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Improved estimation of gut passage time considerably affects trait-based dispersal models

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Abstract

1. Animals are important vectors for transporting seeds, nutrients and microbes across landscapes. However, models that quantify the magnitude of these ecosystem services across a broad range of taxa often rely on generalised mass-based scaling parameters for gut passage time. This relationship is weak and fundamentally breaks down when considering individual species, indicating that current models may incorrectly attribute or estimate the magnitude of dispersal.

2. We collated a large dataset of gut passage time for endothermic animals measured using undigested markers ($n = 391$ species). For each species, we compiled trait data, including body mass, morphology, gut physiology, diet and phylogeny. We then compared the ability of five statistical models (constant, generalised least squares, phylogenetic generalised least squares, general linear model and random forest) to estimate the time of first marker appearance (transit time; TT) and mean marker retention time (MRT) for particle and solute markers in mammals and birds separately.

3. For mammals, we found that the inclusion of additional traits appreciably reduced the median root-mean squared error across all markers in a leave-one-out cross validation. For birds, however, additional traits did not significantly improve our ability to predict gut passage time across markers. This may have occurred due to the smaller number of bird species included in our analysis or the absence of important explanatory factors such as differences in gastrointestinal morphology.

4. Using the $MRT_{particle}$ random forest model from this study, we updated two trait-based dispersal models for seed and nutrient movement by mammals. The magnitude of dispersal in our updated predictions ranged from 66% to 176% of the original model formulation for different scenarios, highlighting the importance of gut passage time for dispersal models. Furthermore, the contribution by individual or groups of species was found sizeably altered in our updated models.

5. Future modelling studies of dispersal by mammals, for which empirical estimates of gut passage time are absent, will benefit from predicting gut passage time using statistical models that incorporate traits including animal morphology, diet and gut physiology.

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1 | INTRODUCTION

Animals are important vectors of seed, nutrient and microbe dispersal across a wide diversity of landscapes in both terrestrial and marine ecosystems (reviewed in Côrtes & Uriarte, 2013; McInturf et al., 2019; Subalusky & Post, 2019). These biotic dispersal networks are, however, often not appreciated until changes in ecological demographics occur. Following the late-Pleistocene extinctions, there has been a concomitant reduction in the transport of seeds, nutrients and microbes throughout the world. Recent studies by Doughty, Wolf, Morueta-Holme, et al. (2016) and Pires et al. (2018) show that megafauna-dispersed plants across Amazonian forests have contracted their range by 26%–31% over the last 10,000 years due to a reduction in long-distance seed-dispersal by 66%–95%. Similarly, lateral nutrient movement by terrestrial mammals has been estimated to have reduced by >90% following the downsizing of mammals over the last 10,000 years (Doughty, Roman, et al., 2016; Hempson et al., 2017) while global microbe dispersal in faeces has decreased seven-fold, possibly increasing independent microbial evolution through an 'island biogeography effect', which is believed to increase the emergence of infectious diseases (Doughty et al., 2020). Likewise, significant reductions in seed dispersal have been shown following changes to populations of large frugivorous bird species (Donoso et al., 2020; Jordano et al., 2007; Wotton & Kelly, 2012).

At present, dispersal models that assess biological dispersal of seeds, nutrients and microbes across a broad suite of taxa often use generalised mass-based scaling parameters for gut passage time (e.g. Donoso et al., 2020; Doughty et al., 2020; Doughty, Roman, et al., 2016; Hempson et al., 2017; Pires et al., 2018; Sorensen et al., 2020; Viana et al., 2013; Wolf et al., 2013; Yoshikawa et al., 2019). The reasoning behind the choice of allometric scaling is based on theoretical grounds as gut capacity scales linearly to body mass ($BM^{1.00}$) and dry matter intake to the metabolic rate ($BM^{0.75}$; Demment & Van Soest, 1985). But this has been refuted (see Müller et al., 2013) and crucially breaks down when individual species, or groups of closely related species, are considered (Clauss et al., 2007; De Cuyper et al., 2020; Frei et al., 2015; Jackson, 1992; Steuer et al., 2011; Pryzbylo et al., 2019; Robbins, 1993). As certain species have unique characteristics that make them disproportionately important for dispersal processes (e.g. their population density, gut passage time, or daily movement), it is critical to estimate parameters for each species as accurately as possible when using trait-based dispersal models. The compound interaction of traits may otherwise result in models that incorrectly attribute or estimate the magnitude of dispersal. For example, Elephantidae are key agents of dispersal due to their high consumption, large daily movement and high population densities (Bunney et al., 2017; Campos-Arceiz et al., 2012). Yet, their mean gut passage time is much shorter (~30 hr; Beirne et al., 2019; Bunney et al., 2017; Hackenberger, 1987; Rees, 1982; Steuer et al., 2011) than would be predicted based on their mass alone (Clauss et al., 2003). Consequently, models that rely on a generalised scaling parameter for gut passage time may significantly overestimate the magnitude of dispersal-related processes by this taxonomic family—an effect that may not be compensated for by the underestimation of other species within the mass-based scaling framework.

