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# Phylogeny is a stronger predictor of activity than allometry in an African mammal community

HERBERT KASOZI[1,*], REMINGTON J. MOLL[2], ROBERT M. KITYO[3] and ROBERT A. MONTGOMERY[4]

[1]*Department of Fisheries and Wildlife, Michigan State University, 14 Natural Resources, 480 Wilson Road, East Lansing, MI 48824, USA*
[2]*Department of Natural Resources and the Environment, 56 College Road, University of New Hampshire, Durham, NH 03824, USA*
[3]*Department of Zoology, Entomology and Fisheries Sciences, Makerere University, PO Box 7062, Kampala, Uganda*
[4]*Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Abingdon Road, Tubney, Oxfordshire OX13 5QL, UK*

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In promoting coexistence, sympatric species often partition shared resources along spatio-temporal domains. Similarly sized and phylogenetically close species, for instance, partition the times of day in which they are active to limit interference competition. Given that variation in species body mass has evolutionary underpinnings, species activity levels (time spent active in a 24-h daily cycle) within animal communities might be structured by phylogeny. However, few studies have tested this hypothesis across animal communities, and none among medium-sized to large mammals. We quantified the relative contributions of phylogeny and body mass in predicting activity levels in a community of 22 sympatric mammal species in Murchison Falls National Park, Uganda. We show that phylogeny is a stronger predictor of species activity levels than body mass. Our findings provide empirical evidence for the phylogenetic structuring of mammal activity in diverse communities. More broadly, our results suggest that evolutionary relationships mask allometry in predicting species traits in diverse animal communities.

ADDITIONAL KEYWORDS: activity level – body mass – coexistence – mammals – phylogeny – temporal niche partitioning.

## INTRODUCTION

Species coexistence in animal communities is often facilitated by niche partitioning across spatio-temporal domains (Schoener, 1974; Amarasekare, 2003; Laporta & Sallum, 2014). Spatially, animals often partition habitats or reduce competition via movements including dispersal and migration (Jeltsch *et al.*, 2013). When spatial partitioning is not possible, animals may partition time by altering their activity schedules (Schoener, 1974; Walter, 1991; Richards, 2002; Bennie *et al.*, 2014). Such temporal niche partitioning can minimize interference competition among similarly sized and phylogenetically close sympatric species (Kronfeld-Schor *et al.*, 2001; Kronfeld-Schor & Dayan, 2003). Similarly, many prey species have evolved to be active when their predators are not, to minimize predation risk (Schoener, 1974; Kronfeld-Schor & Dayan, 2003). Furthermore, increased nocturnality has been detected among several animal species and interpreted as a strategy to avoid anthropogenic disturbance (Carter *et al.*, 2012; Gaynor *et al.*, 2018; Patten *et al.*, 2019). Thus, competition, predation and anthropogenic disturbance are forces that drive temporal variation in species activity (Schoener, 1974; Kronfeld-Schor & Dayan, 2003).

Through their life history, animals structure their activity schedules with both active and passive behaviours (Halle & Stenseth, 2000). Active behavioural states include foraging, reproduction, care for young and predator avoidance, whereas passive states include resting and sleeping (Halle & Stenseth, 2000).

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*Corresponding author. E-mail: kasozihe@msu.edu

In deciding when to be active, animals navigate potentially fitness-compromising trade-offs that partly reflect adaptability to environmental variability over time (Enright, 1970; Halle, 2000; Vazquez *et al.*, 2020). For example, foraging activity is required for animal sustenance and survival (Moermond, 1990) but also carries potential costs incurred from risks of inter- and intraspecies interactions such as competition and predation (Halle & Stenseth, 2000; Downes, 2001). Animals routinely make such trade-offs within ecological communities that are allometrically and phylogenetically diverse. The proportion of time an animal spends active in a day (cf. activity level; Rowcliffe *et al.*, 2014) has been adopted as a critical metric for examining the trade-offs within species activity schedules (Rowcliffe *et al.*, 2014).

Body mass has been identified as a predominant factor determining species activity levels (Peters, 1983; West *et al.*, 1997; Brown *et al.*, 2004). The active behavioural states that constitute an animal's activity level and underlying schedule are constrained by body mass, which partly determines the rate at which animals acquire, process and transform energy (Smith & Lyons, 2011). For example, dietary needs and home range scale allometrically across mammal taxonomic groups such as carnivores and herbivores (Peters, 1983; Swihart *et al.*, 1988). As such, larger mammals spend more time foraging over wider areas than smaller mammals (Peters, 1983; Calder, 1984). Thus, a mammal's body size has a critical bearing on time spent active. Additionally, species differences in body mass are related to their evolutionary relationships as revealed by phylogeny (Smith & Lyons, 2011). The fact that variation in species body mass has evolutionary underpinnings suggests that temporal partitioning of activity within communities might in turn be structured by species phylogenies. However, few studies have formally evaluated the hypothesis that phylogeny predicts species activity (Webb *et al.*, 2002). Communities of medium-sized to large mammals present an opportunity for pursuit of this line of inquiry. Phylogeny reflects evolutionary differences among species, which may be related to ecological processes and dynamics (Felsenstein, 1985; Harvey & Pagel, 1991; Faith, 1992). Therefore, an understanding of the mechanisms generating species differences in the timing of their activity must be inclusive of the evolutionary components of species divergence (Webb *et al.*, 2002; Narwani *et al.*, 2015). Thus, an investigation of the relative contributions of body mass and phylogeny to patterns of variation among animal species activity levels may reveal the ecological and evolutionary processes underlying animal coexistence and community assembly.

