Received: 20 May 2025 | Accepted: 22 June 2026

DOI: 10.1111/1365-2656.70316

Journal of Animal Ecology

RESEARCH ARTICLE

Relationship between spatial and social phenotypes in an avian scavenger

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Funding information
National Science Foundation Graduate Research Fellowship Program, Grant/Award Number: DGE-2034835; United States-Israel Binational Science Foundation, Grant/Award Number: 2015662 and 2019822

Handling Editor: Antica Mrs Culina

Abstract

1. Animals may interact incidentally, by sharing space, or intentionally, by seeking out interactions. Understanding which elements of social interactions can be explained by spatial behaviour and which cannot may uncover drivers of individual fitness and population functioning.
2. In an avian scavenger, we tested how space use covaried with social position while flying, feeding, and roosting. We also identified the deviation of observed social centrality from chance and examined how this non-incidental social centrality covaried with space use.
3. In flight, space use was positively associated only with observed social centrality, suggesting that interactions while flying emerge primarily from co-movement. In contrast, space use covaried with non-incidental social centrality while roosting, suggesting a stronger importance of social preferences when interacting at roost sites.
4. Our work demonstrates that the role of animal movements in shaping social interactions differs across social situations. Such an understanding of the spatial–social interface is essential for predicting population responses to environmental changes and conserving threatened species.

KEYWORDS
behaviour, conspecific attraction, movement, social interactions, social networks, space use, spatial, vulture

1 | INTRODUCTION

Individual animals differ in their social behaviour, and their position in the social network can have important fitness consequences. Social position can contribute to an individual's likelihood of contracting disease (Balasubramaniam et al., 2019; Corner et al., 2003; Godfrey et al., 2009; Romano et al., 2018), reproducing successfully (Formica et al., 2012; Silk et al., 2003; Wyman et al., 2021),

or obtaining information about food resources (Aplin et al., 2012). Social position has been associated with a variety of traits such as sex (Beisner et al., 2020; Lavista Ferres et al., 2021; Spiegel et al., 2018; Wey et al., 2013), age (Acácio et al., 2024; Wyman et al., 2021), and exploratory behaviour (Moyers et al., 2018; Snijders et al., 2014), as well as physiological conditions such as developmental stress (Boogert, Farine, & Spencer, 2014; Brandl et al., 2019). The causes and consequences of social position are complex and varied, and understanding them can reveal how animal social systems emerge.

Because social interactions arise when individuals encounter each other physically, and because social position may in turn influence spatial behaviour, social and spatial traits often covary (Sih et al., 2018). In their framework, Webber et al. (2023) characterized the variation in patterns of animal movement and space use as the *spatial phenotype*, and an animal's social position arising from its social interactions as the *social phenotype*. Recent studies have shed light on the covariance between spatial and social phenotypes in animals. For example, ground squirrels' spatial phenotype is associated with their social behaviour, with space use more strongly predicting affiliative encounters than agonistic encounters (Person et al., 2024). Spatial behaviours in red deer, such as range size and range overlap, are associated with individuals' positions in the social network of the population (Albery et al., 2021). However, it can be difficult to disentangle spatial–social relationships because causality can go both ways.

Social interactions with conspecifics may occur incidentally, as a consequence of movement when two individuals share the same space, or non-incidentally, for example, as a result of social attraction, when individuals seek each other out. Both of these processes can generate social-spatial covariance: on the one hand, such covariance may arise when similar movements incidentally bring individuals into proximity with each other, such as during movement towards a shared resource (Noonan et al., 2021; Payne et al., 2022). By contrast, individuals actively seeking out (or avoiding) other individuals can also result in social interactions (Frère et al., 2024; Pinter-Wollman et al., 2009; Smith-Aguilar et al., 2016; Spiegel et al., 2016). These 'non-incidental' interactions may include choosing particular conspecifics, such as in mate choice (Rosenthal, 2017), cooperation (Carter & Wilkinson, 2013; Helms Cahan, 2001; Laub et al., 2024), or agonistic territorial interactions (Spiegel et al., 2018); or individuals may seek to aggregate with conspecifics for the benefits that group association provides, such as thermoregulation, mating opportunities, predator defence, and foraging efficiency (e.g. Allee, 1927; Clark & Mangel, 1986; Pöysä, 1992). An individual's observed rate of social interactions (or its position in a social network), therefore, arises from a combination of incidental and preferential processes, but the observed interactions do not distinguish these causes. This challenge is particularly pronounced when interactions are inferred from spatial proximity using tracking data rather than from direct observations (Spiegel et al., 2016).

Being able to dissect the different elements that underlie observed social position is important for understanding why animals interact (Whitehead & James, 2015). Reference, or 'null' models are a useful tool to test hypotheses about potential explanations for social interactions (Farine, 2017; Hobson et al., 2021). Reference models that explicitly account for movement patterns can help to determine what portion of the observed interactions would be expected from animal movements alone, by comparing observed social position to expected values from the reference models (Gahm et al., 2024; Spiegel et al., 2016) (Figure 1). An alternative approach is to explicitly incorporate variation in the spatial environment into statistical models, for instance by including location-specific population density (Albery et al., 2021, 2025). However, the latter approach leaves the estimate vulnerable to spatial variance in data quality, such as when observation or tagging effort declines at the edges of a population. By comparing the social position of each individual against an expected distribution generated from a permutation of movement trajectories (Gahm et al., 2024; Spiegel et al., 2016), we can account for spatial edge effects and measure more accurately the extent to which interaction patterns are explainable by movement alone. While a trajectory permutation approach cannot fully resolve the causes of social interaction patterns, situations in which social-spatial covariance exceeds null expectations are candidates for further research on the mechanistic drivers of animal social interactions.

