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The multilevel society of a small-brained bird

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Animal societies can be organised in multiple hierarchical tiers [1]. Such multilevel societies, where stable groups move together through the landscape, overlapping and associating preferentially with specific other groups, are thought to represent one of the most complex forms of social structure in vertebrates. For example, hamadryas baboons (*Papio hamadryas*) live in units consisting of one male and one or several females, or of several solitary males, that group into clans. These clans then come together with solitary bachelor males to form larger bands [2]. This social structure means that individuals have to track many different types of relationships at the same time [1,3]. Here, we provide detailed quantitative evidence for the presence of a multilevel society in a small-brained bird, the vulturine guineafowl (*Acryllium vulturinum*). We demonstrate that this species lives in large, multi-male, multi-female groups that associate preferentially with specific other groups, both during the day and at night-time communal roosts.

Multilevel societies have been exclusively reported in large-brained mammals, including humans [4] and other primates [2], as well as elephants [5], giraffes [6] and cetaceans [7]. Some cooperatively-breeding birds, such as bell miners (*Manorina melanophrys*), exhibit a form of multi-tiered social organisation at breeding colonies, but do not exhibit interactions between higher-tier social units [8]. Thus, multilevel societies are thought to be unique to animals with the cognitive capacity to track the identities of conspecifics both within their own group and at higher tiers [9]. Here, we study the gregarious and predominantly terrestrial vulturine guineafowl at the Mpala Research Centre in Laikipia, Kenya. We combine daily observations from 441 marked individuals, representing 97% of all adults, with high-resolution GPS movements of 58 individuals to characterise the structure of a population containing 18 distinct social groups.

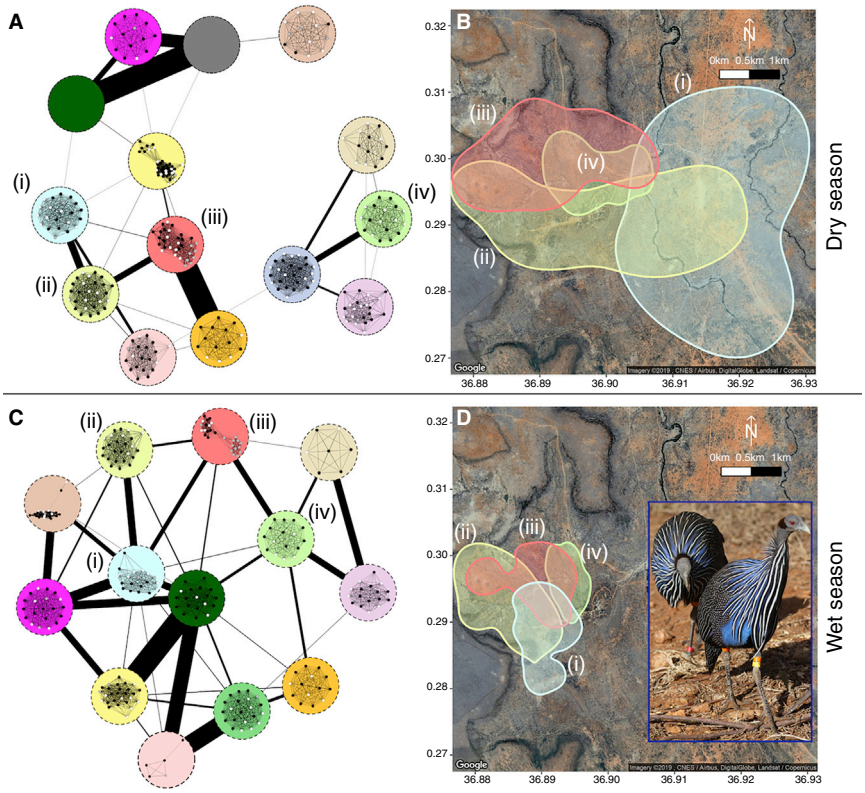

Figure 1. Data summary showing that vulturine guineafowl form stable multi-male, multi-female groups that overlap in space and time with other groups.
(A) Network representing intergroup contacts during one dry season (February–April 2019). Networks that are embedded within larger nodes represent group membership inferred from census data (white nodes represent females, black nodes represent males, and grey nodes are unsexed birds). Groups were clearly demarcated in both census and GPS data (median within-group inter-individual distance = 23.72 m, mean between-group inter-individual distance = 1621.13 m). Connection between larger nodes, each representing one group, capture the proportion of time each pair of groups was in contact (calculated from GPS proximity data using one random individual from each group, see Supplemental Information). (B) Map of four distinct social groups demonstrating their overlapping home ranges for the same season as in panel A. (C) Data per panel A for one wet season (July–August 2018). (D) Map of the same four distinct social groups demonstrating their overlapping ranges for the same season as in panel C. Inset shows two marked adult male vulturine guineafowl from the same group. Group (i)–(iv) represent the same groups across all four panels, and groups are assigned the same colours in all four panels. Missing group membership networks in Panel A represent two groups that were not censused more than three times in that season.

