Socioecology and the role of scramble competition

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Ecological explanations for social organization and behavior are central to behavioral ecology. Unfortunately, the continuing mismatch between theoretical predictions and some empirical data led to increasingly complex hypotheses with numerous factors, raising doubts about their predictive value or even falsifiability. Moreover, several taxon-specific socioecological hypotheses have been developed that are seemingly detached from one another. We discuss how an integration of different hypotheses may help to clarify theoretical arguments and empirical discrepancies. We will first integrate two major socioecological hypotheses developed for carnivores and primates respectively, namely the Resource Dispersion Hypothesis (RDH) and the Socioecological Model (SEM). We then discuss how both hypotheses can benefit each other, particularly by implementing new perspectives about the role of scramble competition. First, the RDH proposes that under certain widespread conditions, territories provide surplus resources that can maintain stable groups without any costs and thus also without any need for direct benefits to the territory owners. We argue that such cost-free group formation requires strong within-group contest competition that assures priority of access to the territory owners, but would not withstand within-group scramble competition, which inevitably causes costs for all group members. Second, the SEM proposes that under pure within-group scramble competition, resources cannot be monopolized and thus dominance rank and social tolerance are pointless. We argue that rank-dependent eviction and group fission into territory holders and leavers as proposed by the RDH provides rank-dependent benefits and allows for social tolerance in terms of granted group membership even under pure within-group scramble competition.

Keywords: Socioecological Model, Resource Dispersion Hypothesis, social tolerance, dominance hierarchy, social style

Animals are either solitary or live in social groups that can range from temporary aggregations to permanent groups. The formation of social groups is facilitated if the benefits (e.g. reduced risk of predation and infanticide, enhanced access to and defense of food resources against other groups and species, support of kin, access to mating partners and social thermoregulation) outweigh the costs, which relate largely to increased within-group competition for resources but also e.g. disease transmission (Ward and Webster 2016). The competition for resources can be high or low, or even negligible, and can be of two forms: contest or scramble competition (Nicholson 1954; Łomnicki 2009). Under pure contest competition, individuals compete for Priority of Access (PoA) to a monopolizable resource, so an individual's access to the resource is independent of group size and depends only on the number of individuals ranking above it (queuing for access; Altmann 1962; van Schaik 1989; Koenig 2002; Alberts et al. 2003; Łomnicki 2009). Under pure scramble competition, a resource cannot be economically monopolized, e.g. because it is too widely distributed or too large, and is therefore equally accessible and exploited by all individuals, so individual access to the resource depends only on group size (or, more generally, population density; van Schaik 1989; Koenig 2002; Majolo et al. 2008; Łomnicki 2009). Under natural conditions, resources are rarely completely monopolizable or unmonopolizable but rather intermediate, with contest competition replacing scramble competition whenever the conditions allow (van Schaik 1989; Łomnicki 2009). Hence, individual access typically depends on both individual rank and group size (van Schaik 1989; Łomnicki 2009).

Within this basic framework, several taxon-specific socioecological hypotheses have been formulated (Macdonald 1983; van Schaik 1989; Sterck et al. 1997; Johnstone and Cant 1999; Lacey and Sherman 2007; Clutton-Brock and Janson 2012; Thierry 2013; Macdonald and Johnson 2015; Macdonald et al. 2019). We will focus on the two most prevalent and comprehensive hypotheses that address mammalian socioecology, namely the Socioecological Model (SEM), which was primarily developed to explain primate social behavior (Wrangham 1980; van Schaik 1989; Isbell 1991; Sterck et al. 1997; Clutton-Brock and Janson 2012), and the Resource Dispersion Hypothesis (including its derivatives), which was primarily developed to explain carnivore sociality (Macdonald 1983; Johnson et al. 2002; Macdonald and Johnson 2015), though both have been applied broadly across taxa (e.g. Sterck et al. 1997; Mann et al. 2000b; Wittemyer et al. 2005; Macdonald and Johnson 2015; Peignier et al. 2019; Karandikar et al. 2023; Makuya and Schradin 2024). The two theories address different aspects and are not mutually exclusive but complementary (Macdonald and Johnson 2015; see below).

We will first integrate them into a single terminological framework and then discuss how this integrative perspective may advance our understanding of socioecological patterns. Most important, we will show how both theories may have underestimated the potential impact of scramble competition on the formation of stable groups and dominance relationships.

The Socioecological Model (SEM)