Mammals are a diverse taxonomic group with ~6399 described extant species (Burgin *et al.*, 2018). Species in the Class Mammalia span eight orders of magnitude in body mass (Baker *et al.*, 2015) and exhibit a variety of activity levels and schedules (Halle & Stenseth, 2000). Using sympatric mammals as research subjects, we explored (1) the relative contributions of phylogeny and body mass in predicting variation in mammal activity levels and (2) whether evident differences in mammal activity levels are phylogenetically structured. We examined these questions in a diverse mammal community in Murchison Falls National Park (MFNP), Uganda. The species included in our analysis varied broadly in taxonomy, body mass and activity. We investigated pairwise overlap among activity schedules of species within the same taxonomic orders to assess temporal niche partitioning. Our results provide insights into the role of phylogeny and body mass in structuring mammal activity within communities, with implications for temporal niche partitioning and species coexistence.

## MATERIALS AND METHODS

### STUDY AREA

We conducted our study in MFNP, located in north-western Uganda (Fig. 1). Covering an estimated land area of ~3898 km², MFNP is the largest national park in Uganda. A section of the River Nile (i.e. Victoria Nile) flowing east to west bisects MFNP into northern and southern sections. The vegetation of the southern section comprises dense woodlands, wooded grassland savannahs, riverine forest and tropical high forest. The northern section, on the other hand, comprises open grasslands, acacia woodland and borassus woodland as the dominant vegetation types (Fig. 1). MFNP has a hot and dry tropical climate characterized by wet (April to May, and September to November) and dry seasons (December to February, and June to August). It also supports a diversity of mammals including ~76 species (Mudumba *et al.*, 2020).

### MAMMAL SURVEYS

We deployed camera traps at 144 sites between May 2012 and August 2013 to obtain records of activity of medium-sized to large mammal species (Fig. 1). We placed cameras systematically on a grid of 1.5 × 1.5-km resolution (Fig. 1). We also placed cameras at some opportunistic locations considered important landscape features for mammals (such as water pools, river, trails and salt licks). Via this strategy, we ensured broad coverage of all habitat types in the study area (Fig. 1). We mounted the camera traps on tree trunks, at most 1 m off the ground to capture species of varied sizes, and to avoid destruction of the cameras, particularly by spotted hyenas (*Crocuta crocuta*

