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Abstract

Many species show intra-specific variation in their social organization (IVSO), which means the composition of their social groups can change between solitary living, pair-living or living in groups. Understanding IVSO is important because it demonstrates species resilience to environmental change and can help us to study ultimate and proximate reasons for group-living by comparing solitary and group-living individuals in a single species. It has long been realized that the environment plays a key role in explaining the occurrence of IVSO. IVSO is expected to have evolved in variable environments and can thus be a key adaptation to environmental change. It has previously been shown that four different mechanisms relying on the environment exist that can lead to IVSO: environmental disrupters, genetic differentiation, developmental plasticity, and social flexibility. All four mechanisms depend on the environment such that focusing only on environmental factors alone cannot explain IVSO. Importantly, only three represent evolved mechanisms, while environmental disrupters leading to the death of important group members induce non-adaptive IVSO. Environmental disrupters can be expected to cause IVSO even in species where IVSO is also an adaptive response. Here we focus on the questions of why IVSO occurs and why it evolved. To understand IVSO at the species level it is important to conduct continuous long-term studies to differentiate between non-adaptive and adaptive IVSO. We predict that IVSO evolves in environments that vary in important ecological variables, such as rainfall, food availability, and population density. IVSO might also depend on life history factors, especially longevity. IVSO is predicted to be more common in species with a short lifespan and that breed only for one breeding season, being selected to respond optimally to the prevailing environmental situation. Finally, we emphasise the importance of accounting for IVSO when studying social evolution, especially in comparative studies, since not every species can be assigned to one single form of social organization. For such comparative studies, it is important to have reliable data-bases based on the primary literature.

Introduction

Formerly, it was assumed that every species has a specific social system and deviations from it were regarded as abnormal or noise. However, it has been recognized that each of the three components of a species social system (Kappeler & Schaik 2002) can vary within the species (Lott 1984; Lott 1991): i.e. its mating system (who mates with whom), its social structure (how individuals interact with each other), and its social organization (whether they are solitary, pair-living or living in groups of different composition). Most information is available for the social organization of species. The social organization can affect the social structure and the mating system, influencing the entire social system.

Intra-specific variation in social organization (IVSO) during breeding occurs when a species shows two or more of the following forms of social organization (Lott 1991; Schradin 2013): living solitarily, in pairs, one breeding male with several breeding females, one breeding female with several breeding males, or multi-male multi-female groups. Each form of social organization must be composed of breeding individuals, not only dispersing solitary individuals or bachelor groups. Variation in group-size and optimal group size are important topics in behavioral ecology (Markham & Gesquiere 2017), but, following our definition, do not indicate IVSO if the relative numbers of breeders of each sex does not change.

IVSO occurs in several taxa, including insects and vertebrates. For example, burying beetles (*Nicrophorus vespilloides*) can be solitary, form pairs or communal groups with two or more breeding females (Eggert 1992), depending on the size of the carrion for which they compete, with more beetles associating at larger carrion (Müller et al. 2006). Similarly, pied kingfishers (*Ceryle rudis*) can live in pairs, in family groups with philopatric adult offspring, or in polygynous groups, depending on the availability of good nesting sites (Reyer 1980; Reyer 1984). The house mouse (*Mus musculus*) can live solitarily, in pairs or in communal groups, with resource availability modifying the intensity of intra-specific competition (intra-sexual aggression in males and female infanticide) (Latham & Mason 2004; Berry et al. 2008).

Dunnocks (*Prunella modularis*) also show varying forms of social organization to maximize individual fitness (Davies 1992), which was used as a model system to study the evolution of sexual conflict, mating systems, parental effort and life histories (Burke et al. 1989; Davies et al. 1996). Male and female dunnocks can change their mating system (monandry, polygyny and polyandry) and social organization (pairs, one female and several males, or multi male multi female groups). In a series of sophisticated experiments, including measuring individual fitness, it was demonstrated that IVSO is the consequence of individual dunnocks choosing the reproductive tactic with the highest fitness depending on the prevailing ecological conditions (Davies 1992).