The aim of this study is to more accurately predict gut passage time across endothermic taxa and to assess the impact this has on trait-based dispersal models. We consider two aspects of gut retention time: (a) the time of first appearance between marker ingestion and excretion (transit time [TT]) and (b) the integrated, average time between marker ingestion and excretion (mean retention time [MRT]; Robbins, 1993). We focus on endothermic taxa because these organisms are considered to be the major vectors of lateral biotic dispersal (Doughty, Roman, et al., 2016; Wolf et al., 2013). However, future research should also consider refining TT and MRT in dispersal models that incorporate ectothermic species.

2 | MATERIALS AND METHODS

2.1 | Literature survey

Mean retention time can be assessed with marker substances that are not normally secreted, digested or absorbed in the gut; that are not toxic to the gut microbiota and that are easily assayed in digesta and faeces (Stevens & Hume, 2004; Warner, 1981). We collected TT and MRT data for all endothermic species that have been recorded in laboratory and field studies available to us. To start, we collated data that have been previously published from Clauss et al. (2007), Müller et al. (2013), Yoshikawa et al. (2019) and De Cuyper et al. (2020). We then conducted our own extensive literature search through until 31 July 2019 to include recently published works and animal groups that were not represented in the original datasets. To do this, we systematically reviewed relevant papers in the ISI Web of Science and Google Scholar using combinations of the following keywords: (mean, gut, passage, retention, time, transit). Some studies presented TT and MRT graphically. In these cases, we used GraphClick v3.0.2. software (Arizona Software Inc., 2010) to extract the data. In total, 351 individual studies were included in our final database, representing 261 mammal and 130 bird species.

Age can impact TT and MRT in animals (Kastelein et al., 2003; Munn & Dawson, 2006; Robbins, 1993; Warner, 1981). For this study, we focused on gut passage time in adult individuals only.

Where studies did not explicitly state the maturity of individuals, we used body size as a metric for inclusion. If the experimental animal body mass was <50% of the body mass reported in Elton Traits v1.0 (Wilman et al., 2014), we removed it from our analysis.

Solute and particle markers travel through the gut at different rates and therefore must be considered separately (Robbins, 1993). Additional marker characteristics, such as particle size, have also been shown to influence gut passage time in specific taxa (Matsuda et al., 2015; Wilson & Downs, 2012), and depending on the mathematical approach, the frequency of faecal sampling in passage experiments can affect the resulting MRT. Please refer to Supplementary Text 1 for further discussion of these factors. To heed differences in marker characteristics, in this study we analysed particle and solute markers separately.

For each study where several particle markers were used, we calculated a mean TT and MRT across particle markers. From this, we then calculated a mean TT and MRT across studies for each species from which to undertake our analysis. This procedure was undertaken to reduce individual study bias and has been practiced in other assessments of TT and MRT evaluation (Clauss et al., 2007; Sorensen et al., 2020; Steuer et al., 2011; Yoshikawa et al., 2019).

2.2 | Animal traits

Many traits have been proposed to impact TT and MRT in endothermic animals including body mass (Demment & Van Soest, 1985; Warner, 1981), dry matter intake (Clauss et al., 2007; Müller et al., 2013), diet (De Cuyper et al., 2020; Murray et al., 1994), gut physiology (Robbins, 1993; Stevens & Hume, 2004), rumination (Przybyło et al., 2019; Steuer et al., 2011), volancy (Frei et al., 2015; Hilton et al., 1998), foraging strata (Jackson, 1992) and physical activity level (Beirne et al., 2019; Kleyheeg et al., 2015). Table S1 details an extensive list of traits that have been shown to impact TT and MRT.

Here, we calculate pertinent trait data for each species included in our TT and MRT database. We only included trait data if it could be reliably obtained for all species in each taxonomic group. Ideally, traits should be measured on the same animals used to calculate gut passage time. However, the number of studies where all traits were measured is very small. Therefore, we utilised averaged species-level data from published sources. Table 1 includes a list of traits used in this study and supplementary text 2 details specifically how we compiled these traits.

2.3 | Statistical models

All statistical models were fitted using the natural logarithm of species mean TT or MRT. Mammal and bird datasets were analysed separately in R version 3.6.1 (R_Core_Team, 2019).

