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# Kappeler's framework for animal social systems and its impact on behavioral ecology and sociobiology

Loren Hayes<sup>1</sup> · C. Schradin<sup>2,3</sup>

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## Abstract

Peter Kappeler's seminal work on animal social systems has built a strong conceptual foundation for generations of researchers (Kappeler (2019) Behav Ecol Sociobiol 73:13). The most notable and important contribution of his work has been a clear framework for animal social systems, clarifying the muddling of definitions. Unfortunately, many have used flawed definitions in their research on social systems, or even worse, no definitions at all. In contrast, Kappeler's framework emphasizes that there are four inter-related components of the social system: (i) social organization, (ii) social structure, (iii) mating system, and (iv) care system. The framework is powerful for numerous reasons. Most importantly, these clearly defined components promote empirical and comparative research that does not confuse or confound behaviours coming under different forms of selection. Moreover, the framework permits the study of how these components are interconnected, instead of taking mixed definitions as an *a priori*. It allows for the identification of > 1000 types of social systems. Even so, the framework has not solved all challenges, most notably how to quantify social structure, which is arguably, the most complex social system component. Despite this limitation, the framework has enormous potential to shape our understanding of social diversity across a broad range of taxa. This Topical Collection advocates for the greater use of the framework in behavioural ecology and sociobiology while allowing for space to critically address its limitations.

## Significance Statement

For decades, a major effort of behavioral ecology and sociobiology research has been to explain the remarkable diversity in animal social systems. As an introduction to a Topical Collection on animal social systems, we emphasize the impact of Peter Kappeler's (2019); this journal) framework and advocate for its application to a wide range of taxa. Kappeler's framework is powerful because it relies on clear definitions that allow for clear quantitative assessments and the identification of thousands of animal social systems. By facilitating discussion on how Kappeler's framework has advanced our understanding and compares to other frameworks, this Topical Collection will help us move towards an unifying framework.

**Keywords** Definition · Social organization · Social structure · Mating system · Care · Social evolution

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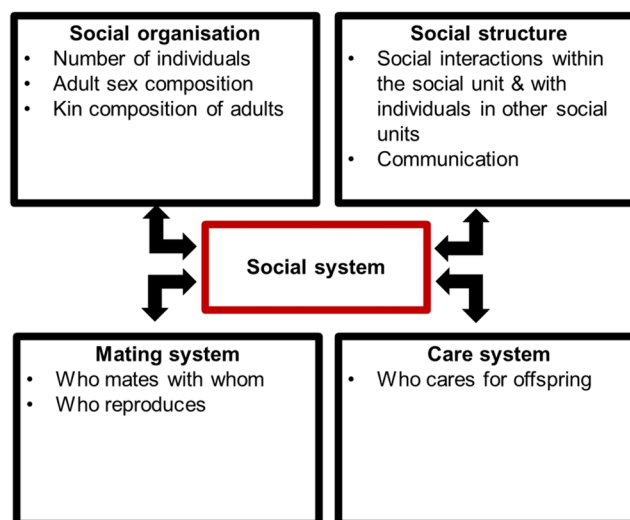
## Introduction

A major aim of behavioral ecology and sociobiology has been to explain the extensive diversity and complexity in animal social systems. Key advances have been made in how we define different aspects of social systems, including social organisation (Jarman 1974) and social structure (Hinde 1976), and the expected relationships between mating and care strategies (Brown 1978; Reynolds 1996). Rubenstein and Abbot (2017) advanced the field by highlighting the similarities and differences between taxonomic groups. Critically, advancements have been limited by unclear terminology (e.g., social

monogamy) that has been inconsistently applied across taxa (Rubenstein and Abbot 2017). This confused research on how natural selection shapes social systems (Kvarnemo 2018; Huck et al. 2020). For example, Jarman's (1974) original verbal hypothesis that the ancestral artiodactyl was monogamous and that group living and polygyny evolved as artiodactyls radiated into open habitats was later supported by a comparative study that used a dataset that confused social organisation (pair-living) and mating system (monogamy) and relied on an incorrect definition of monogamy (some based on 2 females and one male) (Pérez-Barbería et al. 2002). Using a dataset that did not confuse social organisation and mating systems and that accounted for intraspecific variation within populations, Jaeggi et al. (2020) determined that Jarman's framework was only partially correct. Although the ancestral artiodactyl population was most likely to be pair-living, there was also evidence that it had a variable social organisation. In contrast to the original hypothesis, Jaeggi et al. (2020) found only minimal support for the assumption that open habitats predict the evolution of group-living. Similarly, the widespread confusion of monogamy being either a mating system or the social organization of pair-living or the social structure of pair-bonding, or a combination of all three, hindered studies on the evolution of all three components (Huck et al. 2020). Thus, the missing 'holy grail' for those studying animal social systems has been the lack of a broadly applicable framework based on clear definitions and distinctions between potential units of selection.