The social position of an individual can differ across social contexts (Gazda et al., 2015), and contribute differently to the overall population social structure (Sharma et al., 2023). Animals engage in social interactions in a variety of behavioural situations, and those interactions may have different consequences. For example,

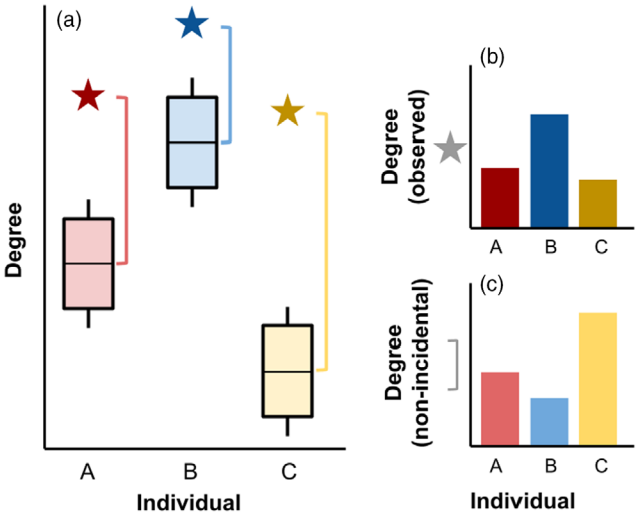

FIGURE 1 Observed degree in three hypothetical individuals (A, B, and C) reflects both incidental and non-incidental components of social interactions. (a) Non-incidental degree (brackets) is the observed degree (stars; number of unique interaction partners) minus the mean, divided by the standard deviation of the expected distribution (boxplots) that is generated from the spatially explicit wrap-around randomization of individuals' movement tracks. (b) Individual B has the highest observed degree, followed by A and then C. (c) Non-incidental degree is highest for individual C, reflecting a large deviation between its high observed degree and its low expected degree distribution.

in starlings, social transmission of foraging skills occurs through interactions while perching, but not when co-foraging (Boogert, Nightingale, et al., 2014). Disentangling the spatial and other components of social position in different behavioural situations can suggest which social situations may be most affected by movement patterns and the spatial environment, and which social situations are affected by other processes, such as social preference. For example, behavioural situations in which social network structure mostly arises from environmental effects on interactions might be the most susceptible to drastic seasonal changes, such as when elephants gather during the wet season (Wittemyer et al., 2005). On the other hand, the social network structure in a situation that is strongly related to other processes, such as social preference, could be expected to change if social preferences change over time, such as between breeding and non-breeding seasons in the case of mate choice.

Griffon vultures (*Gyps fulvus*, 'griffons') are long-lived obligate scavengers that forage for carcasses of large animals, an unpredictable and ephemeral resource (Mundy et al., 1993). They must travel over great distances to do so, relying on energy-efficient soaring flight (Houston, 1974). These traits make them a particularly good system in which to study the relationship between spatial and social behaviour because both social and environmental factors are consequential to their ability to find food and access roosts. Vultures interact in several behavioural situations, including while flying, at roosts, and at feeding sites. A combination of conspecific attraction and incidental encounters due to shared space use is likely important for shaping the social structure of griffon vultures. For example, griffons' flight interactions might arise incidentally, as they utilize geographic features that produce thermals, which reduce energetic expenditure while flying (Harel et al., 2016). Griffons may also fly jointly or rely on social attraction to find food (Jackson et al., 2008; Harel et al., 2017). Interactions at roost sites may have important social consequences because communal roost sites function as social information centres and serve as breeding sites during the breeding season (Harel et al., 2017). Finally, interactions while feeding at carcasses may have direct fitness consequences, as individuals compete for access to resources and may transmit disease at close range.

In this work, we examine the relationship between spatial and social phenotypes. First, we examined how the spatial phenotype relates to an individual's observed social position. We predicted that vultures with greater space use (as defined below) would encounter more unique individuals (higher degree) and have fewer social interactions (lower strength) because they spread their activity across larger ranges compared with vultures with smaller and more concentrated home ranges. The latter are more likely to encounter the same individuals repeatedly (lower degree) and spend less time in transit (i.e., have more time for social interactions that are not during flight). We also predicted that there would be a stronger relationship between space use (i.e., spatial phenotype) and observed social position in behavioural situations that are more intrinsically tied to movement (e.g., co-flight) than in stationary behavioural situations (e.g., co-roosting and diurnal ground interactions at feeding sites). Then, we examined whether a covariance between space use and social position persists after accounting for encounters expected due to movement alone (i.e., incidental encounters). Because incidental social encounters may either mask or reinforce the relationship between space use and an individuals' tendency towards sociality, we expected space use to have a different relationship with incidental than with non-incidental social positions.

2 | MATERIALS AND METHODS

2.1 | Study system

We studied the relationship between spatial and social phenotypes in a population of GPS-tagged Eurasian griffon vultures in the eastern Mediterranean (Figure 2a,b). Griffon vultures are locally critically endangered in Israel, and the population has declined substantially over the past several decades (Mayrose et al., 2017). As part of a management programme led by the Israel Nature and Parks Authority (INPA), around 100 vultures are captured annually in cages baited with carcasses (permit #42166). Most of the captured individuals are fitted with GPS-GSM-Accelerometer tags (Ornitrack-50 3G transmitters) using a Teflon leg-loop harness (see Acácio et al., 2024; Nemtzov, 2021). This research was conducted with permissions from Israel Nature and Parks Authority (permit no. 2020/42529). The GPS tags record location information approximately every 10 min during the daylight hours, and one or two locations overnight, when the vultures are not active, to preserve battery life. We cleaned the GPS data as detailed in the supplementary material.

