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# Intra-specific variation in social organization of Strepsirrhines

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Strepsirrhines, that is, lemurs, galagos, and lorises, are considered basal primates, making them important to understand the evolution of primate sociality. Apart from some lemurs, they are nocturnal and solitary living, though the view of their sociality nature has changed with field studies being completed. We conducted a review of the primary literature about the social organization (group composition) of strepsirrhines, with the aim to determine whether intra-specific variation in social organization (IVSO) occurs and to determine how many species are pair-living, group-living, or solitary living. We found data in 83 peer-reviewed studies for 43 of the 132 strepsirrhine species and compared our results using two databases on social systems of mammals published in 2011 and 2013. While it is often assumed that primates show relatively fixed social organizations, we found that 60.5% of species for which data exist have IVSO. We found only 7% of the species to be truly solitary living (with 34.9% additional species to be sometimes solitary living), which is in contrast to the other databases, which had reported 60.9% and 37.7% of species to be solitary. We further explored group compositions by designating "functional groups" (e.g., foraging, breeding, and infant care groups). While functional groups might explain IVSO within a single species, this was not consistent over species with IVSO, such that IVSO was poorly explained by functional groups. Our study supports the view that most strepsirrhines are social (58.1% of species with another 34.9% of species sometimes living in pairs or groups) and show complex and often variable social organizations; reinforcing the assumption that the ancestor of all primates was social and not solitary.

**KEY WORDS**

comparative studies, prosimian, social organization, social system, Strepsirrhines

## 1 | INTRODUCTION

Understanding the evolution of primate social systems, which show high degree of variability between species, is one of the main aims of primatology (Chapman et al., 2017; Kappeler & van Schaik, 2002; Kappeler et al., 2017). The social system of a species is characterized by three inter-related components (Kappeler & van Schaik, 2002): the social structure which refers to the pattern of social interactions among members of a group and the resulting relationships; the mating system which describes who mates with whom (mating decisions) and reproductive consequences (timing of mating); and the social

organization, that is, the composition of groups, including the number of reproducing males and females. Social organization influences who can interact with whom, impacting both the social structure and the mating system. Furthermore, social organization might vary depending on the function of groups, that is, group composition might differ between foraging and sleeping or between the breeding and the non-breeding season. Thus, understanding social organization is a key to understanding the evolution of sociality. Practically, it is easier to determine group composition than social structure, particularly infant care, and mating system, both of which may be concealed. Moreover, quantifying the mating system also requires the use of molecular

markers to determine maternity and paternity. Given these challenges, it is not surprising that there is more information on social organization than social structure or mating systems.

Social organization has been traditionally used to characterize primate societies (Crook & Gartlan, 1966; Eisenberg et al., 1972) and is one of the most frequently examined component of the social system in studies of primate social evolution, that is, when and why sociality evolved and how variation in social systems can be explained. Most of the Galagidae and Lemuridae are thought to live solitarily, in pairs or in multimale/multifemale groups (Clark, 1985; Nash & Harcourt, 1986; Overdorff, 1993; Tan, 1999) while generally Cercopithecidae live in one male/multifemale and sometimes in larger multimale/multifemale associations (Henzi et al., 2000; Quris, 1976). Cebidae and Atelidae live mainly in large multimale/multifemale groups (Shultz et al., 2011) and Hylobatidae usually live in one male/one female groups that might change over the years (Brockelman et al., 1998; Palombit, 1994). Here we focus on the social organization of `strepsirrhines (lemurs, galagos, and lorises) to come to a better understanding of primate social systems.

Historically, most of the strepsirrhines were believed to be solitary living (Eisenberg et al., 1972), possibly due to their nocturnal and shy nature (with the exception of some diurnal lemurs). The social organization of most strepsirrhines was believed to be dispersed polygyny (solitary males mate with several solitary living females) (Martin, 1972), but a published review of field studies conducted at the end of the 20th century found that most strepsirrhines live either in multimale/multifemale groups (with polygyny as mating system) or in pairs (Müller & Thalmann, 2000). Bearder et al. (2003) reported that species of the genera *Galagooides*, *Galago*, *Euoticus*, *Sciurocheirus*, and *Otolemur* often sleep alone, indicating solitary living, but that sleeping in groups can also occur; pertaining to a variation in social organization in these genera. On the other hand, lorises had been rarely reported to form groups, with the exception of one study in Cameroon reporting adult pairs of *Perodicticus potto* at the same sleeping site (Pimley, Bearder, & Dixson, 2003). Later, Schülke & Ostner, (2005) pointed out that the six well-studied species of cheirogaleidae vary greatly in their social organization. Only one species (*Mirza coquerili*) was found to be truly solitary (Kappeler, 1997), while other species lived either as solitary foraging pairs who slept together or formed larger groups of variable composition. In sum, while it was originally believed that strepsirrhines are solitary living, we now know that many strepsirrhines form more complex forms of social organization. To our knowledge, a recent review taking into account field studies of the last 15 years has not been conducted.

