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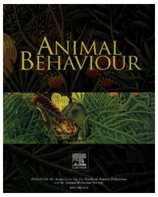

Special Issue: Multilayer Networks for Animal Sociality

Selection of timescales to study social network temporal dynamics in vultures

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Animal social interaction patterns change over time, but the continuous nature of social interactions makes selecting a timescale for studying the temporal dynamics of social networks challenging. We applied both a heuristic approach and a multilayer reducibility analysis approach to study timescales of change in social networks of free-ranging griffon vultures, *Gyps fulvus*. We analysed social networks in two behavioural situations: in-flight interactions, which we expected to fluctuate seasonally but to exhibit a relatively constant pattern of change at subseasonal scales; and diurnal ground interactions, such as while feeding, which we expected to show a pulsed temporal pattern following carcass availability. The heuristic method confirmed the suitability of a 3—10-day aggregation window for studying temporal change in vulture social networks, which matches their feeding dynamics. It also highlighted how examining a variety of timescales of aggregation can offer different insights about network change patterns. Multilayer reducibility analysis confirmed that substantial change occurred at every aggregation timescale we tested, with no redundancy in network layers; that is, social interactions in this population were not oversampled. However, it revealed more similarity between chronologically nonadjacent layers in the feeding networks as compared to the flight networks, further supporting the influence of carcass availability as a driver of co-feeding network structure. Multilayer reducibility analysis over a multiseason timescale did not reveal structural similarities by season, likely due to substantial differences in population composition and tag coverage between seasons. We discuss the benefits and limitations of both the heuristic method and multilayer reducibility network analysis as tools for studying long-term animal social network structural change.

The patterns of interaction among animals in a social group or population change over time. These changes may result from extrinsic or intrinsic reasons. Extrinsic factors include environmental perturbations such as daily weather fluctuations or seasonality (Monk et al., 2023; Patriquin et al., 2016; Shizuka et al., 2014; Welklin et al., 2023), temporal variability in food resource abundance, or larger or more abrupt environmental shifts, such as extreme weather events (Borthwick et al., 2024; Motes-Rodrigo et al., 2025; Pavelka et al., 2003). Changes in population composition can impose important changes to network structure; for example, dominance hierarchies and organization of interactions may change in response to the loss of high-ranking individuals (Flack et al., 2006; van der Marel et al., 2023), or when individuals leave or join a population due to dispersal or mortality (Cantor et al., 2012; Elliser & Herzing, 2014; Ilany et al., 2015; Shizuka & Johnson, 2020). Individuals may also change their interaction patterns as they age (Albery et al., 2022; Wild et al., 2024) or as their movements throughout their home ranges bring them into contact with more, fewer or different individuals (Peignier et al., 2019; Strauss et al., 2024). For example, the social networks of Eurasian griffon vultures, *Gyps fulvus*, change both throughout an individual's lifetime and across seasons and years, due to changes in weather conditions and breeding cycles (Acácio et al., 2024). These changes to social interactions can have consequences for individual fitness and for population level stability.

Social networks have been widely used to study animal social interactions (Croft et al., 2016; Farine & Whitehead, 2015; Pinter-Wollman et al., 2014; Wey et al., 2008). However, because networks depict aggregations of interactions over a set period of time,

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there are challenges in using them to study temporal change (Blonder et al., 2012). Time-ordered interaction networks provide one method of analysing temporal change in continuous time (Blonder & Dornhaus, 2011; Blonder et al., 2012). Still, methods for quantifying time-ordered network measures have not been extensively developed or tested in animal systems (Silk, 2023). In practice, most studies of change in social networks over time use time-aggregated networks, for which a time range and temporal resolution for aggregation must be chosen (Blonder et al., 2012; Pinter-Wollman et al., 2014). A suitable timescale for analysis should capture biologically relevant changes, while minimizing the 'noise' of fluctuating social interactions inherent to any dynamic process (Ogino et al., 2023). Choosing a long timescale risks missing fine-scale temporal changes that are biologically important. Aggregating interactions on very short timescales can provide high-resolution information about interactions, but it risks loss of statistical power due to too sparse networks or capturing redundant information. It may also result in using an overly complicated network representation when a simpler one would capture the biological dynamics just as well. These challenges have become more urgent with the improvement of GPS and proximity sensors, which permit inference of social interactions from spatial proximity while enabling analysis, at least in theory, of interactions at high temporal resolutions (Smith & Pinter-Wollman, 2021). For some research questions, the biologically relevant timescale of interest is evident, and networks should be segmented accordingly. For example, when examining social changes in response to seasonal changes in prey availability (Holekamp et al., 2012) or rainfall (de Silva et al., 2011), the interactions should be aggregated on a timescale of seasons. Alternatively, or additionally, social networks may have underlying cyclicity or periodicity (referred to as an 'inherent rhythm' by Caceres et al., 2011) that points to a particular timescale that may be appropriate for network aggregation. Detecting these rhythms can help confirm whether the chosen timescale is appropriate for the focal biological question, and possibly reveal social dynamics that occur at timescales other than those that had previously been considered.

Two approaches to detect biologically relevant timescales in animal social networks include a heuristic and a multilayer network approach. Using a heuristic approach (Caceres et al., 2011), social network measures are computed for networks in which interactions are aggregated over a variety of time windows (e.g. weekly, biweekly, monthly, etc.). The shape of the relationship between each network measure and the time window size can indicate which timescale is biologically important. Caceres et al. (2011) used this approach to examine simulated and empirical networks with and without underlying periodicity. Robitaille et al. (2021) used a similar approach to select an appropriate spatial scale for a study of caribou, *Rangifer tarandus*, interactions, although they did not apply the method to selecting a temporal scale. A second approach is to use multilayer network analysis. Multilayer networks are a mathematical representation that allows for the analysis of many interconnected networks as 'layers' within a single framework (Kivelä et al., 2014). Layers may represent different behaviours, concepts or time points (Finn et al., 2019; Silk et al., 2018). To assess redundancy of layers, a process of sequential aggregation, known as 'multilayer reducibility analysis', can be applied, either to multilayer networks in which each layer represents a different social situation (e.g. Pinter-Wollman & Rosenthal, 2026; in this Special Issue), or to temporal aspect multiplex networks in which layers represent sequential time-aggregated networks. When time windows are treated as layers, multilayer reducibility analysis can help determine a timescale of aggregation that appropriately captures network dynamics. Multilayer reducibility analysis seeks an optimal representation of a multiplex network by sequentially aggregating the most similar layers and comparing each reduced multiplex to the fully aggregated network (De Domenico et al., 2015). The optimal network will be the one with the fewest layers that is maximally different from the fully aggregated network, trading off simplicity with information loss. Reducibility analysis has been used to demonstrate that the social networks of social spiders change meaningfully over the timescales at which they were measured (three times per week for 6 weeks) (Fisher & Pinter-Wollman, 2021), and, conversely, that the social networks of spider monkeys are stable at monthly or submonthly timescales (S. Smith Aguilar, personal communication).