To account for seasonal differences in social network structure, we divided the data based on vultures' breeding timelines into the breeding season (15 December–14 May), the summer post-breeding season (15 May–14 September), and the transient pre-breeding season (15 September–14 December). We analysed data collected between 15 September 2020 and 14 September 2023 for a total of nine seasons (three of each season type) across four calendar years.

2.2 | Construction of social networks

We inferred social interactions from spatial proximity in three different behavioural situations: co-roosting, co-flight, and diurnal ground interactions (Figure 2c). Because griffons do not usually land during the day except to feed, diurnal ground interactions usually occur at or near food and therefore we refer to them as 'co-feeding' interactions. To define proximity-based interactions, we selected distance thresholds for each behavioural situation according to the biological interpretation of interactions and features of the GPS data. In flight, vultures can see each other at great distances (Cortés-Avizanda et al., 2014; Jackson et al., 2008; Pennycuick, 1973), so being within 1000 m distance of another vulture is sufficient for vultures to cue in on each other's flight patterns (Harel et al., 2017). Accordingly, we recorded a co-flight interaction when two individuals were in

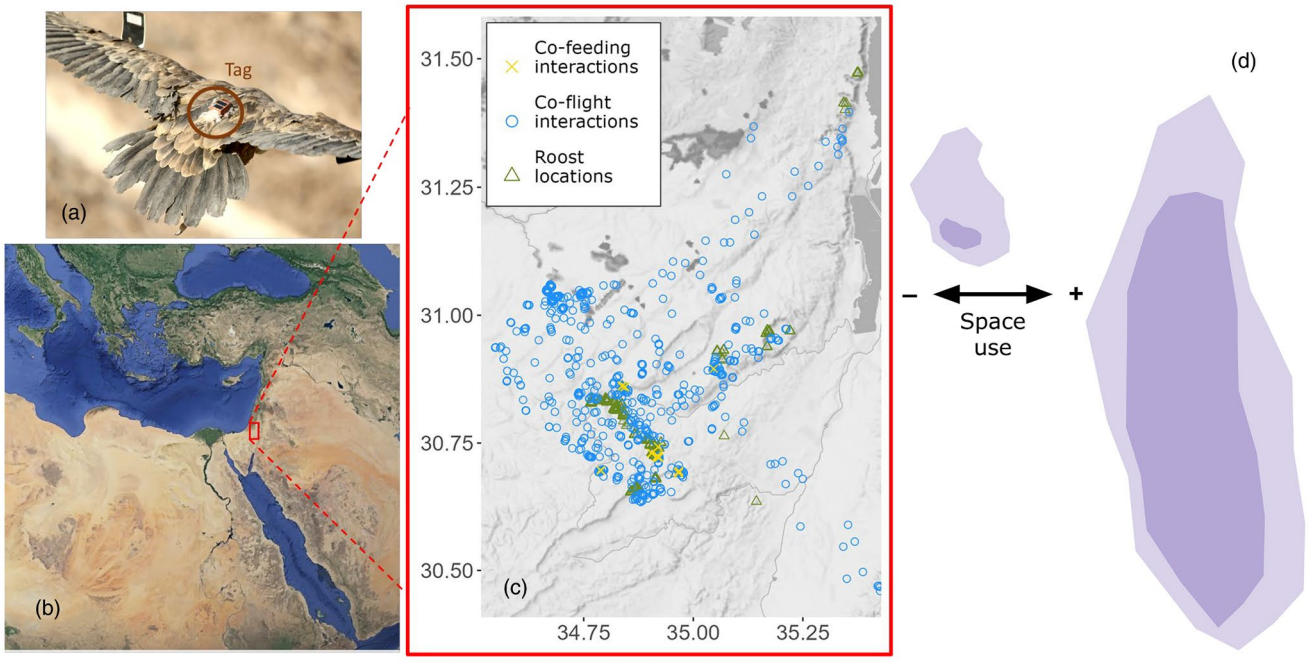

FIGURE 2 Study region, interaction locations, and spatial behaviour measure. (a) A GPS-tagged vulture (photo credit: Tovale Solomon); (b) red rectangle indicates the location of the study site on a map of the eastern mediterranean; (c) Map of the study site with co-roosting interaction locations (green triangles), the locations of co-flight interactions (blue circles), and co-feeding interactions (yellow crosses) during the first 5 days of July 2023. (d) Schematic representation of the 'space use' measure which includes overall home range (light purple, 95% KDE) and core use (dark purple; 50% KDE) areas. The home ranges and core areas of two hypothetical vultures are shown – –the one at left has a lower space use than the one on the right.

flight (ground speed >5 m/s) within 1000 m of each other during two consecutive daytime 10-min time intervals (to measure sustained interactions, rather than brief fly-bys). Interactions at food (carcasses) can include physical contact, aggression, and sharing of the same resource (Bosè & Sarrazin, 2007), therefore a much smaller distance threshold was used to detect such interactions; we chose 50 m as a conservative threshold that accounts for potential GPS errors of several metres. We recorded a diurnal ground (co-feeding) interaction if two individuals were not flying (ground speed <=5 m/s) and were within 50 m of each other, outside of a roost area, for two consecutive daytime 10-min intervals (similar to co-flight: to measure sustained interactions). To determine co-roosting interactions we first defined the nightly roost locations for each individual using a combination of their evening and morning GPS positions, according to the method described by Acácio et al. (2024). We recorded a co-roosting interaction when two individuals roosted within 500 m of each other, to identify co-roosting interactions that include both potential physical proximity and account for visual information about other vultures at the roost.