The SEM aims to explain how socioecological conditions (e.g. kinship, predation and food distribution) influence group formation and maintenance as well as the nature of social relationships within and between groups (van Schaik 1989; Sterck et al. 1997; Kappeler and van Schaik 2002; van Schaik et al. 2006; Ostner and Schülke 2014). The SEM rests on the assumption that group formation is costly due to within group competition over resources and thus must yield compensatory benefits (Wrangham 1980; van Schaik 1989; Isbell 1991; Sterck et al. 1997; Koenig and Borries 2009; Clutton-Brock and Janson 2012). Originally developed for animals in general, but applied mostly to primates, the SEM postulates that social group formation evolves primarily as an adaptive strategy to reduce the risk of predation and infanticide, enhance the detection of, access to and joint defense of food resources against other groups and species, and enable other group benefits like social thermoregulation (van Schaik 1989; Isbell 1991; Sterck et al. 1997; van Schaik and Janson 2000; Clutton-Brock and Janson 2012; Koenig et al. 2013; McFarland et al. 2015; Henzi et al. 2017; Liz A. D. Campbell et al. 2018; Majolo et al. 2020; Port et al. 2020). The SEM postulates that, if resources are limited, social relationships should be characterized by contest competition for key resources resulting in a despotic social style (van Schaik 1989; Sterck et al. 1997). However, the realized level of contest competition and despotism is assumed to be regularly alleviated, resulting in a more equal access to resources. This can be because resources cannot be completely monopolized (scramble-like competition would shift a population towards a more egalitarian social style) or because complete monopolization is not the most adaptive strategy as collective actions yield higher benefits but also require concessions by top-rankers towards subordinates (shift towards a more tolerant social style, van Schaik 1989; Sterck et al. 1997; Kappeler and van Schaik 2002)(for a comparison between different social styles see Table 1).

Corresponding to the continuum between pure scramble and pure contest competition, social relationships between group members can range from purely egalitarian to purely despotic but are usually intermediate (van Schaik 1989; Isbell 1991; Sterck et al. 1997; Clutton-Brock and Janson 2012). Under pure scramble competition, access to resources is equally distributed across group members (van Schaik 1989; Isbell 1991; Koenig 2002; Łomnicki 2009; Clutton-Brock and Janson 2012) and social relationships are assumed to be characterized by the absence of agonistic interactions and dominance hierarchies as they cannot yield benefits due to the absence of direct competition (egalitarian social style) (van Schaik 1989; Sterck et al. 1997; Koenig 2002; Dammhahn and Kappeler

2009; Koenig et al. 2013). Individual access to resources decreases with increasing group size. Consequently, group formation occurs only if compensating benefits are present (van Schaik 1989; Janson and Goldsmith 1995; Sterck et al. 1997; Preuschoft and van Schaik 2000; Majolo et al. 2008; Łomnicki 2009; Port et al. 2020). Such benefits, often arising from success during between-group competition and reduced predation risk, may actually be quite common (Isbell 1991; Sterck et al. 1997; Majolo et al. 2020).

Under pure contest competition, resources are completely monopolizable and access is determined by rank (van Schaik 1989; Sterck et al. 1997; Koenig 2002; Łomnicki 2009; Macdonald and Johnson 2015). Dominance hierarchies are pronounced and steep, and agonistic interactions have unidirectional outcomes along the hierarchy and a high escalation potential due to the high potential gains, resulting in a despotic social style (van Schaik 1989; Sterck et al. 1997; Preuschoft and van Schaik 2000; Koenig et al. 2013). In intermediate states featuring both scramble and contest components, high-rankers may still monopolize resources to some extent, albeit with incomplete PoA. Meanwhile, lower-rankers can exploit non-monopolizable resources and level the PoA skew beyond the effects of mere queuing (van Schaik 1989; Koenig 2002; Koenig et al. 2013). Social relationships are characterized by clear but less pronounced and steep hierarchies, and by less intense aggression during less frequent contests, but conflict initiations and outcomes are still largely unidirectional along the hierarchy (Preuschoft and van Schaik 2000).

In despotic societies, group size is largely constrained by PoA, potentially leading to sub-optimally small groups or even solitary individuals with disadvantages in collective actions like defense of territory and resources and against predators (van Schaik 1989; Koenig 2002; Dammhahn and Kappeler 2009; Clutton-Brock and Janson 2012). Hence top-rankers may benefit most if they do not insist on their PoA, but make concessions to their lower-ranking partners, which could otherwise cease cooperation and leave the group. This creates a social market of interdependence where dominants are encouraged to suppress their monopolization potential and exhibit a tolerant social style towards subordinates (Sterck et al. 1997; Preuschoft and van Schaik 2000; Kappeler and van Schaik 2002). This opens the door for cheating and collective action problems, and it has been argued that social tolerance is particularly likely to emerge if concessions yield fitness benefits via kin selection, promoting nepotistic bonds and alliances especially in the philopatric sex where offspring stays with their parents (Sterck et al. 1997; Koenig 2002; Puga-Gonzalez and Sueur 2017; Smith 2014; Schülke and Ostner 2008; De Moor et al. 2020). However, strong and stable affiliative social bonds between unrelated individuals may also facilitate cooperation by increased mutual confidence and interdependence (Clutton-Brock 2009; Berghänel et al. 2011; Ostner and Schülke 2014; West et al. 2021; Schülke et al. 2024).

Although the resulting levelling of the PoA skew mirrors the influence of scramble competition on social structure and behavior, the mechanism is fundamentally different. In contrast to scramble effects, dominants are able to monopolize resources, and social tolerance reflects a form of cooperation rather than being a consequence of inefficient monopolization capacity (Sterck et al. 1997; Preuschoft and van Schaik 2000). As interdependence grows, subordinates gain greater leverage, making access to resources more open to negotiation and increasing the likelihood of subordinates engaging in conflicts (De Waal and Luttrell 1989; Preuschoft and van Schaik 2000). This results in more frequent cofeeding but also more frequent but less intense aggression and more aggression up the hierarchy (De Waal and Luttrell 1989; Preuschoft and van Schaik 2000). The low mutual avoidance and highly cooperative and negotiating nature of tolerant societies, as well as their high interdependence, should result in dense groups with rather peaceful coexistence and frequent affiliation and reconciliation to reduce social tension and disruption (De Waal and Luttrell 1989; Preuschoft and van Schaik 2000; Thierry 2004; Arnold and Aureli 2007; Lazzaroni et al. 2017; Puga-Gonzalez and Sueur 2017).