Here, we applied both the heuristic and the multilayer reducibility analysis methods to find biologically appropriate timescales for studying social interactions in a GPS-tagged population of free-ranging Eurasian griffon vultures in southern Israel. Griffon vultures are long-lived social scavengers that interact at communal roost sites (Harel et al., 2017), at food resources (i.e. carcasses) (Bosè & Sarrazin, 2007; Duriez et al., 2012) and in flight, where they glean information about carcass locations and favourable thermal air currents (Harel et al., 2016; Sassi et al., 2024). Vultures interact with conspecifics as they fly to and from communal roosts and foraging sites. They feed and interact with conspecifics at carcasses, whose presence is fairly unpredictable in space and time because they include naturally occurring wildlife carcasses, roadkill and dead livestock near human settlements. Additionally, the Israel Nature and Parks Authority provisions carcasses at supplementary feeding stations ('vulture restaurants') (Harel et al., 2017; Spiegel et al., 2013). Overall, this system provides a suitable case study for testing methods of analysing temporal dynamics of two contrasting social situations in a free-ranging animal population.

In this study, we focused on two behaviours, feeding and flight, in which we have an a priori expectation of different temporal dynamics of social interactions and different biologically relevant timescales (Sharma et al., 2023). On the ground near carcasses, griffon vultures may come into close proximity while approaching the carcass and feeding, and at close ranges they may engage in competitive interactions at the carcass (Bosè & Sarrazin, 2007). A network of diurnal ground interactions (i.e. feeding interactions), therefore, captures individuals' patterns of engagement with conspecifics around carcasses, providing potential pathways for disease transmission through co-feeding on the same food source (D'Bastiani et al., 2024) and competitive interactions. Flying within sight of conspecifics provides griffon vultures with important visual information about the location of resources (i.e. carcasses, roost sites and favourable thermal air currents for flight), even at long distances (Harel et al., 2017; Sassi et al., 2024). A social network of in-flight proximity, therefore, captures important pathways of social information transmission in this species. We asked two questions. (1) At what timescale is each network stable, minimizing redundancy of information and stochastic noise? (2) What timescale of analysis is needed, in each social situation, to capture substantial change in the network? Vultures feed at intermittently available carcasses, which can remain on the landscape approximately 1–3 days and may go up to more than a week between feedings, although they usually feed every 3–4 days (Spiegel et al., 2013; Vaadia, 2025). Furthermore, feeding events often involve large numbers of interacting vultures. Therefore, we expected feeding interactions in this population to exhibit a pulsed temporal distribution that fluctuates on the order of 3–10 days. Vulture interactions when feeding are of particular conservation interest because of mass poisoning events, which have occurred several times in the last few years in this population (Anglister et al., 2023; Nemtzov, 2021). These poisonings cause abrupt mortality and may pose a significant disruption to the vultures' social structures and population health (Anglister et al., 2023; Ives et al., 2022). Therefore, it is particularly important to understand the timescale of unperturbed temporal rhythms of feeding interactions to detect deviations and uncover the long-term effects of these perturbations on Israel's vulture population, particularly due to their high dependency on social information for survival. Interactions in flight may occur during movements across the population's geographical range, with individuals generally responding to weather that creates more or less favourable conditions for energy-efficient soaring flight (Nathan et al., 2012; Shamoun-Baranes et al., 2003). We therefore hypothesized that interactions while flying would exhibit meaningful fluctuations over seasonal timescales, potentially in response to changes in weather patterns or in response to seasonal dispersal and long-range movements (Acácio et al., 2023; Spiegel et al., 2015), but that flight interactions would be steadier than feeding interactions over daily to weekly timescales. These dynamics of breeding cycles and environmental conditions also led to the expectation that the same season across different years would have similar network structure.

METHODS

Study System

We analysed data from a population of GPS-tagged Eurasian griffon vultures (hereafter referred to as 'griffons') in southern Israel. Griffons are captured annually as part of a monitoring programme and most are fitted with GPS tags using a Teflon leg-loop harness (Acácio et al., 2023, 2024; D'Bastiani et al., 2024; Nemtzov, 2021). The species is locally critically endangered, and a high proportion of the small population in the region is GPS-tagged (Acácio et al., 2023, 2024; D'Bastiani et al., 2024; Gahm et al., 2024; Sharma et al., 2023; Spiegel et al., 2013). The GPS tags record location fixes approximately every 10 min during daylight hours, and twice overnight, to preserve battery life given the griffons' diurnal habit. We cleaned the GPS data, including removing erroneous fixes and restricting the analysis to the southern population, as detailed in Gahm et al. (2025). To study the seasonal timescale of changes to social behaviour, we divided the data set (spanning from September 2020 through September 2023) into seasons, with three seasons per year: a prebreeding season during which dispersal may occur (mid-September through mid-December; 90 days), a breeding season (mid-December through mid-May; 150 days), when vultures incubate and attend to chicks if they have successfully bred), and a post-breeding season (mid-May through mid-September; 122 days), when thermal conditions are most favourable for soaring flight, and chicks are either near fledging or have already fledged. Overall, the seasonal scale analysis included data from nine seasons, three of each type of season (mean ± SD = 66 ± 22.26 individuals per season, range 33–91 individuals; Gahm et al., 2025). To examine temporal dynamics at a subseasonal scale, we focused on data from the most recent season in our data set, postbreeding season 2023 (15 May – 14 September 2023), which included 86 individual vultures. We considered two individuals within 50 m of another when on the ground (moving less than 5 m/s) during the day and outside a known roost as interacting on the ground, and we refer to these as 'feeding interactions' because most interactions on the ground during the day occur near a food source. We defined a proximity-based interaction between two individuals if they were within 1000 m during flight (moving faster than 5 m/s) and refer to these as 'flight interactions'. These spatial proximity values had to be sustained for at least two consecutive 10 min time intervals to be considered a proximity-based social interaction (Acácio et al., 2024; Gahm, 2023; Gahm et al., 2025; Sharma et al., 2023). We selected 50 m for the feeding interactions as a conservative distance threshold that captured close social interactions, such as fighting and sharing food, as well as somewhat more distant associations, when vultures are gathered near a carcass and can use social information about the food by seeing other vultures feeding. This 50 m distance threshold further allowed us to include direct social interactions that might be missed due to GPS errors of several metres, which are common when vultures are on the ground. We selected 1000 m as the distance threshold for flight co-occurrences because flying vultures can see to great distances (Cortés-Avizanda et al., 2014; Jackson et al., 2008; Pennycuick, 1972). Flight interactions are intended to capture the vultures' ability to obtain visual information about the location of conspecifics, for example, to cue in on the location of food or thermals.

