Chown et al., 2011; Pintor et al., 2016; Pirtle et al., 2019; Riddell et al., 2019). As a result, body hydration state is homeostatically maintained within a safety zone by compensating water loss with input from metabolic, food and drinking water to avoid the acute and chronic, potentially lethal, effects of dehydration. Total evaporative loss (TEWL) comprises both the water lost through the skin epidermis or exoskeleton (cutaneous water loss, CWL) and via the respiratory system (respiratory water loss, RWL). Although functional traits such as desiccation resistance and behavioural traits are also important for hydroregulation, the standard rate of EWL has proven to be a relevant metric to assess water regulation strategies, and to scale the susceptibility of organisms to drought, habitat aridity or salinity in birds (Albright et al., 2017; Boyle et al., 2020), mammals (Van Sant et al., 2012), non-avian reptiles (Brischoux et al., 2012; Cox & Cox, 2015), amphibians (Lertzman-Lepofsky et al., 2020) and insects (Addo-Bediako et al., 2001). However, to our knowledge, there has been no attempt to compile and annotate a global database of all published EWL records in terrestrial animals, including those of squamate reptiles.

Squamate reptiles share proximate mechanisms of water loss (Mautz, 1982). They are ideal model systems to study the relevance of water regulation strategies under a macroecological mechanistic approach since these dry-skinned ectothermic organisms exhibit great phylogenetic and ecological diversification, broad variation in body size and shape, and are found in most habitats across the globe (Meiri, 2018). In addition, their performance and life history strategies are greatly influenced by the availability of water in their environment (Kearney & Porter, 2004; Lillywhite, 2017; Rozen-Rechels et al., 2020). Rates of TEWL vary with micro-climatic conditions, morphological and functional adaptations, life stages and behavioural strategies (e.g., space use and activity, Pirtle et al., 2019). In squamates, EWL is not as tightly associated with body temperature regulation as in endothermic animals. Indeed, heat loss due to CWL and RWL, that is, evaporative cooling, is generally negligible in squamate reptiles, except under extreme conditions such as panting in some desert species or under extreme heat stress (Loughran & Wolf, 2020; Tattersall et al., 2006). Although CWL is generally the dominant avenue of water loss in squamate reptiles, the partitioning between RWL and CWL, which includes trans-epidermal, ocular and cloacal water loss, varies between and within species (Mautz, 1982; Pirtle et al., 2019). One important factor affecting the partitioning between CWL and RWL is body size, which is largely determined by the fact that surface area and skin thickness (the primary determinants of CWL) scale differently with body size than respiration rate and lung size (primary determinants of RWL, Mautz, 1980, 1982) do. Changes in patterns and rates of EWL can rapidly evolve in squamates, and there is evidence of adaptive plastic responses of TEWL to fluctuating temperatures or hydric conditions (Cox & Cox, 2015; Garcia-Porta et al., 2019; Kattan & Lillywhite, 1989; Moen et al., 2005; Sannolo et al., 2020). Yet, estimates of TEWL are influenced by methodological choices, sampling methods (e.g., size class or seasonal factors), acclimation procedures and statistical reporting methods, which makes comparisons across studies difficult without an unambiguously defined vocabulary and a broad set of standardized metadata (see Figure 1b).

Here, we assembled a global and annotated database of rates of evaporative water loss in squamate reptiles of the world using published information and unpublished data we collected in recent years. Our initiative differs from previously published datasets by (a) its broad taxonomic scope spanning all available data for all squamate reptiles including lizards, snakes and amphisbaenians, (b) its exhaustiveness since we gathered all identified published estimates from a pre-established list of acceptable methodologies and recorded samples and units from the original publications without a priori exclusion of particular data or ad hoc calculations of statistics,