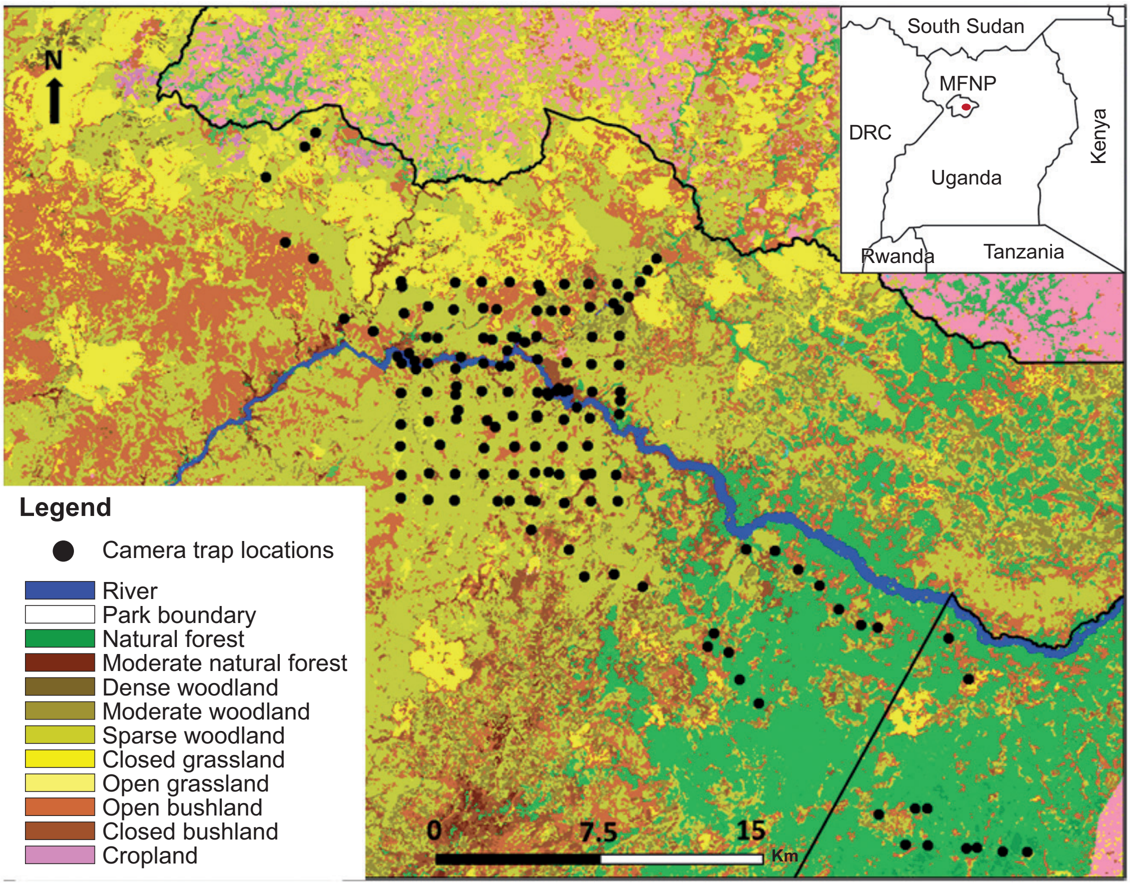

**Figure 1.** Layout of camera traps used to study mammal activity in Murchison Falls National Park (MFNP), Uganda, between May 2012 and August 2013. Inset: location of MFNP in Uganda; the red dot signifies the extent of the study area covered by the survey.

Erxleben, 1777). Given this height, we slightly tilted the traps downwards to enable detection of a range of mammal species (Majelantle *et al.*, 2020). Additionally, we avoided facing cameras directly at vegetation to minimize false triggers from vegetation movement in windy conditions. We programmed the cameras to take three photos per trigger with a 1-min lapse between triggers (Lepard *et al.*, 2018). We conducted this survey in a backcountry area of MFNP where recreational human activity and park staff residence were absent. We set the traps unbaited and left them to run for the entire 16-month survey period.

### Estimating mammal activity levels

We assumed independence in species detections by enforcing a 30-min temporal window between intraspecific detection events at each camera location, unless individuals of the same species were distinguishable (Kelly & Holub, 2008; Davis *et al.*, 2011; Monterroso *et al.*, 2013). We used the function 'fitact' in the activity R package (v.1.3; Rowcliffe, 2019) to estimate activity levels for species with >30 independent detections across the survey period (cf. Cid *et al.*, 2020). We fitted circular von Mises kernels to the time of day associated with each independent animal detection event and generated activity levels (A) for 22 species. We defined activity levels as the portion of the 24-h daily cycle the mammals spent active (cf. Rowcliffe *et al.*, 2014). Activity levels corresponded to the area under the kernel density curve for each species, estimated with 95% confidence limits generated with 1000 bootstraps (Rowcliffe *et al.*, 2014).

### Phylogenetic signal in species activity levels and body mass

We used the function 'phylosig' in the phytools R package (v.0.7.80; Revell, 2012) to calculate phylogenetic signal in species activity levels and body mass using Blomberg's $K$ (Blomberg *et al.*, 2003). We defined phylogenetic signal as the extent to which trait values of closely related species tend to be more similar compared to those of other species drawn at random from the phylogenetic tree (Münkemüller *et al.*, 2012). $K = 0$ indicates no phylogenetic signal (i.e. the trait variation is random with respect to the phylogeny), $K = 1$ indicates that a trait perfectly fits a Brownian motion model of evolution and $K > 1$ indicates that trait values are more similar than expected under Brownian motion. We used 1000 randomizations to generate $P$ values associated with $K$.

### MODELLING

We used Phylogenetic Eigenvector Maps (PEM; Guenard *et al.*, 2013), linear regression and phylogenetic generalized least squares to model relationships between species activity levels, body mass and phylogeny. We used eigenvectors generated via PEM as predictors representing phylogeny in modelling species activity levels. The PEM procedure involves decomposing the topology of a phylogeny into a binary influence matrix representing evolutionary relationships between ancestors and their descendants. We rescaled the binary influence matrix based on the amount of phylogenetic signal in species activity levels by multiplying all values off the main diagonal by $K$ (Molina-Venegas *et al.*, 2018). We then transformed the influence matrix, assuming an evolutionary model and taking into account the quantified species trait values, to represent trait change patterns along the branches of the phylogeny. PEM uses edge weighting to represent information on trait evolutionary dynamics across branches of the phylogenetic tree. An edge (branch) is assigned a weight $w_{a,\psi}$ proportional to the extent of the change that is expected to occur along that edge based on the following monotonic function:

$$w_{a,\psi}\left(\Phi_j\right) = \begin{cases} \psi\Phi^{\frac{1-a}{2}} & \Phi_j > 0 \\ 0 & otherwise, \end{cases}$$

where $a$ ($0 \leq a \leq 1$) is the steepness parameter quantifying abrupt evolutionary changes along branches after each split, whereas $\psi$ ($0 < \psi < \infty$) indicates the relative evolutionary rate of species activity levels, and $\Phi_j$ is the length of edge/branch $j$. The steepness parameter $a$ is related to Pagel's (1999) $\kappa$ (i.e. $a = 1 - \kappa$). We assumed neutral trait evolution under Brownian motion throughout the rescaled phylogeny, and assigned a single pair of values for $a$ and $\psi$. Under Brownian motion, $a = 0$, and the expected changes are proportional to the square root of the branch lengths (Guenard *et al.*, 2013). A trait evolving neutrally under Brownian motion changes gradually along the branches. Conversely, when $a = 1$, evolutionary changes occur at a fixed rate $\psi$ whenever species diverge irrespective of branch length. We set $\psi = 1$, the default state suggested by Guenard *et al.* (2013). Evolutionary rate, $\psi$, has no effect when assumed to be constant across the phylogeny.

