resource (the colony) [9]. By contrast, vulturine guineafowl (*Acryllium vulturinum*) move cohesively in groups that are stable across seasons (intermediate level), and groups roost and move preferentially with other groups (upper level), but the reproductive units within the group (lower level) can change from one season to the next [10]. Thus, stability is not necessarily equally distributed across levels, and birds may provide an ideal set of species to develop a deeper understanding of how cohesion and social stability define different types of multilevel societies (Figure 1). Although Grueter *et al.* [1] defined the lower level as the core unit, this might misrepresent societies where membership in the society is clearest at intermediate (e.g., groups of vulturine guineafowl) or higher (e.g., colonies of slender-billed gulls) levels. Studies from birds can also allow social versus nonsocial drivers of nestedness to be disentangled. While multilevel societies can emerge from social preferences, seemingly identical patterns can arise from spatial and resource-driven processes. Simply studying patterns of social structure arising at larger ecological scales will undoubtedly uncover community substructuring driven by resource distribution and habitat configuration [11]. For example, songbirds can maintain consistent community structure, at two spatial scales, that is sufficiently stable to maintain experimentally induced local traditions across generations [12]. However, such community structure arises through a combination of individual differences in microhabitat preferences (lower level), and habitat geometry restricting the movement of individuals across the woodland (upper level) [11]. This example highlights how studies in birds can help reveal mechanisms that generate patterns of social structure that are consistent with those from multilevel societies, even to the point of exhibiting some of the same seemingly adaptive behaviours as multilevel societies (local traditions), but without any social preferences taking place at higher levels.

We hope that the work of Grueter *et al.* [1] will inspire research on multilevel societies in birds. Much can be gained by expanding existing evidence of complex and nested avian societies into the multilevel society framework. When implementing this framework, studies will need to explicitly consider the number of levels, their stability and cohesion, and the mechanisms underlying the emergence and/or maintenance of each level. In doing so, studies on birds will help with developing a better mechanistic understanding of multilevel societies, and whether, regardless of the drivers, individuals can reap benefits from living in a nested population structure, such as information transmission.

[1]Max Planck Institute of Animal Behaviour, Department of Collective Behaviour, Universitätsstraße 10, Konstanz, 78457, Germany
[2]Department of Biology, University of Konstanz, Universitätsstraße 10, Konstanz, 78457, Germany
[3]Centre for the Advanced Study of Collective Behaviour, University of Konstanz, Universitätsstraße 10, Konstanz, 78457, Germany
[4]These authors contributed equally

*Correspondence:
dpapageorgiou@ab.mpg.de (D. Papageorgiou) and dfarine@ab.mpg.de (D.R. Farine).
@Twitter: @DanPapageorgiou (D. Papageorgiou) and @DamienFarine (D. Farine).
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Letter

On Multifaceted Definitions of Multilevel Societies: Response to Papageorgiou and Farine

Cyril C. Grueter,[1,2,3,*] Xiaoguang Qi,[4] Dietmar Zinner,[5,6] Thore Bergman,[7,8] Ming Li,[9,10] Zuofu Xiang,[11] Pingfen Zhu,[9] Alex Miller,[1] Michael Krützen,[12] Julia Fischer,[5,13] Daniel I. Rubenstein,[14] T.N.C. Vidya,[15] Baoguo Li,[4,10] Maurício Cantor,[16,17,18,19,20,21] and Larissa Swedell[22,23,24,25]

Papageorgiou and Farine [1], in their comment on our recent synthesis of animal multilevel societies [2], provide several examples of nestedness in avian social systems and call for a fuller incorporation of birds into our theoretical framework. We focused mainly on mammals to construct our proposed framework because multilevel societies are best known from this taxonomic group. Papageorgiou and Farine [1] point out several bird species that form nested social arrangements and argue that, by diving deeply into examples from birds, there may be variations in form that meet our criteria for a multilevel society: a social system with a stable core level and at least one recognizable upper level. Papageorgiou and Farine [1] raise two questions: (i) whether the operational definition of multilevel societies should be relaxed to accommodate

bird species that show more stability at higher levels of society; and (ii) whether societies with multiple tiers resulting solely from habitat preferences instead of social preferences should be classified as multilevel societies.

Papageorgiou and Farine [1] argue that our criteria should be relaxed to include social stability at any level of a nested society and that the core unit does not necessarily need to be the lowest level. However, we maintain that: (i) encompassing every society with a demonstrable modular structure would invalidate the inclusion criteria we developed for distinguishing multilevel societies from other types of systems with detectable substructure; and (ii) a more permissive definition would hamper efforts in identifying the eco-evolutionary drivers of multilevel societies *sensu stricto*. Moreover, maintaining this distinction between multilevel societies with at least two consistent levels and societies with a single stable level combined with other unstable associations (as seen in several bird taxa) is crucial because evolutionary processes such as information flow and disease transmission are expected to differ between these types of societies. That said, we are not opposed to the idea that the most stable levels can be higher levels rather than the core unit. Societies with stable intermediate and upper levels, yet unstable lower levels (as exemplified by vulturine guineafowl *Acryllium vulturinum* [3]), could constitute multilevel societies, as we originally acknowledged [2]. In fact, in our discussion of the multilevel alliance system of the Shark Bay bottlenose dolphins (*Tursiops* sp.) we pointed out that this system deviates from our definition in that the highly cohesive and stable units (second-order alliances) occur at a level above the core unit. According to our framework, however, a society with unstable core units, no intermediate level, and clearest membership at a higher level would not represent a multilevel society but instead a system with atomistic fission–fusion dynamics. This is exemplified by the northern muriqui (*Brachyteles hypoxanthus*), which exhibits flexible association patterns at basal levels but cohesiveness at the upper level, both spatially and temporally [4].