To understand IVSO, it is not sufficient to study the related environmental factors. Tinbergen proposed in his four questions that behavior must be understood from the perspectives of ontogeny, causation, phylogeny and function (Tinbergen 1963), and the environment plays a crucial role in all four questions (Schradin 2018). Physiological mechanisms are evolved traits (Hofmann et al. 2014) and thus to understand why IVSO evolved, one must understand the mechanisms leading to IVSO. Thus, the first step to understand why IVSO occurs is to describe and differentiate the mechanisms of IVSO.

After summarizing a previous review on IVSO (Schradin 2013), we outline three important new aspects. First, we show the importance of differentiating between adaptive and non-adaptive IVSO. Second, we focus on the questions of why IVSO occurs and why it evolved. Third, we show the importance of accounting for IVSO when studying social evolution, particularly in comparative studies. Finally, we summarise hypotheses and predications about the evolution of IVSO. Our major aim is thus to encourage more research on evolutionary reasons of IVSO and to emphasise the importance of considering IVSO in comparative studies.

The four mechanisms that can lead to IVSO

In a 2013 review, Schradin proposed four different mechanisms that can lead to IVSO, each mechanism depending on environmental factors (Schradin 2013): environmental disrupters (entirely extrinsic factors), genetic differentiation, developmental plasticity, and social flexibility. Environmental disrupters occur when natural mortality due to old age or predation changes the social organization, which represents a non-adaptive change imposed on the group. IVSO is thus not caused by the remaining individuals which will respond to this new situation with adaptive tactics. This is discussed in detail below. Genetic differentiation refers to the possibility that sub-populations of one species might differ genetically which could influence the resulting social organization. By genetic differences we refer to heritable differences of the genome (for behavior see (Hu & Hoekstra 2017) for social behaviors (Bendesky et al. 2017); (Dochtermann et al. 2015), which includes not only differences in genes and alleles, but also differences in genomic regions that regulate gene expression. However, while genetic differences between populations of the same species could explain the occurrence of IVSO, evidence for this process is rare to absent. The best example could be fire ants (*Solenopsis invicta*) which have two social forms (polygynous with several breeding females and monogynous with one breeding female) and it is a single polymorphism at the locus Gp-9 that determines the social organization of a colony. Queens that are homozygous BB at this locus attempt to found a colony alone, while Bb and bb queens do not fly far but attempt to join a colony (Gotzek & Ross 2007; Gotzek & Ross 2009; Keller 2009; Ometto et al. 2011). Future studies might reveal more examples where genetic differentiation could explain IVSO, but to date empirical evidence does not indicate that it is a common mechanism of IVSO.

IVSO can be caused by phenotypic plasticity. Non-reversible phenotypic plasticity is called developmental plasticity, depending on organizational effects during early development (Phoenix et al. 1959; West-Eberhard 2003) or puberty (Zimmermann et al. 2017). In developmental plasticity, the environment determines which one of two or more alternative phenotypes develops. If the social behavioral phenotype is permanently influenced during early development, the social organization of this population could differ either from generation to generation, or compared to another population, in both cases leading to IVSO. However, to date there is no empirical evidence that developmental plasticity causes IVSO; yet, future studies might reveal species in which developmental plasticity causes IVSO.

Social flexibility, i.e. reversible phenotypic plasticity (Piersma & Drent 2003) of individual social tactics, is the best empirically documented mechanism leading to IVSO. Flexibility in social behavior is common, because individuals have to respond flexibly depending on the social situation. In primates, flexible dominance hierarchies enable individuals to cope with conflict, enabling them to remain in their group even if new conflict arises (Judge 2000). This is an important social ability in many obligatory group-living species, in which living solitarily is very costly and leads to increased mortality. Individuals` flexibility in social behavior stabilizes the social system including the social organization of the species, which can explain why social organization in primates is very stable (Shultz et al. 2011). In social species where individuals are less flexible in their social response, alternative and reversible social tactics might exist. Therefore, social flexibility leading to IVSO might be particularly common in species with low flexibility in social behavior, while flexibility in social behavior can maintain the existing social organization. Flexibility in social tactics in both sexes can change the social organization of the entire population. This mechanism is called social flexibility (Schradin et al. 2012) and has been shown to cause IVSO in burying beetles (Eggert 1992; Müller et al. 2006), pied kingfishers (Reyer 1980; Reyer 1984), house mice (Latham & Mason 2004; Berry et al. 2008), great gerbil (*Rhombomys opimus;* (Randall et al. 2005) and African striped mice (*Rhabdomys pumilio*; Schradin et al. 2012).