Heuristic Method

Subseasonal scale

To investigate how timescale affected our understanding of social network change over time using the heuristic approach (subseasonal scale), we divided the data from the 2023 post-breeding season into consecutive, nonoverlapping temporal windows of varying sizes (1, 3, 5, 7, 10, 15, 20 and 25 days, out of a total season length of 122 days) and used these data subsets to construct time-aggregated networks (Blonder & Dornhaus, 2011) for feeding and flight interactions (Fig. 1) (e.g. 122 1-day networks; 12 10-day networks). We selected these window sizes to explore a wide range of possible timescales without the computational demands inherent to testing every possible window size. Furthermore, we chose 25 days as the longest window size because dividing the 122-day season into larger window sizes would have resulted in too few network slices for an accurate coefficient of variation (CV) calculation. We chose to analyse data from the summer of 2023 because it was the most recent season at the time of the analysis and had a high number of tagged vultures. For each network, we calculated density (number of observed edges divided by number of possible edges) using the 'igraph' package (Csardi & Nepusz, 2005). For each behaviour (feeding and flight), at each window size (1, 3, 5, 7, 10, 15, 20, 25 days), we calculated the CV (standard deviation divided by mean) of network density for all networks of that window size (e.g. 6 networks for a 20-day time window in a 122-day season). We used CV because it is unitless and allows for comparison of variance between systems with different mean values. For example, if all networks in a sample are very sparse, network densities will be much lower overall than a system in which all networks are very dense. Dividing the variance by the mean accounts for different network density values. This is relevant for feeding and flight networks, which have very different densities, as might networks resulting from different windows of aggregation. Following previous applications of the heuristic method (Caceres et al., 2011; Robitaille et al., 2021), we visually examined density CV patterns over different time windows for inflection points to determine the window size(s) that captured meaningful changes in the subseasonal networks.

Multilayer Reducibility Analysis

Subseasonal scale

To apply an alternative approach for understanding which timescales capture meaningful changes in the social network (subseasonal scale), we used multilayer reducibility analysis (De Domenico et al., 2015; Fisher & Pinter-Wollman, 2021). We performed reducibility analysis for each behaviour (feeding and flight) by dividing the postbreeding 2023 data into consecutive,

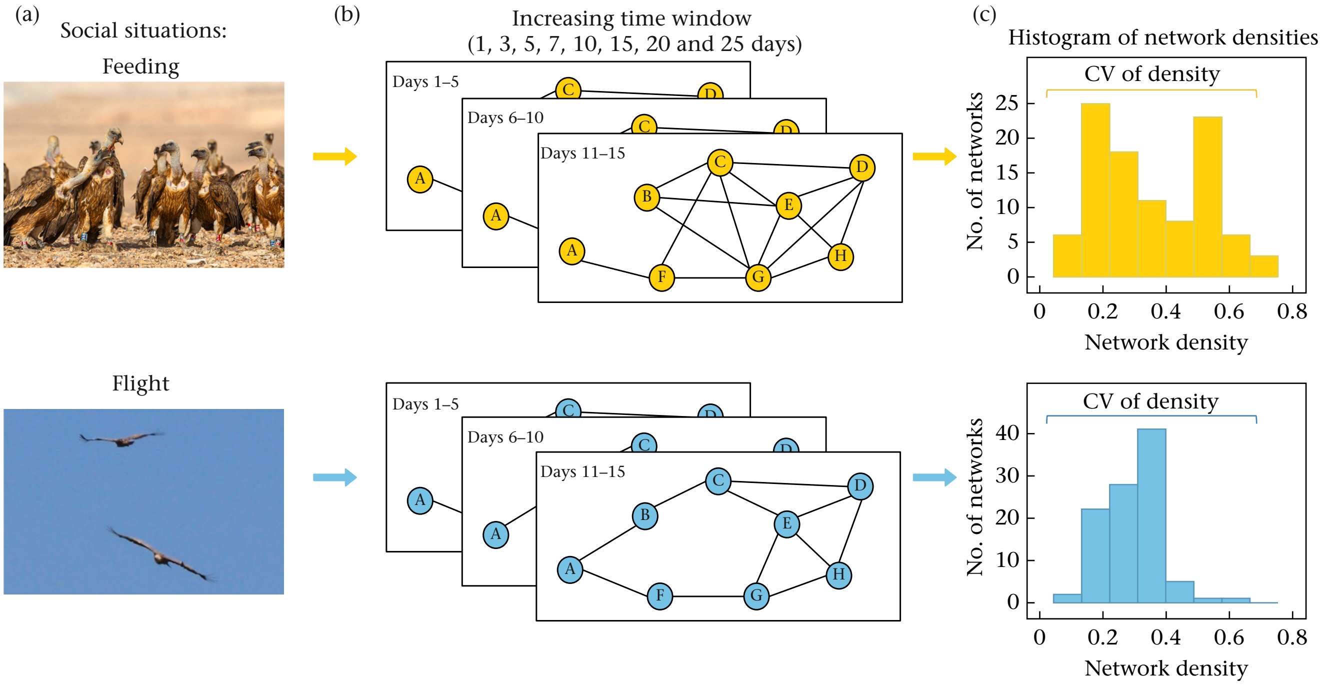

Figure 1. Conceptual illustration of the heuristic method. (a) Photographs illustrating social interactions during feeding (photo credit: Yoram Shpirer) and flight (photo credit: Noa Pinter-Wollman). (b) Feeding and flight situations were aggregated into social networks with time windows ranging from 1 to 25 days. The graphs show an example using 5-day windows. (c) The edge density of each network was then calculated, and the coefficient of variation (CV) of edge densities of all networks from a given window size were calculated. In (b, c), yellow denotes feeding and blue denotes flight.