To test whether the relationship between spatial and social phenotypes differed across social situations, we constructed weighted, undirected social networks for each behavioural situation and season (see Supplementary Material for details on these networks). Networks included between 33 and 91 vultures per season (Table S1). To account for different amounts of data collected by each GPS tag, we defined the edge weights in the co-feeding and co-flight networks using a version of the simple ratio index (SRI) (Cairns & Schwager, 1987; Ginsberg & Young, 1992) modified for GPS data (Spiegel et al., 2016). We calculated SRI by dividing the number of 10-min time periods during which two vultures were observed interacting by the number of time periods during which both vultures had a recorded GPS fix for that behavioural situation, whether or not they were interacting during that period. Thus, two tagged vultures who never interacted in a given social situation would have an SRI of 0, while two individuals who interacted in every time period during which a GPS fix was collected for both of them in a given social situation would have an SRI of 1. Similarly, for the co-roosting network, edge weights represent the number of nights on which two individuals co-roosted divided by the number of nights when both individuals had a known roost location (i.e., they theoretically could have been observed co-roosting). For summaries of various network statistics see Tables S1–S4.

2.3 | Observed social network measures

For each individual in each social network, we recorded two social centrality measures, **degree** and **strength**, using the igraph package (Csárdi et al., 2026). Degree measures how many unique contacts an individual has (i.e., the number of unique conspecifics that it is connected to), indicating the number of potential sources of social information. Strength measures the weight of all social interactions

for each individual (i.e., the sum of the SRI values of all the edges of an individual), indicating how many social interactions an individual has. A vulture with many social interactions (high strength) may encounter only few unique individuals (low degree) if it is choosy about its social partners, while a vulture with relatively few interactions overall might still spread those interactions over many unique individuals over the course of an entire season.

2.4 | Disentangling incidental and non-incidental contributions to social position

To measure how much non-incidental factors contributed to individuals' position in the social network, we compared observed degree and strength values to distributions of values that would be expected to occur if potential synchrony in movements was broken. We used a wrap-around datastream randomization (i.e., re-sampling) method, which maintains individuals' explicit movements but decouples co-movements of individuals by shifting the observed movement trajectories in time (Gahm et al., 2024). This randomization procedure breaks the temporal signature of movement trajectories to disentangle the effects of movement on social interactions from any other potential drivers of social interactions (including social preference). We conducted 100 randomization iterations for each season of data separately using a time shift of 0 or 1 days backward or forward (i.e., −24, 0, or 24 h) (Gahm, Acácio, et al., 2026; Gahm et al., 2024; Gahm, D'Bastiani, et al., 2026). We obtained degree and strength measures from social networks constructed from the permuted movement data and compared each individual's observed degree and strength value to these expected distributions. We defined non-incidental sociality (non-incidental degree and non-incidental strength) as the z-score of the observed value compared with the distribution of expected values (i.e., the non-incidental value is the observed value minus the mean of the expected distribution, divided by the standard deviation of the expected distribution, Figure 1). As shown in Figure 1, any observed degree or strength value could be associated with either high or low non-incidental degree or strength, and two individuals with similar observed values could have very different underlying expected distributions and therefore different non-incidental sociality values.

2.5 | Spatial phenotype

We measured each vulture's spatial phenotype as its 'space use', which is a measure that combines both home range size and the evenness in which home range is used. Because griffons exhibit rare long-range movements (Spiegel et al., 2015), home range estimates may be inflated because they would include areas that are less frequently used. Accounting for the evenness in which the home ranges are used takes into consideration the movement biology of the study species. We used autocorrelated kernel density estimates (AKDEs) of daytime movement data, computed using the 'ctmm' R package (Fleming & Calabrese, 2023), to calculate home ranges sizes. To measure how individuals used space, we calculated the ratio between the core area size (50% AKDE) and the home range size (95% AKDE). To combine both the size of a home range as well as the way in which it is used, we defined 'space use' as the first principal component (capturing 84.56% of the variation in the data) of a PCA (Figure S3) containing both the core area to home range ratio and home range size (log-transformed to minimize the leverage of high values in the highly skewed distribution of home range sizes) (Jolliffe, 2014). Individuals with low space use had smaller home ranges that are less evenly used (lower KDE50/95 ratio) and individuals with high space use had larger home ranges that were used more evenly (Figure 2d).

2.6 | Statistical analysis

To determine the relationship between observed or non-incidental social positions (degree and strength) and space use, we fit four generalized linear mixed-effects models (GLMM) using the 'glmmTMB and lmerTest' packages (Brooks et al., 2017; Kuznetsova et al., 2017). The response variable in each model was observed or non-incidental degree or strength for each vulture in a single season and a specific situation. The observed degree model used a Poisson distribution with a log link function; all other models (observed strength, non-incidental degree, and strength) had Gaussian distributions with identity link functions. Each model had a response variable with different units: observed degree is measured in units of individuals; observed strength values are the sum of decimal SRI values; and non-incidental degree and strength are in units of standard deviations relative to the mean of the observed values. The model predictors were space use, season (breeding, summer, or fall), and behavioural situation (feeding, flight, or roosting). Because social interactions in each behavioural situation have different ecological functions and may have very different relationships to the spatial phenotype, we included an interaction term between space use and behavioural situation in all models. Because we did not find a significant effect of season on any social position measure tested, and to minimize model complexity and ensure convergence, we did not include an interaction term between season and behavioural situation (Engqvist, 2005). To account for potential differences among seasons, including different numbers of tracked individuals in the network, we included a random effect of season-year (e.g. fall 2022). Because individuals were tracked for different numbers of days within a season (Figure S6), we included an interaction term between behavioural situation and proportion of the season tracked (# of days an individual had valid GPS data divided by the total number of days in the season). Finally, to account for differences among individuals in network position or behaviour, we included a random effect of individual ID. For each of the four models, we calculated conditional effects using the emmeans package (Lenth, 2023) and created visualizations using ggeffects and ggplot2 (Lüdecke, 2018; Wickham, 2016). Data and analysis code are available on the Dryad Digital Repository (Gahm, Acácio, et al., 2026; Gahm, D'Bastiani, et al., 2026).