First, we built a constant model by simply calculating the mean TT/MRT across all species. We then explored the allometric relationships between TT/MRT and body mass, both with and without

TABLE 1 Animal traits included for mammals and birds

Trait	Details	Database
Mammals		
Activity time	Nocturnal/crepuscular/diurnal	Wilman et al. (2014)
Body mass	Adult body mass (kg)	Wilman et al. (2014)
Coprophagy	Yes/no	Individual studies
Diet	Consumption from 10 diet classes in Elton Traits v1.0 (%)	Wilman et al. (2014)
Feeding strata	Marine/ground/scansorial/arboreal/aerial	Wilman et al. (2014)
Gut physiology	Simple/hindgut/foregut	Stevens and Hume (2004)
Morphology	Adult body length (mm)	Nowak and Walker (1999)
Phylogeny	Consensus tree from PHYLACINE v1.2	Faurby et al. (2018)
Ruminant	Yes/no	Nowak and Walker (1999)
Volancy	Yes/no	Nowak and Walker (1999)
Birds		
Activity time	Nocturnal/diurnal	Wilman et al. (2014)
Body mass	Adult body mass (kg)	Wilman et al. (2014)
Coprophagy	Yes/no	Individual studies
Diet	Consumption from 10 diet classes in Elton Traits v1.0 (%)	Wilman et al. (2014)
Feeding strata	Below water/water surface/ground/understory/mid-canopy/canopy/aerial	Wilman et al. (2014)
Gut physiology	Simple/foregut	Stevens and Hume (2004)
Morphology	Morphological principal components 1–9	Pigot et al. (2020)
Phylogeny	Consensus tree from BirdTree	Jetz et al. (2014)
Volancy	Yes/no	del Hoyo et al. (2017)

consideration of the phylogenetic relatedness of the target species. These techniques have been undertaken before on select groups of animals (Clauss et al., 2007; De Cuyper et al., 2020; Robbins, 1993; Sorensen et al., 2020; Steuer et al., 2011; Yoshikawa et al., 2019). We performed simple generalised least squares (GLS) with log body mass as a single explanatory variable using the 'NLME' package (Pinheiro et al., 2014) and phylogenetic generalised least squares (PGLS) using the 'CAPER' package (Orme et al., 2013). PGLS incorporates potential bias arising between biological traits by assuming that the similarity

of model residuals between species depends upon their phylogenetic relatedness (Symonds & Blomberg, 2014). The strength of the phylogenetic signal is set using Pagel's λ, which can vary from 0 (no phylogenetic signal) to 1 (strong phylogenetic signal). We estimated λ using the maximum likelihood method. For comparison to previous studies that have considered allometric scaling differences between trophic groups, we also undertook GLS and PGLS scaling on subsets of our data for each taxon, where species were grouped by their dominant feeding mode. Groups were defined using the dominant diet categories in Elton Traits v1.0 (Wilman et al., 2014).

To include additional traits into our predictive models, we utilised the 'CARET' package, which provides a framework for training more complex linear and nonlinear statistical models (Kuhn, 2015). Within 'CARET', we used the 'GLMNET' package (Friedman et al., 2010) to build a L1-regularised generalised linear model with square loss (LASSO) for predicting TT/MRT using the animal traits outlined in Table 1. Lasso regression uses a regularisation parameter to shrink or eliminate predictor variables that contribute least to model fit (Tibshirani, 1996). To do this, the GLMNET method continuously optimises each parameter in the model and executes cyclical coordinate descent until model convergence is reached. This procedure helps prevent model overfitting while allowing all potential variables to be included in the final general linear model. We used an identity link function and assumed a Gaussian error distribution. To incorporate phylogeny into our lasso general linear model, we added separate predictor variables for each scientific order and family found in our database. The regularisation parameter was optimally selected using k-fold cross-validation with $k = 10$ folds.

Finally, we built a random forest model using the 'RANDOMFOREST' package (Liaw & Wiener, 2002) to assess nonlinearity between predictor variables in predicting TT/MRT. To our knowledge, machine learning techniques have not previously been applied to the prediction of gut passage time in animals. Random forest is generally considered the most powerful implementation of regression tree techniques for prediction. Again, we incorporated phylogeny using separate predictor variables for each scientific order and family. The number of variables randomly sampled at each split in the tree (mtry) was optimised within the 'CARET' package using a predefined hyperparameter grid from 1 to the total number of variables.

To compare models, we performed a 'leave-one-out' cross validation, whereby we removed each species in turn, trained the five statistical models on the remaining data and then tested each model on that removed species. We calculated the root-mean squared error (RMSE) between the predicted and observed values for each species and assessed model performance for each marker separately by comparing the median RMSE across models.

2.4 | Updating MRT in trait-based diffusion models

As an application of our improved MRT estimates for mammals, we updated two ecological models that explicitly require an MRT parameter for seed and nutrient dispersal, respectively. The first model,

developed by Pires et al. (2018), mechanistically encompasses seed ingestion, gut retention, animal movement and seed deposition to understand seed dispersal by Pleistocene megafauna in South America. We replaced the original body mass scaled MRT equation of $10 \times BM^{0.22}$ with predictions obtained from our mammal MRT$_{particle}$ model with the lowest median RMSE for two representative genera: (a) a 5,000 kg elephant (*Loxodonta* spp) and (b) a 200 kg tapir (*Tapirus* spp). For each genus, we built a model using all available data except with that genus removed. In this way, we could evaluate the performance of MRT models for species that are not included in our training database. We then compared seed dispersal kernels using the original and our newly predicted estimate of MRT to that arising using an estimate directly from empirical studies. For elephants, we calculated a mean empirical MRT from Hackenberger (1987), Steuer et al. (2011), Bunney et al. (2017) and Beirne et al. (2019). For tapir, we used data from Clauss et al. (2010) and Campos-Arceiz et al. (2012). We used a Levy walk scenario and ran 1,000 individual simulations to generate a seed dispersal kernel for each genus. All other parameters were kept constant as used by Pires et al. (2018).