In 2002, a seminal paper by Peter Kappeler and Carel van Schaik provided a comprehensive framework on animal social systems. Building on previous work by Hinde (1976) and Di Fiore and Rendall (1994), Kappeler and van Schaik suggested social systems consist of three components: social organization, social structure, and mating system. In a *Behavioral Ecology and Sociobiology* paper published in 2019, Kappeler advocated for an updated framework that included the original three components as well as an additional component, the care system (Fig. 1). The addition of the care system completed the distinction of the potential types of interactions among conspecifics (social, sexual, and care), resulting in a comprehensive framework for studying animal social systems. As such, the revised framework provides clarity to operational definitions that can be qualitatively and quantitatively compared within and between species.

The aim of this Topical Collection is to bring greater attention to Kappeler's framework while creating a space for debate about the broad utility of it. In this introductory paper, we highlight what we believe are the most important contributions of this framework: clear terms and the interrelation between social system components. These ideas set the stage for a series of contributions highlighting both advancements in our understanding and debate over the



**Fig. 1** Representation of animal social systems, including the four components (social organisation, mating system, social structure, care system). Double arrows indicate that the four components shape the entire social system and can be shaped by other components. Adapted from (Kappeler and van Schaik 2002; Kappeler 2019) and (Jaeggi et al. 2020)

impact on Kappeler's framework on behavioral ecology and sociobiology. Table 1 summarises what some of the contributors to this topical collection think are the main advantages of Kappeler's framework.

One of the most important contributions of Kappeler's framework is that it is based on operational definitions and thus, lays a groundwork for quantitative assessments. *Social organization* describes the size and composition of social units and can be described in terms of numbers, age, sex, relatedness. Understanding of this definition has allowed comparative studies focusing on the evolution of the composition of social units (Kappeler and Pozzi 2019; Olivier et al. 2024). The *care system* identifies who cares for offspring and may be classified as no parental care, uni-parental, bi-parental, or allo-parental care. Separation of these terms reduces the risk of confusing selective pressures (Huck et al. 2020).

The *mating system* refers to mating interactions leading to reproduction and thus is distinct from non-sexual interactions characterized as *social structure*. Emergent patterns of mating interactions result into well-known classifications such as monogamy, polygyny, polyandry, and polygynandry or promiscuity, though it is now recognized that a more continuous rather than categorical classification of mating systems is often needed, for example when studying multiple paternity (Dobson et al. 2025). Critically, Kappeler's framework highlights that these mating system classifications should not be confused with other social system components (Huck et al. 2020).

The last component, social structure describing social interactions, is the most complex and hardest to

**Table 1** Advantages of Kappeler’s Framework to study social systems, as identified by some of the authors of this topical collection

Personal communication	Advantages
Peter Kappeler	(1) A clear terminology that links up with previous influential work which ends the arbitrary use of “social” in combination with various nouns (end of “social-ism”) (2) A conceptual categorization that facilitates comparative work (at least across vertebrates) on particular components of social systems. (3) A framework for more comprehensive and holistic studies of different components of the social systems of a given species.
Carsten Schradin and Loren Hayes	(1) Clear definitions allow for quantitative assessments. (2) Providing a framework that allows us to reliably describe the remarkable biodiversity of animal social systems.
Claudia Fitchel	(1) Refined concepts and terminology related to animal sociality, emphasizing the need for clear definitions when comparing social systems across different species (2) Importance of developing a clear conceptual framework for studying social complexity in animals, allowing for more precise and comparative analyses of the different aspects of the evolution of social complexity in animal societies.
Lindelani Makuya	(1) Kappeler’s framework allows us to recognize that solitary living species can have many different social systems. (2) It allows us to move beyond simple “solitary” versus “group-living” classifications by examining these components not only separately but as interconnected parts of the whole.
Michael Taborsky and Dustin Rubenstein	Peter Kappeler stressed the need to clarify terms and underlying concepts in the study of sociality. At the same time, his framework caused some confusion as ‘social complexity’ was virtually used synonymously with the ‘social system’. An inflationary use of the term ‘social complexity’ may render it useless and should be prevented because the complexity of social relationships among group members raises interesting questions worth being scrutinized.