3 | RESULTS

Vultures with greater space use encountered significantly more conspecifics in flight (higher observed degree) than individuals with more constrained ranges (conditional estimate ± SE 0.048±0.007; 95% CI: 0.035, 0.062). Yet, surprisingly, they had significantly fewer unique roostmates (lower observed degree) (conditional estimate ± SE −0.013±0.006; 95% CI: −0.025, −0.001). We did not find a statistically significant relationship between space use and number of co-feeding partners (conditional estimate ± SE −0.007±0.007; 95% CI: −0.02, 0.006) (Figure 3a, Table 1). Vultures with greater space use had significantly fewer interactions (lower observed strength) at roosts (conditional estimate ± SE −0.398±0.182; 95% CI: −0.755, −0.042) and during feeding (conditional estimate ± SE −0.432±0.182; 95% CI: −0.789, −0.076), and significantly more interactions in flight (conditional estimate ± SE 0.407±0.182; 95% CI: 0.05, 0.763, Figure 3c, Table 1). We did not find an effect of season (breeding, summer, or fall) on observed degree or strength (Table S5, Figure S4).

Nearly all vultures' observed degree and strength values exceeded chance expectations by several standard deviations (i.e., non-incidental degree and strength greater than zero, Figure S2), consistent with previous findings in this species (Gahm et al., 2024). The magnitude of the non-incidental social position differed between behavioural situations, with non-incidental strength values being highest when co-roosting (Figure 3d, Figure S2). Non-incidental social position while flying or feeding was not predicted by individuals' space use (Figure 3b,d; Table 1), suggesting that spatial and social phenotypes are independent in these contexts. However, space use was a significant predictor of both non-incidental degree (conditional estimate ± SE −0.358±0.046; 95% CI: −0.448, −0.267) and non-incidental strength (conditional estimate ± SE −4.367±0.334; 95% CI: −5.023, −3.711) while roosting (Figure 3b,d, Table 1). In other words, vultures with smaller, more constrained home ranges (lower space use) tended to interact with more conspecifics than expected by chance (higher non-incidental degree) and had more interactions than expected by chance (higher non-incidental strength). Meanwhile, wider ranging vultures showed roosting interactions that were closest to the expected rates from their movements alone (lower non-incidental). We did not detect a statistically significant effect of season on non-incidental social position. Figure S5 shows raw data points in addition to the conditional model predictions shown in Figure 3. Full model statistics are reported in Table S5 and the variance explained by random effects in the models is reported in Table S6.

4 | DISCUSSION

In our study population of free-living griffon vultures, we found different patterns of socio-spatial covariance in different behavioural

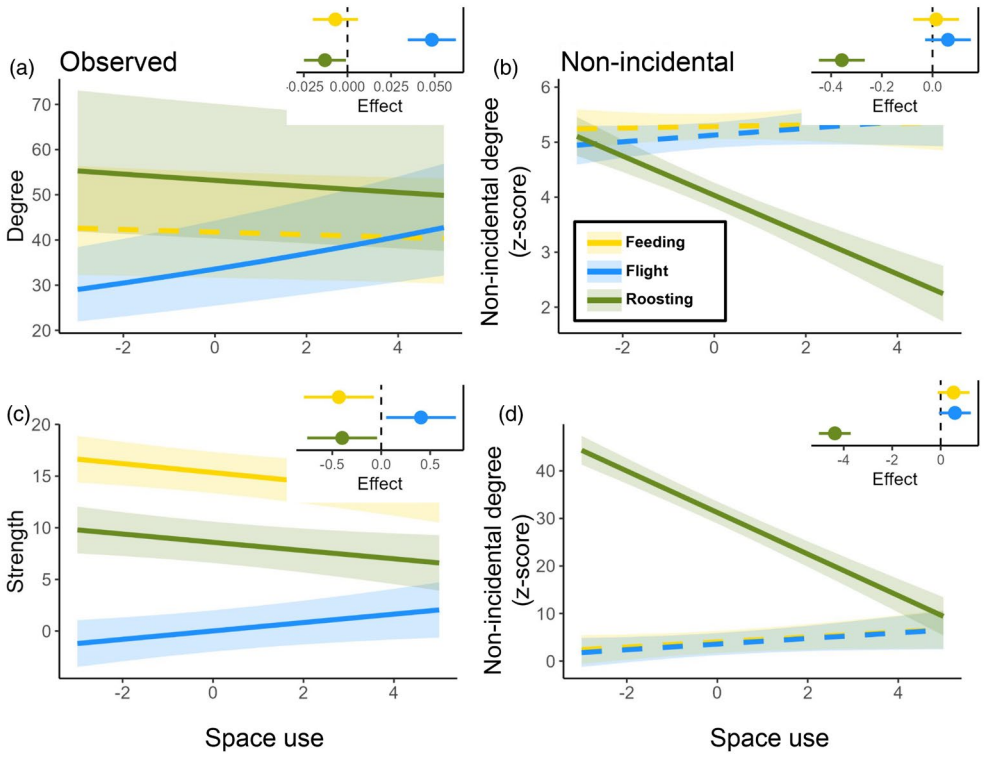

FIGURE 3 Relationship between space use and social position. Line plots (main panels a–d) show the conditional effect of space use on observed (a, c) and non-incidental (b, d) degree (a, b) and strength (c, d) for each behavioural situation: Feeding–yellow, flight–blue, and roosting–green. Solid lines indicate statistically significant relationships, while dashed lines indicate trends that are not statistically significant. Shading around the lines represents 95% confidence intervals. The inset plots show effect sizes, with error bars representing 95% confidence intervals. Error bars that do not overlap the dashed vertical line at 0 indicate statistically significant relationships. The same plots with data points added can be found in the Supplementary Material (Figure S5).