nonoverlapping subsets of 1, 5, 10 and 25 days. We represented the networks for each social situation and window size as a temporal multiplex using functions adapted from the ‘muxViz’ package (De Domenico, 2022). Reducibility analysis computes pairwise quantum Jensen—Shannon distances to measure the dissimilarity between each pair of layers. We also visualized the Von Neumann relative entropy (a measure of how distinguishable the multilayer network is from the corresponding fully aggregated graph) against the number of aggregation steps for each multilayer network (De Domenico et al., 2015). For a conceptual illustration of how multilayer reducibility analysis works, and for a more detailed discussion of the computation of the Von Neumann relative entropy, see De Domenico et al. (2015).

Seasonal scale

We additionally performed a multilayer reducibility analysis at a seasonal scale, treating each full-season network as a layer and allowing aggregation of nonconsecutive layers. Individuals that were not present in a given season, either because they had left or had not yet joined the population, or because they were not yet tagged, were represented in the multilayer slices as unconnected nodes, to create a multiplex for aggregation. To examine whether similarities in the seasonal networks followed seasonal rhythms or were temporally sequential, we created heatmaps of network similarity and ordered the seasons either temporally (seasons in temporal order) or categorically (sorted by type of season, with subsequent years in temporal order within each season type). We compared both heatmaps to the heatmap outputted by the reducibility analysis. Close resemblance between the observed heatmap and a heatmap ordered by season type would imply that networks of the same season are more similar to each other across years than to their immediate temporal neighbours. In contrast, if the heatmap with networks chronologically ordered is more similar to the observed heatmap, then it implies that temporal changes in the data set are more important than the effect of season per se (see Results).

We conducted all statistical analyses in R, version 4.5.0 (R Core Team, 2025), using the ‘targets’ package for data pipeline management (Landau, 2021). Figures were created in ‘ggplot2’ (Wickham, 2016) and ‘gplots’ (Warnes et al., 2024). Other packages used for data analysis were ‘tidyverse’ (Wickham et al., 2019), ‘sf’ (Pebesma & Bivand, 2023) and ‘Matrix’ (Bates et al., 2025).

Ethical Note

The study was conducted under Israel Nature and Parks Authority (INPA) permit number 42166. Vultures were tagged as part of the annual health inspection conducted by the INPA, by a team of expert wildlife biologists and veterinarians who are trained in handling wildlife to minimize stress. No designated captures of vultures were made for this study.

RESULTS

Heuristic Method

Subseasonal scale

At all window sizes, the feeding network showed more variation in network density between time slices than the flight network (Fig. 2a). In both social situations, network density was the most variable when networks were aggregated at fine temporal resolutions (i.e. shorter windows). Also, for both behaviours there was a clear inflection point between the 5- and 10-day window sizes, with the CV of density decreasing more slowly at longer time windows (Fig. 2a). Peaks in network density were particularly evident in the co-feeding network every few days,

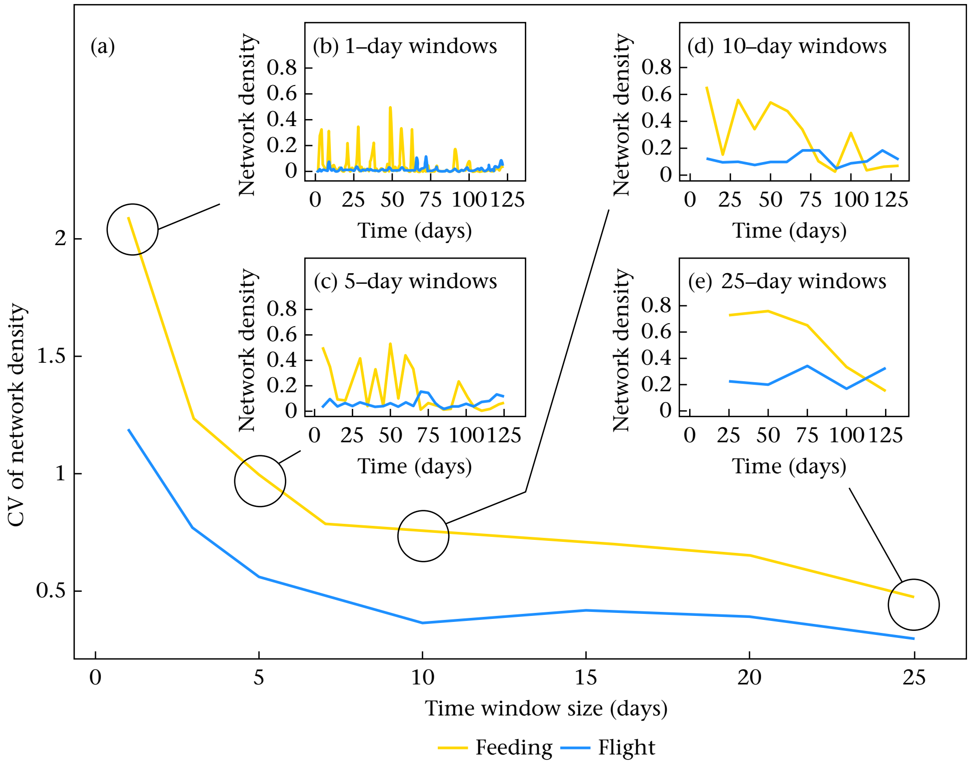

Figure 2. Heuristic analysis of time window sizes. (a) Thick lines show the coefficient of variation (CV) of network density for feeding (yellow) and flight (blue) interaction networks over time windows ranging from 1 to 25 days. Inset panels show network density (number of observed edges, divided by the number of all possible edges in the network) over time, for four window sizes of (b) 1 day, (c) 5 days, (d) 10 days and (e) 25 days. Data are presented only for the postbreeding season in 2023.

with density peaks around 0.2—0.4 (i.e. 20—40% of all possible pairs of GPS-tagged vultures interacted), compared to densities very close to 0 on days in between (Fig. 2b). Meanwhile, the co-flight network exhibited much fewer density peaks, with network densities being around 0—0.05 most days and only a few days with higher densities (around 0.1—0.15; Fig. 2b).