Previously, it has been assumed that most species have only one type of social organization; either the species was regarded to be solitary, living in pairs, or living in groups. Now we know that many species show intra-specific variation in their social organization (IVSO), and that IVSO is more common in other mammals than previously thought (Valomy et al., 2015). Crook & Gartlan (1966) noticed that primate societies can be flexible, which was confirmed in later field studies. For example, IVSO had been reported when comparing different populations of *Microcebus murinus* (Schülke & Ostner, 2005). Richard (1974) reported that social organization of *Propithecus verreauxi*

in the north-western and southern Madagascar was variable, with individuals living in pairs, in one male/multifemale groups, multimale/one female groups, or in multimale/multifemale groups. This variation in social organization was observed between different areas as well as between groups living in the same forest. Based on these observations, it is not accurate to characterize many species based on only one form of social organization. Instead, IVSO must be taken into account in order to understand the evolution of social systems, especially the phylogeny (evolutionary history; e.g., Lukas & Clutton-Brock, 2013; Shultz et al., 2011), one of Tinbergen's four questions (Tinbergen, 1963).

IVSO can be induced by four different mechanisms: genetic variation, developmental plasticity, social flexibility and entirely extrinsic factors (Schradin, 2013). Genetic variation is involved when individuals of a species differ genetically in a way that influence their social behavior, leading to different forms of social organization. For example, these differences might influence their ability to form pair-bonds or to show parental care (Hammock & Young, 2005; Rymer & Pillay, 2011) contributing to different social organizations. Developmental plasticity is involved when environmental variation activates alternative developmental pathways of one genotype early in life in a non-reversible way (Piersma & Drent, 2003). Social flexibility is involved when adult individuals change their social tactics in response to short-term changes of environment, modifying the social organization of a species or population, which is reversible. IVSO can also be induced by extrinsic factors (stochastic processes) resulting to non-adaptive changes of social organization. IVSO due to extrinsic factors has no ultimate or proximate explanation and is not a response to environment change itself, but the result of a demographic interruption. It is therefore a non-adaptive form of enforced IVSO that then might trigger adaptive individual responses to cope with the new situation and possibly return to the adaptive form of social organization (Schradin, 2013).

Here, we present a primary literature review on field studies that report the social organization in naturally occurring strepsirrhines. Our aims were, first: to describe the extent of IVSO in strepsirrhines, and, second: to compare our database to that of two previously published databases including information on strepsirrhine social organization (Lukas & Clutton-Brock, 2013 who studied the evolution of social monogamy in mammals and Shultz et al., 2011, who worked on the evolution of stable sociality in primates). We also searched for information on whether IVSO might occur in different functional groups such as sleeping and foraging groups.

## 2 | METHODS

This research adheres to the American Society of Primatologists principles for the ethical treatment of primates.

### 2.1 | Primary literature search on social organization

We used the Web of Science (Thomson Reuters) to search for primary literature on the social organization of 132 extant species of strepsirrhines listed by the IUCN (International Union for Conservation

of Nature) website. For each species, we initially searched the Latin name of the species and the term "social." If no literature on social organization was found, only the genus and the term "social" were used, and if still no information was found, only the Latin name. All review articles and studies of captive strepsirrhines were discarded and only primary field studies were considered. The abstract of each study was then read and the PDFs were searched for the terms: "social," "group," "herd," "territorial," "solitary," "bachelor," "plural," and "singular." Further, all figures, tables, and supplemental documents, were checked for potential information.

For each species, we recorded the social organization (adult sex composition) reported in published papers (Table 1). Publications reporting group sizes without providing details about adult sex composition of groups were not included in our database. As a single population could be used in multiple papers, we also determined the number of published studies on social organization and number of populations in which studies were conducted for each species. For example, if social organization in one population was reported in 10 papers, we counted this as one population, but as 10 published studies.