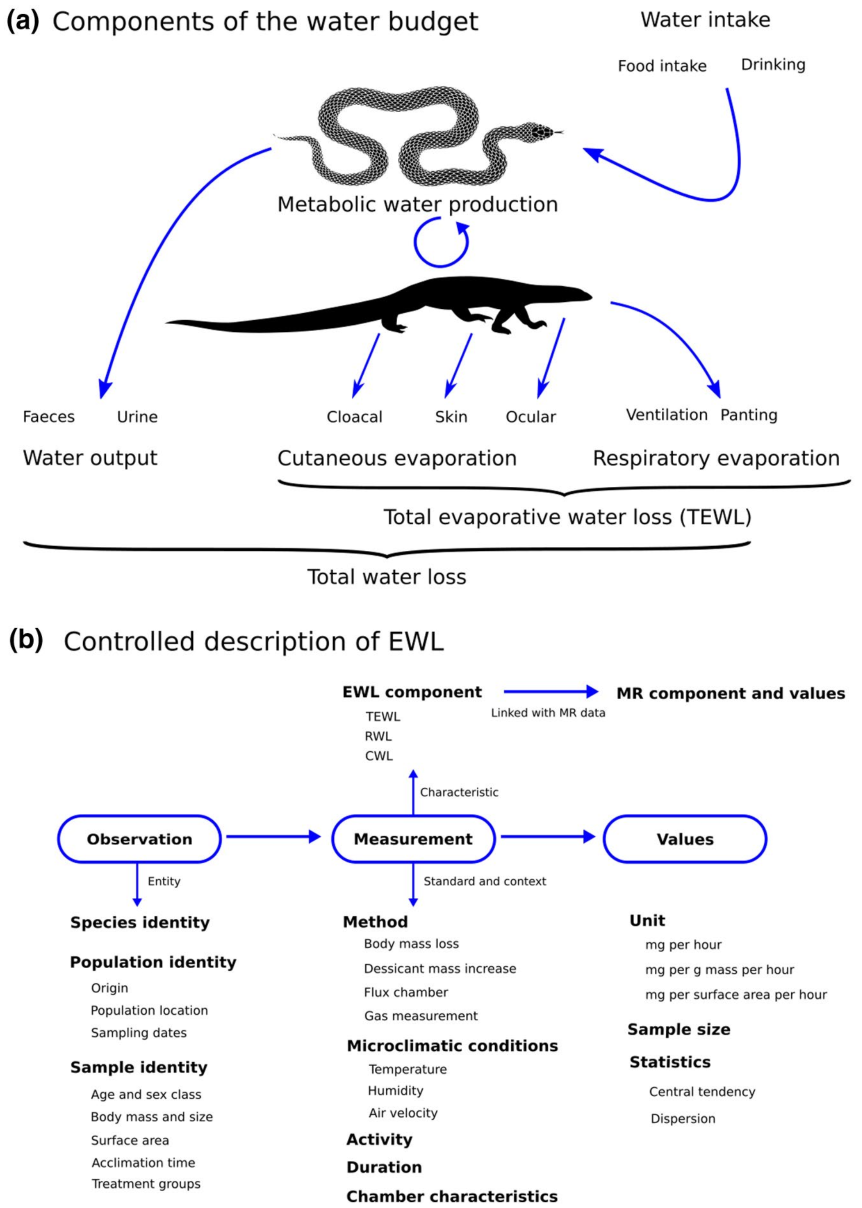

FIGURE 1 Components of water loss in squamate reptiles and metadata required to describe evaporative water loss (EWL). (a) The total water budget of the animal depends on the balance between water intake from food and drinking of rain, free standing water or moisture, metabolic water production and water loss from respiratory evaporation (RWL), water loss from skin, ocular or cloacal evaporation (cutaneous water loss, CWL) and water loss from faeces and excreta. Total evaporative water loss (TEWL) is the sum of total respiratory and cutaneous evaporative water loss and can be measured from post-absorptive animals in controlled laboratory conditions provided they do not produce faeces or excreta. (b) Controlled description of EWL rates data using metadata describing properties of entities (observations, including species, population and animals), measurements (including characteristics, protocols and context) and values. Rich metadata are needed to describe the methodology and the environmental conditions when EWL was measured. Each concept in this figure refers to one or several columns of metadata in our database (see Table 1 for details). The database was linked with associated data on metabolic rate (MR) whenever the study reported concurrent estimates of MR for the same animals

and (c) its comprehensiveness since we compiled information on 30 metadata variables. We provide a computing script to facilitate future use of these data. Whenever available, we recovered and report all the variables necessary for the calculation of skin resistance to evaporation R_s, a functional trait relevant to the predictive modelling of water-flow balance (Kearney et al., 2021) and of central relevance in mechanistic niche distribution models (Riddell et al., 2017). We also compiled a second companion database on metabolic rate (oxygen consumption VO_2 and carbon dioxide production VCO_2) for those cases in which this information was also available in the same source material examined for the construction of the EWL database. We judge this companion database relevant under the primary goal of this paper, since it may ease future studies focusing on the partitioning between CWL and RWL (Gates, 1980; Pirtle et al., 2019).

We make the compiled database freely available to stimulate future research on water balance in reptiles, particularly on water conservation mechanisms and even more so on the geographic, ecological and phylogenetic correlates of evaporative water loss. We hope to encourage other researchers to work on the expansion of the database and consult it to identify understudied groups and which sets of variables are relevant to be measured and reported. Finally, we hope that our database will be useful for those willing to use it to parameterize mechanistic niche models (Kearney & Porter, 2020).

2 | METHODS AND DATASET

We searched for published literature and referenced reports providing potential data on water loss rates in squamate reptiles in Web of Science and Google Scholar using relevant search terms in the title, abstract and content with the following query: ("water loss" OR "water balance" OR "hydroregulation") AND ("reptile*" OR "snake*" OR "lizard*" OR "squamate*"). In addition, we extracted all

TABLE 1 Database of standard water loss (WL) data descriptors and summary statistics data extracted from published studies and raw material