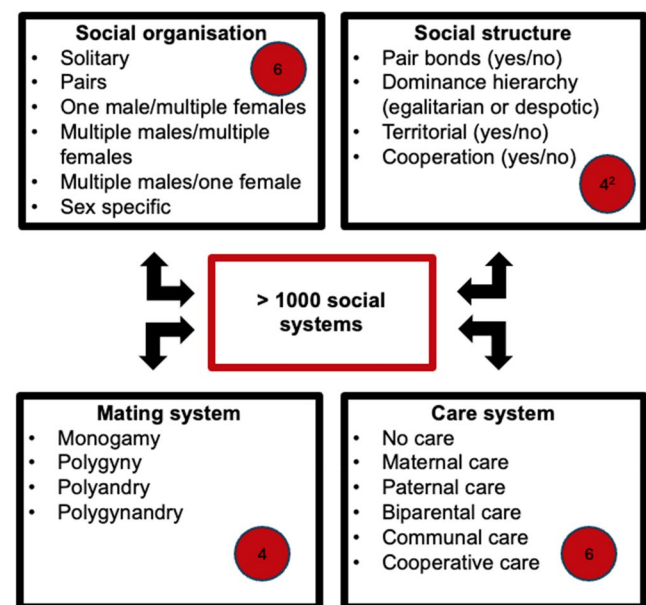
conceptualize, as it has multiple sub-categories, including but not limited to: social bonds (including pair-bonds, parent-offspring bonds, social bonds with adult kin, cooperation partners, sexual partners), dominance hierarchy, levels of cooperation and territoriality, and also communication. Species can vary dramatically in their social structure and thus, express very different social systems even when their group size, mating system, and care system are identical.

Kappeler (2019) states that the “Social structure is defined by the content, quality, and patterning of social relationships emerging from repeated interactions between pairs of individuals belonging to the same social unit”. These definitions are

based on Hinde’s (1976) framework highlighting that social structure is an emergent property of the observable social interactions between conspecifics, which arise from and characterise social relationships, such as pair-bonds, coalitions, competition, and place in a social hierarchy. Social interactions are observed and quantified and their analysis and interpretation then leads to a classification of the social structure. While not originally stated by Kappeler and van Schaik (2002) and Kappeler (2019), social interactions between neighbours should also be regarded as part of the social structure. Whether neighbours are ignored or attacked by territorial aggression, and whether all neighbours are treated the same or differently, are important aspects of the social structure. Accordingly, even solitary species have important and often complex social structure with non-random interactions between neighbours, for example differentiating them by kinship and by sex (Makuya and Schradin 2024a, b).

### Combining the 4 components into multiple systems

Kappeler’s framework is powerful because it first separates concepts such as social organization and social structure and then brings them back together without muddling theory. Importantly, acknowledging that there are four components emphasizes that the different components can be shaped by different selection pressures. For example, social



**Fig. 2** Components of social systems. Social systems are comprised of four different components, each of which can have multiple categories (Kappeler 2019). There are more than 1000 possible combinations of these four components, which means more than 1000 possible social systems. Derived from (Makuya and Schradin 2024b)

groups (social organization) may form because individuals benefit from reduced predation risk. However, sexual interactions among group members (mating system) often selects for only one adult male per group. On the other hand, emphasizing the inter-relatedness of these components acknowledges that events impacting one component can lead to changes in another. For example, the loss of a group member (a change in social organization) could influence the benefits and costs of social, mating, and care interactions among the remaining members. In this way, Kappeler's framework is uniquely powerful because it allows for proper quantitative assessment of what is changing.