## 2.2 | Functional groups

Whenever possible, we determined functional group composition and whether intraspecific variation occurred between these functional groups. Functional groups were defined in the following way: Foraging groups: individuals that were observed during foraging. Sleeping groups: individuals sharing a sleeping site such as a tree-hole, determined via radio-tracking and/or direct observations. Breeding groups: groups observed during the breeding (mating) season before infants were born. Infant care groups: groups observed during periods when dependent infants were present in the group. Non-breeding groups: groups that were observed outside the breeding season or infant care period.

## 2.3 | Existing databases

For comparison, we compiled information on strepsirrhine social organization from two existing databases (Lukas & Clutton-Brock, 2013; Shultz et al., 2011), both of which were available as electronic

supplements. Neither of these databases included information on male-female social organization, but regarded species as "group-living" which had groups composed of multiple adults (Table 1). Thus, we compared the proportion of species in our database that were solitary, pair-living, group-living, or some combination of these social organizations to that in both Lukas and Clutton-Brock (2013) and Shultz et al. (2011).

## 2.4 | Statistical analysis

Fisher's exact tests and chi-square tests were performed using GraphPad InStat Inc. (La Jolla, CA) to compare ratios of the different social organizations reported in our database with the ratio of social organization from Lukas and Clutton-Brock (2013) and Shultz et al. (2011). For example, we compare the ratio of solitary to social species between databases using contingency tables. Statistical significance was determined using an alpha level of  $p < 0.05$ .

## 3 | RESULTS

From the 132 extant species of strepsirrhines listed by the IUCN, information on adult male-female social organization was found for only 43 species (32.6% of all species, see Table 2; electronic supplement 1); because detailed field studies are missing for the remaining 89 species. By comparison, Lukas and Clutton-Brock (2013) and Shultz et al. (2011) reported social organization for 80 and 67 species, respectively. Out of the 43 species for which we did find primary information from field studies, 41 (Lukas and Clutton-Brock) and 38 (Shultz et al.) were included in the two other databases. Unlike the other two datasets, our dataset did not include information from secondary literature (e.g., Nowak, 1999) or from captive studies. Moreover, we did not assume that closely related species have the same form of social organization (Schradin, 2017).

## 3.1 | IVSO in Strepsirrhini

Species such as *Cheirogaleus medius* or *Loris lydekkerianus* showed a high variation in social organization with individuals of both sexes observed solitarily, in pairs or in male/female groups of different

**TABLE 1** Types of social organization reported in our database

Social organization	Definition
Solitary M	One breeding male
Solitary F	One breeding female
F-M	Pair (adult female, adult male, plus possibly dependent offspring)
FM + adult off	Pair + adult offspring
Different forms of group-living	
MFF	Multiple breeding females and one breeding male
FMM	One breeding female and multiple breeding males
FFMM	Multiple breeding females and multiple breeding males
FF	Multiple adult females
MM	Multiple adult males

**TABLE 2** Number of strepsirrhine species for which primary literature was found regarding their social organization, in comparison with the number of species reported in the databases of Lukas and Clutton-Brock (2013) and Shultz et al. (2011)

Strepsirrhines family	Number of species for which primary data were found	Number of species reported in Lukas and Clutton-Brock (2013)	Number of species reported in Shultz et al. (2011)	Number of existing species
Cheirogaleidae	9	19	8	36
Daubentoniidae	1	1	1	1
Galagidae	3	19	9	19
Indriidae	7	11	8	19
Lemuridae	16	14	21	21
Lepilemuridae	4	8	13	26
Lorisidae	3	8	7	10
Total	43	80	67	132

Number of existing species refers to the species recognized by the IUCN (International Union for Conservation of Nature).

compositions. Species of the genus *Microcebus* (*M. berthae*, *M. griseorufus*, *M. murinus*, and *M. ravelobensis*) also showed a high degree of variation while in *Eulemur* very little variation was reported within most species (*E. albifrons*, *E. flavifrons*, *E. fulvus*, *E. rubriventer*, *E. rufifrons*, and *E. rufus*). IVSO was reported for only three species of the genus (*E. collaris*, *E. macaco*, and *E. mongoz*). Over the entire genus, variation in social organization was limited, with mainly pair-living and multi-male multi-female groups (see also Kappeler & Fichtel, 2016).