The overall pulsed pattern of network density in the feeding network, and the relatively low nonpulsed density in the flight network, remained evident in the 5-day time window (Fig. 2c). A 10-day window still showed some network density pulses in the feeding network, compared with relative stability in the flight network, with adjacent pulses in the shorter time window networks being merged together in the 10-day time window. Additionally, an overall downward tendency in feeding network density over the course of the season began to emerge with 10-day time windows. This pattern was not mirrored in the flight network, which, if anything, seemed to become slightly denser towards the end of the season (Fig. 2d). A 25-day aggregation window showed no evidence of a pulsed pattern in the feeding network density; instead, feeding network density declined smoothly over the course of the season, while flight network density retained its pattern of relative consistency of low density with minor fluctuations (Fig. 2e).

Multilayer Reducibility Analysis

Subseasonal scale

At all time window sizes and in both the feeding and flight networks, relative entropy declined consistently with greater aggregation of network layers, indicating that the network had salient temporal changes that were lost with increasing aggregation of the layers. The fully expanded, nonaggregated networks (i.e. the leftmost point on each curve) had the highest relative entropy (Fig. 3). This indicates that the window size being tested did not have sufficient structural redundancy that layers could be combined without losing information. However, the shape of the relative entropy curves differed between feeding and flight interactions. For the flight networks at all window sizes, relative entropy declined near-linearly with increasing aggregation of layers. In contrast, the relative entropy curves for the feeding networks were more concave (Fig. 3), indicating that some layers were more structurally redundant (i.e. aggregating them caused a smaller decrease in relative entropy) than others. In other words, for the feeding networks, the initial aggregation steps affected the relative entropy less than subsequent ones. Fig. 3c, for example, shows that up to four 10-day windows can be aggregated with minimal loss of information. At all four window sizes, the steepness of the curve increased approximately halfway through the aggregation; this was especially evident at 10- and 25-day windows (Fig. 3c—d).

Seasonal scale

At the seasonal scale, both the feeding and flight networks showed approximately linear, and nearly identical, declines in relative entropy with increasing layer aggregation (Fig. 4a). The three most similar pairs of layers (smallest Jensen—Shannon distances) were temporally adjacent: breeding 2023 and postbreeding 2023; breeding 2022 and postbreeding 2022; and prebreeding 2020 and breeding 2021, with another temporally adjacent layer being the next most similar (Fig. 4c). In other words, the aggregation of seasonal layers by similarity recapitulated their actual temporal order, rather than nonadjacent layers of the same season being most similar to each other (Fig. 4b).

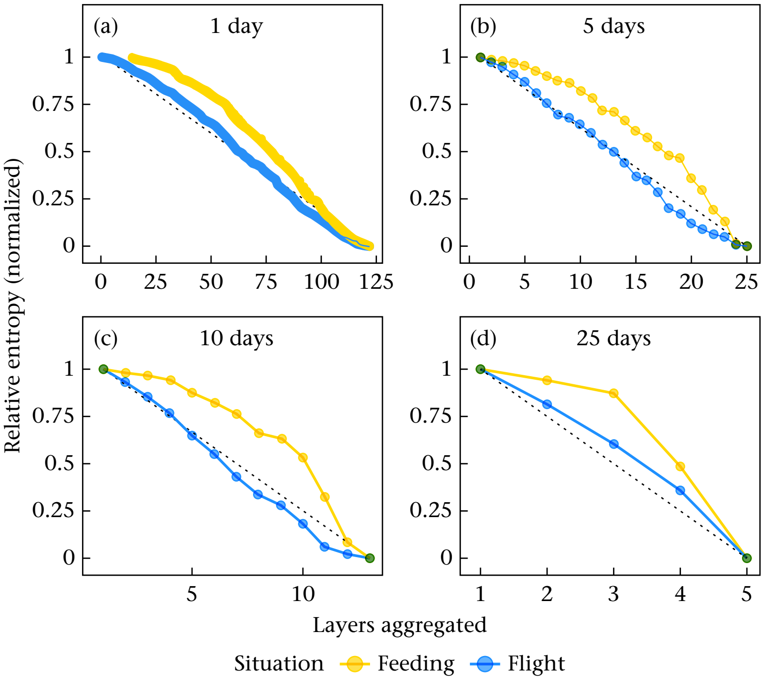

Figure 3. Multilayer reducibility curves at different aggregation window sizes. Feeding (yellow) and flight (blue) social networks for the postbreeding season in 2023. Each panel shows a different timescale: (a) 1 day, (b) 5 days, (c) 10 days and (d) 25 days. The *Y* axis shows the Von Neumann relative entropy of the current reduced multilayer network compared to the fully aggregated network, normalized to the maximum value for each curve; the *X* axis shows how many layers have been aggregated. The dotted black line represents the hypothetical linear decrease in entropy that is expected if each layer contributed exactly the same amount of information.

DISCUSSION

We examined the temporal dynamics of social networks of feeding and flight interactions in a population of free-ranging griffon vultures. We were interested in whether biologically meaningful interactions in these two social situations occurred at timescales varying from 1 day to nearly a month. We used two methods previously described in the literature for determining an appropriate timescale for each social situation. The heuristic method generally confirmed our expectation that interactions in a feeding context follow a pulsed pattern every few days, in alignment with the timing of food resource availability, and that interactions in flight were sparser and more consistent across the season. Multilayer reducibility analysis of networks at a subseasonal scale confirmed different temporal dynamics between the two social situations. Reducibility analysis did not reveal structural redundancy in social networks at any of the window sizes we tested, indicating that our GPS fix frequencies did not oversample the underlying biological processes. Multilayer reducibility analysis of networks aggregated at a seasonal timescale confirmed the importance of temporal sequencing in social network structure, over and above similarities between nonconsecutive seasons, in both the feeding and flight networks. However, it also highlighted the sensitivity of this method to changes in the number of individuals included in each layer, which may result from demographic turnover. This sensitivity could severely limit its applicability for the study of temporal dynamics in some free-living animal populations over long timescales.