TABLE 1 Effect of space use on sociality, conditional on behavioural situation.

	Situation	Estimate ± SE	95% CI
Degree (observed)	Feeding	−0.007 ± 0.007	−0.02, 0.006
	Flight	0.048 ± 0.007	**0.035, 0.062**
	Roosting	−0.013 ± 0.006	**−0.025, −0.001**
Degree (non-incidental)	Feeding	0.014 ± 0.046	−0.076, 0.105
	Flight	0.061 ± 0.046	−0.029, 0.151
	Roosting	−0.358 ± 0.046	**−0.448, −0.267**
Strength (observed)	Feeding	−0.432 ± 0.182	**−0.789, −0.076**
	Flight	0.407 ± 0.182	**0.05, 0.763**
	Roosting	−0.398 ± 0.182	**−0.755, −0.042**
Strength (non-incidental)	Feeding	0.533 ± 0.334	−0.123, 1.188
	Flight	0.589 ± 0.334	−0.066, 1.245
	Roosting	−4.367 ± 0.334	**−5.023, −3.711**

Conditional effects of space use on social network measures for each behavioural situation (feeding, flight, or roosting). If 95% confidence intervals do not include 0, they are indicated in bold. For full model results, see Table S5.

situations. First, we found that vultures consistently interacted more, and with more individuals than expected by chance based on their movements alone, suggesting that they seek out conspecifics (as seen in the positive values of non-incidental interactions in Figure S2). Second, space use covaried significantly with observed sociality in all behavioural situations (Figure 2a,c), but space use was negatively associated with non-incidental social position only in roosting networks (Figure 2b,d). In situations that require substantial moving (i.e., flight), wider ranging vultures generally had more observed interactions than vultures that used less space. However, the opposite was true when roosting: individuals with smaller and more concentrated space use were more central in co-roosting networks. Furthermore, the observed strength of social interactions when roosting or feeding decreased with space use. The different effect of space use on observed and non-incidental social position suggests that different mechanisms may drive the structure of social networks at roosts compared with when flying or feeding. Our results point to the importance of disentangling spatial and social components of social behaviour in animal societies, as well as understanding which parts of animals' social phenotypes arise from their spatial phenotype and the environment, and which parts arise from other sources, such as social preferences. Uncovering such patterns is essential for predicting how social behaviour is expected to adjust to changing environmental conditions on rapid ecological timescales.

Space use predicted observed, but not non-incidental, social position in flight, suggesting that flight interactions may be primarily driven by incidental encounters that result from movement patterns (e.g., towards shared resources or along favoured routes). As we predicted, vultures with larger home ranges had more unique flight partners and more co-flight interactions (Figure 3a,c). The positive relationship between space use and degree in flight likely reflects the fact that wide-ranging individuals fly through areas occupied by a variety of individuals. These results are consistent with our expectations, and with findings in other species. For example, space use and social position are positively associated in free-living red deer (Albery et al., 2021), California ground squirrels (*Otospermophilus beecheyi*) (Person et al., 2024), and Australian sleepy lizards (Spiegel et al., 2015). Similarly, great tits (*Parus major*) that were more exploratory interacted with more conspecifics (Aplin et al., 2012). In vultures, the fact that the positive relationship with space use did not hold for non-incidental degree and strength in flight (Figure 3b,d) further suggests that movement towards spatial attractors or along energetically efficient paths, rather than conspecific attraction or avoidance, drives co-flight interactions in the system. Sociality is important for vultures' flight patterns because they rely on social information to locate both food resources and thermals (Cortés-Avizanda et al., 2014; Harel et al., 2017; Pennycuick, 1973; Sassi et al., 2024). However, while individual vultures differ in their tendency to be social (Figure S2; Harel et al., 2016, Sharma et al., 2023, D'Bastiani et al., 2024), the absence of covariance between space use and non-incidental social position in flight networks suggests that this variation is independent of differences in spatial behaviour.

At roosts, we found evidence that movement patterns and conspecific attraction may drive social position. Vultures that used more space had fewer unique roostmates (Figure 2a) and fewer social interactions at roosts (Figure 2c). This negative relationship between space use and social position when roosting could reflect spatial variation in population density. For example, if the vulture population and roost locations are most dense at a few specific roosts located near the centre of the study site, then vultures that range widely may be more likely to spend nights in smaller roosts farther from most other individuals. Indeed, the largest and most popular roosts in the study population are generally located close to active feeding stations (Acácio et al., 2024) at the geographical centre of the study site. Our observations could also be explained by edge effects. We estimate that more than 70% of the study population is GPS-tagged (Acácio et al., 2024). While this is a notably higher proportion than is typical of studies of free-ranging animals (Silk et al., 2015), tagging efforts

have been greatest in the area nearest to the geographic centre of the study site—near main feeding stations and popular roosts (Acácio et al., 2023; Spiegel, Harel, et al., 2013). Therefore, wide-ranging vultures may encounter more untagged conspecifics, artificially lowering their observed degree and strength values. However, we highlight that edge effects cannot explain the negative relationship between space use and non-incidental co-roosting social position. Our measures of non-incidental social position use explicit movement trajectories to account for spatial variation in the density of tagged conspecifics. For example, if an individual's home range lies in an area of low population density and the individual encounters few conspecifics as a result, its temporally shifted trajectories will retain this spatial context; non-incidental social position would measure any deviation of that individual's observed position from the (low) values expected given its home range. Therefore, the non-incidental social position measure accounts for spatial edge effects through the randomization procedure that generates expected sociality.