We found IVSO in 26 species (60% of all species with available information; Table 3). Lukas and Clutton-Brock did not consider any species to have multiple types of social organization, and Shultz et al. reported IVSO in 20 species (30% of their species), a significantly lower proportion than we did (Fisher's Exact Test,  $p = 0.003$ ). We found that 11.6% of the 43 species with available information lived in groups consisting of different male-female compositions, 9.3% of species as solitary or pair living, 14% of species as pair-living and group-living, and 25.6% of species as solitary, pair-living and group-living (Table 3; for details see electronic supplement 1).

We found significant differences in the distributions of social organizations among databases when we categorized social organization by solitary living and being social (pair-living + group-living; Chi-square test for trend  $p$ -value = 0.02). Solitary living was reported in significantly more species in Lukas & Clutton-Brock than in our database (Fisher's Exact Test,  $p < 0.01$ ). Even when we considered all species with IVSO for which solitary living had also been recorded (total of 15 species), our ratio differed from Lukas & Clutton-Brock (Fisher's Exact Test,  $p < 0.01$ ). Exclusive solitary living was more commonly reported in Shultz et al. than in our database (Fisher's Exact Test,  $p < 0.01$ ), but not when we considered all species with IVSO for which solitary living had also been recorded (Fisher's Exact Test,  $p = 0.08$ ). Accordingly, we report relatively more species to be pair-living and to be exclusively group-living than what was found in both other databases (Table 3).

### 3.2 | Is IVSO associated with functional groups?

For 31 of the 43 (72%) strepsirrhine species, social organization was reported for more than one of the functional groups ( $3.5 \pm 1.2$  functional groups per species; Table 3). For 20 species (65%), social

organization did not differ over functional groups, while for 11 species (35%) it did. For the 11 species where intra-specific variation in social organization was observed between functional groups, there was no obvious functional group associated with the variation (Table 4; for details on all species, see electronic supplement 2). For four species (13%), social organization was different for sleeping groups, for three (10%) in infant-care groups for three (10%) there was population specific variation. For the very well-studied species *Lemur catta* no specific categorization was possible, as variation in social organization was reported in foraging groups, sleeping groups breeding groups, infant care groups and non-breeding groups in which groups of multiple males and multiples females were the dominant social organization.

## 4 | DISCUSSION

We found that only 7% of Strepsirrhini species are exclusively solitary living, while most species are social, living in pairs or in groups. This is different from other databases that in contrast to our study, also used secondary literature and in which many more (38% Shultz et al., 2011) or even the majority of Strepsirrhini are considered solitary living (61% in Lukas & Clutton-Brock, 2013). We found an additional 34.9% of the species to be sometimes solitary living, but also to live in pairs or in groups, showing intra-specific variation of social organization (IVSO). Thus, our review indicates that it is important to focus only on primary literature and not on secondary literature that might also include broad assumptions, and to take IVSO into account in the study of strepsirrhine social organization.

We chose to classify each species in which more than one form of social organization was observed as showing IVSO. As such, our classification takes more information into account than the traditional classification. As a result, it is possible to study the variation of IVSO which in turn, allows researchers to study the evolution of IVSO. In our current analysis, a species in which nine groups and one pair were reported in a single study were classified in the same way as a species with five groups and five pairs, even though important species differences might exist. However, the database we provide includes

**TABLE 3** Number of strepsirrhine species reported with different kinds of social organization in primary literature, in the databases of Lukas and Clutton-Brock (2013) and Shultz et al. (2011)

Social organization	All Strepsirrhini		
	Research in primary literature	Lukas and Clutton-Brock database (2013)	Shultz et al. database (2011)
Solitary	3 (7%)	53 (60.9%)	26 (37.7%)
Pair-living	6 (14%)	14 (16.1%)	8 (11.6%)
Group-living	13 (30.2%)	20 (23%)	15 (21.7%)
No IVSO	8 (18.6%)	NA	NA
With IVSO	5 (11.6%)	NA	NA
Solitary and pair-living	4 (9.3%)	0	5 (7.3%)
Solitary and group-living	0	0	6 (8.7%)
Pair-living and group-living	6 (13.9%)	0	6 (8.7%)
Solitary, pair and group-living	11 (25.6%)	0	3 (4.3%)
Total species with data	<b>43 (32.6%)</b>	<b>87 (100.0%)</b>	<b>69 (84.1%)</b>
Total species with data showing IVSO	<b>26 (60.5%)</b>	<b>0 (0.0%)</b>	<b>20 (29.0%)</b>
Total species with data showing stability in social organization	<b>16 (39.5%)</b>	<b>87 (100.0%)</b>	<b>49 (71.0%)</b>
Total species NA	89 (67.4%)	0 (0.0%)	13 (15.8%)
Total species	<b>132</b>	<b>87</b>	<b>82</b>

