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Research

The effect of body size on co-occurrence patterns within an African carnivore guild

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EDITOR'S CHOICE

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Intraguild interactions among mammalian carnivores are important in shaping carnivore guild composition. Competing species may inhabit different areas and/or being active during different times to reduce the risk of aggressive interactions, but the role of body size in intraguild interactions within carnivore guilds remains largely unknown. We determined spatial and temporal co-occurrence of small, medium-sized and large carnivores of the carnivore guild in central Tuli, Botswana: lion *Panthera leo*, leopard *Panthera pardus*, spotted hyena *Crocuta crocuta*, brown hyena *Parahyaena brunnea*, black-backed jackal *Canis mesomelas*, bat-eared fox *Otocyon megalotis*, African wildcat *Felis sylvestris lybica*, African civet *Civettictis civetta*, honey badger *Mellivora capensis* and small-spotted genet *Genetta genetta*. We used camera trap data over a two-year period and quantified the degree of temporal and spatial overlap by comparing activity patterns and calculating Pianka's index respectively. Our results showed that temporal overlap in activity between all carnivore species was high, but complete overlap was possibly reduced by differences in peak activity periods. In addition, low to moderate levels of spatial overlap were found between the different carnivore species, supporting the idea that small carnivore species inhabit different areas than large species to reduce the risk of interference competition. Due to the possible strong competition amongst sympatric carnivores there is a need for more knowledge on co-existence patterns for successful management and conservation of carnivore species, for example when carnivore species are (re)introduced in an area.

Keywords: camera trap, carnivores, central Tuli, interference competition, spatial partitioning, temporal partitioning

Introduction

Intraguild interactions among mammalian carnivores are important in shaping carnivore guild composition (Palomares and Caro 1999, Linnell and Strand 2000). Competing species may inhabit different areas and/or being active during different times to reduce the risk of aggressive interactions (Palomares and Caro 1999, Hunter and Caro 2008, Di Bitetti et al. 2010). Carnivore body size influences the outcome

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of interference interactions, with larger carnivores able to exclude or kill smaller carnivores (Palomares and Caro 1999, Donadio and Buskirk 2006). Small mammalian carnivore species possibly experience the strongest effects as they are more likely to be killed by other carnivores (Palomares and Caro 1999, Hunter and Caro 2008, Bischof et al. 2014). However, small carnivore species are often wide-ranging generalists whose diets overlap with numerous sympatric larger carnivore species whereby they possible experience the strongest effects due to exploitative competition from dietary overlap and interspecific killing (Caro and Stoner 2003, de Satgé et al. 2017). Alternatively, some smaller carnivores may also benefit from larger carnivores through food provisioning at kills (Prugh and Sivy 2020). Consequently, smaller carnivore species may alter habitat use (Fedriani et al. 1999, Palomares and Caro 1999, Durant 2000, Linnell and Strand 2000, St-Pierre et al. 2006, Prigioni et al. 2008) and activity patterns when larger carnivore species are present (Hayward and Slotow 2009, Bischof et al. 2014).

Most studies on spatial and temporal overlap or avoidance among mammalian carnivore species have focused on either large and medium-sized carnivore species (Fedriani et al. 1999, Buskirk 2000) or small carnivore species (Martinoli et al. 2006, St-Pierre et al. 2006, Prigioni et al. 2008, Chen et al. 2009) and comparatively little research has been done on species interactions within an extensive carnivore guild with small, medium-sized and large carnivore species (but see Rich et al. 2017, Monterroso et al. 2020, Zhao et al. 2020). Knowledge on co-existence patterns in these guilds is vital for successful conservation and management since they might be affected by (re)introduction or local extinction of carnivore species (Slotow and Hunter 2009). Since carnivores are important in protecting ecosystem functioning a decline in carnivore populations may result in changes in the structure and function of ecosystems with cascading effects on prey or sympatric mesopredators (Ripple et al. 2014).