Schradin (2013) identified that for all four possible mechanisms, the environment plays a critical role. Thus, to understand which mechanism is at play, it is not sufficient to study the environmental factors. One must also establish whether the underlying physiological mechanisms are genetically determined, organizational, or activational (Table 2 in Schradin, 2013). In accordance with Piersma & Gils (2011), Schradin (2013; Table 2) hypothesized that the predictability of the environment will determine which mechanism evolved such that: (i) genetic differentiation evolves in predictable environments (two or more populations with different but predictable environments); (ii) developmental plasticity occurs in short-term, predictable environments (the individual can predict from the environment in which it grows up the environment in which it will breed); and (iii) social flexibility evolves in unpredictable environments. As environmental disrupters do not represent an evolved mechanism of IVSO, it is also not associated to a specific physiological mechanisms nor a specific environment (Schradin 2013).

How to recognize the different mechanisms?

Schradin (2013) identified two questions one needs to answer to show which one of the four mechanisms explains an observed IVSO (Table 3 and 4 in Schradin 2013). 1. Does IVSO occur within or between individuals? This differentiates between genetic variation and developmental plasticity (IVSO between individuals) on the one hand and entirely extrinsic factors and social flexibility on the other (IVSO occurs within individuals). 2. If IVSO occurs between individuals, to differentiate between genetic variation and developmental plasticity one would have to answer the question ‘to what extent does the genotype or the environment determine the social tactics shown by individuals? If IVSO occurs within individuals, one has to (i) establish whether the environment induces changes in individual behavior which in turn, leads to a new form of social organization (social flexibility), or (ii) whether the social organization is changed due to one (or more) individuals disappearing (environmental disrupters).

IVSO can be non-adaptive

Environmental disrupters are common reasons of IVSO but do not represent an adaptation, but a case where a change in social organization is imposed on the individuals by the environment. If an important group member dies, the social organization of the entire group might change (Fig. 1). For example, in pair-living species, if one of the two breeders dies, the other individual automatically becomes solitary living (Fig. 1). The death of a single individual in pair-living Scandinavian wolves often results in temporarily solitary individuals (Milleret et al. 2017). Individuals might then respond adaptively to this imposed change, such as by re-pairing as reported in beavers (*Castor fiber*; (Mayer et al. 2017). In pair-living species where the offspring remain in their natal family after reaching adulthood and help in raising their younger siblings, the death of one of the two breeders often leads to reproductive conflicts between the adult non-breeders, which can lead to several forms of social organization. For example, cooperatively breeding callitrichid primates reportedly show considerable IVSO, which has been typically interpreted as an adaptive strategy (Garber 1997; Garber et al. 2016). However, IVSO in callitrichids is often induced by the disappearance of a dominant breeder, for example a breeding male in Goeldi`s monkeys (*Callimico goeldii*) (Porter et al. 2001), in black faced lion tamarins (*Leontopithecus caissara*) (Martins et al. 2015), or in mustached tamarins (*Saguinus mystax*) (Löttker et al. 2007). In these examples, the changes in social behavior observed in the remaining individuals can be regarded as adaptive, since each individual attempted to optimize its fitness under the new social conditions and to obtain a breeding position. However, the observed IVSO itself was not caused by the individuals. IVSO due to environmental disrupters therefore seems to be very common.