Vultures with the greatest space use exhibited the smallest deviation from the degree and strength that were expected by chance when roosting (Figure 2b,d). This finding suggests that, in this species, the tendency to prioritize social associations when roosting seems to be related to the tendency to move less. Given the importance of roosting sites for social information exchange (Harel et al., 2017), our findings suggest a trade-off between self-exploration and obtaining social information at the roost. Vultures that move less can gather less information through individual exploration about the location of resources, compared with individuals that have wider ranges. However, vultures that move less, have more social interactions, potentially providing them with social information about resources, which could compensate for their lower space use. In contrast, individuals with large space use have fewer social interactions at roosts, suggesting that they prioritize individual exploration through wide-ranging movement over social information that can be obtained at roosts. While social information use is generally considered more advantageous than individual foraging for vultures (Buckley, 1996; Jackson et al., 2008; Spiegel, Getz, & Nathan, 2013), adopting a variety of foraging strategies could help individuals within the same population avoid competition (Curk et al., 2025). There is some evidence of differentiation in behavioural strategies in this study system. Subadult griffon vultures are more likely to feed at naturally occurring carcasses, rather than the busier, more spatially central feeding stations, likely because they are outcompeted by adults at feeding stations (Vaadia et al., 2025). Furthermore, as vultures age, they are more likely to occupy the most popular and most central roost sites, and they show greater site fidelity and more routine roosting patterns (Acácio et al., 2024), characteristics that may be associated with lower space use. If the negative covariance between space use and non-incidental social position indicates an exploration-sociality trade-off in our population, then age is a likely predictor of individuals' choice of movement strategy. We did not include age in our models due to incomplete information that would have limited our sample size, and because the 3-year study period is too short to effectively investigate age-related changes in a long-lived scavenger (wild lifespan often >20 years; reproductive maturity around 5 years (Acácio et al., 2024; Chantepie et al., 2016)). However, future work should examine whether factors other than age affect individual foraging strategies, and whether there is evidence of consistent individual differences in movement and social position (i.e., socio-spatial behavioural types).

The relationship between space use and social position when feeding was less straightforward than in the other two behavioural situations. Vultures with greater space use had fewer social interactions when feeding (i.e., lower observed strength; Figure 2c), but we did not find a statistically significant relationship between space use and the number of unique co-feeding partners (Figure 2a). Furthermore, space use did not significantly predict non-incidental degree or strength in the co-feeding networks (Figure 2b,d). The vultures in this study population exploit both food provisioned at supplementary feeding stations and naturally occurring carcasses found elsewhere on the landscape (Anglister et al., 2023; Spiegel, Harel, et al., 2013; Vaadia et al., 2025). Naturally occurring carcasses tend to be less predictable (in time and space) and to attract smaller aggregations of vultures compared with provisioned carcasses that are placed at feeding stations (Vaadia et al., 2025). If wider ranging vultures are more likely to find naturally occurring food, they might have fewer opportunities to interact with conspecifics. Meanwhile, vultures with smaller ranges might be those who feed at busy and spatially central feeding stations. It is also possible that vultures that range more widely spend more time flying and less time at or near carcasses, resulting in fewer social interactions when feeding. Finally, in general, the wrap-around method cannot rule out that some interactions classified as non-incidental are a result of incidental interactions due to attraction to feeding sites. However, in this system, the timescale of the shift in the randomization and the timescale at which carcasses persist in the environment (Gahm, Acácio, et al., 2026; Gahm, D'Bastiani, et al., 2026) are similar to one another (1–3 days). Therefore, shifting the trajectories with randomization decouples interactions that result from incidental attraction to a food sources, reducing the likelihood that non-incidental interactions are misclassified as incidental interactions.

Our findings highlight the value in analysing social interactions in more than one behavioural situation and using reference models to distinguish between social and spatial components of interactions. Because observed social position comprises both incidental encounters and non-incidental social interactions (Figure 1), studying only observed social network centrality measures can mask important covariances between movement behaviour and tendency towards sociality (De Moor et al., 2025). In addition, comparing results for incidental and non-incidental components of social position can begin to shed light on which social patterns are a consequence of movement towards shared attractors, and which could be attributable to conspecific attraction per se. Importantly, we cannot be certain of the direction of causality when it comes to social encounters. Our reference model allows us to identify rates of social interactions that result from co-movement. We note that our method may overestimate incidental social interactions, especially in cases when social

preferences drive movements. In such cases, our method would provide conservative estimates of rates of 'non-incidental' encounters, because it might classify some interactions as 'incidental' even though they were driven by social motivation to go to the same place. For research questions that require accurately measuring the rate of truly incidental encounters, other methods would be needed to rule out the influence of socially driven movements on incidental encounters.

Understanding which behavioural situations are the most salient for social choice can help us focus future research on those situations in particular. Incidental encounters are driven mostly by the distribution of resources and threats, and are thus expected to change rapidly with changing environmental conditions. Therefore, social network positions in situations that are heavily influenced by incidental encounters are likely to be particularly changeable in response to changes in the environment. Meanwhile, the tendency to seek out social interactions is more likely to be stable and subject to change under selection over longer timescales. Social situations in which social attraction is salient may be resilient to environmental change if individuals can alter their behaviour to preserve specific social relationships or their positions in the population social network when their physical environment changes (Blumstein et al., 2023). Alternatively, behavioural plasticity may be insufficient to respond to rapid environmental change; this would lead to increased change in social position when the environment changes more rapidly than evolutionary timescales. Decoupling the social and spatial drivers of movement and social interactions will help us understand how social behaviours adjust and help animals cope with a changing world.