The SEM has inspired intense research in primates and other species, and recent reviews discuss the empirical support for and against the concept (Janson 2000; Mann et al. 2000a; Wittemyer et al.

2005; Koenig and Borries 2006, 2009; Thierry 2008, 2013; Clutton-Brock and Janson 2012; Lukas and Clutton-Brock 2018; Strier 2018). Across mammals, group formation and large group size are related to and advantageous under predation risk and between-group contest competition (Clutton-Brock and Janson 2012). Increasing group size leads to increasing competition for resources within groups, and increasing between-group competition increases group cohesion (Majolo et al. 2008; Clutton-Brock and Janson 2012; Samuni et al. 2019). Within single primate species, the rates and forms of affiliative and agonistic interactions often show the predicted relationship to gradients in resource monopolizability, including sex differences in key resources (Clutton-Brock and Janson 2012; Strier 2018). However, different behavioral indices of social style (Table 1) do not always co-vary as predicted (Snaith and Chapman 2005; Clutton-Brock and Janson 2012; Kaburu and Newton-Fisher 2015; Balasubramaniam et al. 2020), questioning the general validity of the concepts of social egalitarism, despotism and tolerance. Interspecies comparisons between primates and across mammals often found patterns that were inconsistent with various predictions of the SEM (Clutton-Brock and Janson 2012; Thierry 2022). To some degree this may be due to phylogenetic constraints (i.e., similar social behavior in related species despite different ecologies) but also species differences in e.g. scale (e.g., what constitutes a small or large food patch) or physiology (e.g., digestive systems), as well as methodological differences between studies (Koenig 2002; Koenig and Borries 2006; Clutton-Brock and Janson 2012; Thierry 2013). While some scientists have suggested abandoning the SEM entirely as an unsupported, overly complex or even unfalsifiable hypothesis, others have called for a more comprehensive approach including studies on non-primate mammals and considering a wide continuum of socioecological conditions (Sterck et al. 1997; Thierry 2008; Koenig and Borries 2009; Clutton-Brock and Janson 2012; Koenig et al. 2013).

Table 1: Behavioral predictions of the SEM for egalitarian, despotic-intolerant and despotic-tolerant social styles

	Egalitarian - Prevailing Scramble competition	Despotic - Prevailing Contest competition	
Behavior		**Intolerant**	**Tolerant**
Aggression rate	Low	Low	High
Aggression intensity	Low	High	Low
Spatial avoidance	Low	High	Low
Steepness & DCI of hierarchy	Low	High	Medium
Main formal hierarchy signals	None	Unidirectional Submission	Unidirectional Dominance
% of dyadic conflicts…			
… with counteraggression	High	Low	High
… submission against hierarchy	High	Low	High
… won against hierarchy	High	Low	High
… initiated against hierarchy	High	Low	High
Coalitionary support	absent	rare, nepotistic	frequent
Priority of access	Low rank skew	Strong rank skew, queuing	Moderate rank skew, queuing rare
Co-feeding	/	Rare	Frequent
Respect of ownership against hierarchy	/	Rare	Frequent
Affiliation time	Moderate	Low	High
% Affiliation up the hierarchy	Equal	High	Equal
Play time	Moderate	Low	High
Post-conflict reconciliation	Low	Low	High
Social integration/cohesion	Low	Low	High
Social bonds kin	Low	Low	High
Social bonds non-kin	Low	Low	Medium

Resource Dispersion Hypothesis (RDH)

The RDH postulates that, under certain conditions, stable social groups can form and persist without incurring any costs, eliminating the need for compensatory benefits (Macdonald 1983; Carr and Macdonald 1986; Johnson et al. 2002; Macdonald and Johnson 2015). This provides an interesting null hypothesis for stable group formation (Johnson et al. 2002). Here, the formation and maintenance of social groups is enabled by resource abundance, because patches are either habitually or temporarily super-rich (Fig. 1; for a detailed description and discussion of the RDH see Macdonald and Johnson 2015). There are two versions of the RDH, a spatial and a temporal one (Macdonald 1983; Johnson et al. 2002; Macdonald and Johnson 2015). In the spatial version, the smallest possible territory size habitually includes sufficient resources to sustain multiple individuals, e.g. because food patches are super-rich such as large prey items and congregations or large patches of human refuse such as rubbish dumps (Macdonald and Johnson 2015; Noonan et al. 2015).