Via weighting and centring the influence matrix, PEM returns $N - 1$ eigenvectors (where $N$ is the number of species analysed), some of which are not useful in explaining trait variation. Each eigenvector describes a pattern of phylogenetic variation stemming from the structure of the phylogenetic tree, and that is orthogonal (linearly independent) with respect to the other eigenvectors in the set. We selected a subset of significant eigenvectors which explained the majority of the variation in species activity levels using a forward stepwise procedure based on Akaike's Information Criterion corrected for small samples (AICc; Hurvich & Tsai, 1993). We then regressed activity levels against the selected subset of significant eigenvectors (i.e. *Activity level* ~ *eigenvectors* + $\varepsilon$) and activity levels against eigenvectors and body mass (i.e. *Activity level* ~ *eigenvectors* + *body mass* + $\varepsilon$). We implemented PEM using functions in the R package MPSEM (v.0.3-6; Guenard & Legendre, 2019).

We modelled the influence of body mass on species activity levels (i.e. *Activity level* ~ *body mass* + $\varepsilon$) using a generalized least squares model. Within this framework, we simultaneously fitted a regression model and estimated Pagel's $\lambda$ (Pagel, 1999), which represents the phylogenetic signal in the residuals. Pagel's $\lambda$ transforms the phylogeny to ensure the best fit of trait data to a Brownian motion model (Münkemüller *et al.*, 2012). Lambda values range from 0 to 1. A $\lambda$ value of 0 indicates that model residuals are completely independent of the phylogeny, resulting in a model that is equivalent to a standard linear model (Frckleton *et al.*, 2002). A $\lambda$ value of 1 indicates that the model's residuals perfectly follow a Brownian motion model of evolution.

### VARIATION PARTITIONING

We used variation partitioning analysis (Borcard *et al.*, 1992) to investigate the relative contributions of body mass and phylogeny in explaining the variation in species activity levels. We partitioned the variation of species activity levels into four proportions, namely (1) a part strictly due to body mass (A), (2) a part strictly due to phylogeny (C), (3) shared variation explained by both phylogeny and body mass (B), and (4) a part unexplained by either phylogeny or body mass (i.e. residual variation, D; Fig. 2). We obtained values of the different activity level variation proportions (A–D) either directly via adjusted $R^2$ statistics from the phylogenetic linear regressions or arithmetically (Table 1).

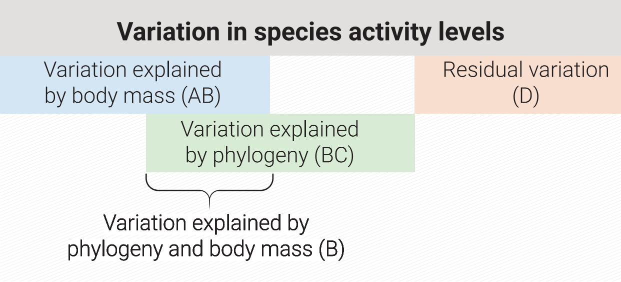

**Figure 2.** Partitioning protocol for variation of species activity levels (time spent active in 24 h) as explained by body mass and phylogeny.

**Table 1.** Calculation of components of variation in activity levels (proportion of the 24-h day spent active) from a community of 22 mammal species inhabiting Murchison Falls National Park, Uganda. Variation explained by the first three components is derived directly from adjusted $R^2$ values of their respective regression equations. The remaining components were derived arithmetically

| Variance component due to: | Formula |
|---|---|
| Phylogeny and body mass (ABC) | Activity level ~ Phylogeny + Body mass |
| Body mass (AB) | Activity level ~ Body mass |
| Phylogeny (BC) | Activity level ~ Phylogeny |
| Body mass only (A) | ABC – BC |
| Common influence of phylogeny and body mass (B) | AB + BC – ABC |
| Phylogeny only (C) | ABC – AB |
| Unexplained variance (D) | 1 – (ABC) |

### ESTIMATING OVERLAP IN SPECIES ACTIVITY SCHEDULES

We estimated overlap in activity schedules among species within the same taxonomic orders using the coefficient of overlap (Δ; Ridout & Linkie, 2009). The Δ value ranges from 0 (for completely dissimilar curves) to 1 (for identical curves). We generated 95% confidence limits for each overlap estimate using 10 000 smoothed bootstraps. We performed a Watson's two-sample test of homogeneity using an alpha level of ≤ 0.05 to test for statistical significance in differences between species activity schedules. We implemented the overlap analysis in the R package 'overlap' (v.0.3.3; Ridout & Linkie, 2009).

We omitted the effect of weather and season in our analysis because we observed no differences in species activity schedules across the dry and rainy seasons (Supporting Information, Fig. S1). We conducted analyses using log-transformed body mass and activity level data to reduce skew and to linearize the relationship between the two variables (Desdevises *et al.*, 2003). We adopted the phylogeny used in this analysis from the super tree of Fritz *et al.* (2009) and obtained body mass data from Faurby *et al.* (2019). Phylogeny included topology and branch lengths. We conducted analyses on an informative ultrametric phylogenetic tree, where distance from the root to all tips is constant for all tips/species. We conducted all analyses using RStudio v.1.3.1073 running R v.4.0 (R Core Team, 2020).

