

Multilevel societies in birds

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Author contributions: Both authors conceived the study and contributed equally to the writing.

Keywords: avian societies, complex sociality, social structure, social organisation

30 **Letter**

31 There is growing interest in the study of multilevel societies, where social units comprising
32 several individual animals (human and non-human) come together to form higher-level
33 groupings. Grueter et al. [1] provide a useful definition of multilevel societies, highlighting
34 that key characteristics of multilevel societies should include stability across different social
35 levels and that stability should be driven by active social preferences rather than attraction to
36 the same resource or spatial overlap. Despite their framework being predominately focused on
37 mammals, and in particular primates, we argue it applies to a much wider-range of taxa. Here,
38 we highlight the important contribution that studies on birds can make to distinguish different
39 evolutionary pathways that can lead to multilevel societies and mechanisms that might
40 maintain these.

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42 Birds have a wide diversity of social systems, with many species living in nested societies.
43 Studies on birds have a long history of conducting comparative studies within and across
44 phylogenetic lineages [2]. It is now also abundantly clear that birds can possess cognitive
45 abilities similar to mammals [3], and the means of communicating through group- and
46 subgroup-level acoustic signatures [4], thereby highlighting that birds have the capacity to
47 maintain multilevel societies. They therefore represent an ideal taxonomic group to help with
48 defining and distinguishing multilevel societies from other forms of nested social structures.
49 For example, species living in two-level societies exhibit different combinations of stability
50 and cohesion at upper (e.g. groups or colonies) and lower levels (e.g. pairs or breeding units).
51 Colonial cooperative-breeding sociable weavers (*Philetairus socius*) collectively build large
52 nests and maintain long-term colony membership. Colony members forage together, with
53 individuals expressing stronger cohesion with members of the same cooperative unit within
54 foraging flocks [5]. In non-cooperative colonial breeders, such as zebra finches (*Taeniopygia*
55 *guttata*), individuals maintain long-term stable pair bonds, and forage cohesively with other
56 pairs with whom they breed synchronously, carrying-over these between-pair bonds into
57 subsequent breeding seasons [6]. While colony membership in zebra finches is unstable
58 within and across years, other species such as slender-billed gulls (*Chroicocephalus genei*)
59 maintain long-term colony membership despite colonies relocating large distances between
60 years [7], forming a stable upper level that suggests underlying social structure. Beyond
61 colonial breeders, clans of thornbills (e.g. the buff-rumped thornbill *Acanthiza reguloides*) can
62 be stable and consist of multiple cooperative-breeding groups, with clans foraging cohesively
63 but splitting into smaller groups during breeding [8].

64

65 There is also emerging evidence that group-living birds can form three-level societies. Bell
66 miners (*Manorina melanophrys*) live in large colonies that comprise of cooperative-breeding
67 units (lower level) that are members of coterries (intermediate level) which are then part of a
68 colony (upper level), although there is no evidence that the upper level is socially-driven and
69 not arising simply from attraction to the same resource (the colony) [9]. By contrast, vulturine
70 guineafowl (*Acryllium vulturinum*) move cohesively in groups that are stable across seasons
71 (intermediate level), and groups roost and move preferentially with other groups (upper level),
72 but the reproductive units within the group (lower level) can change from one season to the
73 next [10]. Thus, stability is not necessarily equally distributed across levels, and birds may
74 provide an ideal set of species to develop a deeper understanding of how cohesion and social
75 stability define different types of multilevel societies (**Fig. 1**). Although Grueter et al. [1]
76 defines the lower level as the core unit, this might misrepresent societies where membership
77 in the society is clearest at intermediate (e.g. groups of vulturine guineafowl) or higher (e.g.
78 colonies of slender-billed gulls) levels. Studies from birds can also allow social versus non-
79 social drivers of nestedness to be disentangled. While multilevel societies can emerge from
80 social preferences, seemingly identical patterns can arise from spatial and resource-driven
81 processes. Simply studying patterns of social structure arising at larger ecological scales will
82 undoubtedly uncover community sub-structuring driven by resource distribution and habitat
83 configuration [11]. For example, songbirds can maintain consistent community structure, at
84 two spatial scales, that is sufficiently stable to maintain experimentally-induced local
85 traditions across generations [12]. However, such community structure arises through a
86 combination of individual differences in micro-habitat preferences (lower level), and habitat
87 geometry restricting the movement of individuals across the woodland (upper level) (see
88 [11]). This example highlights how studies in birds can help reveal mechanisms that generate
89 patterns of social structure that are consistent with those from multilevel societies, even to the
90 point of exhibiting some of the same seemingly-adaptive ‘behaviours’ as multilevel societies
91 (local traditions), but without any social preferences taking place at higher levels.

92

93 We hope that Grueter et al. [1]’s work will inspire research on multilevel societies in birds.
94 Much can be gained by expanding existing evidence of complex and nested avian societies
95 into the multilevel society framework. When implementing this framework, studies will need
96 to explicitly consider the number of levels, their stability and cohesion, and the mechanisms
97 underlying the emergence and/or maintenance of each level. In doing so, studies on birds will

98 help with developing a better mechanistic understanding of multilevel societies, and whether,
99 regardless of the drivers, individuals can reap benefits from living in a nested population
100 structure, such as information transmission.