The second model, used by Hempson et al. (2017), quantifies lateral nutrient transport across sub-Saharan Africa by mammalian herbivores in the pre-colonial era (approximately 1,000 years before present) and present day. Here, we updated MRT for 92 extant native herbivores and three domestic livestock species from the original mass-based formulation of $0.29 \times BM^{0.26}$ to results arising from our mammal MRT$_{particle}$ model with the lowest median RMSE. In all, 13 of the 95 species included in the model were represented in our gut passage database for mammal MRT$_{particle}$, allowing a comparison between the original and newly modelled estimates of MRT to empirical data for these species. All other model parameters were kept as used by Hempson et al. (2017). We summed lateral nutrient movement by all species within $0.5 \times 0.5°$ grid cells to investigate spatial differences between the original model and that using our new estimates of MRT. Finally, we aggregated total nutrient transport across the continent into bins based on the $\log_{10}$ of their body mass to compare differences between size classes using the different iterations of MRT.

3 | RESULTS

3.1 | Model estimates of TT and MRT

In total, we collated data for 261 mammal and 130 bird species. For both taxa, there was a general positive increase in gut passage time with body mass across markers (Figure 1). However, the strength of these relationships varied between taxon and markers from R^2 equal to 0.13 (mammal MRT$_{solute}$) to 0.69 (bird MRT$_{solute}$). Birds consistently demonstrated a larger allometric scaling exponent ('slope') than mammals across markers (Table S2). Analyses of allometric scaling broken down by dominant feeding strategy demonstrates that gut passage time varies according to diet (Figures S1 and S2). In general, herbivorous species had a longer gut passage time for a given body mass than carnivorous species. However, there was no consistent
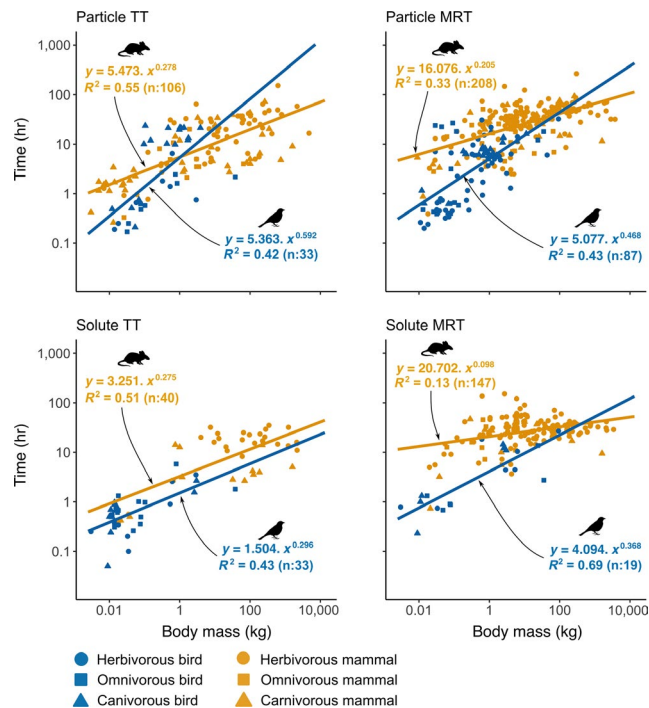
FIGURE 1 Allometric relationships between body mass and gut passage time for mammal (orange) and bird (blue) species using particle and solute markers to assess transit time (TT) and mean retention time (MRT). Point shape denotes dominant feeding strategy. Lines indicate the results of allometry based on generalised least squares (GLS) for mammals and birds separately. For results of allometry based on phylogenetic generalised least squares (PGLS), see Table S2

difference in scaling exponents between these different feeding strategies (Tables S3 and S4).

When comparing the five statistical models for predicting gut passage time in mammals, the inclusion of additional traits improved prediction with the GLMNET and random forest models displaying the lowest median RMSE across all marker types. For birds, the inclusion of additional traits did not significantly reduce the median RMSE (Table S5; Figure 2).