Column title	Column type	Description
Unique_id	*Integer*	Unique row identification number.
Person_name	*Character*	Name of the person who extracted the data.
Species_name	*Character*	Given species name, including subspecies identity, at the time of publication as given in the source publication. This is provided in the standard format Genus name + species name + subspecies names separated by the '_' character.
Species_name_ ReptileDB	*Character*	Accepted species names based on the Reptile Database as of December 2019 extraction, including subspecies name, given in the standard format Genus name + species name + subspecies names separated by the '_' character. If the species identity could not be extracted from the publication, this column was filled with 'NA'. In cases where multiple species are pooled together, the 'spp.' species name is provided.
Publication_id	*Text*	Source publication reported as https://doi.org/10.1000/xyz123 or with the URL of the journal publication. All articles are also listed in a freely available Zotero group bibliography.
Publication_year	*Integer*	Year of the publication
Sample_type	*Factor* Laboratory housing Semi-natural population Wild population Not specified	'Laboratory housing' Describes the sample type. Implies that animals from the sample were all maintained indoors in captivity for their entire life. 'Semi-natural population' implies that animals were maintained outdoors in semi-natural habitats for their entire life. This corresponds to rare cases where animals were kept in outdoor enclosures. 'Wild population' implies that animals were obtained from natural populations. If this is not specified in the manuscript, this column was filled with 'Not specified'.
Locality_name	*Character*	Full name from the specific location of the study as specified in the source publication. Usually provided with locality name, region or district name and country name with comma separation. Full name was extracted for wild populations (i.e., name of the origin locality) and for semi-natural populations whenever available. Sometimes, only a country or a district locality could be retrieved from the original publication. If this is not specified in the manuscript, this column was filled with 'NA'.
Locality_latitude	*Float*	Decimal degree GPS latitude coordinate of the locality (extracted from the publication or obtained from the centre of the average locality using Google Maps service). Provided with a minimum three decimal places whenever possible in the WGS 84 format. If this is not available, reported as 'NA'.
Locality_longitude	*Float*	Decimal degree GPS longitude coordinate of the locality (extracted from the publication or obtained from the centre of the average locality using Google Maps service). Provided with a minimum three decimal places whenever possible in the WGS 84 format. If this is not available, reported as 'NA'.
Locality_altitude	*Integer*	Elevation (metres above sea level) of the locality. If this is not available, this column was filled with 'NA'.
Altitude_source	*Factor* Author GPS visualizer Publication None	Source of altitude data. Can be the publication, an extraction based on locality GPS coordinates using GPS visualizer tool online or data provided by the author. When no source was found, this column was filled with 'None'.
Start_day Start_month Start_year	*Integer* *Integer* *Integer*	Start date of the collection and measurements of animals when provided. This can be useful to determine season when animals were sampled and measured for example. Depending on details, this can be given with a year, month, week or day accuracy. When this is not available (e.g., laboratory bred animals), this column was filled with 'NA'.
End_day End_month End_year	*Integer* *Integer* *Integer*	End date of the collection and measurements of animals when provided. This can be useful to determine season when animals were sampled and measured for example. Depending on details, this can be given with a year, month, week, or day accuracy. When this is not available (e.g., laboratory bred animals), this column was filled with 'NA'.

(Continues)

TABLE 1 (Continued)

Column title	Column type	Description
Sample_sex	*Factor* Females Males Both sexes Not specified	Sex of animals from the study sample for which statistics are reported. If this is not specified in the manuscript, this column was filled with 'Not specified'.
Sample_age	*Factor* Juveniles Adults Both age classes Not specified	Age class of animals from the study sample for which statistics are reported. If this is not specified in the manuscript, this column was filled with 'Not specified'.
Treatment_group	*Factor* Controls Abnormal animals Acclimation manipulation Activity manipulation Other manipulation	Sample group of the study animals to differentiate between data from non-manipulated individuals ('Controls') and data from treatment groups of manipulated individuals (other categories). The treatment type is described with a main category type; these categories might be useful to calculate effect size of manipulative studies. This column was included to facilitate removal of data from manipulated individuals for which interspecific comparisons of water loss rates are less meaningful.
Treatment_type	*Text*	Free text providing some details about the kind of manipulation performed on sampled animals. Additional details are provided in the All_comments column at the end of the dataset.
Acclimation_time	*Integer*	Number of days of acclimation in the laboratory prior to measurements for field-caught animals from wild or semi-natural populations. If this is not specified in the manuscript or if animals were from a laboratory colony, this column was filled with 'NA'.
WL_method	*Factor* Change in mass of a desiccant Doubly labeled water Flux chamber Loss of body mass Gas measurement	General protocol used to quantify water loss rates (see main text for more detailed description).
WL_VPDair	*Float*	Water vapour pressure deficit (VPD) of the surrounding air during water loss rate measurements when available (kPa). When temperature and relative humidity are provided, VPD was calculated with the Magnus equation from Alduchov and Eskridge (1996). The relative humidity is assumed to be 10% when air was dried with silica gel or another chemical in a flow-through system and no exact humidity value is reported in the manuscript. Additional information about the calculation is provided as free comments in the All_comments column whenever necessary. Provided with at least three decimal places whenever possible. If this could not be calculated, this column was filled with 'NA'. This calculation assumes that body and surface temperatures of the animals are at equilibrium with air temperature. See below.
WL_TPair WL_TPskin WL_TPbody	*Float*	Temperature of the surrounding air during water loss rate measurements when available (mean value or midpoint temperature from the given range, °C). Provided with at least one decimal place whenever possible. If this is not specified in the manuscript, this column was filled with 'NA'. Temperature is also provided whenever available for the surface skin of the animals and for the core body temperature of the animals.
WL_flow	*Integer*	Air flow in mL per min during water loss rate measurements when available. If this is not specified in the manuscript, this column was filled with 'NA'. The air flow is assumed to be zero for measurements performed in sealed or semi-sealed boxes.

(Continues)

TABLE 1 (Continued)