## RESULTS

Our analysis included 22 species from eight taxonomic orders and 15 families (Fig. 3) detected across 23 753 independent camera trap observations. The most commonly detected species were Uganda kob (*Kobus kob* Erxleben, 1777; $N$ = 4833 detections) followed by hippopotamus (*Hippopotamus amphibius* Linnaeus, 1758; $N$ = 4166 detections, Supporting Information, Table S1). The least detected species included ground pangolin (*Manis temminckii* Smuts, 1832; $N$ = 31 detections) and banded mongoose (*Mungos mungo* Gmelin, 1788; $N$ = 38 detections).

Activity level estimates varied across species, both within and across taxonomic orders. Among carnivores, the banded mongoose was the most active, with ~17 h of activity in a day [A = 0.71, 95% confidence interval (CI) 0.42–0.81; Fig. 4]. The remaining carnivores spent ~11 h active per day (Supporting Information, Table S1, Fig. S2). Among the Cetartiodactyls, the hartebeest (*Alcelaphus buselaphus* Pallas, 1766) was the most active species, spending ~18 h active per day (A = 0.76, 95% CI 0.65–0.85; Fig. 4). The least active species within the order Cetartiodactyla was the bush duiker (*Sylvicapra grimmia* Linnaeus, 1758) spending ~9 h active (A = 0.38, 95% CI 0.28–0.57). The elephant (*Loxodonta africana* Blumenbach, 1797) was equally active as the hartebeest, whereas the aardvark (*Orycteropus afer* Pallas, 1766) was the least active among all species (A = 0.35, 95% CI 0.31–0.44, ~8 h active; Table S1; Fig. 4).

We found activity levels to have moderate phylogenetic signal ($K$ = 0.5, $P$ > 0.01) and body mass to have high phylogenetic signal ($K$ = 0.8, $P$ < 0.01). We obtained a total of 21 phylogenetic eigenvectors from the tree of 22 species. Four eigenvectors were chosen to represent phylogeny in subsequent regression analyses. Body mass with an embedded part of phylogeny (component AB; Table 1) explained a small proportion (5%) of the variation in species activity levels ($R^2_{adj}$ = 0.05, $P$ > 0.01), whereas body mass only (component A;

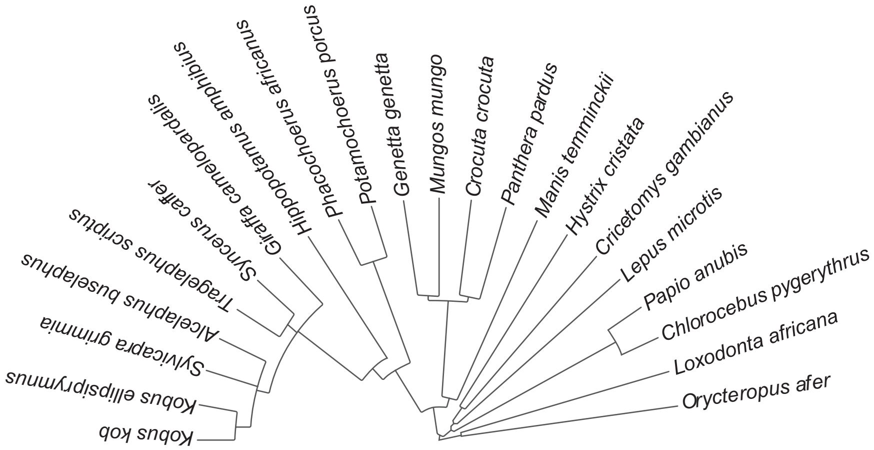

**Figure 3.** Phylogeny of the 22 mammal species observed in Murchison Falls National Park, Uganda, from a camera trap survey conducted between May 2012 and August 2013. The tree is adapted from Fritz *et al.* (2009) after removing species that were not observed in the current surveys.