3.2 | Updated trait-based diffusion models

Replacing MRT in dispersal-related models by Pires et al. (2018) and Hempson et al. (2017) with the random forest prediction for $MRT_{particle}$ made a significant impact. In the Pires et al.'s (2018) seed dispersal model, using the $MRT_{particle}$ random forest predictions decreased mean transport of seeds by 34% for a 5,000 kg elephant (*Loxodonta* spp), but increased mean distanced transported by 31% for a 200 kg tapir (*Tapirus* spp) when compared to original model formulations (Table S6). For elephants, this results in a seed dispersal kernel that is more consistent with a model that is parameterised using an empirical estimate of MRT (Figure 3). However, for tapir, the seed dispersal kernel is midway between that produced using the original formulation and the empirical estimate.
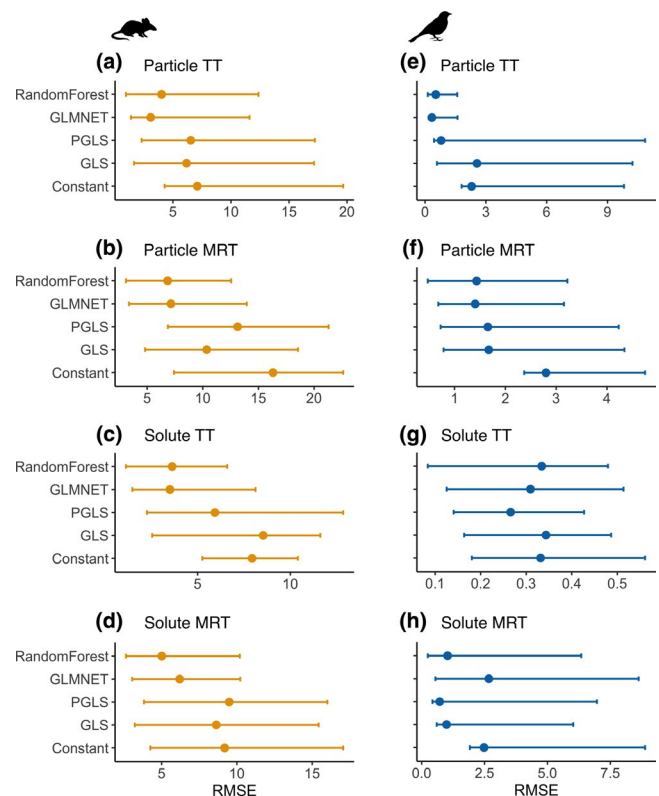

FIGURE 2 Leave-one-out cross validation plots comparing RMSE values arising from the five statistical models for (a) mammal $TT_{particle}$, (b) mammal $MRT_{particle}$, (c) mammal TT_{solute}, (d) mammal MRT_{solute}, (e) bird $TT_{particle}$, (f) bird $MRT_{particle}$, (g) bird TT_{solute} and (h) bird MRT_{solute}. Filled points represent the median root-mean squared error (RMSE) and error bars indicate the interquartile range
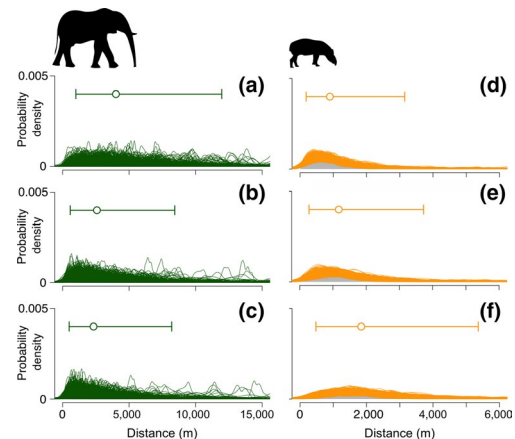

FIGURE 3 Seed dispersal kernels for three predictors of MRT in the Pires et al. (2018) model, depicting seed dispersal of a large seeded plant by a 5,000 kg elephant (*Loxodonta* spp) and a 200 kg tapir (*Tapirus* spp). Panels (a) and (d) estimate MRT using the original mass-based scaling formulation of $10 \times BM^{0.22}$, (b) and (e) using the mammal $MRT_{particle}$ random forest model presented in this paper, except with that genus removed from the training data, and (c) and (f), an empirical calculated mean across studies for each genus. Animal movement was simulated as a Levy walk. Each line represents one of 1,000 simulations. Circles represent the median and bars determine the 5th and 95th percentiles