AUTHOR CONTRIBUTIONS

Noa Pinter-Wollman, Orr Spiegel, Kaija Gahm, and Marta Acácio conceptualized the study; Nili Anglister, Gideon Vaadia, Marta Acácio, and Orr Spiegel collected and curated the data; Kaija Gahm cleaned the data, performed statistical analyses, and created figures and tables. Marta Acácio wrote portions of the data cleaning and analysis code. Kaija Gahm and Noa Pinter-Wollman wrote the first draft of the manuscript, and all authors contributed substantially to revisions. Kaija Gahm and Noa Pinter-Wollman incorporated revisions and wrote the final draft of the manuscript. All authors gave final approval for publication.

ACKNOWLEDGEMENTS

We gratefully acknowledge the GPS tagging and vulture data collection efforts undertaken by rangers from the Israel Nature and Parks Authority over many years, in particular Ohad Hatzofe, Ygal Miller, Asher Perez, Avishai Bar-On, Roni Elias-Ofri, Nikita Podobreyer, Hanan Levavi, Lior Iev, Sappir Simchi, Ron Efrat, and Elya Maatuf. We further thank Elvira D'Bastiani, Cassidy Sadowski, Emily Laub, Nitika Sharma, Sean O'Fallon, and Alejandra Gamboa for helpful suggestions during the preparation of this manuscript.

FUNDING INFORMATION

Funding from NSF-BSF, grant #2015662 and #2019822, and from NSF GRFP, grant #DGE-2034835.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.7sqv9s54b (Gahm, Acácio, et al., 2026; Gahm, D'Bastiani, et al., 2026). The code used to generate this analysis is available on GitHub via Zenodo, https://zenodo.org/records/19446286. To protect this sensitive species, all GPS coordinates have been shifted in space.

STATEMENT ON INCLUSION

Our study brings together authors from different countries, including scientists based in the country where the fieldwork was carried out. All authors were engaged throughout with the research and study design to ensure that a diverse set of perspectives is represented. Whenever relevant, literature published by scientists from the region was cited, including consideration of relevant work in the local language. The research was performed in close collaboration with local stakeholders, including the country's nature and parks authority that played a vital part in our ability to perform the research.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Identifying southern vultures. Histograms of the centroid (mean) latitudes of all vultures in each season. Vultures that spent most of their time in the north (grey-shaded region of each histogram) were excluded from this study.

Figure S2. Social network measures. Distributions of observed (left) and non-incidental (right) degree (top) and strength (bottom) values in each of three behavioural situations: co-feeding (yellow), co-flight (blue), and co-roosting (green) in fall (F), breeding (B), and summer (S) seasons and years (2020–2023) in chronological order. Almost

all non-incidental values are greater than 0, indicating that nearly all individual vultures interacted more often, or with more unique partners, than would have been expected by chance, given their movements.

Figure S3. Space use PCA. Components are log-transformed home range (95% AKDE) and the ratio of the core area (50% AKDE) to the home range (95% AKDE). Space use was defined as the first principal component, which explains 84.56% of the variability in the data.

Figure S4. Effect of season on social position. Model-predicted marginal means (open circles), standard error (thick lines) and 95% confidence intervals (thin lines) for observed (left) and non-incidental (right) degree (top) and strength (bottom). Seasons are breeding (turquoise), summer (magenta), and fall (gold). Marginal effects were calculated with the 'ggeffects' package (Lüdecke, 2018).

Figure S5. Relationship between space use and social position, with points. Line plots (main panels a–d) show the conditional effect of space use on observed (a, c) and non-incidental (b, d) degree (a, b) and strength (c, d) for each behavioural situation: feeding – yellow, flight – blue, and roosting – green. Solid lines indicate statistically significant relationships, while dashed lines indicate trends that are not statistically significant. Shading around the regression lines represents 95% confidence intervals. The inset plots show effect sizes, with error bars representing 95% confidence intervals. Error bars that do not overlap the dashed vertical line at 0 indicate statistically significant relationships. Each point represents the measured (observed) or calculated (non-incidental) degree or strength value for a single vulture in a single season and situation. Point shapes, as well as colours, correspond to social situations (feeding – yellow circle, flight – blue triangle, roosting – green x).

Table S1. Sample sizes. Total number of vultures included in the social network for each season and behavioural situation, as well as the number of individuals for which space use was calculated.

Table S2. Social network measures. Each cell shows mean (SD) values (top row) as well as the range (min–max) (bottom row) of observed or non-incidental degree or strength for each season and behavioural situation.

Table S3. Observations per dyad. Cells show mean (min, max) number of raw observations for each dyad (i.e., the mean and range of the numerator of the SRI values) for each network.

Table S4. SRI values for each network. Cells show mean and range (min, max) SRI values for each behavioural situation in each season.

Table S5. Model results. Model summaries for LMMs including individual identity and season by year (e.g., Fall_2022) as random effects. Significant results ($p < 0.05$) are indicated in bold.

Table S6. Model results. Random effect variance estimates for each model.

How to cite this article: Gahm, K., Acácio, M., Anglister, N., Vaadia, G., Spiegel, O., & Pinter-Wollman, N. (2026). Relationship between spatial and social phenotypes in an avian scavenger. *Journal of Animal Ecology*, *00*, 1–12. https://doi.org/10.1111/1365-2656.70316