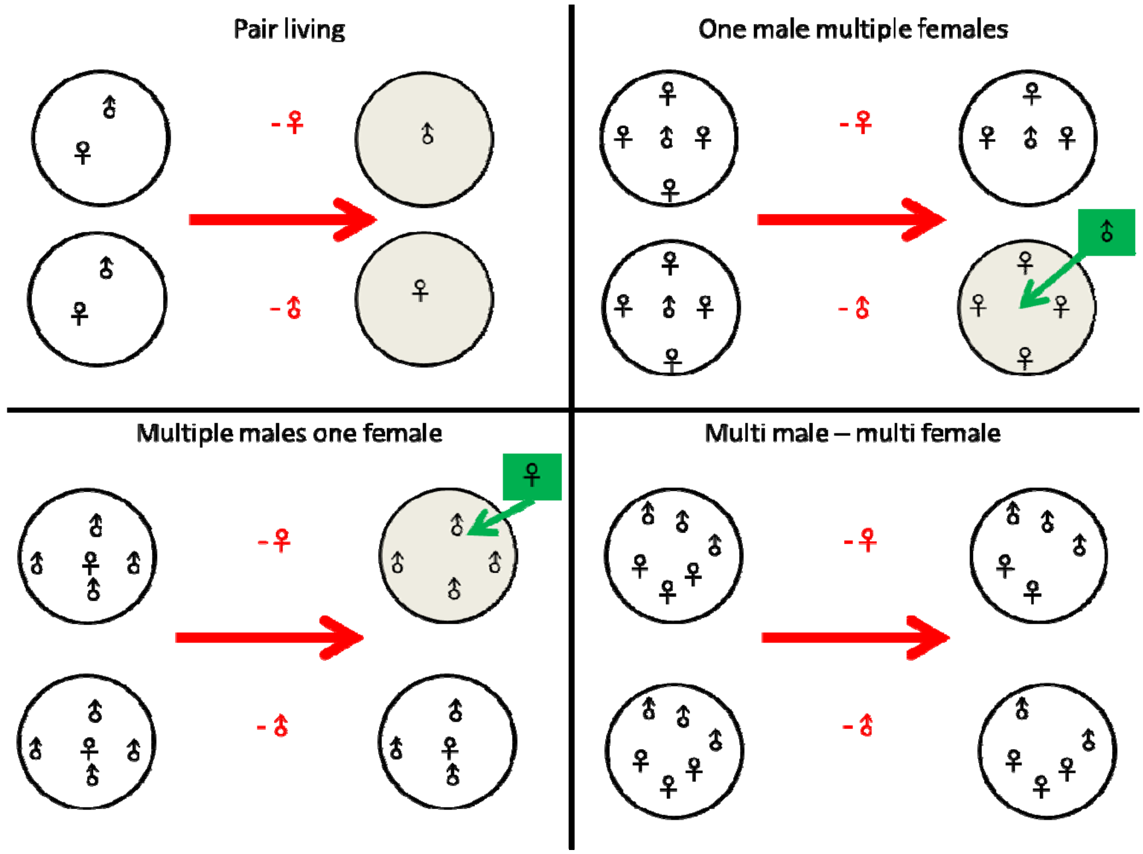

Fig. 1

Mortality of a single individual (indicated by a red arrow and red sex specific symbol) can change the social organization if there is no other breeding individual of the same sex in the group (indicated in grey). This is especially the case in pair-living species (top left), but not in species living in multi-male multi-female groups (bottom right). In species where groups typically consist of only one individual of one sex and multiple individuals of the other sex, mortality of only the individual of the rarer sex changes the social organization (one male multi female groups top right, and multiple males one female groups bottom left). However, in these species, often the vacant breeding position is taken over very quickly (for example from males in bachelor groups), such that no IVSO might be observed (green insets). Note that pair-living species often have groups that also contain adult non-breeders, for example in cooperatively breeding species such as wolves and callitrichids. In these species, mortality of a dominant breeder typically leads to conflict between the remaining group members about who will become a breeder.