The temporal version proposes that group formation is facilitated in territories with temporal fluctuations in resource abundance, with increasing temporal heterogeneity facilitating the formation of larger groups (Fig. 1): In order to guarantee survival and reproduction, territory holders need to defend territories large enough to guarantee resources during low abundance periods. However in richer periods such territories provide surplus resources which can then sustain additional (secondary) individuals. Central to the RDH is the assumption and preposition that this doesn't cause costs to the primary territory holder(s), who still has primary access to resources at any time (Johnson et al. 2002; Macdonald and Johnson 2015). The secondary individuals may face costs as they must queue for and thus rely on residual resources, potentially leading to suboptimal reproduction or even mere survival without reproduction (Schradin 2013; Macdonald and Johnson 2015). Secondary individuals only stay if other options are even worse, making the best of a bad job (Johnson et al. 2002; Schradin 2013). The resulting groups may often be temporary and fluctuating in size, more or less reflecting a simple "ideal free distribution" where individuals distribute according to spatial resource distribution. But the resulting groups may also be stable over long periods and also bridge and resist periods of scarcity if the costs of leaving the group are high and/or the opportunities elsewhere are low for the lower-ranking or secondary individuals (Johnson et al. 2002; Macdonald and Johnson 2015).

Central to both versions of the RDH is the assumption that periods of minimal abundance are rare (representing the lower end of the probability distribution, Fig. 1) and that sufficiently rich periods are the norm, so overall access to resources can be almost identical for the primary and a number of secondary individuals (Altmann 1962; Macdonald and Johnson 2015). Temporal heterogeneity and thus periods of excess resource abundance are inevitable in most environments, and habitual supra-optimal food abundances may occur often (Macdonald and Johnson 2015).

The RDH describes how ecological conditions could allow for more or less stable group formation and maintenance without the necessity of group-derived benefits like reduced predation risk or enhanced territory defense. The RDH is rooted in basic ecological principles, positing that animals distribute themselves based on resource availability (a framework consistent with the ideal free and despotic distribution hypotheses). The novel contribution of the RDH is the emphasis that in many environments, resources are patchily and unevenly distributed in a way that could enable group formation even under strict territoriality (despotic distribution), without necessitating any direct benefits from group formation and sociality itself. Furthermore, when habitats are saturated—a common condition in natural environments—stable groups can be maintained. Secondary individuals may derive greater benefits from remaining in the area and resisting periods of resource scarcity rather than leaving, making the best of a bad job (Schradin 2013; Macdonald and Johnson 2015). This way, the RDH pertains to both the formation and maintenance of animal groups.

Importantly, the RDH does not discount the possibility that groups may form and persist due to the inherent benefits of sociality, as proposed by e.g. the SEM (Macdonald and Johnson 2015), but offers a purely proximate explanation of group formation and maintenance. Notably, group formation and maintenance due to benefits of sociality can typically only emerge through social evolution. Animals are not rational agents that assess the benefits of sociality and then decide to form and stay together in groups. To enable directed selection for the benefits of sociality, some animals have to form groups at least for some time. In an ideal free distribution, group formation is simply facilitated by animals aggregating according to the resource distribution (e.g. around a waterhole, food patches or nesting sites). Here, group sizes adjust to resource distribution in a way that provides equal consumption rates per individual, reflecting pure scramble competition (Davies et al. 2012). The RDH provides a further proximate mechanism of group formation also in territorial species. However, even though the RDH does not rule out the possibility that benefits of sociality can drive group formation and maintenance, the underlying evolutionary processes are not part of the proximate RDH framework (Johnson et al. 2002; Macdonald and Johnson 2015).

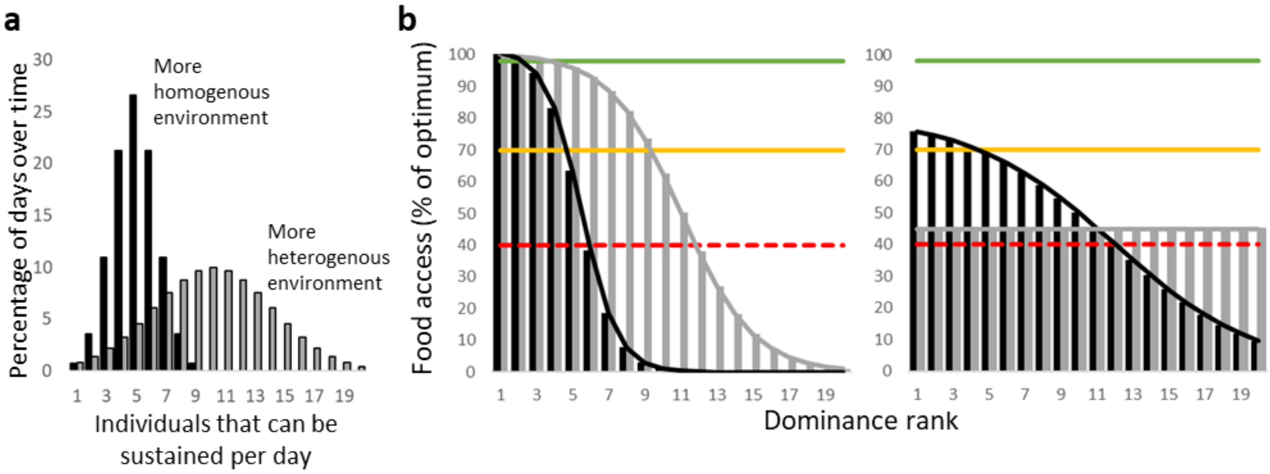

Figure 1: The temporal Resource Dispersion Hypothesis (RDH; schematic). Colored lines: Minimal resources required for optimal reproduction (green), suboptimal reproduction (orange) and survival (red and dotted). **(a)** Territory holders must hold a territory that provides sufficient resources also at the worst times, which in a temporally more heterogeneous (grey) than homogenous (black) environment means a territory with higher mean resource abundance and a higher proportion of days with high food abundance over time that allows for additional individuals (adopted from (Macdonald and Johnson 2015)). **(b)** *Left:* Translated into PoA-curves, only a few individuals can optimally reproduce, with a few more being able to reproduce sub-optimally and some more to survive without reproduction, with the respective numbers being larger in a more (grey) compared to a less (black) heterogeneous environment. *Right:* Under scramble competition (black: mixed contest and scramble, grey: pure scramble) territory holders face costs because they cannot hold complete PoA to resources and may even fail to reproduce, or would have to maintain a larger territory.