Heuristic Method

Because of the temporally pulsed pattern of carcass availability on the landscape, we had predicted that patterns of social interactions in the feeding network would also be temporally pulsed. This prediction was supported by our finding that the feeding network was consistently more variable, relative to its mean, than the flight network across window sizes (i.e. yellow line consistently higher than the blue line in Fig. 2a). In the feeding network (yellow), the curve of network density CV showed an inflection point at window sizes between 5 and 10 days, which is consistent with the biologically informed timescale we expected based on our knowledge of griffons' feeding patterns and carcass availability on the landscape. Carcasses attract griffons for 3–10 days, facilitating close physical proximity (<50 m) and social interactions that would not occur otherwise. During the day, griffons are predominantly in the air or in their main roosts; if they land, it is either to rest in the shade of a cliff or at a carcass. Even when roosting, griffons are not often close enough to other individuals during the day to meet our distance threshold of 50 m. Thus, only when carcases were available in the landscape did we detect such close social interactions on the ground (presumably while feeding). The inflection point around window sizes of 5–10 days indicates that while networks aggregated over 1-day windows can provide information about fine-scale temporal dynamics, a wider time window, around 5 or 7 days, is still sufficient to capture fluctuations in network density that correspond to biologically meaningful feeding events. Indeed, this rate is supported by the ‘lifetime’ of a given carcass being less than 3 days (O. Spiegel, personal communication), as well as by the INPA provisioning rate (carcasses were provisioned every 2–20 days at most of the feeding stations).

We had predicted that the flight network would be relatively constant at subseasonal window sizes. Overall, the CV of network density among networks decreased with increasing window size. This decrease could be a result of increasing mean network density with increased aggregation, decreasing variability between slices, or both. Future work could more thoroughly explore the relationship between time window size, network density and number

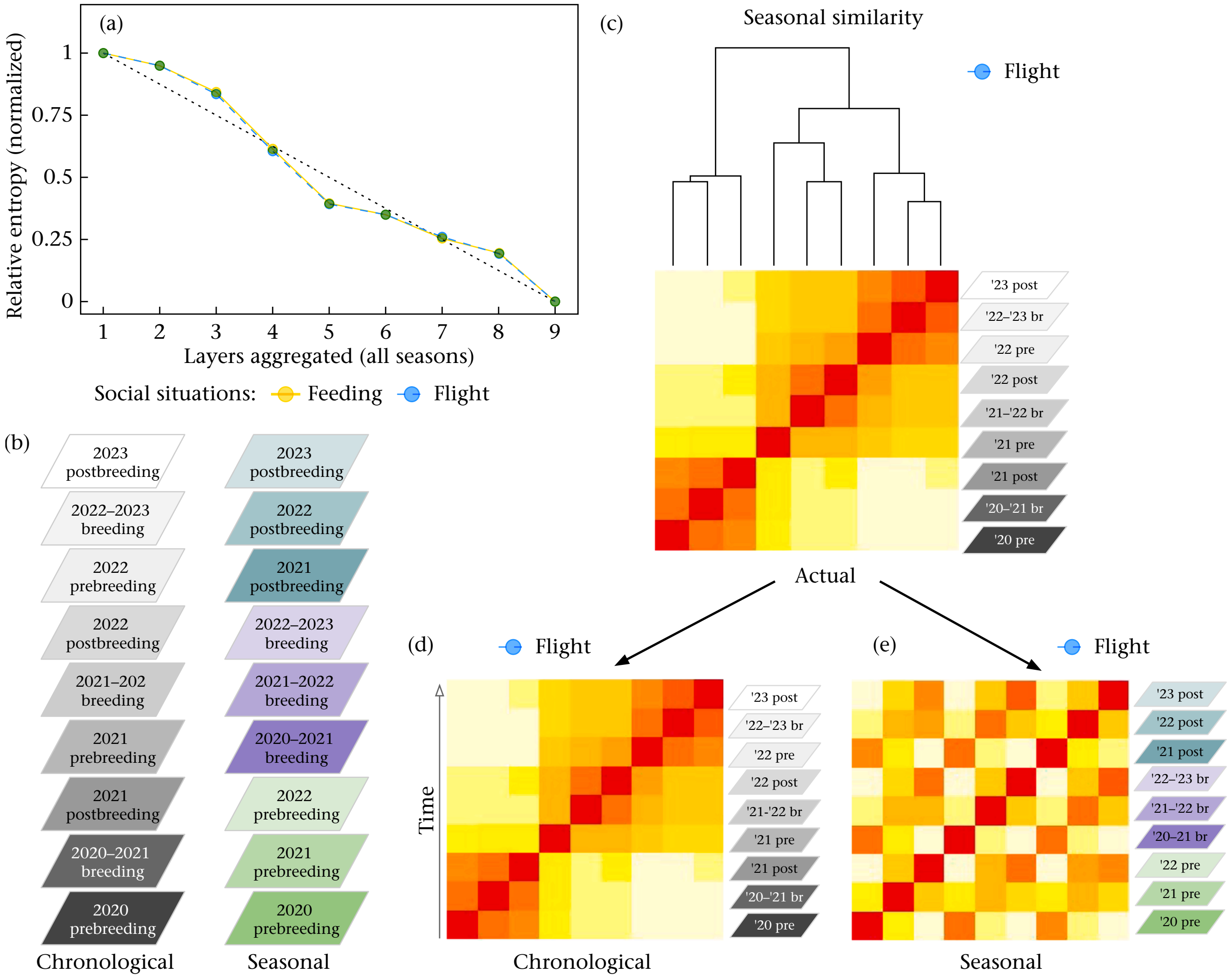

Figure 4. Seasonal scale multilayer reducibility analysis. (a) Reducibility curves showing approximately linear decreases in relative entropy with increasing aggregation for both feeding (yellow, solid line) and flight (blue, dashed line) networks. The dotted black line represents the hypothetical linear decrease in entropy expected if each layer contributes exactly the same amount of information. (b) Expected patterns of layer similarity if the social network structure is driven either by chronological continuity (left) or by recurring seasonal patterns (right). (c) A heatmap with accompanying dendrogram showing observed pairwise similarity between all seasonal flight network layers, where darker (redder) colors indicate more similar layers. (d) The same heatmap of similarity among flight network layers as in (c), but with rows and columns reordered to match the chronological order of the layers. In this case, the observed heatmap in (c) is identical to the heatmap in (d), indicating that the most similar layers were chronologically adjacent. (e) The same heatmap of similarity among flight network layers as in (c), with rows and columns reordered by season type (postbreeding, breeding, prebreeding), and then by year within each season type. Each layer represents a specific time point across years and seasons. Feeding networks showed essentially the same pattern (Supplementary Fig. S2).