It is important to know whether the observed IVSO is due to an environmental disrupter or due to the adaptive choice of individuals. In facultative group-living African striped mice, solitary breeding in females has been described as an adaptive tactic to avoid reproductive competition within groups (Schradin et al. 2010). However, long-term studies revealed that solitary breeding in female striped mice could be the result of two alternative mechanisms: 1. females leaving the communal group to become solitary breeders, indicating an individual choice; or 2. females becoming solitary breeders because all other females of their group have disappeared, probably due to predation (Hill et al. 2015a). This difference in mechanisms is also represented in differences between females, with solitary females that left the group having a higher body mass and lower corticosterone levels than females that remained in the group, whereas females that became solitary due to environmental disrupters did not differ from group-living females in body size or hormonally (Hill et al. 2015a; Hill et al. 2015b). However, females that chose to become solitary differed significantly in body mass and in hormone levels from females that became solitary due to environmental disrupters (Hill et al. 2015a; Hill et al. 2015b). Thus, to understand the proximate mechanisms and ultimate consequences of solitary breeding, it is important to know whether solitary breeding has been caused by an environmental disrupter or by adaptive individual choices.

The importance of long—term field studies with continuous monitoring

Identifying IVSO is challenging, especially for long-lived species. It requires long-term field studies (Hayes & Schradin 2017) which are difficult to initiate and sustain (Schradin & Hayes 2017). The history of the group must be known for an extended period of time to identify whether changes in social organization are the result of individual choices, indicating adaptive IVSO, or due to environmental disrupters changing the group organization. Thus, long-term field studies must contain continuous observations over several years, not just several extended field trips to the same field site over a few years. This is in contrast to many projects, which are typically funded for only three years, with periods between study years when no field data are collected, and when important members of the study population might disappear for then unknown reasons (Porter et al. 2001). While it is easy to provide adaptive interpretations to explain the observed IVSO, whether or not it is really adaptive or the consequence of environmental disrupters remains unknown. It is important to be aware that cases of non-adaptive IVSO due to environmental disrupters can also occur in species where adaptive IVSO occurs, as was demonstrated in the case of solitary breeding in African striped mice (Hill et al. 2015b).

Why did IVSO evolve?

Regarding the evolution of IVSO, one can ask several questions. 1. Which environmental factors lead to the evolution of IVSO? 2. How do environmental factors differ between the three described adaptive mechanisms? 3. Which life history traits are related to the evolution of IVSO?

IVSO may represent an adaptive response to spatio-temporal variation in environmental conditions (Table 1). Accordingly, stable social organizations can be expected in stable or predictable environments. Such social stability is beneficial because all forms of phenotypic plasticity have costs such as gathering the correct information to decide which phenotype to develop, costs of nervous system tissue to make fitness-enhancing decisions (e.g., dispersal vs. natal philopatry), the risk of developing the wrong phenotype, and the time cost to change (for reviews see (VanBuskirk & Steiner 2009; Auld et al. 2010; Piersma & Gils 2011). To avoid these costs, having a stable social organization might be the optimal solution for species evolving in stable or predictable environments. However, if the costs and benefits of social stability differ between sexes (Ebensperger et al. 2016), inter-sexual conflict could facilitate changes in social organization within populations. IVSO might be expected in species that have large geographical ranges encompassing very different environments. Variation in ecological conditions between populations could lead to genetic differentiation affecting the social system and thus IVSO between populations. This could be the starting point of speciation (Meynard et al. 2012; Rymer et al. 2013; Nonaka et al. 2015).

Adaptive phenotypic plasticity within populations, including IVSO, can evolve in environments that are variable (Table 1). For an adaptive response to evolve, this variation must be repeatable in different generations. For example, IVSO could evolve in environments characterized by repeated, predictable environmental disrupters resulting in periods of high and low availability of resources, such as periodic El Niño-Southern Oscillation (ENSO) events (Zabel & Taggart 1989; Dickman et al. 2010). Any given ENSO cannot be predicted precisely, but it is predictable that ENSO will occur again in the future. Thus, animals that evolved in areas where ENSOs occur experience periodic but predictable variation, to which IVSO could be an adaptation (Zabel & Taggart 1989; Dickman et al. 2010).

Variation in population density may drive IVSO as it influences the availability of breeding territories (habitat saturation hypothesis: (Emlen 1982; Koenig et al. 1992). For example, the social organization of striped mice in the Succulent Karoo is mainly dependent on population density, with solitary living occurring in generations experiencing low population density and communal breeding in generations experiencing high population density (Schradin et al. 2010). Whether developmental plasticity or social flexibility evolves in varying environments would then depend on the predictability of this variation. For developmental plasticity, the environment in which an individual grows up must contain reliable (predictable) information about the environment in which it will breed. In this case, the individual could develop an alternative phenotype via developmental plasticity with the highest reproductive success occurring in the future environment.