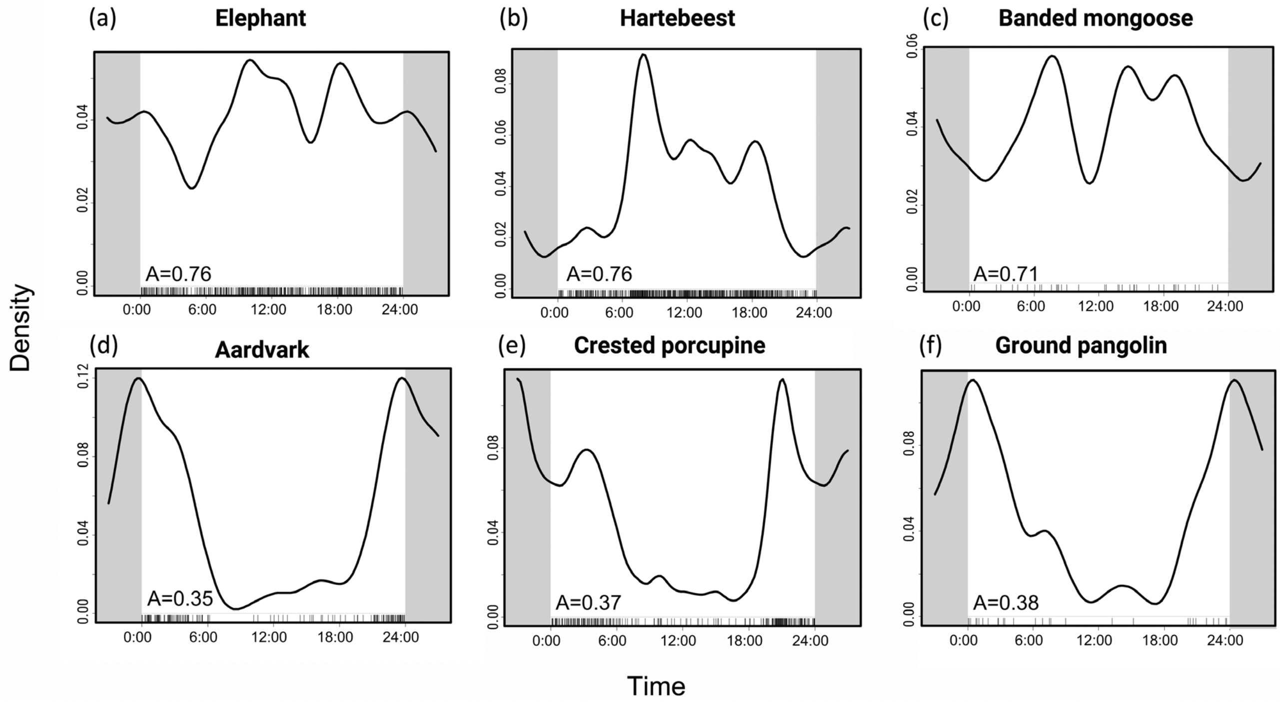

**Figure 4.** Activity schedules of mammal species with the highest (A–C) and lowest (D–F) activity levels (A) in Murchison Falls National Park, Uganda, estimated using camera trap temporal records. The activity curves are fitted circular von Mises kernel density curves showing patterns of species activity across a 24-h daily cycle.

Table 1) explained 1%. Both phylogeny and body mass (component ABC; Table 1) explained 61.5% of the variation in species activity levels ($R^2_{\mathrm{adj}} = 0.62$, $P < 0.01$). Phylogeny and body mass explained a shared variation (component B; Fig. 2) of 4%. Phylogeny with an embedded component of body mass (component BC; Fig. 2) explained 61% of the variation in species activity levels ($R^2_{\mathrm{adj}} = 0.61$, $P < 0.01$), while phylogeny only (component C; Fig. 2) explained 56%. The component of variation in species activity levels unexplained by either of the two factors (component D; Table 1) was 39%. There was no phylogenetic signal in the residuals of the regression of activity levels against body mass ($\lambda = 0.00$, 95% CI −1.13, 0.27).

Across all taxonomic orders, we detected considerable pairwise overlap among species activity schedules (Fig. 5; Supporting Information, Table S2, Fig. S3). Species pairs with highly overlapping activity schedules included olive baboon (*Papio anubis* Lesson, 1827) and vervet monkey (*Cercopithecus pygerythrus* Lesson, 1827), Uganda kob and waterbuck (*Kobus ellipsiprymnus* Ogilby, 1833), Uganda kob and hartebeest, and waterbuck and hartebeest; these all had overlap coefficients of at least 0.90 (range 0.90–0.91; Table S2; Fig. 5). On the other hand, species pairs with the least overlapping activity schedules included hippopotamus and warthog (*Phacochoerus africanus* Gmelin, 1788), giraffe (*Giraffa camelopardalis rothschildi* Lydekker, 1903) and hippopotamus, and bush duiker and hippopotamus, all with overlap coefficients of < 0.4 (range 0.33–0.35; Table S2; Fig. 5). Despite the high overlap among activity schedules across several species, Watson's test indicated significant differences in the majority of pairwise species activity schedule comparisons ($P < 0.05$; Table S2).

## DISCUSSION

Our analysis highlights varied activity levels in a community of 22 mammal species inhabiting MFNP, Uganda. Activity levels of phylogenetically close species tended to be similar, indicating a strong influence of phylogeny in structuring the variation in species activity levels. Comparatively, there was less of an influence of body mass in explaining variation in species activity levels. This was exemplified by the general lack of a trend between body mass and activity levels among species across the phylogeny. Exploring such phylogenetically explicit relationships among species traits is important (Desdevises *et al.*, 2003), given that species have shared ancestry (Burgin *et al.*, 2018). Within this context, the residual variation represents independent evolution of the trait within each species (Diniz-Filho *et al.*, 1998; Desdevises *et al.*, 2003). Our analysis illustrates the broad applicability and relevance of multispecies phylogenetically explicit modelling in exploring patterns of species traits.