Column title	Column type	Description
Chamber_type	*Factor*	Main category of chambers used to measure evaporative water loss (EWL): a flow-through chamber (typically a tube with air coming in and out from opposite sides), a flow flask (typically a glass vessel with air coming in and out from port inlets and outlets of the roof), a sealed box for measurements of water loss in closed conditions, a ventilated box for measurements of water loss in semi-open boxes (typically installed in a temperature control cabinet) or no chamber (typically for field studies or laboratory studies inside enclosures).
Chamber_diam	*Float*	Diameter (cm) of the measurement chamber to calculate air velocity when air is flowing over the animal at a given flow rate. Velocity depends on air fluxes (often reported) and chamber dimensions (not often reported). This applies only to tubular or semi-tubular set-ups. Provided with one decimal place.
WL_duration	*Float*	Duration of the water loss measurements in number of hours. Provided with at least two decimal places whenever possible. If this is not specified in the source, this column was filled with 'NA'.
WL_activity	*Factor* Yes No Not specified	A variable describing if animals were active or not during the water loss measurements. This information was provided only when the original publication specifies that animals were active during measurements ('Yes') or were not active or minimally active during measurements ('No'). Otherwise, when there is no detailed information on animal activity from the protocols or data, this column was filled with 'Not specified'.
WL_Other	*Text*	Free text providing other useful characteristics about the protocol (acclimation type, apparatus, etc.)
Sample_id	*Character*	Unique identifier of the study sample. This identifier is used to identify records from the same group of individuals obtained in different conditions or reported with different units. The unique identifier is given in the standard format Name first author + Abbreviated journal name + Year + Identification-Number separated with the '_' character. When there were small differences in sample size for statistics of the group of animals due to a few missing data points or some outliers, we decided to give the same identifier for all statistics.
WL_component	*Factor* TEWL RWL CWL	A variable describing the component of water loss measured in the sample with this protocol, which includes only three possibilities here: total evaporative water loss (TEWL), respiratory water loss (RWL) and cutaneous water loss (CWL, see Figure 1).
WL_unit	*Factor* mg/h mg/g/h %/h mg per cm2 per hour %	A variable describing the unit of the water loss rates as provided in the original publication, which includes four possibilities: absolute water loss in mg water per hour (mg/hr), relative water loss in mg water per g animal per hour (mg/g/hr), relative proportional water loss in % initial mass per hour (%/hr) and surface specific water loss in mg water per cm^2 body surface ($mg/cm^2/hr$). One record was reported in % without time unit.
WL_mean	*Float*	The central statistics (mean) of the water loss rate from the sample expressed with three decimal places whenever possible.
WL_mean_type	*Factor* Dataset Table Figure Text Other	A variable describing how mean statistics were extracted from the source publication, which includes five possibilities: direct extraction from raw data provided by the source publication or obtained from authors and/or collaborators ('Dataset'), direct extraction from a table ('Table'), direct extraction from a figure ('Figure'), direct extraction from the text ('Text') or other techniques (e.g., statistical modelling of the data, calculation from sum of respiratory and cutaneous water loss; see also details in the All_comments column)
WL_error	*Float*	A measure of the dispersion (error around the mean) of WL values with three decimal places whenever possible. When this could not be extracted or when sample size equals 1, this column was filled with 'NA'.

(Continues)

TABLE 1 (Continued)

Column title	Column type	Description
WL_error_type	*Factor* SD SE Range	A variable describing the kind of dispersion statistics reported in the source, which includes three possibilities: sample standard deviation (*SD*), standard error (standard deviation of the mean, *SE*) or range (difference between maximum and minimum values). When this could not be extracted or when sample size equals 1, this column was filled with 'NA'.
WL_error_details	*Factor* Sample error Error in a statistical model	A variable describing if the dispersion statistics are calculated from sample statistics (Sample error) or using a statistical model from the variance components.
WL_N	*Integer*	Sample size for the WL statistics (total number of individuals in the sample). When this could not be extracted, this column was filled with 'NA'.
SVL_mean	*Float*	Mean snout to vent length of animals from the sample (mm) provided with a maximum of two decimal places. When this could not be extracted, this column was filled with 'NA'.
TL_mean	*Float*	Mean total length of animals from the sample (mm) provided with a maximum of two decimal places. When this could not be extracted, this column was filled with 'NA'.
Shape_score	*Factor* Juvenile lizard Juvenile snake Lizard Snake Worm lizard	Factor describing the general shape of the animals, essentially to make test checks of the size, length and mass data.
BM_mean	*Float*	Mean body mass of animals from the sample (g) provided with a maximum of two decimal places. When this could not be extracted, this column was filled with 'NA'.
BM_error	*Float*	A measure of the dispersion of body mass values with two decimal places whenever possible. When this could not be extracted or when sample size equals 1, this column was filled with 'NA'.
BM_error_type	*Factor* SD SE Range	A variable describing the kind of dispersion statistics reported for body mass, which includes three possibilities: sample standard deviation (*SD*), standard error (standard deviation of the mean, *SE*) or range (difference between maximum and minimum values). When this could not be extracted or when sample size equals 1, this column was filled with 'NA'.
SA_mean	*Float*	Mean surface area of animals (cm^2) provided with a maximum of two decimal places. When this could not be extracted, this column was filled with 'NA'.
Quality_code	*Factor*	A complex categorical variable allowing data quality to be ranked using a set of comments separated by commas. First comment describes data quality and extraction mode. Second and third comments describe the kinds of abnormality in the data, which may refer to the condition and state of the animals, the test conditions or some kind of pre-measurement manipulative protocol. Regarding quality, it is a subjective score with 'high' (good methodology, metadata are all reported and statistics are provided with enough details), 'low' (poor methodology, conditions are not reported and statistics are poorly reported) and 'medium' (one of the critical aspects of a 'high' score is missing). Further details are provided in the All_comments column to justify further the study quality and explain environmental conditions before and during measurements.
Study_standards	*Factor* Low quality Medium quality High quality	A simple categorical variable describing the quality of the data (low, medium or high scores from the Quality_code). This is useful for future analysis of the data to select a subset of the dataset with the best standards.
Data_standards	*Factor* Usable data Not usable data	A simple categorical variable describing if the data can be used to compare standard water loss rates within and between species. Further details are provided in the All_comments column to justify why a data record should not be used. This is useful for future analysis of the data to select a subset of the dataset with the best standards.
All_comments	*Text*	Free text giving detailed contextual information about the methods and data compilation.