There is considerable evidence consistent with the RDH (reviewed in Macdonald and Johnson 2015), particularly from carnivore species that show shifts from solitariness to grouping (Marino et al. 2012; Macdonald and Johnson 2015; Mosser et al. 2015; Mbizah et al. 2019) related to food abundance. Similarly, territory size often correlates positively with dispersion of food patches or negatively with richness of food patches (Macdonald and Johnson 2015). However, these findings are not only consistent with the RDH but with most ecological hypotheses, including concepts of ideal free and despotic distributions and optimality models of foraging, territory size and economic defendability (Brown 1964; Ricklefs 2008; Davies et al. 2012). Central predictions of the RDH are that under the same ecological conditions, group size is not correlated to territory size (which is always defined by the needs of the primary territory holders only) and that group size is also not related to any other direct benefits of group-living (Johnson et al. 2002; Macdonald and Johnson 2015). However, it is hard to obtain support for this prediction as non-correlations may be due to methodical or statistical issues, and potential benefits of group formation may have been overlooked (e.g. Elbroch et al. 2017). Even proponents of the RDH agree that, although there is plenty of empirical evidence that conforms with predictions from the RDH, there is only marginal evidence that provides direct, exclusive support for it, whereas others have even questioned its falsifiability (Johnson and Macdonald 2003; Johnson et al. 2003; Macdonald and Johnson 2015). One reason might be that group-derived benefits may often emerge automatically even in loose short-term aggregations, which makes it difficult to test whether groups would have formed and maintained without these benefits.

RDH vs SEM

The RDH and the SEM address different aspects and are not mutually exclusive but complementary, allowing to integrate the two hypotheses into a single model. The main difference between the RDH and the SEM is that the RDH provides a proximate explanation whereas the SEM mainly addresses ultimate explanations based on the evolutionary relevant fitness costs and benefits of sociality. Under the same feeding competition, the SEM allows larger and more stable groups depending on the mitigation of the costs through group benefits and social tolerance (van Schaik 1989; Sterck et al. 1997; Macdonald and Johnson 2015). The RDH lacks such mitigating mechanisms (Macdonald and Johnson 2015), potentially leading to fluctuations in group size in reaction to changes in local key resource abundance and the opportunities that are available elsewhere. The SEM therefore complements the RDH by a) providing comprehensive explanations for stable group maintenance when gregariousness is or becomes costly and b) going beyond explanations for social organization by addressing variation in social structure and behavior (Macdonald and Johnson 2015). In contrast, the SEM does not explicitly address the proximate formation of stable groups in the absence of group benefits, as outlined by the RDH.

Despite their different perspectives, the two hypotheses normally make similar predictions. If food resources are plentiful, feeding competition is negligible and individuals can peacefully coexist in both cases. Prevailing scramble competition promotes a reduction in group size under both hypotheses (see below; van Schaik 1989; Sterck et al. 1997; Łomnicki 2009; Berghänel et al. 2010), although the SEM allows larger optimal group sizes depending on the benefits of group living (van Schaik 1989; Isbell 1991, 2004; Sterck et al. 1997; Majolo et al. 2008; Macdonald and Johnson 2015; Port et al. 2017, 2020). Under prevailing contest competition, both hypotheses predict negligible costs for top-ranking individuals, whereas lower-ranking individuals may face costs depending on the actual food abundance. Here, the RDH differs from the SEM by hypothesizing that in a typical heterogeneous environment, periods of very low food abundance are rare and the costs to secondaries negligible, whereas the SEM emphasizes the inevitable costs to lower-ranking individuals and the need for compensating benefits and/or social tolerance for them to stay (van Schaik 1989; Sterck et al. 1997; Macdonald and Johnson 2015). However, the RDH primarily aims to explain the widespread formation of small groups in carnivores with a handful of secondaries, including occasional stable group formation in rather solitary species (Carr and Macdonald 1986; Johnson et al. 2002; Macdonald and Johnson 2015), whereas the SEM typically aims to explain the evolution and maintenance of large groups of 50 or more individuals that are typical for primates. The typical number of secondaries maintained under a RDH scenario would thus often describe the top-ranking individuals in a typical SEM scenario. Some top-predator carnivore species may also differ from non-carnivore species like primates by a) mobile food patches that may cross territory boundaries (depending on their own territoriality) and introduce between-group scramble or contest competition and b) fierce competition with scavengers like ravens and hyenas. However, qualitatively similar effects will also be caused by home range overlap, scroungers and between-species contest competition in primates. Hence these differences are unlikely to explain qualitative differences between the SEM and the RDH.