Updating MRT in the Hempson et al. (2017), lateral nutrient diffusion model had similarly large effects. For the 13 species for which empirical estimates of $MRT_{particle}$ were present in our database, the random forest predictions were generally much closer to empirical estimates than those predicted using the original allometric scaling relationship (Figure 4). Across sub-Saharan Africa, the replacement of the body mass estimate of MRT with the $MRT_{particle}$ random forest predictions reduces total nutrient transport by 20% in the historic model (Figure 5c insert). In contrast, total nutrient transport increases
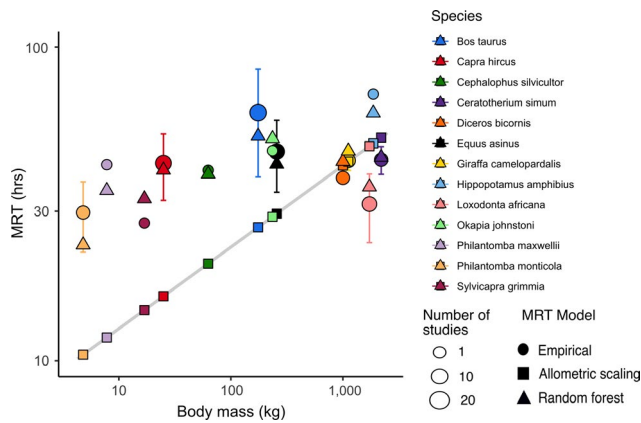
by 76% in the present-day model (Figure 5d insert). Spatially, the largest decreases for the historic model are in tropical West Africa, the Sahel, northern Mozambique and the east coast of South Africa, primarily driven by a reduced contribution of nutrient transport by elephants (Figure 5a). For the present-day model, largest increases in nutrient transport are in southern Africa, Angola, the Sahel and the Horn of Africa (Figure 5b). In the historic model, changes in total nutrient transport are driven by a decrease in lateral nutrient dispersal by megaherbivores (herbivores >1,000 kg; Figure 5c). In contrast, changes in total nutrient transport in the present-day model are driven by herbivores with body mass between 11 and 1,000 kg (Figure 5d), which primarily comprise livestock.

4 | DISCUSSION

4.1 | TT and MRT model performance

Our expanded database confirms previous findings for a general pattern of positive allometric scaling in all markers for mammals and birds. Tables S3 and S4 provide the allometric exponent scaling ('slope') values for different feeding strategies in mammals and birds using GLS and PGLS regression. These are broadly similar to studies that have previously undertaken allometric scaling of gut passage time on select groups of animals (e.g. Clauss et al., 2007; De Cuyper et al., 2020; Demment & Van Soest, 1985; Sorensen et al., 2020; Steuer et al., 2011; Warner, 1981; Yoshikawa et al., 2019). The raw data and derived scaling exponents from our database will help improve the output of ecological models that must rely on allometric

FIGURE 4 A comparison of modelled mean gut retention time (MRT) for 13 species included in the Hempson et al. (2017) model for which there are empirical data. Error bars represent the standard deviation across empirical studies for each species with >2 studies. The grey line represents the allometric scaling equation ($0.29 \times BM^{0.26}$) used in the original model formulation by Hempson et al. (2017). Both axes represent $\log_{10}$ scales

FIGURE 5 Lateral nutrient transport across sub-Saharan Africa calculated using the Hempson et al. (2017) model with different formulations of mean gut passage time. Lateral nutrient transport as a percentage of the original estimate by Hempson et al. (2017) after replacing the original allometric formulation for $MRT_{particle}$ with the random forest $MRT_{particle}$ model presented in this study mapped spatially at a 0.5° resolution for (a) historic (~1,000 years before present) and (b) current-day scenarios. Bar charts for total lateral nutrient movement by animals grouped by their $\log_{10}$ body mass for (c) historic and (d) current-day scenarios. BM refers to the original body mass relationship of $0.29 \times BM^{0.26}$ for $MRT_{particle}$. RF refers to the random forest model presented in this study for $MRT_{particle}$
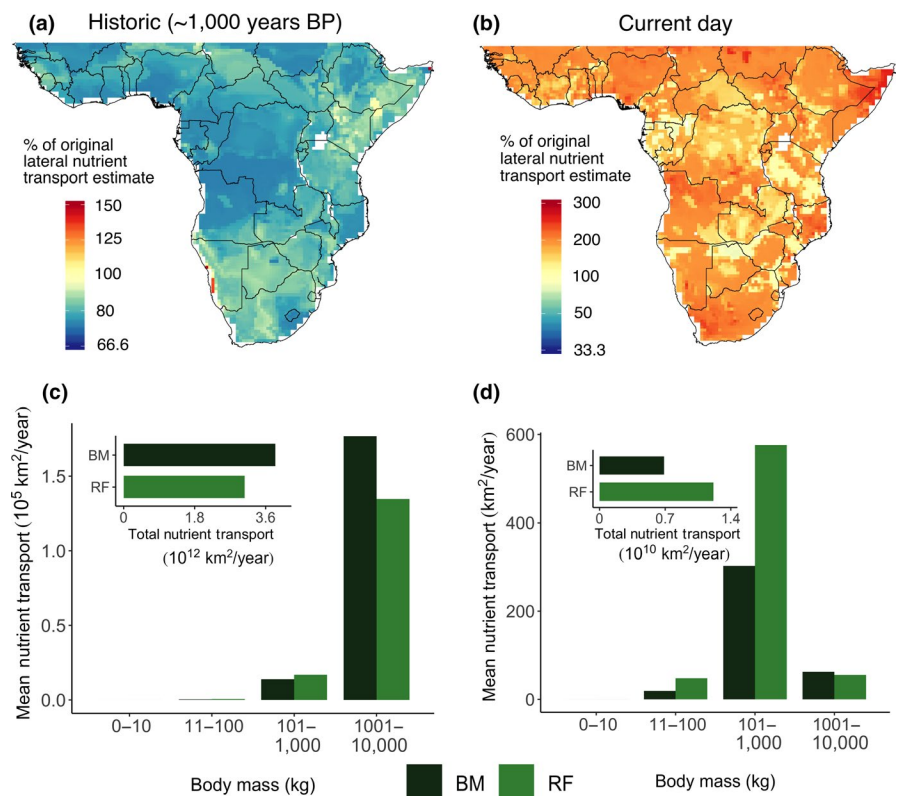
scaling of gut passage time. For example, a recent study by Enquist et al. (2020) found that the magnitude of global nutrient dispersal altered 8-fold when using different plausible mass-based MRT scaling coefficients. In addition, at present most ecological models utilise $MRT_{particle}$ for which many empirical studies have been undertaken. However, our database also includes relationships between animal body size and solute marker passage time, which may be a more appropriate marker signal for some studies (e.g. for models dealing with water-soluble elements such as sodium in Doughty, Wolf, Baraloto, et al., 2016). Furthermore, our database also presents allometric relationships for the time of first marker appearance (TT). These data can help further refine the shape of gut passage time distribution curves, as have commonly been used to generate seed dispersal kernels (e.g. Guttal et al., 2011; Pires et al., 2018; Viana et al., 2013).

