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The secret social life of solitary mammals

Lindelani Makuya³ and Carsten Schradin^{a,b,1} 

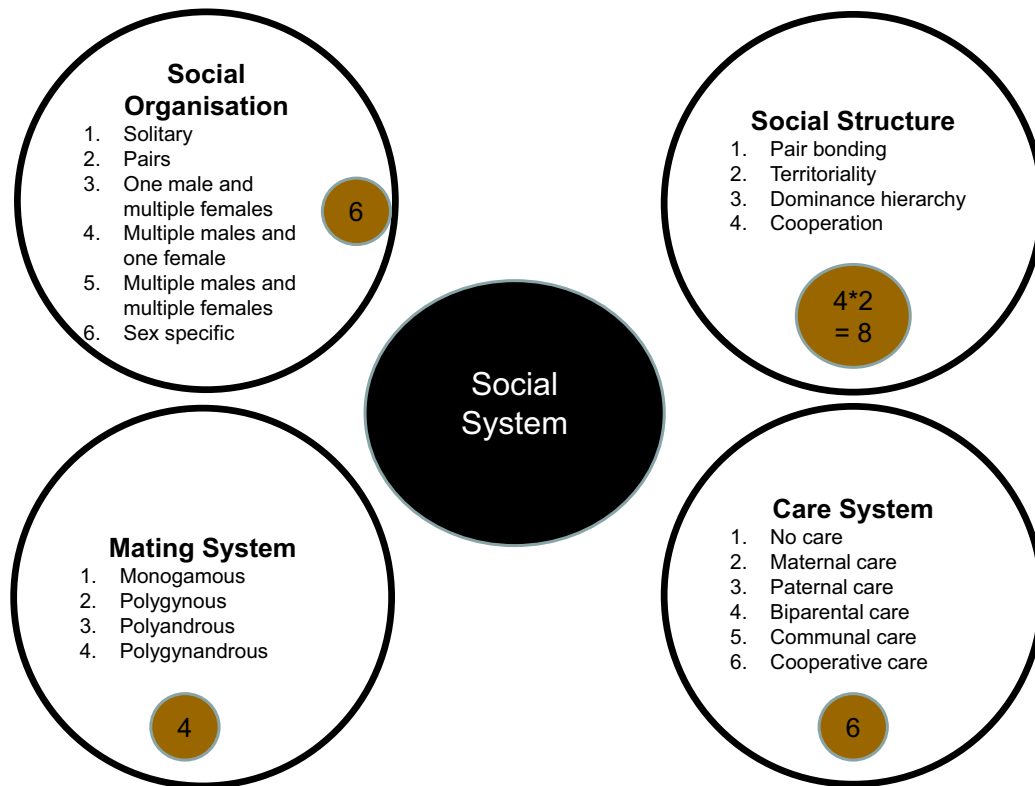


Fig. 1. Components of social systems. Social systems are composed of four different components, each of which can have multiple categories (4). For example, animals can live in six different forms of social organization. Social structure is complex, and animals can have pair bonds or not, be territorial or not, etc. (Note: The figure does not list all potential aspects of social structure.) This leads to multiple possible combinations. Note for the care system: “No care” is not an option in mammals but in other taxa. Using such a categorical classification of components of social systems indicates that more than 1,000 ($6 \times 8 \times 4 \times 6$) different forms of social systems are possible. However, as most components are not categorical but continuous (for example, the degree of territoriality, the frequency of extrapair young) or variable (one species showing intraspecific variation in social organization), even more forms of social systems are possible.

Solitary living has been regarded as a primitive ancestral state in mammals (1). Thus, behavioral ecologists studied for decades pair- and group-living species, while solitary species have been ignored (1, 2). However, we cannot understand the ecological and evolutionary reasons of group-living if we do not understand the costs and benefits of the alternative, which is solitary living (1). So far, it has been assumed that individuals of solitary species are aggressive toward each other, only interacting during mating and territorial disputes (1, 2). In a study published in the current issue of PNAS, Twining and a consortium of 38 coworkers present evidence for seven species of solitary mustelids that their social life is much more complex than previously believed (3). This study adds to growing evidence that solitary living mammals are not unsocial per se (1). Here, we argue that solitary living in mammals is not a primitive ancestral stage but an adaptation to local environments.

Social systems are complex, and the simplistic dualism of solitary versus social species cannot represent this complexity (3). Kappeler (4) provides a useful tool to handle this

complexity by dividing the social systems into four components (Fig. 1): the social organization (composition of groups), the social structure (interactions), the mating systems (who mates with whom), and the care system (who takes care of the offspring). Each of these components can have multiple categories, with more than 1,000 possible combinations between them (Fig. 1). In reality, the components do not vary categorically, but continuously, and thus, even more combinations are possible. For example, the degree of multiple

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See companion article, “Using global remote camera data of a solitary species complex to evaluate the drivers of group formation,” [10.1073/pnas.2312252121](https://doi.org/10.1073/pnas.2312252121).