Interspecific interactions can be evaluated by assessing co-occurrence patterns (MacKenzie et al. 2004, Richmond et al. 2010). Here we evaluate temporal and spatial overlap and avoidance of small, medium-sized and large African mammalian carnivore species as indexed by spatial and temporal co-occurrence data from camera traps. In the African savannas, the mammalian carnivore guild consists of multiple large, medium-sized and small carnivore species, and as a result co-existence is likely facilitated by spatial avoidance or differences in activity patterns (Palomares and Caro 1999, Di Bitetti et al. 2010). Previous studies focused on analysis of interspecific killing events and suggested that body size ratio between different carnivore species is the most important factor for the strength of intraguild interactions (Palomares and Caro 1999, Donadio and Buskirk 2006, Monterroso et al. 2020). For example, Monterroso et al. (2020) found that larger carnivore species dominate over smaller ones with body size ratios of ~4, above which local intraguild coexistence is unlikely.

However, carnivore interactions can also be non-lethal and more subtle but still result in temporal and/or spatial avoidance. We predicted that species pairs that are different in body size would be more likely to display niche segregation as a result of dominance hierarchies. Conversely, niche segregation between similar sized species may occur due to competition for the same resources and hence are more likely to display spatial and temporal avoidance. Furthermore, smaller carnivore species may reduce competition by using areas with high habitat complexity resulting in lower encounter rates (Janssen et al. 2007) that may be in areas with high vegetation cover, especially during the wet season. Consequently, we hypothesize that spatial and temporal overlap for the different species pairs is higher when vegetation cover is high and during the wet season due to higher habitat complexity.

Material and methods

Study area

We collected camera trap data in central Tuli, Botswana, which is an approximate 600 km^2 protected area consisting of privately-owned properties. Most of the properties host small-scale tourism enterprises or private holiday houses and a few properties have livestock. There are no internal fences between the different properties allowing for free animal movement between the properties while there is a boundary fence between central Tuli and the communal lands. A 200 km^2 area was delineated in central Tuli where a camera trap grid was used to capture mammalian carnivore species. Human pressure on carnivore populations in central Tuli is minimal with little road traffic and few cases of subsistence poaching.

The dominant flora is riverine woodlands with large bands of large fever berry trees *Croton megalobotrys* and mopane *Mopane-Combretum* shrub savanna. Most precipitation falls during the wet summer months, spanning from November to April, with 350 mm average annual rainfall. The mammalian carnivore guild is rich with lion *Panthera leo*, leopard *Panthera pardus*, spotted hyena *Crocuta crocuta*, brown hyena *Parahyaena brunnea*, black-backed jackal *Canis mesomelas*, bat-eared fox *Otocyon megalotis*, African wildcat *Felis sylvestris lybica*, African civet *Civettictis civetta*, honey badger *Mellivora capensis* and small-spotted genet *Genetta genetta* all being present in central Tuli.

Sampling design and field methods

An average of 12 camera trap stations were set in rotation in a block-survey design spaced 1–2 km apart, placed on trees at a height of 40–60 cm. Each of the three blocks was surveyed successively for 24–33 days after which the stations were moved to a different block. Each station consisted of two motion-activated cameras (Bushnell, E3) and were placed at game trails, roads or drainage lines to maximize capture probability of mammalian carnivore species. No baits or lures were used to increase detection rates of carnivores. Cameras were checked weekly to change batteries and download

Table 1. Description of variables and models evaluated for both temporal and spatial overlap.

Model	Predictor variable	Description
M1	Body size ratio (^{10}log)	Body size ratio was calculated using the mean weight ratio (heavier:lighter species) and was ^{10}log-transformed
M2	Vegetation	Vegetation was classified in 1) low vegetation and 2) high vegetation
M3	Season	Season was classified in 1) dry season and 2) wet season

images. Cameras were set to run continuously and to take three photos per trigger with a 5 s delay. To ensure independence of photographic capture events any photographs of the same species captured within 15 min were recorded as a single event unless it could be confidently determined it was a different individual (Kolowski and Forrester 2017).