NA, not available; no IVSO, group-living species that always show the same type of social organization; with IVSO, species showing different types of group-living social organization (FFMM, MFF, FMM). Bold values represent total number of species and main results.

this information, allowing other researchers to extract more detailed information. Taking IVSO into account allows researchers to use more accurate information instead of ignoring cases of social organization that differ from the norm (Sandel et al., 2016).

We used female-male group composition as the most general measurement of social organization, that is, differentiating between solitary, pair-, and group-living species (Kappeler & van Schaik 2002). However, valuable information could be gained by differentiating among functional groups (foraging, sleeping, infant care, breeding, or non-breeding season). IVSO was reported between functional groups for only 11 out of 26 species with IVSO. For all strepsirrhines combined, IVSO could not be explained by taking the different functional groups into account (Table 4; for details on all species, see electronic supplement 2). Even though IVSO was related to sleeping groups in some species and infant care in others, there was not a general pattern for all species. While, IVSO in the strepsirrhines was poorly explained by differentiating between function, considering functional groups could help explaining IVSO on the species level. For example, in African striped mice (*Rhabdomys pumilio*) differentiating between breeding and non-breeding groups helped to understand IVSO (Schradin et al., 2010). It is now understood that solitary living is an alternative form of social organization that only occurs when free breeding territories are available during the breeding season and is an adaptive mechanism to avoid reproductive competition (Schoepf & Schradin, 2012). It would be interesting and important to conduct similar studies in strepsirrhini taxa such as *Cheirogaleus medius* or, on the genus level, *Microcebus* and *Eulemur* (Kappeler & Fichtel, 2016). Thus, while for our comparative approach differentiating between functional groups did not help to

understand when IVSO occurs, on the species level this could help us in future to understand why IVSO occurs.

Most strepsirrhines were believed to be solitary living (Eisenberg et al., 1972), mainly due to the solitary foraging tactic of nocturnal species (Müller & Thalmann, 2000). Numerous strepsirrhines are still considered to be solitary living in recently published databases on mammalian social organization even though this perception changed as field studies on these species documented that many species have at least social networks (Kappeler et al., 2017; Müller & Thalmann, 2000). Two other databases (Lukas & Clutton-Brock, 2013; Shultz et al 2011) included a large number of species for which we did not find primary literature from field studies (e.g., *Cheirogaleus crossleyi*,

**TABLE 4** Number of strepsirrhine species for which the social organization was described for at least two of the five different functional groups

Species with no IVSO between functional groups	<b>20</b>
Species with IVSO between functional groups	<b>11</b>
Of these, related to:	
Foraging groups	0
Sleeping groups	4
Mating season	0
Infant care	3
Non-breeding season	0
None of the above, but population specific	3
Unspecific	1

*Lepilemur ankaranensis*, *Eulemur coronatus*, *Euoticus elegantulus*, *Microcebus rufus*, *Otolemur monteiri*, *Propithecus coquereli*, and many other species; for details see electronic supplement 3). This indicates that in other databases, the social organization was obtained from secondary literature (including captive studies) or from the assumption that closely related species have the same form of social organization (Lukas and Clutton-Brock), which has been criticized as being unreliable, as assumptions should not enter databases (Schradin, 2017). Relying on secondary literature or using compiled data can lead to biased conclusions regarding primate group size (Patterson et al., 2014) and social organization (Valomys et al., 2015). As Patterson showed for group-size, we show here for group composition that significantly different results are obtained if one invests time and energy into getting the most accurate information from primary literature.