Abbreviation: WGS 84, World Geodetic System 1984.

references from a recent comparative analysis of water loss in reptiles (Cox & Cox, 2015). The availability of water loss data on samples of individuals (excluding eggs or embryos) from known reptile species was then checked by a single person (JFLG) who stored all such references, source files as well as available online data in a Zotero group library (see https://tinyurl.com/y2nclru5). Using tags, all publications were then assigned to a single person who oversaw confirming availability of water loss data, extracting the data and adding relevant metadata to a spreadsheet. If additional relevant publications were identified, those were added to the Zotero library and processed by the same individual. This procedure was performed first in September 2018 and repeated in October 2019, February 2020 and September 2020 and spans data sources published from 1932 to late 2020. Additionally, unpublished data were also contributed by our research group. In March 2021, we added metadata following up on review requests, extracted additional information on metabolism and validated the database again.

We produced a library of 160 publications, reports or academic contributions (monographs, dissertations and theses) from which we extracted complete or partial data (see PRISMA workflow in Supporting Information Figure S1). EWL data were then added into a spreadsheet together with all the available metadata describing the relevant conditions of water loss measurements, species and sample characteristics, and contextual information regarding animal morphology, location, sampling dates and habitat. The species and subspecies identities were standardized using the European Molecular Biology Laboratory (EMBL)/European Bioinformatics Institute (EBI) Reptile DataBase release of 21 December 2019 (Uetz & Etzold, 1996). We performed data extraction accepting a sample data point as defined by a unique group of animals composed of a fixed set of individuals, subjected to the same experimental protocol, and measured under the same conditions. For each sample, we extracted the mean and dispersion statistics (*SD*, *SE* or range) of EWL rates (total water loss, respiratory water loss or cutaneous water loss) and the mean and dispersion statistics (*SD*, *SE* or range) of body mass as well as mean statistics for body size (snout to vent and total length) and body surface area. Data were taken from published or shared datasets, extracted from tables and text, or extracted from figures using scanned images of the plots and the Plot Digitizer program in Java (https://sourceforge.net/projects/plotdigitizer/). Information on measurement method, temperature (air, skin surface and core body temperature), water vapour pressure deficit (VPD) in the air, air flow, measurement duration, and activity statuses of animals were extracted whenever available or requested from the corresponding authors. We added additional information on chamber characteristics and average diameter of the chambers to make it possible to calculate air velocity from air flow. All data are presented as values on the scales chosen for reporting, although, whenever possible, the possibility for scale conversion is provided (see below). These metadata were selected because they provide important contextual information about dominant factors of methodological variation in measurements of EWL (Mautz, 1980).

A mechanistic understanding of water balance requires a careful quantification of the functional traits governing variation in CWL and RWL among species and the use of biophysical models of EWL (Gates, 1980; Kearney & Porter, 2009; Pirtle et al., 2019). In RWL, water is lost by evaporation from the lung respiratory surface to air contained in it at a rate determined by the water vapour density gradient. The establishment of the water vapour density gradient, in turn, depends on the relative humidity and temperature of the inhaled air and the pace at which the air inside the lungs is renewed, that is, total ventilation (Gates, 1980). Total ventilation is determined by a combination of breathing frequency and tidal volume and is linked to the adequate match of metabolic demand (Pirtle et al., 2019). Thus, RWL should increase monotonically with air temperature, air dryness, body temperature, and increased metabolic activity. CWL is mostly determined by the water vapour gradient between the skin surface and the air, which is established by the interaction of air temperature and relative humidity, air convection rate, an animal's shape and size, both of which affect skin surface area, and, finally, the intrinsic resistance of the skin to evaporative water loss or R_s (Gates, 1980; Mautz, 1980). Thus, from a functional standpoint, R_s informs on a central organismal determinant of the animal's susceptibility to lose water via evaporation being, possibly, the best standardized metric to compare samples, populations and species (Gates, 1980; Pirtle et al., 2019). Several studies have quantified and compared R_s among closely related squamate reptile species (Dmi'el, 1998, 2001; Oufiero & Van Sant, 2018), but accurate values of R_s are generally unavailable for most species to date (Mautz, 1982). Therefore, for those cases in which the information could be recovered, we collected and reported all the components necessary for calculating R_s, even though we have not added it as a separate variable in the dataset (Kearney & Porter, 2020). Note that there are potential caveats with respect to this approach because of unknowns in the regional variation of skin and body temperatures (Barroso et al., 2016), difficulties in partitioning sub-components of EWL (Senzano & Andrade, 2018), and further study or species-specific features that make it difficult to calculate *Rs* (Mautz, 1982).

We also included variables describing study design (groups and treatments) and a quality score permitting the exclusion of data (abnormal animals, animals maintained under manipulated conditions or measurements performed in non-standard conditions) in future extraction and analysis. Each of us scored a study data quality ranging from high (appropriate protocols, protocols are well reported, and data statistics are detailed), medium (one item is missing) to low (poorly designed, poorly reported protocols and poorly detailed data statistics). One person then check all scores and also categorized the record as either usable to not usable data (because of low study standards or inappropriate metadata, detailed comments about these scores are also provided as a free text column in the dataset). The content of the database is outlined in Table 1, which provides additional information on each field of the data table. Upon data extraction, each record was checked by the data collectors and the content and integrity of the whole database was checked by two individuals prior to uploading the first version, called SquamEWL, in a public repository available at DOI: https://doi.org/10.5281/zenodo.3666172 (Le Galliard et al., 2020). Routines for data extraction, database integrity checks and data cleaning were coded in the R statistical language, and are briefly described below. The fully annotated code written for R version 3.6.3 (R Core Team, 2020) is also available in the public repository and includes functions to convert records between measurement scales.