At each camera trap station, we recorded characteristics of the habitat, such as vegetation cover (low/high), and season (dry/wet) when the camera trap was active, as these covariables may affect opportunities for competing species to co-occur (Cozzi et al. 2012, Vanak et al. 2013, Rich et al. 2017). In order to determine vegetation cover, six photos were taken at knee height at each camera trap station at 30 m distance on either side of the camera at 90- and 270-degree angles from the road/track. Subsequently, photos were divided into sixteen squares and squares in which vegetation cover was over 50% were summed (Van der Weyde et al. 2018). Vegetation cover was classified as high when ≥ 8 squares had a vegetation cover over 50%. In central Tuli the wet season spans from November to April and dry season from May to October.

Camera trap data was collected from September 2018 to December 2018 and June 2019 to September 2020. Ridout and Linkie (2009) conducted analyses on sample sizes as small as 25 capture events to test overlap analyses and similarly we decided to have a minimum sample size of 24 capture events so lion could be included in the analysis. We considered lion, leopard, spotted hyena and brown hyena as large carnivores (> 20 kg) based on average weight, black-backed jackal, African civet and honey badger as medium-sized carnivores (5–20 kg) and bat-eared fox, African wild cat and small-spotted genet as small carnivores (≤ 5 kg). Body size categorisation and calculations were based on Mills (1997).

Data analyses

To examine temporal overlap between all different carnivore species the coefficient of overlap (Δ) was calculated using the overlap package in R (Ridout and Linkie 2009, Meredith and Ridout 2014). Kernel density estimates of activity patterns were estimated for every carnivore species and subsequently a measure of overlap between different carnivore species distributions was calculated (Ridout and Linkie 2009, Linkie and Ridout 2011, Meredith and Ridout 2016). We used the estimators Δ_1 and Δ_4 for respectively sample sizes less than 75 and sample sizes more than 75, following recommendations of Meredith and Ridout (2016). We generated 10 000 bootstrapping iterations to calculate 95% confidence intervals for activity overlap.

To investigate the spatial co-occurrence of species at camera trap stations, we calculated Pianka's overlap index between different carnivore species (Pianka 1973). The index ranges from 0 (no overlap) to 1 (complete overlap), and overlap was considered low (0–0.39), intermediate (0.4–0.6) or high (0.61–1) (Grossman 1986, Maitra et al. 2020). To test the spatial autocorrelation in capture events of the camera stations, we calculated Moran's I per carnivore species (de Knegt et al. 2010).

Our main prediction was that greater difference in body size of species pairs would affect temporal and spatial overlap. We calculated body size ratio as body size of heavier/body size of lighter species). The body size ratio was then log transformed. We investigated whether body size, vegetation and season would influence the found temporal and spatial overlap of carnivore species in central Tuli. As the spatial and temporal overlap indices were bounded by 0 and 1, we used beta-regression to test these effects using the 'betareg' package in R (Cribari-Neto and Zeileis 2010) with temporal and spatial overlap as dependent variables and body size ratio, vegetation and season as independent variables (Table 1).

Results

From 4886 trap nights (mean 27.1 ± 3.0), a high number of capture events (≥ 24) were obtained for brown hyena, spotted hyena, leopard, civet, genet, jackal, wild cat, bat-eared fox, lion and honey badger. The number of capture events for

Table 2. Numbers of independent camera trap events for all different carnivore species in central Tuli, Botswana.

Species	Total	Species	Total	Species	Total
Large		Medium		Small	
Brown hyena	1584	Civet	255	Genet	93
Spotted hyena	1370	Black-backed jackal	151	Bat-eared fox	27
Leopard	377	Wild cat	61	White-tailed mongoose	18
Lion	24	Honeybadger	66		
Wild dog	13	Caracal	11		
		Aardwolf	3		