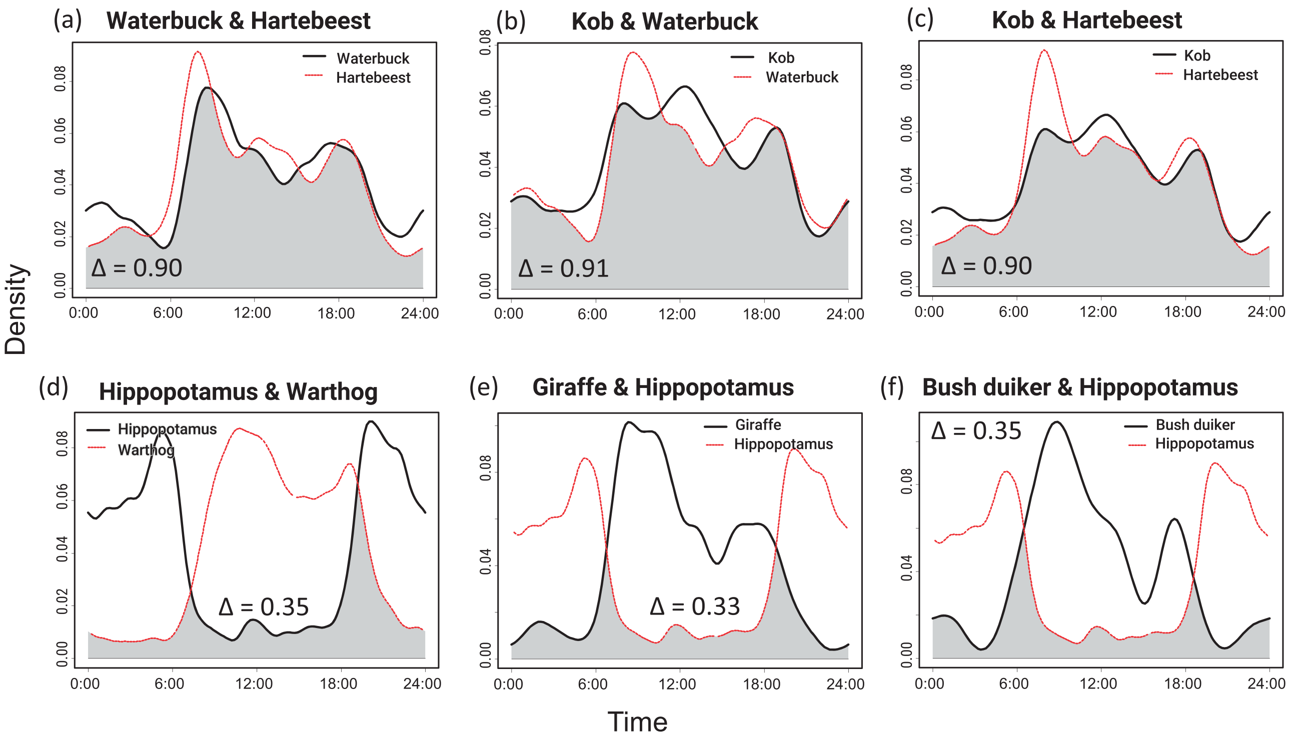

**Figure 5.** Pairwise overlap of activity schedules between selected mammal species in Murchison Falls National Park, Uganda, as estimated using camera trap temporal records. The highest activity overlap was between (A) waterbuck (*Kobus ellipsiprymnus* Ogilby, 1833) and hartebeest (*Alcelaphus buselaphus* Pallas, 1766), (B) kob (*Kobus kob* Erxleben, 1777) and hartebeest, and (C) kob and water buck, all with overlap coefficients of 0.9 (95% CI 0.87–0.94, Supporting Information, Table S5). The least activity overlap was between (D) hippopotamus (*Hippopotamus amphibius* Linnaeus, 1758) and warthog (*Phacochoerus africanus* Gmelin, 1788), (E) hippopotamus and giraffe (*Giraffa camelopardalis rothschildi* Lydekker, 1903), and (F) hippopotamus and bush duiker (*Sylvicapra grimmia* Linnaeus, 1758), all with overlap coefficients of 0.3 (95% CI 0.24–0.46, Table S3).

Such methods could be employed to examine the multiple factors that facilitate species assembly and coexistence as they relate to phylogenetic structure within communities across other taxonomic groups.