3 | PRELIMINARY ANALYSES

The SquamEWL dataset includes 2,536 water loss records of 325 species and subspecies (301 unique species) of squamate reptiles for 793 unique samples (mean number of individuals per sample = 10.15 ± 11.5 SD, median = 6, range = 1–169) with most measurements obtained for TEWL (*n* = 2,146) and substantially fewer for CWL (264) and RWL (126). The vast majority of records is from field-captured animals (*n* = 2015) in comparison to laboratory acclimated animals or those raised in outdoor enclosures (*n* = 203). There is substantial variation in the acclimation time of animals (time spent in the laboratory prior to measurement), even after excluding laboratory-raised animals (range = 0–750 days, mean = 46.45 ± 119.4 *SD*, median = 7). The predominant protocol involves measurements of body mass loss in the laboratory (*n* = 1,391), followed by direct measurements of water vapour changes in flow-through chambers (*n* = 760), measurements of the mass increase of a desiccant (*n* = 296), doubly-labelled water techniques in active animals (*n* = 56) and, in more recent studies, flux chamber protocols for measurements of trans-epidermal water loss (*n* = 33). The variation in micro-climatic environmental conditions during sampling is wide, with air temperatures ranging from 5.3 to 45 °C (mean = 28 ± 6.47 *SD*, median = 27), VPD in the air ranging from *c*. 0 to 9.10 kPa (mean = 2.83 ± 1.73 *SD*, median = 2.53) and air flow ranging from zero to several hundred mL per min (mean = 146.5 ± 267.8 *SD*, about half of the records were obtained in still air).

The geographic origin is available for 1,923 records comprising 316 unique localities (Figure 2a) predominantly located in northern and Central America, Europe and Australia, with under-representation in pan-tropical diversity hotspots including South America, Africa, and Asia as well as several semi-arid and arid regions of Africa, the Arabian Peninsula and remaining Asia sub-tropical regions (Roll et al., 2017). The altitudinal range varied from sea level up to 3,718 m above sea level with most records below 500 m (mean = 367.7 m, median = 74 m), which reflects the prevalent altitudinal range for Squamata (Buckley et al., 2008, 2012). The dataset contains representatives of 34 families but only 2.71% of the total species richness estimated for squamates. Given the contribution of different families to the total species richness of squamate reptiles worldwide (Roll et al., 2017; Uetz & Etzold, 1996), there is an 'over-representation' of species from Lacertidae, Phrynosomatidae, Teiidae, Diplodactylidae, Sphaerodactylidae and Viperidae and an 'under-representation' of species from Gekkonidae, Gymnophthalmidae, Elapidae, Scincidae and Colubridae (Figure 2b).

In addition to heterogeneity in sampling, measurements conditions and laboratory methods, calculations of water loss rates vary among studies. In particular, EWL rates are reported on three different scales, namely as mass-relative values (% of initial body mass or mg per g per hour, 1,544 records), absolute values (mg water per hour, 715 records), or surface-relative values (mg per cm^2 per hour, 270 records). To convert all EWL records to a single scale (mg per hour), we gathered records reported for the same samples under the same conditions on different scales and used a statistical procedure to fit a calibration function to convert data from relative to absolute scale (see Supporting Information File S1). Using this approach, we calculated 1,884 unique estimates of absolute EWL rates, including TEWL, CWL and RWL components. Preliminary non-phylogenetic analyses indicated that TEWL and CWL rates scale allometrically with body mass with an exponent of *c*. 0.6–0.7 (linear regression on a log-log scale, TEWL: slope = 0.66 ± 0.0154 *SE*, CWL: slope = 0.59 ± 0.048 *SE*; see Figure 2c), which is close to the 2/3 allometric exponent for the geometric increment of surface area with the increment in body mass. The RWL component is generally smaller than the CWL component of TEWL in small-sized species and increases faster with body mass (linear regression on a log-log scale, RWL: slope = 0.88 ± 0.058 *SE*), as expected from the 3/4 allometric exponent relating ventilation and metabolic rates to body mass. After correction for body mass but not for experimental conditions, records of TEWL showed no clear altitudinal cline across all samples (linear regression with log-transformed WL and mass, $F_{1,959} = 0.56$, $p = .09$), but a small negative latitudinal cline (linear regression with log-transformed WL and mass, $F_{1,960} = 5.25$, $p = .02$). Future analyses should explore more in depth the effects of species characteristics and environmental conditions (e.g., temperature and humidity, habitat aridity) on interspecific variation in EWL.

Physical equations of TEWL require additional information on the temperature of the animals, the body shape and air velocity, and the metabolism (see above). Surface (*n* = 90) and body (*n* = 190) temperatures were very rarely reported because they are usually difficult to measure and it is often assumed that they are at equilibrium with air temperature, which is not true in general (Warburg, 1965). Air velocity could be calculated for most records (*n* = 2,204) and ranged from 0 to 0.017 m per second (mean = 0.0014 ± 0.0029 *SD*). We extracted 394 usable metabolic data values from the same sources as in the SquamEWL database including 105 unique species and subspecies from 184 samples, which we present in a separate companion dataset. Notwithstanding that, we provide the necessary functions to merge these data with those of the SquamEWL database for users potentially interested in mechanistic modelling of CWL and RWL using the NicheMapR software (Pirtle et al., 2019).