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102 **References**

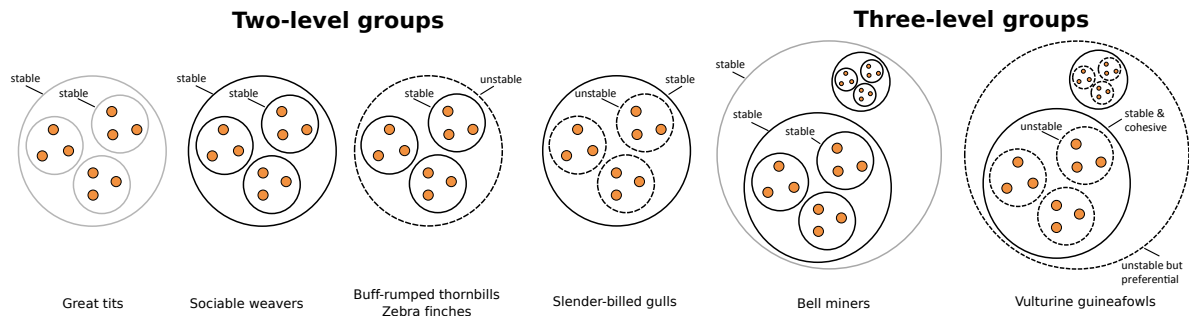
103

- 104 1 Grueter, C.C. *et al.* (2020) Multilevel Organisation of Animal Sociality. *Trends Ecol.*
105 *Evol* 9, 834-847.
- 106 2 Riehl, C. (2013) Evolutionary routes to non-kin cooperative breeding in birds. *Proc. R.*
107 *Soc. B Biol. Sci.* 280, 20132245.
- 108 3 Stacho, M. *et al.* (2020) A cortex-like canonical circuit in the avian forebrain. *Science*
109 369, eabc5534.
- 110 4 Henry, L. *et al.* (2015) Dialects in Animals: Evidence, Development and Potential
111 Functions. *Anim. Behav. Cogn.* 2, 132–155
- 112 5 Ferreira, A.C. *et al.* (2020) How to make methodological decisions when inferring
113 social networks. *Ecol. Evol.* 17, 9132-9143.
- 114 6 Brandl, H.B. *et al.* (2019) Wild zebra finches that nest synchronously have long-term
115 stable social ties. *J. Anim. Ecol.* 00: 1– 11
- 116 7 Francesiaz, C. *et al.* (2017) Familiarity drives social philopatry in an obligate colonial
117 breeder with weak interannual breeding-site fidelity. *Anim. Behav.* 124, 125–133
- 118 8 Bell, H.L. and Ford, H.A. (1986) A comparison of the social organization of three
119 syntopic species of Australian thornbill, *Acanthiza*. *Behav. Ecol. Sociobiol.* 19, 381–
120 392
- 121 9 Painter, J.N. *et al.* (2000) Complex social organization reflects genetic structure and
122 relatedness in the cooperatively breeding bell miner, *Manorina melanophrys*. *Mol.*
123 *Ecol.* 9, 1339–1347
- 124 10 Papageorgiou, D. *et al.* (2019) The multilevel society of a small-brained bird. *Curr.*
125 *Biol.* 29, R1120–R1121
- 126 11 He, P. *et al.* (2019) The role of habitat configuration in shaping social structure: a gap
127 in studies of animal social complexity. *Behav. Ecol. Sociobiol.* 73, 9
- 128 12 Aplin, L.M. *et al.* (2015) Experimentally induced innovations lead to persistent culture
129 via conformity in wild birds. *Nature* 518, 538–541

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132 **Figures**



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 134 **Figure 1. The levels of nested societies can differ in their stability and cohesiveness, and non-**
 135 **social drivers can operate at all levels.** Great tits (*Parus major*) form fission-fusion flocks that are
 136 non-randomly drawn from the local population and that live within a repeatable community structure,
 137 but while flocks appear cohesive, their membership is highly dynamic and the social structure at both
 138 levels is driven by underlying habitat characteristics. In sociable weavers (*Philetairus socius*),
 139 individuals form stable breeding groups that maintain long-term membership to a colony, which they
 140 construct, and individuals forage cohesively with members of their cooperative unit and colony. Zebra
 141 finches (*Taeniopygia guttata*) form long-term stable pairs, but membership to the colony is unstable
 142 both within and between reproductive seasons, while slender-billed gulls (*Chroicocephalus genei*)
 143 maintain colony membership across years even when these relocate large distances, but little is known
 144 about their wintering social behaviour. Some species exhibit greater cohesion and stability outside of
 145 breeding. For example, buff-rumped thornbills (*Acanthiza reguloides*) winter in clans, but these break
 146 up into multiple cooperatively-breeding units during the reproductive season. In three-level societies,
 147 bell miners live (*Manorina melanophrys*) in large colonies, which consist of cooperatively-breeding
 148 units that form coterie, but there does not appear to be any social interactions among coterie within
 149 the same colony. Finally, vulturine guineafowl (*Acryllium vulturinum*) form stable and cohesive social
 150 groups that comprise of changing breeding pairs, and social groups preferentially interact with other
 151 social groups. Dashed lines represent lack of stability or social cohesion, and grey lines represent
 152 resource-driven levels.

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 154 Figure 1 was developed using Microsoft Power Point for Mac 2011, version 17.7.7, Inkscape and
 155 XQuartz 2.7.11.

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