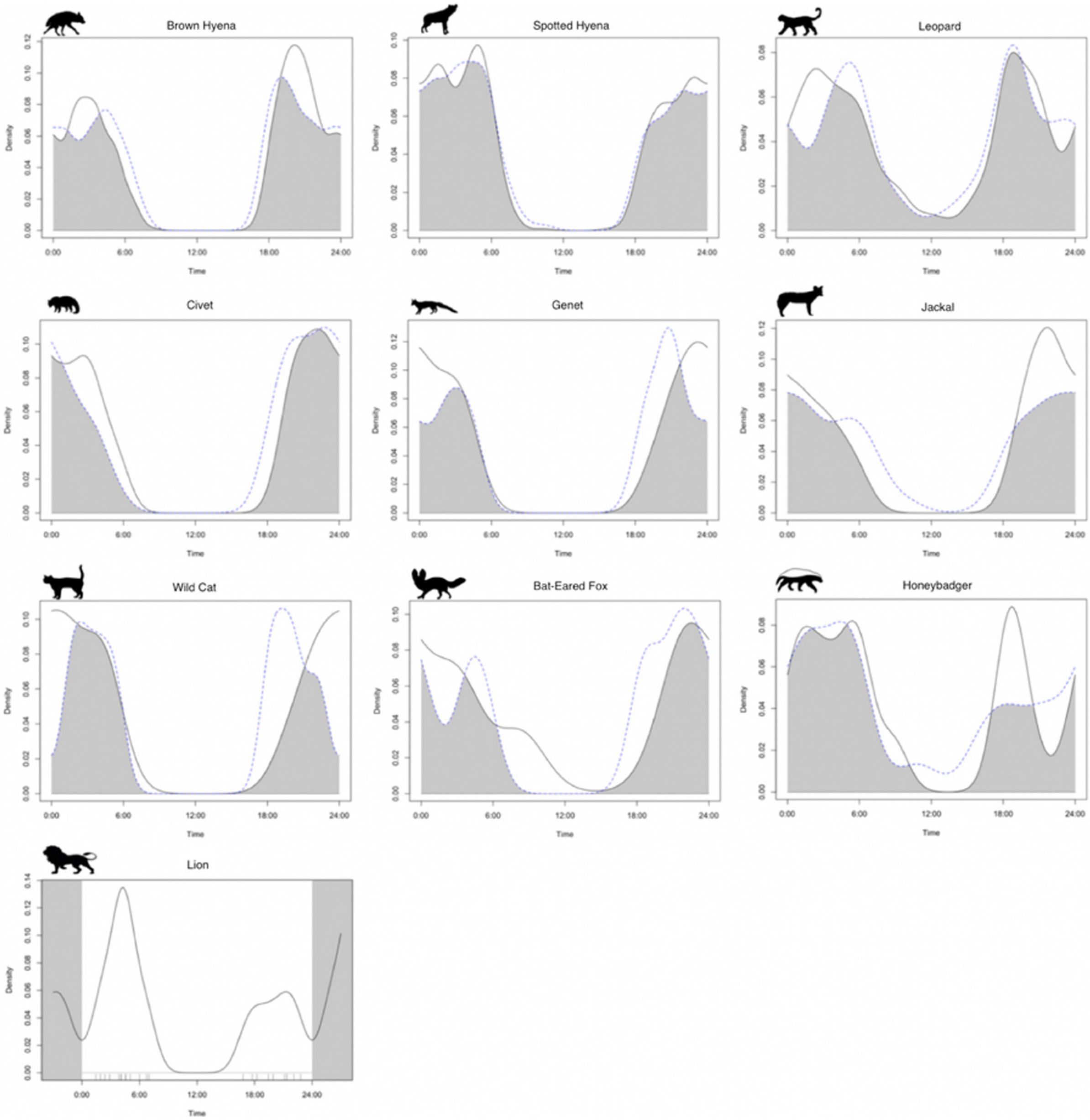

Figure 1. Daily activity patterns of the different carnivore species during the dry season (black solid line) and the wet season (blue dashed line) in central Tuli, Botswana. From left to right: brown hyena, spotted hyena, leopard, civet, genet, jackal, wild cat, bat-eared fox, honey badger and lion.

wild dog, aardwolf, caracal and white-tailed mongoose was low (< 24) and these species were therefore excluded from the analysis (Table 2). We found low values for Moran's I (< 0.01) suggesting spatial independence of the capture events per camera station.