4 | CONCLUSION AND PERSPECTIVES

The present dataset greatly expands previous compilations of EWL in squamate reptiles by nearly doubling the number of species (*c*. 100 species in Mautz, 1982; 139 species in Cox & Cox, 2015). It also provides exhaustive metadata about the methods, contexts

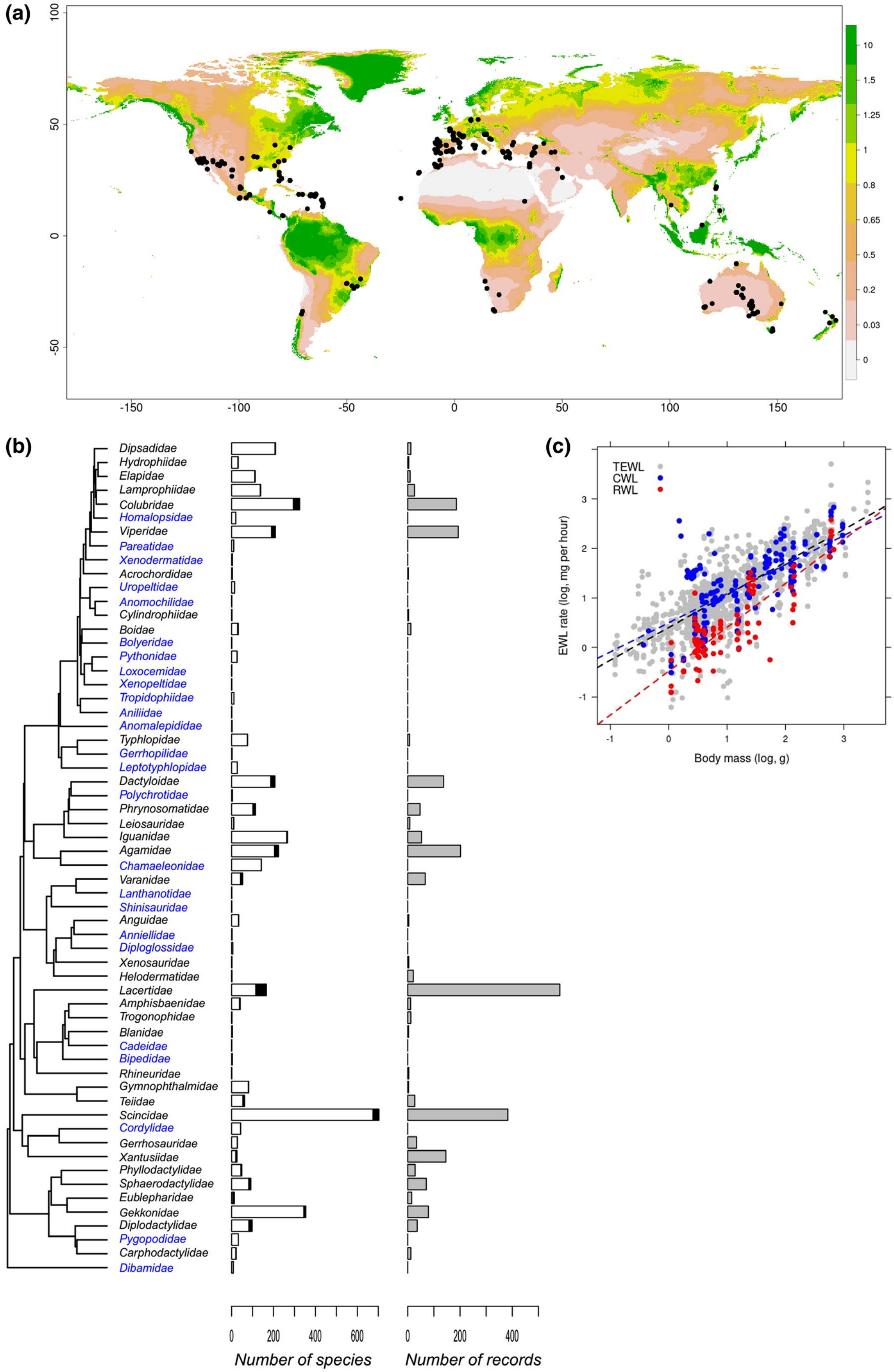
(a)
(b)
(c)
TEWL
CWL
RWL
EWL rate (log, mg per hour)
Body mass (log, g)
Number of species
Number of records
Dipsadidae
Hydrophiidae
Elapidae
Lamprophiidae
Colubridae
Homalopsidae
Viperidae
Pareatidae
Xenodermatidae
Acrochordidae
Uropeltidae
Anomochilidae
Cylindrophiidae
Boidae
Bolyeridae
Pythonidae
Loxocemidae
Xenopeltidae
Tropidophiidae
Aniliidae
Anomalepididae
Typhlopidae
Gerrhopilidae
Leptotyphlopidae
Dactyloidae
Polychrotidae
Phrynosomatidae
Leiosauridae
Iguanidae
Agamidae
Chamaeleonidae
Varanidae
Lanthanotidae
Shinisauridae
Anguidae
Anniellidae
Diploglossidae
Xenosauridae
Helodermatidae
Lacertidae
Amphisbaenidae
Trogonophidae
Blanidae
Cadeidae
Bipedidae
Rhineuridae
Gymnophthalmidae
Teiidae
Scincidae
Cordylidae
Gerrhosauridae
Xantusiidae
Phyllodactylidae
Sphaerodactylidae
Eublepharidae
Gekkonidae
Diplodactylidae
Pygopodidae
Carphodactylidae
Dibamidae