While allometric scaling equations have proved useful for predicting general patterns of how gut passage time relates to animal body size, the best statistical models presented in this study for predicting TT and MRT in mammals incorporate the full suite of traits detailed in Table 1. Across markers, the GLMNET and random forest models reduced the median RMSE error across markers by ~34% compared to the GLS model (Table S5), which has previously been used to describe $MRT_{particle}$ scaling in mammals. However, there is a wide range of RMSE results across all models following our leave-one-out cross validation (Figure 2). This indicates that prediction capacity of all statistical models included in this study is poor when outlier species with idiosyncratic traits are included in the test dataset. For example, the two-toed (*Choloepus didactylus*) and three-toed sloths (*Bradypus tridactylus*) have a very high MRT due to their low metabolism and food intake rate (Vendl et al., 2016), which is not currently accounted for in any of the model predictor variables.

For birds, no statistical model was consistently best across markers. This may partly have arisen due to the stronger relationship between bird body mass and gut passage time (Robbins, 1993; Sorensen et al., 2020; Yoshikawa et al., 2019). However, there was also a large spread of RMSE results across statistical models for birds, suggesting that either the dataset is not large enough for the more complex models to become statistically different, or that important traits pertinent to TT and MRT in birds are missing from our analysis. For example, key information of differences in the gastrointestinal tract, which is known to significantly impact gut passage time in birds (Frei et al., 2015), was lacking. In our dataset, all birds were considered to have a simple gastrointestinal tract, with the exception of the hoatzin *Opisthocomus hoazin*, which is the only known bird with a foregut physiology (Grajal & Parra, 1995). Datasets which facilitate the inclusion of more nuanced traits will improve the ability of more complex statistical models to predict gut passage time for this taxon.

4.2 | Importance of MRT for trait-based dispersal models

The findings in this study highlight the shortcomings of previous dispersal-related ecological models that have relied upon

generalised mass-based scaling parameters for gut passage time. Updating the Pires et al. (2018) model with improved estimates of gut passage time considerably impacts generated seed dispersal kernels (Table S6; Figure 3). This has important ramifications for our understanding of which animal species play an important role in the long-distance dispersal of invasive plant species and migration of native plants in response to climate change (Jordano et al., 2007). Previous studies have argued that at the ecosystem level, the over or underestimation of dispersal by species or functional groups will likely even out when the contribution to a dispersal service is summed across all species (Wolf et al., 2013). However, we have shown in this study that depending on the compound interactions of gut passage time with other pertinent traits, current models may be incorrectly attributing or estimating the magnitude of dispersal. The updated Hempson et al.'s (2017) nutrient dispersal model in this paper succinctly demonstrates this point.

In the historic model, elephants (*Loxodonta* spp) are widely distributed across sub-Saharan Africa. As these animals consume large quantities of vegetation, live at higher population densities and have large daily movement ranges, they contribute disproportionately to nutrient movement (Wolf et al., 2013). However, in the original formulation of the model, which relies on allometric scaling for gut passage time, the contribution of a 1,725 kg elephant to nutrient transport is vastly overestimated as their gut passage time is predicted at 48.3 hr, when the average empirical estimate across a number of gut passage time studies in elephants is 31.6 hr. Likewise, the gut passage time for many meso-herbivores (11–1,000 kg) is significantly underestimated based on their mass alone (Figure 4). We see in the historic model that the original overestimation of elephant contribution to nutrient transport outweighs the underestimation of meso-herbivores, resulting in a 20% overestimate of total continent nutrient dispersal. In contrast, for the present-day scenario in which elephant populations are largely confined to a few key protected areas—and meso-herbivore biomass has been maintained or increased by water provision, supplementary feed and veterinary care for livestock—the underestimation of nutrient transport by meso-herbivores using the original allometric scaling results in a large underestimation of total continent nutrient dispersal by 76%. With the exception of elephants, the species included in the Hempson model did not have particularly large residual error in the allometric scaling of gut passage time (Figure S7). This highlights that the magnitude of change in our updated models may not be unique to this study and the relationship between estimated gut passage time and factors such as population density and daily dispersal can considerably change the total magnitude of dispersal within ecosystems from local to continental scales.