Our phylogenetically explicit models detected a significant influence of phylogeny on mammal activity levels, highlighted by phylogenetic eigenvectors explaining over 60% of the variation. Additionally, our results highlight that the amount of phylogenetic signal in species activity levels corresponds to the percentage of variation explained by phylogeny without an embedded component of body mass. Additional research is necessary to examine the relationship between level of phylogenetic signal in species trait data and the amount of trait variation explained by phylogeny. On the other hand, we did not detect a significant influence of body mass on mammal activity levels. We interpret this result as indicating phylogenetically distant species showing no clear patterns between body mass and activity levels. Body mass may have an effect if modelled across a range of phylogenetically close species, say within one taxonomic order in which species have widely different body masses and activity levels. This may reduce the correlation between body mass and phylogeny, and thus allow detection of an effect of body mass. Additionally, recent studies have detected strong relationships between body mass and mammal activity levels when phylogeny is not included among the predictors (e.g. Rowcliffe *et al.*, 2014; Ramesh *et al.*, 2015). Our results build upon the initial work on rodents to reveal the importance of phylogeny in structuring activity in mammal communities (Roll *et al.*, 2006). Analyses of the allometry of species activity levels tend to be conducted among species of specific dietary guilds such as carnivores or herbivores (e.g. Rowcliffe *et al.*, 2014; Cid *et al.*, 2020) or taxonomic hierarchies (e.g. Roll *et al.*, 2006). While our research is limited in the number of species assessed, we extend the analyses to include species from a diverse range of dietary guilds and taxonomic hierarchies. Additional research including more species could further highlight the role of species body mass and their evolutionary relationships in the generation and maintenance of differences in species activity, temporal niche partitioning and species coexistence. We found that the elephant and hartebeest had the highest activity levels of all species (Fig. 4A, B). Among the carnivores, our results showed the banded mongoose to have higher activity levels than the larger genet (*Genetta genetta* Linnaeus, 1758), hyena and leopard (*Panthera pardus* Linnaeus, 1758) (Supporting Information, Table S1, Fig. S2). Collectively, these results highlighted no consistent patterns between species body mass and activity levels across the phylogeny. These results align with recent analyses suggesting no scaling of diel activity with body mass from a mammal community of Lake Manyara National Park, Tanzania (Clauss *et al.*, 2021). This explains our observation that body mass explained a small proportion of species activity levels across the phylogeny. A critical difference we observed among carnivore activity is that the banded mongoose is cathemeral, exhibiting its peak activity during daylight hours, whereas the genet, hyena and leopard are strictly nocturnal species (Fig. S2). This temporal partitioning of activity among the carnivores aligns with their differences in foraging strategies, and has been suggested to promote their coexistence (Hayward & Slotow, 2009). The mongoose is predominantly insectivorous, but could become prey for the larger nocturnal carnivores, explaining their need to maintain low activity during the night. The species with the lowest estimated activity levels were all obligate nocturnal species [i.e. aardvark, crested porcupine (*Hystrix cristata* Linnaeus, 1758) and ground pangolin (Fig. 4D–F). These animals are shy and elusive burrowing species, which spend the majority of the day in underground tunnels (Felicioli *et al.*, 1997; Nowak, 1999; Taylor & Skinner, 2003; Tabruce *et al.*, 2008). Consequently, their activity estimates may therefore be interpreted as nocturnal given their biased detection above ground.

Despite the high overlaps, differences between activity schedules of the majority of phylogenetically close species were statistically significant (e.g. Fig. 5A–C). A close examination of activity curves for these species revealed considerable variations in their peak activity times (Fig. 5; Supporting Information, Fig. S3). Such variation suggests that temporal niche partitioning among phylogenetically close species is only possible within specific times of day, perhaps highlighted as times of peak activity. Given that phylogenetically close sympatric species use similar resources (Daan, 1981; Roll & Dayan, 2002), it is necessary for them to maximize their resource consumption in times when activity of their relatives is low (Kronfeld-Schor & Dayan, 2003). The variation in species times of peak activity is critical in minimizing interspecific encounters and interference competition, and thus can facilitate coexistence (Schoener, 1974; Daan, 1981; Roll & Dayan, 2002). Our results show that the hippopotamus had the least activity overlap with several species, including warthog, giraffe and bush duiker ($\Delta < 0.5$; Fig. 5D–F; Table S2; Fig. S3). We attribute this result to the fact that hippopotamus predominantly inhabit aquatic environments during the day but forage on land at night (Eltringham, 1999). The nocturnal terrestrial activity of the hippopotamus therefore minimizes potential for activity overlap with diurnal phylogenetically close relatives. Additionally, hippopotamus are obligate grazers, exhibiting dietary niche overlap avoidance with giraffe and duikers which are obligate browsers.

In conclusion, we provide empirical evidence for the phylogenetic structuring of species activity levels within a diverse mammal community. In this regard, our findings suggest that evolutionary relationships are more important in structuring mammal activity than allometry within diverse communities. These results further highlight the need to consider evolutionary relatedness when exploring interspecific variation in species traits (Pignata & Diniz-Filho, 1996; Diniz-Filho & Torres, 2006). More broadly, our findings suggest that evolutionary relatedness can be a useful pathway to reveal mechanisms underlying the structuring of activity, coexistence as well as patterns of assembly in animal communities. In an applied context, insights from this research may be useful when identifying conservation and management priorities based on the phylogenetic comparison of species activity.

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## DATA AVAILABILITY

Much of the data are summarized in the Supporting Information, but the original data will be provided upon reasonable request.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website:

**Figure S1.** Daily activity schedules of mammals in Murchison Falls National Park, Uganda, across seasons (dry and wet) from camera trap data collected between May 2012 and August 2013.

**Figure S2.** Activity schedules for mammals in Murchison Falls National Park, estimated from camera trap records obtained between May 2012 and August 2013. The curves depict activity patterns on a 24-h cycle conforming to a circular distribution.

**Figure S3.** Pairwise overlap of species activity schedules within taxonomic orders in a mammal community in Murchison Falls National Park, Uganda.

**Table S1.** Activity levels (A), in terms of the proportion of time spent active in a day, estimated for 22 mammal species in Murchison Falls National Park, Uganda, using camera trap detections between May 2012 and August 2013.

**Table S2.** Coefficient of overlap (Δ) with corresponding 95% confidence intervals and Watson's two sample test of homogeneity comparing activity curve estimates for mammals in Murchison Falls National park, Uganda. The activity estimates are derived from camera trap data collected between May 2012 and August 2013. Significant Watson U2 values indicate significant differences in species activity schedules.