FIGURE 2 (a) Geographic distribution of data records with exact coordinates of sampling location when available. The geographic location of data records is mapped over a raster map of the global aridity index (GAI) for the 1970–2000 period (Trabucco & Zomer, 2019). The aridity index represents the ratio between rainfall and a measure of potential evapotranspiration (hyper-arid: GAI < 0.03; arid: GAI < 0.2; semi-arid: 0.2 < GAI < 0.5; dry sub-humid: 0.5 < GAI < 0.65; humid: GAI > 0.65; the scale includes a larger range of humid conditions for the sake of visualization). (b) Phylogenetic tree of the Squamata according to a recent time-calibrated phylogeny by Zheng and Wiens (2016). We calculated the proportion of species sampled (black portion of each barplot) according to the Reptile Database (Uetz & Etzold, 1996) and the total number of records for each family. Data deficient families are highlighted in blue. (c) Allometric scaling of water loss rates (mg water loss per hour) with body mass in 1,485 records across 305 species for which total evaporative water loss (TEWL), total water loss from skin, ocular or cloacal evaporation (CWL) and total water loss from respiratory evaporation (RWL) could be calculated. All individual data points are displayed on a log-log scale together with the best linear non-phylogenetic regression line for each EWL component

and protocols by/in which each unique data point was obtained. This expanded and fully annotated dataset will ease transparent and reproducible statistical manipulation of EWL data for future studies, allow the examination of how much variation in EWL is caused by methodological factors instead of ecological or evolutionary drivers, facilitate the estimation of skin resistance for an expanded list of species and will therefore ease comparative analyses of EWL. The dataset may also assist in estimates of TEWL, CWL and RWL, the conversion between different measurement scales and the identification of records performed within pre-defined sets of conditions, such as standard records of EWL with non-manipulated animals at rest. This is particularly important given the substantial differences in methodology among studies and the inherent variability in EWL values caused by air temperature, air humidity and air velocity during measurements. Potential case studies will include methodological analyses of microclimatic factors such as temperature and humidity, partitioning of intra- and interspecific variation and comparative phylogenetic analyses of the diversification of and environmental constraints on EWL across species.

Despite earlier suggestions to better standardize EWL measurement protocols (Mautz, 1982), the current data cover a broad range of methods and contexts, and we found it difficult to suggest an optimal and single method way to measure EWL in squamate reptiles because the exact protocol will always depend on the specific research questions. Obviously, broad-scale comparisons of EWL in poorly explored taxa and geographic areas would benefit from the use of simple approaches where water loss is measured with a gravimetric method on animals at rest for a few hours in controlled conditions in a ventilated box (Garcia-Porta et al., 2019). On the other hand, functional studies will require detailed quantification of the processes and patterns of water loss and therefore continuous-time gas measurements following standard guidelines on animals at rest in controlled conditions in flow-through chambers (Lighton, 2018).

We hope that the compiled metadata information of our database (see Figure 1b) will foster the improvement of data reporting standards. In particular, we recommend that future studies of EWL in squamate reptiles report systematically details of animal origin, husbandry conditions before measurements, protocol and measurement conditions, and provide central tendencies and dispersion statistics on absolute scales (mg per hour) or supply the raw data. We also hope to stimulate future researchers to collect and report all the variables necessary to quantify skin resistance to water loss R_s, a potentially central metric in mechanistic modelling approaches (Riddell et al., 2017). For example, macro-ecological studies may focus on spatial analyses of how climatic and other abiotic aspects of the habitat interact to determine species distributions and their vulnerability to environmental disturbances.

Our dataset further identifies critical geographic and taxonomic gaps that may be valuable in guiding future investigations. The limited geographic and poor taxonomic coverage of our dataset reflect known gaps in herpetological and ecological research (Etard et al., 2020; Meiri, 2018; Roll et al., 2017). Such gaps and biases are also not surprising for functional traits related to physiology for which coverage is much lower than ecological, life history, and morphological traits (> 20% species coverage according to Etard et al., 2020). Given that the water balance physiology of squamate reptiles has been far less investigated than their thermal biology, we insist on the fact that a gap-filling effort be directed to the sampling of more data in undersampled areas and taxonomic groups. More specifically, we wish to draw attention to the scarcity of data for Gekkonidae, Scincidae and Colubridae on a taxonomical basis, and, from areas in South America, Africa, and Asia. The database will be regularly updated with these new data to provide a central resource for ecological and evolutionary research on this particular animal group.

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AUTHOR CONTRIBUTIONS

JFLG and TVD conceived the project, organized the data collection, and collected and checked data. FB, AD, RG and OL contributed to project conception and helped with data collection and management. MC, MS and DOVA contributed data and helped with data collection. CC helped with data collection, data formatting and technical validation. All authors contributed to writing based on a first version produced by JFLG.

DATA AVAILABILITY STATEMENT

Data are available on Zenodo (doi: https://doi.org/10.5281/zenodo.3666172).

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BIOSKETCH

Jean-François Le Galliard is an evolutionary biologist and population ecologist interested in the understanding the diversity of life history and behavioural strategies that animals use to survive and reproduce in their changing environments. For this data project, he worked with a team of ecologists and evolutionary biologists with strong expertise in the ecophysiology and water biology of reptiles.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

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