In the following sections, we discuss how the SEM and the RDH may enhance each other, with a particular focus on how an integrated perspective may change our view on the impact of scramble competition. We argue that

a) under a RDH scenario, scramble competition would cause costs to territory holders or top-ranking individuals which then should evict lower-ranking group members or inhibit group formation entirely,
b) stable group formation requires social tolerance of group membership by primary territory owners and the provision of group benefits to them under prevailing within-group scramble competition, and
c) the striving for high rank and primary territory ownership can be an adaptive strategy even under pure within-group scramble competition if group size regulation and eviction are rank-dependent.

Scramble competition and the RDH

Integrating SEM arguments and the distinction between contest and scramble competition into the RDH helps clarifying the theoretical basis of the RDH. The RDH is a hypothetical, proximate model that, translated into this terminology, is based on a PoA scheme under pure contest competition (Fig. 1). According to the RDH, stable group formation can be cost-free to the primary territory holders, but according to the SEM, this is only true under the rare conditions of pure contest competition, where the territory holders can maintain complete PoA to saturate their needs. Even small scramble components can impose costs on the territory holders and restrict group formation, an important aspect that has been largely neglected (Fig. 1) (Bacon et al. 1991; Wrangham et al. 1993; Buckley and Ruxton 2003; Johnson et al. 2003). Such scramble-imposed costs would theoretically require territory holders to enlarge their territory and ranging area (Clutton-Brock and Parker 1992; Lukas and Clutton-Brock 2013), or to evict secondary, lower-ranking individuals if there are no other benefits of group formation to the primary territory holders such as kin selection and nepotistic effects, enhanced territory defense and access to resources, or reduced predation and infanticide risk (Clutton-Brock and Parker 1992; Port et al. 2017).

Consequently, under temporal resource heterogeneity with a scramble competition component, territory holders can only ensure their needs during periods of minimal food abundance if they prevent access to resources, evict group members or enlarge their territory. Hence the formation and maintenance of stable groups would be constrained and group size would be expected to fluctuate with resource abundance, with complete eviction of others during periods of minimal resource abundance (Johnson and Gaines 1990). Although this would hamper the formation of stable groups, it would allow floaters to visit during periods of higher resource abundance, wandering between multiple territories.

Furthermore, scramble components may cause costs and limit group size and group formation even under high resource abundance, as group sizes beyond the maximal saturable size will impose costs on territory holders in terms of reduced access to resources. In the temporal scenario, it may be difficult for one or two territory holders to limit the group size to the maximal saturable group size if the resource patches are not completely monopolizable. Hence allowing group formation may always incur costs under scramble competition, also during periods of high food abundance. This applies also to many spatial RDH-scenarios where groups aggregate and are maintained around habitually large and rich food patches. Under such conditions, territory holders will often be unable to control group size and limit it to the maximal saturable size, and larger-than-optimal groups may aggregate and swamp the patch, causing strong scramble competition (Berghänel et al. in press; but see Prior and Weatherhead 1991). Indeed, in both the temporal and the spatial RDH scenario, group size limitation at food patches that are not entirely monopolizable by the primary territory holders may require collective patch defense, which then represents an important benefit of group formation. In conclusion, scramble competition may constrain stable group formation in many scenarios, and the primary territory holder(s) will typically do best if they prevent group formation as long as it does not yield benefits through e.g. kin selection, enhanced territory defense or safety (Isbell 2004; Port et al. 2020).

Stable groups may nonetheless form if exclusion and eviction of additional group members bears costs for the primary territory holder(s). This can be particularly the case if secondaries accept escalating fights to resist eviction because leaving causes high reproductive or even survival costs. The resulting coerced aggregations would not be cost-free to the territory holders and should be characterized by agonistic relationships and mutual avoidance rather than social gregariousness (Ostner and Schülke 2014), so would not meet the criteria of the RDH. Similarly, territory holders may benefit from filling "empty slots" with relatives and particularly their own offspring, which would mitigate potential scramble competition costs (Sterck et al. 1997; Isbell 2004; Port et al. 2020). Such kin selection and philopatry would then represent a benefit of group formation though, and group formation would not require an RDH constellation.

Stable group formation under scramble competition can however occur if subordinates or secondaries respond to the threat of eviction by concession to the top rankers respective primary territory holder(s), suppressing their own resource exploitation or even reproduction, thereby mitigating the costs to territory holders (Johnstone and Cant 1999; Cant et al. 2014; Freeman 2021). This would provide the territory holder(s) with PoA and induce a reproductive skew even under pure scramble competition. However, concessions by subordinates to dominants in response to threat of eviction require that eviction is costly, and that group membership provides benefits, although not necessarily to the territory holders.

Translating the RDH into a framework of contest and scramble competition and implementing arguments from the SEM may allow reassessment of certain scenarios and findings that were interpreted as support for the RDH. This applies specifically to cases where territory or group size increase with more dispersed and/or unpredictable occurrence of food patches (Macdonald and Johnson 2015). From an RDH perspective, larger territory size is required under larger fluctuation or uncertainty in food abundance, which in parallel also allows the maintenance of larger groups, thereby supporting the RDH. However, from a SEM perspective, more dispersed and/or unpredictable food patches also reduce food patch monopolizability and increase scramble competition, leading to costs and larger required territories for the primary territory holder(s).