Conclusions from comparative studies using high quality primary data can differ significantly from comparative studies of large databases including data from secondary and tertiary literature (Kappeler & Fichtel, 2016; Lukas & Clutton-Brock, 2013; this study). Using only primary field data on 12 species of *Eulemur*, Kappeler and Fichtel (2016) found that from the two pair-living species (*E. mongoz* and *E. rubriventer*), at least one evolved pair-living from group-living. In contrast, using a dataset that included information from secondary sources, Lukas and Clutton-Brock (2013) concluded that mammalian pair-living nearly exclusively evolved from a solitary ancestor. Our own study indicates that Strepsirrhini have to be considered as primarily social, and that additional field studies are needed on the approximately 90 species for which information is not available. We found that 41.9% of Strepsirrhini were at least sometimes solitary, which was similar to the 38% reported by Shultz et al. (2011). However, 15 of 18 solitary species (83.3%) were also reported either to be pair or group-living. Critically, our review also indicates that the majority of strepsirrhine species (60.5%) show IVSO, and that it is problematic to put each species into single category.

IVSO can be induced by four different mechanisms: genetic variation, developmental plasticity, entirely extrinsic factors, and social flexibility (Schradin, 2013). IVSO due to extrinsic factors (predation, abrupt habitat destruction leading to demographic interruption) is the only mechanism which is not adaptive (i.e., it is not the result of evolution to increase individual fitness). Thus, when trying to understand the evolution of sociality, we must focus on genetic variation, developmental plasticity, and social flexibility, all of which are considered evolved IVSO (Schradin, 2013). One of the main non-adaptive causes of IVSO in Strepsirrhini is supposed to be an individual's death, which could be due to diseases, old age, bad falls from trees, or even infanticide (Lewis et al., 2003; Morland, 1990). However, these cases of non-adaptive IVSO cannot explain why we found so few species to be truly solitary living, as solitary living is the only form of social organization that cannot be changed by the death of important group members.

In a 2000 review paper, Müller and Thalmann concluded that even though strepsirrhines often forage solitarily, social networks exist, often representing a social organization of dispersed males and females (with a promiscuous mating system) or dispersed pairs (e.g.,

solitary foraging pairs that share one territory and either sleep alone or together). Therefore, for Müller and Thalmann (2000) the main difference between strepsirrhines and simians was whether their groups split for solitary foraging (nocturnal strepsirrhines) or remained consistent, representing the gregarious groups typical of diurnal simians. When we differentiated under which conditions social organization was recorded, we found that IVSO was related to sleeping groups in four species with different social organizations. For example, *Cheirogaleus major* was sometimes foraging solitarily but always slept in pairs. *Nycticebus coucang* and *Otolemur garnettii* always foraged solitarily, but sometimes slept in pairs. IVSO was very common in all functional groups of *Phaner pallescens*, but one male/multiple female groups were never reported in sleeping groups but in all other functional groups (see electronic supplement 2). However, these four species do not offer a general explanation of IVSO over all strepsirrhines. Still, the results of our study are in accordance with conclusions of Müller and Thalmann (2000) that most studied strepsirrhines are social and not solitary. Thus, our results support their assumption that the ancestor of all primates was also social and not solitary.

Our results indicate that describing the social organization of species as "dispersed multi-male/multi-female" group-living is not as precise as describing the observed IVSO. For example, studies suggest that multiple *Microcebus murinus* females can sleep with one male (Müller & Thalmann, 2000), but also that males and females can sleep alone (Radespiel, Ehresmann, & Zimmermann, 2003) or in pairs (Radespiel, 2000). Additionally, it has been suggested that some males share a sleeping site without females being present (Radespiel, 2000). In sum, our review indicates that while studying primate social systems, recording different forms of social organization (IVSO) provides more precise information and allows to keep track of small changes in social organization.

Most of the strepsirrhines are sociable and many of them show a complex and often variable form of social organization. Field studies on the remaining 90 strepsirrhine species are needed to fully understand the evolution of strepsirrhine and thus primate social organization. Due to their relatively long lifespans, researchers will require longitudinal data over several years to quantify social organization in most strepsirrhines. These studies should include long term monitoring and radio tracking of neighboring groups along with the recording of ecological factors (food availability, plant composition/coverage, weather, predation exposure) in order to identify the mechanisms leading to IVSO. More field studies assessing geographic range size, habitat breadth, and abundance are also needed (see Lehman et al., 2016). The long-term monitoring and telemetry is needed to identify individual movements and group composition changes, linking this information with ecological factors or direct behavioral observation will then allow us to identify if the IVSO is an adaptive trait or due to environmental disruptors.

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## SUPPORTING INFORMATION

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