To characterise the membership of vulturine guineafowl groups, we first recorded the composition of two habituated groups twice-weekly over three years. These data (Figure 1 and S1A, in Supplemental Information published with this article online) show that group membership is stable, with groups containing multiple breeding pairs together with non-breeders (Data S1A–C). When conditions are suitable for breeding, pairs split from their group for a period of one to two months to nest, and re-join the same group afterwards. We then analysed the structure and temporal stability of group membership in the broader population using daily census observations of marked adults over a full year, broken down into six replicated periods, each two months long, which we call seasons (see Supplemental Information). Our data confirm that vulturine guineafowl

live in large (13 to 65 individuals) and distinct social groups that remain stable over time (inter-season correlations: r = 0.81–0.94, consecutive-season correlations: r = 0.86–0.94, Data S1D), despite regularly overlapping in space and time with other groups.

To quantify the higher-level structure among these distinct social groups, we simultaneously fitted high-resolution solar-powered GPS tags to 58 individuals. We selected one to five individuals per potential group, and fitted tags to all individuals in one group. Analysis of the inter-individual distance among GPS-tagged birds reveals a clear distinction between individuals that live in the same group versus those from different groups. Individuals from the same group were consistently found within 30 meters of each other (see Supplemental Information). GPS-based association networks constructed using this threshold matched our census data (correlations: r = 0.86–1.00, Data S1E, Figure S1A–B) and remained stable over our study period (between-season correlations: r = 0.74–0.98, consecutive-season correlations: r = 0.92–0.98, Data S1F). Proximity data between individuals from different groups further revealed that intergroup contacts were also consistent across seasons, confirming that groups repeatedly encounter the same groups over long time periods (Data S1G). While groups had overlapping home-ranges (mean = 27%, Figure 1), overlap did not explain preferences in intergroup associations (correlations: r = –0.02–0.1, P > 0.05). Groups also frequently roosted communally (mean = 19% of nights each group was tracked), with communal roosts typically containing two to five social groups. Roosting associations (Figure S1C) were also significantly correlated across seasons (Data S1H), but were not correlated with home range overlap (r = –0.01–0.04, P > 0.05). Together, these results show that vulturine guineafowl form stable social groups that fuse and fission preferentially with specific other groups, both during the day and at night. What determines higher-tier social preferences in multilevel societies remains unclear.

One potential factor contributing to the propensity for groups to associate is ecological conditions. Tracking the movement of groups over six seasons enabled us to relate patterns of space use, communal roosting, and inter-group contacts to ecological conditions. Home range overlap (Figure S1D) among different groups was significantly greater during dry seasons than during wet seasons (Data S1I), potentially because groups need to use larger areas during dry seasons to find resources. By contrast, the proportion of nights in which pairs of groups roosted communally (Data S1J) and the proportion of time that pairs of groups were in contact during the day (Data S1K) were both significantly greater during wet seasons than dry seasons, potentially because of greater overlap at areas rich in resources. The GPS data showed that prominent habitat features determined the location of intergroup contacts, and that the importance of these features varied across seasons. Contacts were significantly more likely to occur near water in dry seasons, and near open grassy areas — known as glades — that remain rich in resources in seasons when conditions transition from wet to dry (Figure S1E–I).

Together, our empirical data show that vulturine guineafowl live in a multilevel society, with individuals forming breeding units that are contained within stable groups, and that groups interact preferentially with specific other groups across different contexts. Further, we show that the resulting multilevel social structure is shaped by ecological conditions. Galliformes have a relatively small brain to body-size ratio, and their brains contain a number of neurons that is comparable to much smaller songbirds [10]. Yet, despite their small brains, vulturine guineafowl are able to track and maintain social associations across different temporal and social scales. These results, therefore, challenge the notion that multilevel societies are exclusive to large-brained mammals, and may in fact be more widespread than previously acknowledged.

SUPPLEMENTAL INFORMATION

Supplemental Information contains one figure, experimental procedures, results, acknowledgements, author contributions, and one data file, all of which can be found with this article online at https://doi.org/10.1016/j.cub.2019.09.072.

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