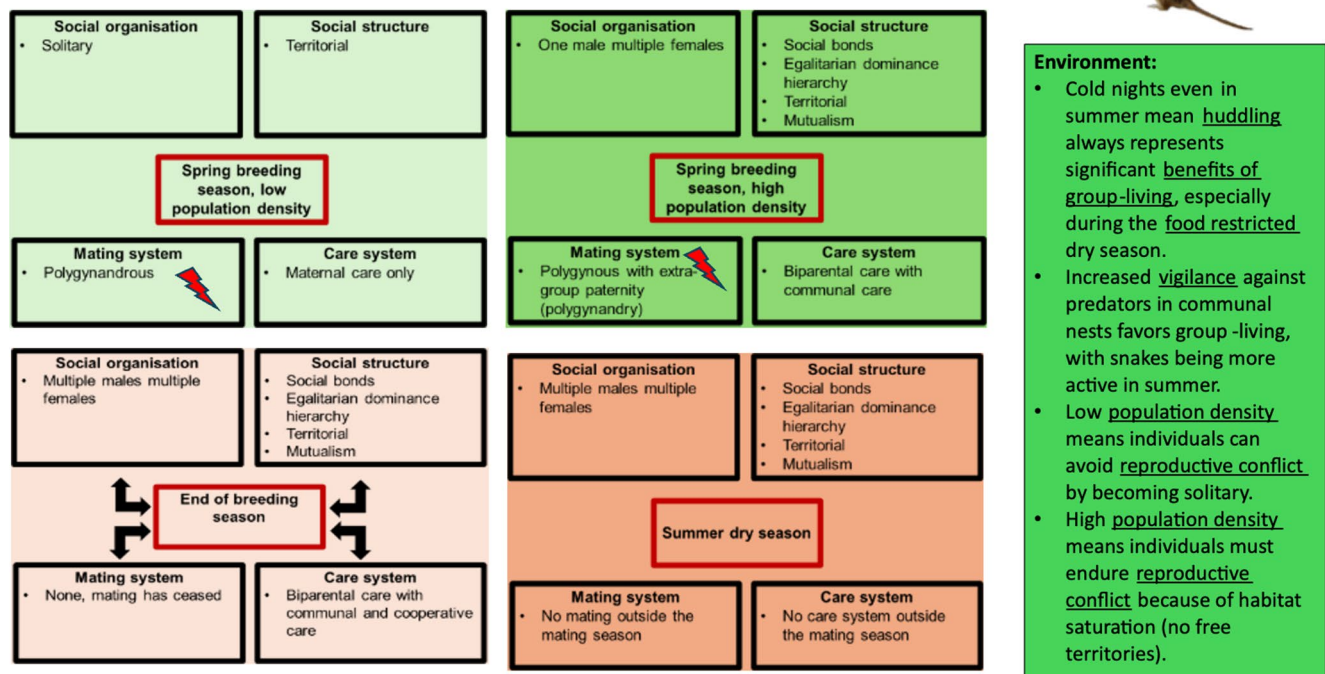
Kappeler's framework allows for the identification of >1000 types of social systems (Fig. 2) and thus, has the potential to improve our understanding of the wide inter- and intraspecific diversity in animal social systems. For example, animals can live in six different forms of social organisation. Social structure is complex, and animals can have pair bonds or not, be territorial or not, etc. (note: the Fig. does not list all

potential aspects of social structure). This leads to multiple possible combinations. Using a categorical classification of components of social systems indicates that more than 1000 ( $6 \cdot 8 \cdot 2^4 \cdot 6$ ) different forms of social systems are possible. In fact, even more forms of social systems are possible because most components are not categorical but continuous (e.g., degree of territoriality; the frequency of extra-pair young) or variable (one species showing intra-specific variation in social organisation). As such, the framework allows describing social systems in detail and to study how social systems change due to environmental changes (Fig. 3).

## Introducing the publications of this topical collection

This Topical Collection will support a collection of papers summarizing the advancements made possible by Kappeler's framework. Papers will address three main themes

### Environmentally induced changes in the social system of striped mice



**Fig. 3** Changing social systems in the African striped mouse. The framework of Kappeler as depicted in Fig. 2 can be used to graph down changes in the social system of striped mice (left) induced by ecological factors (right). Striped mice are always territorial and, when living in group, have an egalitarian social structure without detectable dominance hierarchy, but benefit from sharing a nest via energy savings due to huddling and increased vigilance against predators. The mating system is always polygynandrous. However, the social organisation varies depending on whether there is reproductive competition, which can only occur in the breeding season and is characterised by female infanticide and male sexual suppression. To avoid reproductive competition, mice become solitary living if population density is low. Under

high population density, this becomes impossible and mice are forced to remain philopatric. Thus, whether they start in the breeding season with solitary living or one male multi-female groups depends on population density. In all cases, recruitment due to reproduction means that 3 months later at the end of the breeding season, when mice from the first two litters are adult, all mice live in groups with multiple adults of both sexes. All adults in a group engage in infant care. Accordingly, the care system directly reflects the social organisation when pups are present. This Fig. also illustrates that outside the breeding season, the mating system does not occur, and in many species the care system also not, reducing complexity and as such potential of conflict in social systems

(i) advancements in our understanding of the four components of the social system, (ii) broader impacts of the framework, and (iii) contributions exploring the definition of social complexity and how Kappeler's framework compares to other frameworks. We asked all contributors to review in their paper how Kappeler's framework applies to their system or review topic. In doing so, we hope that it will encourage others to use this framework and move us towards a unifying theory for animal social systems.

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**Data availability** No datasets were generated or analysed during the current study.

## Declarations

**Competing interests** The authors declare no competing interests.

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