of networks, including by comparing observed patterns to reference models in which the null models based on a variety of temporal structure is randomized (Hobson et al., 2021). The CV curve for the flight network showed a lessened version of the same pattern as the feeding network, consistent with our expectation that a pulsed pattern would be less pronounced in this social situation. Networks aggregated over 1-day windows had the highest variation, which then declined with increasing time window sizes. For time windows of 10 days or more, variation remained approximately constant throughout the season. Whereas diurnal ground interactions tend to occur at or around a food resource, vultures may meet in flight any day. Some variation is expected based on daily weather conditions, the spatial localization of thermals, how recently individuals have fed and how far they need to fly to access the carcasses currently on the landscape. Across both social situations, this case study suggests that the heuristic method is appropriate for detecting biologically relevant timescales in the analysis of temporal social networks. Our analysis points to a 5–10-day aggregation window for further analysis of these particular networks, in order to minimize noise but capture short- and long-term trends.

Our findings further emphasize that examining a variety of network aggregation window sizes can validate assumptions about the relationship between social network structure and known biological events, and can suggest future directions for inquiry. When we aggregated the feeding network over 25-day windows (Fig. 2e), we could clearly see a decline in feeding network density over the course of the postbreeding 2023 season, a pattern that was less evident from 1-day networks of the same social situation (Fig. 2a). The flight network showed no such decline in density over the season. These differing patterns for the two social situations raise questions about the relationship between interactions in the two situations and how they are each affected (or not) by long-term seasonal changes. The decline in feeding network density over the course of the season is unlikely to be explained by a decrease in food availability. Carcasses are provisioned more or less evenly over time by the INPA, and vultures in this system are in general not particularly food-limited

(Acácio et al., 2023; Reznikov et al., 2024; Spiegel et al., 2013). Hungry vultures also tend to fly farther and for longer periods than when they are satiated (Spiegel et al., 2013), which would suggest an increase in flight network density that is not present in our data. More feeding interactions early in the season could reflect breeding vultures' need to visit feeding stations more often when their chicks are young, or they could reflect decreased tag coverage over the course of the season. An alternative explanation for decreased feeding density could be a shift towards smaller feeding groups at far-flung carcasses, compared to larger feeding groups at feeding stations (Spiegel et al., 2015). Such a change in feeding habits could occur if food provisioning at feeding stations declines across the season. Future work should examine the availability of naturally occurring carcasses across the year, and the effects of the rate of food provisioning at feeding stations on the structure of long-term feeding networks. Temporal network analysis methodologies should continue to be driven primarily by biological research questions. Still, examining networks at a variety of scales can answer questions and suggest hypotheses that may not have been apparent from examining the data at the scale on which it was collected, revealing potentially important emergent properties of the study system, such as fission–fusion dynamics and metapopulation structure.

Multilayer Reducibility Analysis

Multilayer reducibility analysis helps us to determine whether a chosen window size is an appropriate representation of the complexity of the social network, or whether too fine a resolution has introduced redundancy, which could make further computations costly and mask real biological dynamics with statistical noise. Our analysis did not identify structural redundancy at any of the chosen window sizes, indicating that all of the window sizes appropriately captured change in the social network. The feeding networks did have some layers that were quite similar to others, indicated by the downward curvature of the reducibility curves (yellow lines in Fig. 3), but no layers were similar enough to justify excluding them from the multiplex. Likewise, social interactions in flight did not exhibit consistent enough social structures to provide any redundant information, or even much similarity between any of the layers. This pattern of relatively constant change in the flight networks over the course of the season would be consistent with interactions arising as an incidental consequence of foraging movements, or as a result of consistent conspecific attraction, in the absence of strong dyadic social preferences. Our forthcoming findings that social interaction patterns in vulture flight networks are a consequence of movement rather than conspecific social attraction provide evidence for the former explanation (Gahm et al., 2025).

In addition to validating that meaningful change is occurring over a focal window size, reducibility analysis can help us understand drivers of social network change. The concave reducibility curve in the subseasonal feeding networks suggests that it is possible to group similar types of network slices without losing important information. For example, layers that include large feeding aggregations at one or more carcasses may be more similar to each other than to layers that do not contain feeding aggregations, reflecting the strong temporal clustering observed in the heuristic above. Such an aggregation would allow layers of a similar type join more readily with minimal loss of information, while aggregation of layers of different types would result in steeper declines in information (De Domenico et al., 2015). This pattern is supported by heatmaps of 5-day layers in the feeding and flight networks, which showed that the most similar layers in the flight networks were often temporally adjacent, while the most similar layers in the feeding networks tended to be more temporally distant (Supplementary Fig. S1). Future studies could directly test for different types of network layers by slicing the network according to known biological events, such as feeding aggregations or weather events.

Our multilayer reducibility analysis of seasonal networks clearly demonstrates that each season's network is substantially different from the others. In addition, the most similar networks were those that were temporally adjacent (Fig. 4b–d), rather than the same season in different years being clustered together. This finding rejected our hypothesis that network level patterns of social interaction are primarily structured by seasonal scale environmental fluctuations (Fig. 4b–e); however, it is consistent with the hypothesis that networks change gradually over time, and it does not preclude seasonal influence on smaller-scale characteristics of social structure.