The mean temporal overlap value across all species pairs was 0.78 [0.76, 0.80] ([95% CI]) indicating that the vast majority of the species pairs showed on average a high degree of temporal overlap (Fig. 1, Supporting information). Activity patterns for all carnivore species showed strong nocturnal behaviour except leopard and honey badger (Fig. 2) which displayed crepuscular behaviour. Only for wild cat, bat-eared fox, honey badger and lion the estimator Δ_1 was used due to sample size ≤ 75.

The mean spatial overlap value across all species pairs was 0.24 [0.20, 0.28] ([95% CI]) indicating that the vast majority of the species pairs tended on average to spatially avoid each other (Fig. 2). Notably, the spatial overlap between the large carnivore species (brown hyena, spotted hyena and leopard, except lion) was relatively high (Fig. 1, Supporting information).

Our beta-regression analysis indicated that body size ratio did not significantly impact temporal overlap amongst carnivore species pairs (Table 3, pseudo $R^2 = 0.033$, $z = -1.348$,

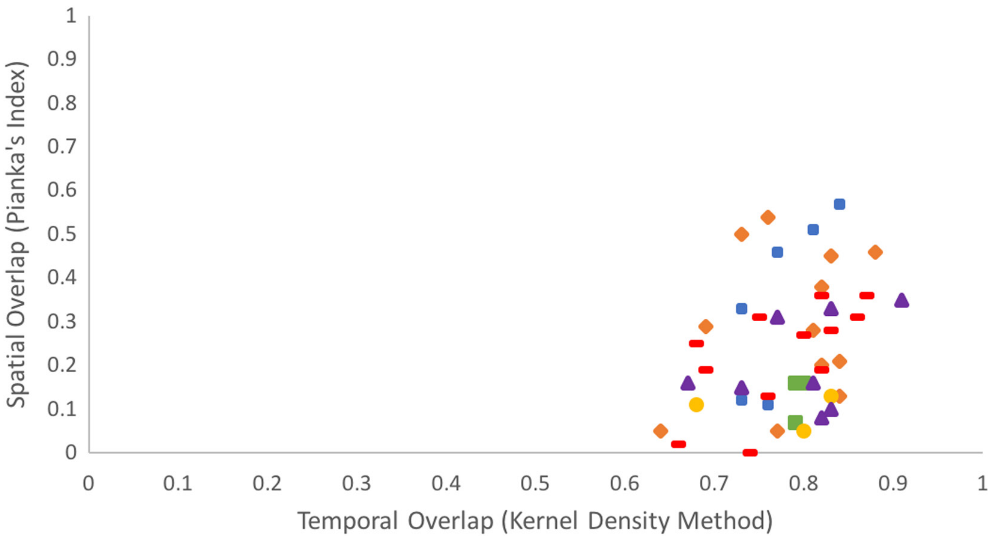

Figure 2. Relationship between temporal overlap and spatial overlap scores of carnivore species pairs. Temporal overlap scores are the Δ1 and Δ4 kernel density estimates. Spatial overlap scores are calculated with the Pianka's overlap index. Colors indicate different pairs of carnivore species: large–large carnivores (small blue square), large–medium-sized (orange diamond), large–small (red dash), medium-sized–medium-sized (big green square), medium-sized–small (orange circle) and small–small (purple triangle).

$p > 0.05$), while temporal overlap was significantly lower in low vegetation compared to high vegetation (pseudo $R^2 = 0.22$, $z = -6.197$, $p < 0.05$). Lastly, temporal overlap was significantly lower during the dry season compared to the wet season (pseudo $R^2 = 0.11$, $z = -4.503$, $p < 0.05$). The beta regression models for spatial overlap between different carnivore species pairs showed a significant negative effect of body size ratio on spatial overlap (pseudo $R^2 = 0.06$, $z = -1.986$, $p < 0.05$). This indicates that higher body size ratio resulted in lower spatial overlap. Secondly, spatial overlap in low vegetation between the different carnivore species pairs was marginally significantly different from spatial overlap in high vegetation (pseudo $R^2 = 0.017$, $z = -1.875$, $p = 0.06$) indicating that spatial overlap tends to be lower in areas with high vegetation. Lastly, season significantly impacted spatial overlap (pseudo $R^2 = 0.034$, $z = -2.531$, $p < 0.05$) which indicates that spatial overlap was lower in the dry season compared to the wet season (Table 3).