Table 1
Environmental conditions under which the four mechanisms leading to IVSO are predicted to evolve. Predictability can occur within generations (i.e., early and later life of an individual) or between generations (i.e., conditions experienced by adults and their offspring).

Mechanisms for IVSO	**Environmental conditions under which it is predicted to evolve**
Environmental disrupter	It is not an evolved trait but enforced and thus occurs in all environments
Genetic differentiation	Environmental variation between populations. Environment is predictable for the individual.
Developmental plasticity	Re-occurring variation within populations which the individuals can predict.
Social flexibility	Non-predictable but re-occurring variation within populations.

If the environment is not predictable but differs significantly from generation to generation, social flexibility enabling an adaptive response at a later life history stage and not during early development should evolve. Social flexibility offers the potential to respond immediately in a number of ways to changing environmental conditions. In most cases of developmental plasticity, such as a response to prevailing predation pressure (Steiner & Buskirk 2008; Lind et al. 2015), there is no or only a very short time lag between the reliable information and the fitness benefit of the alternative phenotype. In contrast, the time lag between the juvenile stage and the breeding stage is often much longer. This could explain why many examples exist of social flexibility explaining IVSO, but not for developmental plasticity (Schradin, 2013). We therefore predict that developmental plasticity as the mechanism for IVSO is most likely to occur in species where the juvenile and the breeding life history stage follow shortly after one another. For example, in common voles (*Microtus arvalis*), precocious fertile mating of non-weaned 14 days old females occurs (Tkadlec & Zejda 1995), being an extreme example of overlap between the juvenile and the breeding stage. Future studies will have to test whether developmental plasticity is the mechanism leading to IVSO in some species and whether this is related to a short time lag between development and reproduction. In sum, all three adaptive mechanisms leading to IVSO are predicted to have evolved as a response to environmental variation (Table 1).

Testing predictions at the species level

Testing for the adaptive value of IVSO requires a comparison of the fitness of individuals living in different types of social organizations under different environmental conditions. For example, male striped mice have alternative reproductive tactics, being either the breeding males of communally breeding groups (called breeding males) or solitary roamers attempting to copulate with females of several groups (Schradin et al. 2009). In striped mice, IVSO occurs within populations. Striped mice of both sexes live solitarily when population density is low, but live in communally breeding groups when population density is high. However, solitary roaming males occur even under high population densities (because the sex ratio at birth is equal but there is only one breeding male per communal group), but have a lower body mass (= competitive ability) than breeding males (Schradin et al. 2009). Breeding males have 10 times higher reproductive success than roamers (Schradin & Lindholm 2011). However, when only roaming males occur, many of them have very high reproductive success (Schradin & Lindholm 2011). Importantly, under intermediate population density, males (and also females) can be solitary or group-living, and the reproductive success of roamers equals the reproductive success of breeding males (Schradin & Lindholm 2011). This indicates that IVSO in this species is the result of selection having acted on individuals to maximize reproductive success.

If adaptive IVSO has been identified in a species, the main expectation would be that the species showing IVSO lives in a variable environment (Table 1). In striped mice, population density is the main predictor of social organization, determining whether individuals live in groups or solitarily (Schradin et al. 2010; Schoepf & Schradin 2012). Population density is highly variable from year to year. This indicates that African striped mice live in a variable and unpredictable environment, favoring the evolution of social flexibility.

Statistically testing whether or not IVSO in a single species is due the variability in its environment can be challenging. If genetic differentiation has been identified as the mechanism of IVSO, one could measure selected environmental factors and compare these between populations with social organization type A with populations showing the different social organization type B. For this, an appropriate sample size is needed in the different populations showing the two forms of social organization. If the identified mechanism is developmental plasticity, it could be shown statistically that the environmental factors are predictable for the individuals by doing autocorrelations or other time series analyses.