These findings are similar to those from a multilayer reducibility analysis over long timescales (seasonal and yearly) in spider monkeys (S. Smith-Aguilar, personal communication). Additionally, the seasonal scale reducibility pattern was nearly identical between the feeding and flight networks (Fig. 4a), an unexpected result given the very different dynamics of these two networks over subseasonal timescales (Fig. 3). We suspect that demographic turnover and changes in tag coverage drive these patterns (Table 1). The number of individuals in the network varied greatly between seasons. This could be due to demographic events (i.e. births, deaths and immigration/emigration events, including introductions of captive-bred individuals in this population); however, the griffon vulture population in this region has stayed

Table 1
Descriptive information about seasonal network layers for all nine seasons included in the analysis

Season	No. of vultures included in network	Start date	End date	Duration (days)	Network density	
					Feeding	Flight
2020 Prebreeding	40	15 Sep 2020	14 Dec 2020	90	0.038	0.067
2021 Breeding	33	15 Dec 2020	14 May 2021	150	0.033	0.026
2021 Postbreeding	52	15 May 2021	14 Sep 2021	122	0.062	0.057
2021 Prebreeding	86	15 Sep 2021	14 Dec 2021	90	0.231	0.159
2022 Breeding	62	15 Dec 2021	14 May 2022	150	0.172	0.126
2022 Postbreeding	62	15 May 2022	14 Sep 2022	122	0.247	0.203
2022 Prebreeding	91	15 Sep 2022	14 Dec 2022	90	0.288	0.265
2023 Breeding	86	15 Dec 2022	14 May 2023	150	0.285	0.198
2023 Postbreeding	86	15 May 2023	14 Sep 2023	122	0.448	0.334

Season boundaries are based on estimates of the biological timing of the vultures' breeding cycle. Edge densities are given for networks including all 124 individuals present in any season, because these complete networks were used for the multilayer reducibility analysis.

relatively constant over the past several years (Hatzofe, 2020). Alternatively, changes in vulture numbers could result from the addition or loss of GPS tags. To create a multiplex for reducibility analysis, missing individuals were represented as unconnected nodes in the network, creating seasonal networks with many unconnected nodes. As a result, demographic, or tagging-related changes, have a potentially larger influence on the similarity and relative entropy calculations than changes in the edges between individual nodes. Even if the edges were somewhat different between the flight and feeding networks, the number of individuals in those two networks changed in a similar way over the seasons, as individuals were lost or gained. Future work should assess the relative influence of demographic, methodological and social changes on apparent temporal changes in social network structure.

Our finding that seasonal networks were most similar to those closest to them chronologically could be explained by changes in the number and composition of individuals in the network. Such changes may be a result of changes in the number of tagged individuals (Table 1) or due to demographic events (Shizuka & Johnson, 2020). One way to circumvent the impact of changes in the number of individuals in the data set over time would be to restrict the reducibility analysis to individuals that are present in all seasons, or to those whose absence is known to be due to a death rather than to a lack of tag coverage. However, such an approach would greatly limit the sample size of individuals in the network (in our case, it would reduce our sample to a multiplex with only 20 individuals, despite individual season networks that can include as many as 90 individuals). To explore the effect of examining only the subset of 20 individuals present in all seasons, we include a reducibility analysis of a multiplex with only these individuals in Supplementary Figs S3–S4. We found that the reducibility curves for the subset were much more concave, indicating that some layers were almost similar enough to each other as to contain redundant information (Supplementary Fig. S3). Additionally, there was more similarity between layers from the same season in different years than we saw for the whole-network reducibility analysis, although chronological adjacency also seemed to drive similarity (Supplementary Fig. S4).

This subset analysis suggests how much can be learned from using multilayer reducibility analysis for a network of the same individuals over time. However, this comes with trade-offs. The longer the timescale of investigation relative to the life span of the study species or the duration of tracking, the harder it will be to study social change over long timescales using reducibility analysis. Because multilayer reducibility analysis requires a multiplex network (i.e. one in which all layers contain the same nodes) and considers changes in node connectivity when assessing layer dissimilarity, it will be especially sensitive to changes in the network composition and size. For example, some of the patterns of similarity in Fig. 4 could be explained by changes in the number of vultures included in the analysis over time (Table 1). For the study of temporal change over longer timescales, the heuristic method, or other methods that focus on network level measures instead of individual or dyad level measures, may be more suitable. Future method development could also consider ways to integrate multiple timescales within a single analysis to allow for explicit exploration of nested temporal structuring (e.g. annual, seasonal and daily all in one analysis).

While multilayer networks can afford us advantages over short periods of time and can excel at detecting whether networks are oversampled, our findings indicate that they are not a good method for studying network level social change in animal social networks across temporal scales of substantial demographic change. Over shorter periods of time, multilayer reducibility analysis is best used as a validation that meaningful change is happening at the chosen time window size, and as an investigative tool that may highlight unexpected temporal patterns in the data that might have otherwise been overlooked. Used on a smaller subset of individuals that are present over a long period, multilayer reducibility analysis could help investigate temporal change in their relationships, potentially helping to differentiate change in social bonds from change that is the result of demographic change or changes to tracking data coverage alone (Shizuka & Johnson, 2020). Meanwhile, the heuristic method can help to identify the time window size at which noisy fluctuations in network structure give way to general stability, as well as revealing longer-term temporal trends that may not have been evident from the raw data. Both methods could potentially be used in tandem; for example, by using the inflection points in the heuristic analysis to identify appropriate timescales and then using reducibility analysis to verify and learn more about the network layers at that scale. Using both methods, we can contrast temporal changes happening at different timescales in different behavioural situations, with implications for how various dimensions of sociality may respond to environmental or demographic change.

Author Contributions

Kaija Gahm: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Elvira D'Bastiani:** Writing – review & editing, Conceptualization. **Nili Anglister:** Writing – review & editing, Validation, Methodology, Data curation. **Gideon Vaadia:** Writing – review & editing, Validation, Methodology, Data curation. **Marta Acácio:** Writing – review & editing, Validation, Methodology, Data curation, Conceptualization. **Orr Spiegel:** Writing – review & editing, Validation, Supervision, Methodology, Funding acquisition, Data curation. **Noa Pinter-Wollman:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

Data Availability

The data that support the findings of this study are available in Dryad (https://datadryad.org/dataset/doi:10.5061/dryad.mpg4f4rcf). To protect this sensitive species, all GPS coordinates have been shifted in space. The code used to generate this analysis is available on GitHub via Zenodo (https://zenodo.org/records/15794961).

Declaration of Interest

None.

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Supplementary Material

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