Discussion

In this study we investigated the temporal and spatial overlap of small, medium-sized and large mammalian carnivore species in central Tuli, Botswana. Our study provides important knowledge on the role of body size, vegetation and season in shaping local carnivore guilds. Our primary finding strongly supports the prediction that body size ratio significantly affects the spatial overlap between different carnivore species pairs. Specifically, we found that an increased body size ratio, i.e. larger body size differences between two species, generally resulted in lower spatial overlap. This suggests that that smaller carnivore species avoid sharing space with larger species most likely because larger species are able to dominate over smaller ones (Monterroso et al. 2020). In addition, temporal overlap was not significantly affected by body size ratio. Our results fail to demonstrate low temporal overlap and actually found high temporal overlap between smaller and larger carnivore species (Ramesh et al. 2017, Miller et al. 2018, Chaudhary et al. 2020, Vissia et al. 2021). These results suggest that subordinate carnivores avoid dominant carnivores in space but not in time.

Our second finding highlighted the significant impact of vegetation on temporal and spatial overlap. Specifically, we found that temporal overlap was lower in low vegetation suggesting that carnivore species more strongly avoided each other in areas with low vegetation compared to high vegetation. Persson and Eklov (1995) and Janssen et al. (2007) showed that smaller carnivores prefer more dense vegetation cover and use habitat structure as refuge hereby reducing the negative effects of possible intraguild predation. A possible explanation might be that there is less of a need for smaller

Table 3. Model comparison table for beta regression models with temporal overlap and spatial overlap as dependent variable and body size ratio (log), vegetation (low versus high) and season (dry versus wet) as independent variables.

		Temporal overlap			Spatial overlap		
Models	Variables	Coef	z	p	Coef	z	p
Model 1	Body size ratio	−0.15	−1.35	0.180	−0.54	−1.99	0.047
Model 2	Vegetation	−1.78	−6.20	< 0.001	−0.40	−1.88	0.061
Model 3	Season	−1.21	−4.50	< 0.001	−0.55	−2.5	0.011

carnivores to avoid more dominant carnivores in time in high vegetation. In addition, spatial overlap was marginally significantly lower in areas with high vegetation compared to areas with low vegetation. This suggest that smaller carnivore species reduce competition by using areas with high habitat complexity resulting in lower encounter rates (Janssen et al. 2007).

We found that temporal overlap was significantly lower during the dry season compared to the wet season. These findings are supported by Finnegan et al. (2021) who found that temporal segregation (e.g. a decrease in temporal overlap) between jaguars and pumas with mesocarnivores occurred more during the dry season than the wet season. Lower temporal overlap between different carnivore species pairs is likely caused by fewer food resources during the dry season and results in an increase in competition during this period (Finnegan et al. 2021). To avoid this competition, temporal segregation will increase between the carnivore species due to smaller carnivore species avoiding more dominate carnivore species. Furthermore, spatial overlap was significantly lower in the dry season compared to the wet season. Subordinate carnivores are known to avoid areas with high resource abundance when they overlapped highly with the activity area of more dominant carnivores (Vanak et al. 2013) and as a result when food sources are concentrated during the dry season, spatial overlap between carnivore species is lower.

We recognize two drawbacks of this study, namely using relatively small data sets for some of the carnivore species in this study and the fact that species might vary in their detection probabilities that we did not account for in our analysis. Although future studies could improve the data set, we conclude that there is increased segregation between species pairs with large body size differences in our extensive carnivore guild. As a result of local predator extinctions and/or reintroductions, changes might occur in the structure and function of ecosystems with cascading effects on prey or sympatric mesopredators (Slotow and Hunter 2009, Ripple et al. 2014). Changes in these ecosystems highlight the need for a better understanding of these interactions within different carnivore guilds and more research for further development of carnivore conservation is essential (Linnell and Strand 2000, Ripple et al. 2014).

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Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.tmpg4f50g> (Vissia and van Langevelde 2021).

Supporting information

The supporting information associated with this article is available from the online version.

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