Social flexibility is characterized by environmental factors that are unpredictable, such that no significant autocorrelation of the factors determining social organization would be expected. For example, the population density experienced as juveniles would not predict (correlate with) the population density when the individual is breeding. Thus, the environmental factor measured at $time_{(breeding-x)}$ does not predict the same factor at $time_{(breeding)}$, which would be the case if an identified cycle (for example 7 years) does not correspond with the life history cycle (e.g. 2 year) of a species, or if no cycles exist at all, indicating environmental unpredictability that results in non-significant statistical relationships. This would be statistically problematic as one would expect the null hypothesis to be true (the variable factor cannot be predicted). There are no tests demonstrating unpredictability, but there are statistical tools such as time series tests to detect structure in a dataset. This can be applied to a time series of environmental data and the absence of any signal at the time scales of the animal's lifetime would indicate that the variable is unpredictable for the individual of this study period. Potential methods include wavelet analysis which generates complementary wavelets with different periodicities to decompose data without gaps. The wavelets are then used to detect periodicity in the environmental time series at different time scales. Another approach is to use a test for autocorrelation (Moran's test, Portmanteau test's, Box-Pierce, Ljung-Box Q test) to detect a structure in the time series (Diggle 1990).

Testing predictions in comparative studies

The comparative method relies on large datasets of many species. Comparative studies could be used to establish whether variation in key environmental factors such as rainfall and food availability or life history are associated with the occurrence of IVSO over a large number of species. There are three important issues we want to address about how to improve future comparative studies. First, despite evidence that IVSO has been observed in mammals (Dalerum 2007; Valomy et al. 2015; Garber et al. 2016; Mann & Karniski 2017), existing databases on the social organization of mammals and other taxa typically do not consider IVSO but assign one form of social organization to each species. Ignoring IVSO in comparative studies can lead to spurious conclusions about social evolution (Silvestro et al. 2015; Sandel et al. 2016). For example, it was previously believed that social carnivores evolved from a solitary ancestor, but taking IVSO into account indicated that the ancestor might rather have been socially flexible (Dalerum 2007). Thus, it is crucial that IVSO is considered in comparative studies of factors influencing social diversity in animals.

Second, to achieve maximum taxonomic breadth, some databases are populated with information from the secondary literature and some data are based on the assumption that closely related species have the same form of social organization, even if only one species has been studied in detail. We advocate for a different approach in which scientists build a smaller dataset based on the most reliable information from the primary literature (Schradin 2017) and that includes IVSO (Valomy et al. 2015). Conclusions from comparative studies using high quality primary data can differ significantly from comparative studies of large databases of low quality data from the secondary and tertiary literature (Kappeler & Fichtel 2016). For example, one database for comparative studies included 90% (399/445) of Eulipotphla in their dataset with >99% assigned a solitary social organization, often based on secondary literature (Lukas & Clutton-Brock 2013). In contrast, Valomy et al. (2015) using only primary literature determined that reliable information was only available for 16 species, of which 56% of species (n=9/16) were social (living in pairs or in groups). Interestingly, IVSO was found in 7 Eulipotyphla species (Valomy et al. 2015). Detailed long-term studies can change our understanding animal social systems even in well studied taxa (Elbroch et al. 2017). Databases used in future comparative studies of IVSO and social evolution should be built from data collected from the primary literature and not include assumptions about the social organization of an entire genus based on observations in a single or a few species (Schradin 2017). This will require that the social organizations of more species are studied in their natural environment (Valomy et al. 2015; Schradin 2017).

Third, the next major challenge with comparative studies is the restriction of analyses to adaptive forms of IVSO. This is difficult because environmental disrupters are a frequent cause of non-adaptive IVSO. Thus, it would be beneficial if databases on the social organization of a taxon do not only include whether IVSO occurs, but also whether it is adaptive or non-adaptive. Unfortunately, this information is normally not available.

Predictions about the factors favouring the evolution of adaptive IVSO

Table 2
Predictions regarding IVSO to be tested in comparative studies.