4.3 | Future of predicting MRT

The measurement of gut passage time in endothermic animals is a complex procedure with multiple logistical, scientific and ethical hurdles (Robbins, 1993; Stevens & Hume, 2004). Consequently,

statistical models that attempt to predict gut passage time from multiple sources are inherently contingent on the quality of individual studies within the database. Here, we have collated a large database of gut passage time in endothermic animals from a total of 351 studies. Our database represents data from 4.8% of all extant mammal and 1.3% of all extant bird species (Wilman et al., 2014). However, of the 391 endothermic species included in our database, 71.8% have a gut passage time derived from only one study and just 9.7% of species have a gut passage time calculated across three or more studies. As a result, there is potential uncertainty around the accuracy of our calculated measures of gut passage time for many species. Future meta-analyses that attempt to statistically predict gut passage time across a broad suite of endotherms will benefit from any expansion and replication of experiments for the studies that we have collated here.

Table S1 provides 20 independent factors that have been suggested to impact gut passage time in endothermic animals found in the literature. We were only able to include ten of these in our traits database, as reliable information was difficult to ascertain across all species for many traits. Importantly, dry matter intake (DMI) was not included in our trait data as they were was unavailable across all studies, but is known to be an important driver (Clauss et al., 2007; Levey & Martínez del Rio, 1999). Furthermore, the trait data that we did include were not directly from the experimental or field trials, but from generalised datasets. For example, while the data pertaining to percentage of diet from 10 Elton Traits v1.0 categories is an improvement on previous attempts to include diet (e.g. Yoshikawa et al., 2019), multiple studies have shown that gut passage time is directly related to the type of food consumed in the experiment and not the dominant feeding preferences (Hilton et al., 1998; Jackson, 1992; Nijboer et al., 2007; Pagan et al., 1998; Remis & Dierenfeld, 2004; Silva et al., 2005; White et al., 2007). Accordingly, trait values calculated in this study may be different to those driving the gut passage in the collated gut passage database.

Despite these issues, the inclusion of the additional traits has considerably improved our prediction capabilities of gut passage time in mammals (Figure 2). This supports the notion that future predictions of gut passage time in mammals, and possibly all endothermic animals, will be further improved by the inclusion and increased sophistication of pertinent traits in statistical models. Of the traits we did include, animal morphology (body mass, body length) was found to be the most important predictor of gut passage time in mammals and birds (Figures S5 and S6). This was followed by traits related to gut physiology and diet. Traits related to habitat, activity time, feeding strata, rumination and volancy, however, were rarely important in our models despite being cited in the literature as important to specific groups of animals (Hilton et al., 1998; Jackson, 1992; Vendl et al., 2016). As a result, future modelling studies, for which empirical estimates of gut passage time are absent, will benefit from predicting gut passage time using statistical models that incorporate at least animal morphology, diet and gut physiology.

In our study, we have updated two trait-based dispersal models to highlight the importance of correctly resolving gut passage time. Statistical models that attempt to estimate gut passage time

for extinct animals, however, may struggle to determine the required traits. For example, it is clear that digestive physiology plays a key role in gut passage time for endothermic animals (Frei et al., 2015; Przybyło et al., 2019; Steuer et al., 2011). However, it is still unknown what the digestive physiology was for many species of extinct animals such as ground sloths (Suborder *Folivora*; Clauss et al., 2003), of which over 80 extinct genera have been described (Faurby et al., 2018). This may provide a significant hurdle for the prediction of gut passage time in extinct animals and the improvement of models that include them (e.g. Doughty, Roman, et al., 2016; Pires et al., 2018).

5 | CONCLUSIONS

We have shown that an improved estimation of gut passage time can have considerable impacts for the attribution and estimation of dispersal-related ecosystem services by communities of animal species. We hope that the databases presented in our study will be used to further understand the underlying mechanisms that drive differences in gut passage time across endothermic animals and will facilitate the development of ecological models that better quantify vital dispersal-related ecosystem services by animals.

AUTHORS' CONTRIBUTIONS
A.J.A., M.C. and C.E.D. conceived the ideas and designed the methodology; A.J.A., A.D.C., T.O.P.-J., M.C. and G.P.H. collected the data; A.J.A., C.E.D., T.O.P.-J., C.R. and T.H. analysed the data; A.J.A. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT
The datasets generated and analysed during the current study are available at https://figshare.com/articles/dataset/Endotherm_Gut_Passage_Data/13182716.

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SUPPORTING INFORMATION

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