European badgers (*Meles meles*) were interpreted as a par excellence case for a RDH scenario because they live in large stable groups and were argued to show no obvious benefits of group living (Macdonald and Johnson 2015). However, they mainly forage on earthworms and thus "food patches that are hard to partition but easy to share" (Macdonald and Johnson 2015; see also Kruuk and Parish 1982), which describes a spatial RDH scenario that is highly prone to scramble competition and thus costs to the primary territory holder(s). In line with our argumentation, badger groups occupy and defend territories (Kilshaw et al. 2009), indicating between-group contest competition and thus direct benefits of stable group formation. Group members mark their territory borders actively at specific latrines, which likely also provide information to neighboring groups like about group numerosity (Stewart et al. 2001; Kilshaw et al. 2009; Tinnesand et al. 2015). They reciprocally exchange affiliative behaviors (grooming) and actively maintain a group odor that provides information about group membership (Buesching et al. 2003; Macdonald and Johnson 2015). At the heart of the territory are large, safe underground dens which are inherited over many generations and provide philopatric benefits, with such fossoriality being generally a strong correlate of sociality in carnivores and rodents (Doncaster and Woodroffe 1993; Noonan et al. 2015). Hence, badgers gain high benefits from group living through collective defense of a valuable territory.

Scramble competition and the SEM

Integrating the RDH perspective may also help clarifying the role of scramble competition in the SEM. Generally, prevailing scramble competition regarding all relevant resources is often seen as leading to an egalitarian and rather peaceful social style without strong or stable dominance relationships (van Schaik 1989; Sterck et al. 1997; Clutton-Brock and Janson 2012). Here the RDH provides a stimulating "null model" perspective on the social dynamics when individual group membership is not fixed but under permanent reconsideration, and eviction from the group is a permanent threat. As outlined above, the RDH perspective highlights two aspects. First, under pure contest competition, group size and its regulation through eviction is not relevant for top rankers from the perspective of competition. Second, if scramble competition occurs, it can be reduced by reducing group size through eviction of subordinate group members and prevention of immigration (Clutton-Brock and Huchard 2013). This option also remains if social group formation provides benefits to the territory owners, leading to different optimal group sizes depending on the actual socioecological costs and benefits and thus a potential for social tolerance of group membership by top-rankers (Isbell 1991, 2004; Parker 2000; Berghänel et al. 2010; Teichroeb and Sicotte 2018; Prox et al. 2023).

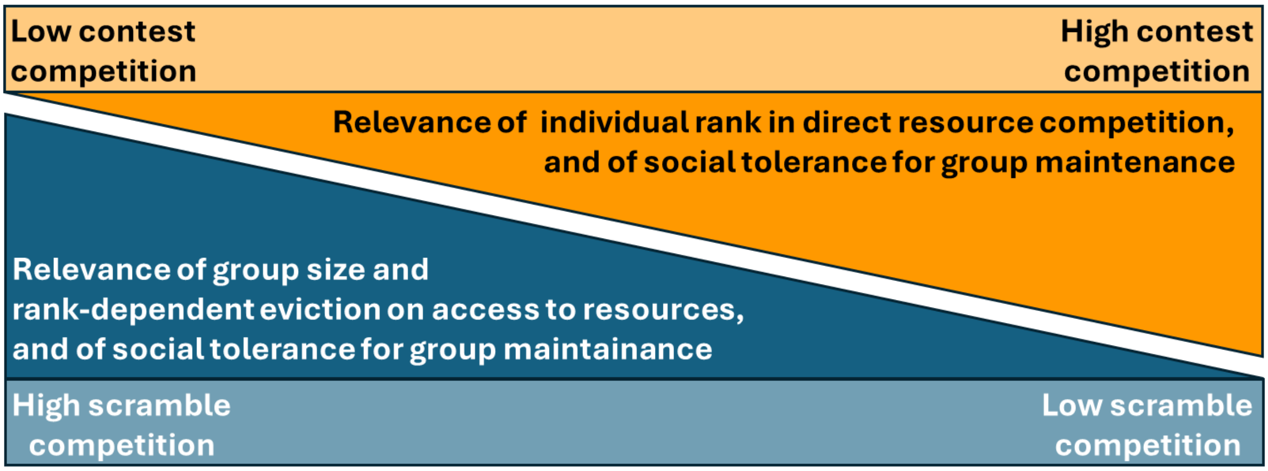

Figure 2: Dominance relationships and social tolerance can be important under within-group contest as well as scramble competition. Orange: Under pure contest competition (direct competition), individual access to resources depends on rank and is independent of group size, and group maintenance may depend on social tolerance towards lower-ranking individuals during direct competition. The relevance and impact of such rank-dependent priority of access and social tolerance during direct competition decreases with decreasing contest and increasing scramble competition. Blue: With increasing scramble competition (indirect competition), individual access to resources depends increasingly on group size and can be regulated by rank-dependent eviction of lower-ranking individuals. Group maintenance may then depend on social tolerance towards lower-ranking individuals regarding group membership.