Papageorgiou and Farine [1] shortlist five possible avian candidates for multilevel societies. But which ones actually fit our definition? Beyond vulturine guineafowls, bell miners (*Manorina melanophrys*) may be a good fit, as discrete social organization manifests itself on at least three levels [5]. Two additional species appear to 'tick the boxes'. In spectacled parrotlets (*Forpus conspicillatus*), monogamous pairs are embedded within putatively stable groups, which then form flocks [6]. This does appear to be a multilevel society, but more data on association patterns are probably needed to rule out alternatives. In white-fronted bee-eaters (*Merops bullockoides*), there is an intermediate social tier between the breeding pair and the larger colony [7], which could qualify their society as multilevel. Careful screening of the literature will likely reveal similar systems in hitherto neglected taxa.

The second major question raised by Papageorgiou and Farine [1] pertains to whether the definition of multilevel societies should include structured societies brought about by shared spatial preferences or other ecological opportunities (e.g., preferences for certain sleeping and foraging sites) instead of social preferences. In some cases it is not known to what degree the formation of a distinct level is ecologically induced or the result of individual expressions of social preference. For some species, we still do not know exactly where the social glue ends and habitat-induced overlap begins (i.e., at which spatial scales the social processes are paramount). While core (and intermediate) levels are undoubtedly genuine social groupings that crystallize for reproductive purposes and social support, we should be open to the idea that assortment into upper-level groupings is not exclusively driven by social preferences but may also involve ecologically driven mechanisms. Apex levels in particular often represent aggregations of individuals resulting entirely from an external factor (e.g., the magnetic effects that localized resources exert on social units, as is the case with rare safe sleeping sites in the classic example of the troop level in hamadryas baboons [8]), which are very different from a 'group' of individuals in which the presence and identify of conspecifics matter. Lack of individualization, however, does not preclude the possibility that individuals derive benefits from being associated with the apex grouping level (e.g., 'safety in numbers').

Because we cannot always ascertain whether a particular level of a multilevel society is socially or ecologically driven, this should not be a decisive factor in classifying a society as multilevel or not. In our view, the critical criteria are: (i) consistency of individual membership in each level over time, and (ii) spatio-temporal cohesion of the core and upper levels. An important goal for future research is to quantify the relative contributions of social processes and ecological factors in shaping additional levels in animal societies. This will require fine-grained data on how animals move relative to each other and, ideally, on how they may perceive each other as individuals and members of distinct social levels. It would also be interesting to compare the consistency of groupings that are purportedly socially versus ecologically driven. Papageorgiou and Farine [1] argue that studies from birds can allow social versus non-social drivers of nested social levels to be disentangled. While we agree that a broader perspective is useful, it is not clear to us how birds are in any way more suitable than mammals for distinguishing the drivers of social levels, particularly as few of their examples are unambiguously

multilevel. Clearly, much further work is needed and data from mammals, birds, and other taxa will be crucial in enriching and refining our understanding of the evolutionary processes responsible for the emergence and maintenance of this intriguing social system.

[1]School of Human Sciences, The University of Western Australia, Perth, WA 6009, Australia
[2]Centre for Evolutionary Biology, School of Biological Sciences, The University of Western Australia, Perth, WA 6009, Australia
[3]International Centre of Biodiversity and Primate Conservation, Dali University, Dali, Yunnan 671003, China
[4]Shaanxi Key Laboratory for Animal Conservation, College of Life Sciences, Northwest University, Xi'an, 710069, China
[5]Cognitive Ethology Laboratory, German Primate Center (DPZ), Leibniz Institute for Primate Research, 37077 Göttingen, Germany
[6]Leibniz ScienceCampus for Primate Cognition, 37077 Göttingen, Germany
[7]Department of Psychology, University of Michigan, Ann Arbor, MI, USA
[8]Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI, USA
[9]CAS Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chaoyang District, Beijing 100101, China
[10]Center for Excellence in Animal Evolution and Genetics, Chinese Academy of Sciences, Kunming 650223, China
[11]College of Life Science and Technology, Central South University of Forestry and Technology, Changsha, Hunan 410004, China
[12]Department of Anthropology, University of Zurich, 8057, Zürich, Switzerland
[13]Department for Primate Cognition, Georg-August-University of Göttingen, Göttingen, Germany
[14]Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ, USA
[15]Evolutionary and Organismal Biology Unit, Jawaharlal Nehru Centre for Advanced Scientific Research (JNCASR), Jakkur, Bengaluru 560064, India
[16]Department for the Ecology of Animal Societies, Max Planck Institute of Animal Behavior, Konstanz, 78464, Germany
[17]Centre for the Advanced Study of Collective Behaviour, University of Konstanz, Konstanz, 78464, Germany
[18]Department of Biology, University of Konstanz, Konstanz, 78464, Germany
[19]Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, Florianópolis, 88048-970, Brazil
[20]Centro de Estudos do Mar, Universidade Federal do Paraná, Pontal do Paraná, 83255-000, Brazil
[21]School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, 2000, South Africa
[22]Department of Anthropology, Queens College, City University of New York, Flushing, NY, USA
[23]New York Consortium in Evolutionary Primatology, New York, NY, USA
[24]Anthropology, Biology and Psychology Programs, CUNY Graduate Center, 365 Fifth Avenue, New York, NY, USA
[25]Department of Archaeology, University of Cape Town, Rondebosch, 7701, Cape Town, South Africa

*Correspondence:
cyril.grueter@uwa.edu.au (C.C. Grueter).
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