Hypothesis	Prediction & mechanisms
Non-adaptive	IVSO is more common in species that are typically characterised by one dominant breeding pair, indicating that environmental disrupters (death of one dominant breeder) cause the observed variation.
Benefits under environmental heterogeneity	IVSO occurs more frequently in species that occur in areas of the world characterized by high inter-annual (among) year variation (coefficient of variation) in rainfall and ambient temperature. This can for example induce significant variation in population density and thus competition for reproduction (and resources). A positive relationship between IVSO and increasing diet breadth and greater IVSO is expected in species found in regions with high within-year and inter-annual variation in rainfall and food availability.
Benefits to short lived species	IVSO is more common in species with a short lifespan and that breed only for one breeding season; these species are selected to respond optimally to the prevailing environmental situation.
Responsiveness to changing environments over a long lifetime	IVSO is greater in species with long lifespans and that reproduce during multiple years than species with short lifespans and that do not produce offspring during multiple breeding seasons and that IVSO is positively associated with habitat breadth.

The main prediction is that environmental factors important for fitness vary more in species with than without IVSO (Table 2). Important factors are variation in rainfall and food availability, which influence population density. Population density in combination with resource availability can influence both the degree of competition within populations and the extent to which ecological constraints limit reproductive and social options (Emlen 1982; Koenig et al. 1992; Schradin 2013). Other environmental factors such as ambient temperature and changes in predation pressure or parasite / infectious disease prevalence could also be important for the evolution of IVSO.

The adaptive value of IVSO may depend on both environmental conditions and life history (Table 2). This is expected when environmental variation has different effects on long-lived versus short-lived species and those with many versus few breeding attempts during a lifetime. Short-lived species will experience less environmental variation during a lifetime and thus must breed in the prevailing environment rather than wait to breed until the environmental conditions have improved. If an individual of a short-lived species chooses a reproductive and social tactic that leads to a comparatively low reproductive success during its only breeding opportunity, its lifetime reproductive success will be below average. In contrast, an individual of a long-lived species that breeds during many breeding seasons can have a relatively high lifetime reproductive success even if its tactic leads to low success in one breeding season. As an extreme example, consider a reproductive tactic that leads to very high reproductive success during years in which multiple preferred foods are abundant but to no reproductive success in years when food availability is restricted. In a long-lived species where individuals breed in many years, this reproductive tactic could still be advantageous. However, in a short-lived species where every generation breeds for only one year and is then replaced by the next generation, individuals with this reproductive tactic would die without having reproduced, resulting in a shift in the frequency of an alternative tactic. In sum, we predict that IVSO is more likely to evolve in short-lived species, particularly species where individuals only breed during one single breeding season. This prediction should be compared to the alternative prediction: long-lived species from heterogeneous environments evolved IVSO as a tactic to cope with inter-annual variation in environmental conditions, thereby using the best strategy for current conditions, while short-lived species are constrained to one social tactic (Table 2).

Conclusions

The fact that a species shows IVSO is no evidence that it is an evolved trait of this species. Environmental disrupters can be expected to cause IVSO even in species where IVSO is also an adaptive response (Hill et al. 2015a; Hill et al. 2015b). Adaptive IVSO is expected to have evolved in variable environments. To understand IVSO at the species level it is important to conduct continuous long-term studies to differentiate between non-adaptive and adaptive IVSO. In addition, it is necessary to measure variation in the environment, and statistical tools such as time series analyses can be used test for structure in the data. One problem is that such statistical analyses mainly demonstrate significant relationships such as cycles, but not non-existing cycles, which would represent unpredictability. Thus, unpredictability is difficult to demonstrate statistically, but an important factor for the evolution of social flexibility causing IVSO.

IVSO is an important consideration when studying social evolution (evolution of monogamy, cooperative breeding, paternal care, group versus solitary living), as not every species can be assigned to one single form of social organization (Lott 1984; Lott 1991). For such comparative studies, it is important to have reliable data based on the primary literature. IVSO is an interesting phenomenon that needs scientific explanation. Understanding IVSO is important because it demonstrates species resilience against environmental change and it can help us to study ultimate and proximate reasons of group-living by comparing between solitary and group-living individuals in a single species (Schradin et al. 2012). Finally, social organization can influence both social structure and mating system, but does not determine these. Thus, once adaptive IVSO has been identified, future studies should investigate its effects on social structure and mating system.

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