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paternity in litters is a more realistic measure of mammalian mating systems (5) than putting it into one of four categories (monogamy, polygyny, polyandry, or polygynandry). Further, most species are not restricted to one form of social organization but show intraspecific variation in social organization (6). In many primarily pair or group-living species such as prairie voles, lions, and many prosimians, some individuals can live solitarily, and as such, there is a gradient of sociality (6). Thus, even social organization represents rather a continuous than a categorical trait.

Social systems are complex, and the simplistic dualism of solitary versus social species cannot represent this complexity.

Using camera traps, Twining et al. found continuous variation in the probability of two or more individuals being photographed together. The probability of occurring with a conspecific varied by more than an order of magnitude between species, being below 5% for five species, 8% in the tayra (*Eira barbara*), and 18% in the yellow-throated marten (*Martes flavigula*). This indicates that there is continuous (and not categorical) variation in how often individuals meet and interact in this species complex. One main reason for this seems to be resource dispersion.

The resource dispersion hypothesis predicts that species would tend to be solitary when resources are distributed evenly, but to be group living when resources (such as fruiting trees) are distributed patchily (7). A growing body of research has shown that the distribution of resources is important in determining the social system of species (8). Twining et al. show that the mustelid species which rely on patchily distributed food resources (such as fruits and large prey) had higher probabilities of aggregating. Further, the interaction between weight and resources had a strong positive impact in explaining the probability of aggregations. Patchily distributed food seems to be one of the key drivers of aggregation in mustelids, increasing tolerance of conspecifics. Thus, Twining et al. provide empirical evidence supporting the resource dispersion hypothesis.

Individuals are group living when they are consistently found together with always the same other individuals with which they share the same home range and sleeping site for extended periods of time (6). Some group-living species are solitary foragers but still share a nest and territory (6). The information that is needed to accurately determine the social organization, i.e., the composition of social units, includes data on the sex of individuals, occupancy of sleeping sites, frequency of observations and trapping events, home range overlap, and the proportion of the individuals monitored in the study area (9). Data from camera trap studies are often not sufficient to determine the social organization, for example, because it is not possible to identify the individual and whether individuals share a territory/sleeping site or just meet sporadically. Data from camera traps at denning sites would be important to determine social organization, especially if individual recognition is possible. The data presented by Twining et al indicate the possibility of interspecific variation in social organization (IVSO) in some primarily solitary mustelids, especially the yellow-throated marten and the

tayra. In stone martens (*Martes foina*) (10) and the stoat (*Mustela erminea*) (11), home range overlap indicates that both solitary individuals and pairs might occur, indicating IVSO in mustelids. Pet ferrets (*Mustela putorius furo*) are often kept in groups (12), providing further evidence that mustelids do not necessarily have asocial tendencies. Overall, Twining et al. found that most of the mustelids meet conspecifics regularly in a nonaggressive context.

Future studies in mustelids, but also in many other mammals, must not only provide detailed information to reliably determine the social organization (as outlined in ref. 9) but also to characterize the social structure. To know who is interacting with whom, individuals must be marked and their life histories including relatedness must be known, and we need detailed behavioral data. While focal animal sampling is the most accurate method, for nocturnal and shy animals, cameras at nesting sites and territory boundaries are a good alternative. Here it is very important that researchers clearly differentiate between social organization and social structure before investigating how these two components influence each other. Finally, to understand variation in both social organization and social structure, detailed ecological data such as resource distribution that can be directly related to the individuals are needed, for example, food abundance in individual territories.

There is growing evidence that many solitary mammals have a complex social structure. Social structure has originally been discussed to represent only interactions between individuals belonging to the same social unit (4). Twining et al. add to an increased body of evidence that social structure must also include interactions with neighboring individuals. Similarly, the solitary puma (*Puma concolor*) forms nonrandom aggregations at prey sites (13). Other examples are solitary species where close kin live close to each other and share part of their home ranges, like giant kangaroo rats (*Dipodomys ingens*) (14) and woodchucks (*Marmota monax*) (15). Solitary prosimians show complex social networks (16, 17). Solitary species can have fitness benefits from living close to kin (18, 19), indicating the adaptive value of social structure in solitary species. Thus, individuals of many solitary species regularly interact with each other, and their social structures are driven by varying factors such as population density (14) and resource distribution (7).

Twining et al. conclude that their results are likely to be widely generalizable, and we agree. Aggregations of otherwise solitary mammals might be common. In conclusion, solitary mammals are often not unsocial but have frequent amicable social interactions with specific conspecifics. The social structure of solitary species is not simple and varies between species. Thus, solitary living is not one form of social system but represents a variety of social systems, from species showing high aggression and intolerance toward conspecifics (20) to tolerant species that have frequent nonrandom interactions (1). The distribution of resources plays a major role in influencing the social structure not only of group-living but also of solitary species. Solitary living in mammals cannot be regarded as a primitive default stage that needs no scientific explanation but most likely represents adaptations to specific

environments. In how far solitary species of other taxa such as reptiles, birds, and insects have a complex social structure that not only consists of aggressive interactions but also of tolerance and even amicable interactions, is even less understood. In sum, we need to understand the costs and benefits of solitary living as an alternative to pair- and group-living,

Complex social structure can probably reduce the costs of solitary living (1).

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