Scramble competition and dominance relationships

In contrast to classic SEM argumentation, the opportunity to evict or at least peripheralize potential competitors suggests that pronounced dominance relationships can also be adaptive under prevailing or even pure within-group scramble competition (Isbell 2004; Port et al. 2017, 2020; Majolo et al. 2020). Under prevailing within-group scramble competition, eviction will increase the share of all remaining individual(s), whereas evicted individuals may face strong fitness costs, ranging from reduced access to resources to reduced reproduction (including abortion of current offspring) to certain death. Hence eviction can induce skews between individuals in access to resources and reproductive success (Clutton-Brock and Huchard 2013), and thus contest competition at the population level (= global competition, (Leimar and Bshary 2022)). Eviction may result in mass eviction and/or group fission, resulting in between-group competition with one group maintaining PoA to the territory and the others loosing access (plus the potential costs of loosing group membership). Such mechanisms may also play a role in lethal agonistic interactions against same-sex immigrants to curtail group size and within-group scramble competition (Clutton-Brock and Huchard 2013; Riveros et al. 2017; Strier 2021), although such interactions may sometimes also aim to prevent rank or group takeovers by new immigrants (e.g. Jones 1980; Clutton-Brock and Huchard 2013; Ostner and Schülke 2014).

As the costs of group size for dominant individuals and thus the benefits of evicting lower-ranking individuals increase with increasing scramble competition, also the impact of dominance rank increases (Fig. 2)(Clutton-Brock and Huchard 2013). Under such conditions, a dominance hierarchy provides a gradient from primary territory holders to those that are most under threat of eviction. Hence if eviction is related to dominance rank, then high dominance ranks are also beneficial under prevailing within-group scramble competition. This notion would be in line with empirical findings. Generally, eviction and permanent group fission follows dominance relationships, with dominant individuals remaining in the territory and maintaining access to the resources, whereas lower-ranking evicted individuals become floaters (Clutton-Brock and Huchard 2013; Okamoto 2004; Port et al. 2017; Hammer et al. 2023; but see Okamoto and Matsumura 2001). This may explain the formation of dominance hierarchies under conditions where no or only weak rank effects on access to resources or reproductive success can be determined within the group. However, under such conditions it might be sufficient to maintain weak dominance relationships and fiercely fight for rank when group size and other socioecological aspects cause increased scramble competition and thus benefits and likelihood of eviction (Dittus 1988; Okamoto 2004; Larson et al. 2018; Alvarado et al. 2020; Hammer et al. 2023). This may, for example, explain matrilineal hierarchies in philopatric females (like in many primate and some carnivore species) under prevailing within-group scramble competition, particularly where fighting for rank a) increases with increasing level of scramble competition (e.g. increasing group size or daily travel distances) and is b) related to an increased likelihood of a subsequent group split, which then c) splits the group into territory holders and evicted individuals. However, within-group scramble competition can also be reduced by marginalization and peripheralization of group members, particularly recent immigrants, which may then reduce the benefits of group membership for those individuals to a degree where it effectively results in their eviction (e.g. in Barbary macaques (Macaca sylvanus) and spider monkeys (Ateles geoffroyi): Kuester and Paul 1997; Asensio et al. 2008; Berghänel et al. 2010; Riveros et al. 2017). Permanent marginalization and peripheralization of group members including reproductive suppression may then relate to rather permanent or seasonally pronounced dominance relationships.

In theory, already the threat of eviction or infanticide can cause permanent dominance hierarchies and contest competition. Just as social tolerance by dominants reduces contest and increases scramble competition (Berghänel et al. in press), threat of eviction can cause the opposite (Johnstone and Cant 1999; Cant et al. 2014). Threat of eviction by dominants can cause concessions by subordinates to avoid eviction, through helping but also through actively reduced competitive power and reduced or suppressed reproduction (Schradin 2013; Cant et al. 2014; Fischer et al. 2014; Buston and Clutton-Brock 2022). If threat of eviction causes concessions by subordinates, then this can induce rank-related skews in access to resources and reproduction within groups even under pure scramble competition, thereby inducing patterns of within-group contest competition even if resources are not monopolizable through direct dyadic competition. Evidence for concessions by subordinates in response to threat of eviction or infanticide comes from fish species, rodents, mongooses and meerkats, typically under conditions of strong within-group scramble competition and high costs of eviction (e.g. high population density) or infanticide for the victims, and threat of infanticide or eviction may also play an important role in reproductive suppression in other species

(Cant 2011; Clutton-Brock and Huchard 2013; Schradin 2013; Cant et al. 2014). However, such concessions seem rare or hidden in many other species like primates (but see Clutton-Brock and Huchard 2013), even though concession-making evolved and occurs in the form of social tolerance towards subordinates (DeTroy et al. 2022). It was argued that threats of eviction or infanticide may be an effective strategy only under certain conditions, such as the ability to direct the threat explicitly and individually at the intended target (for a detailed discussion see (Cant 2011; Cant et al. 2014)). Moreover, whether or not threats of eviction can at all be effective depends on the lost benefits of group membership like safety from predation, or access to resources under high habitat saturation. The costs may be mitigated if eviction causes group splits rather than solitary evictions, since the benefits of group membership maintain and the subordinate subgroup may loose access to resources to some degree but not entirely. Finally, in female philopatric societies and under prevailing within-group scramble competition, eviction and group fission may just occur along "predefined" kinship lines like matrilines (Okamoto and Matsumura 2001; Prox et al. 2023).

Scramble competition and social tolerance

This perspective also challenges classic arguments about the nature and occurrence of social tolerance, i.e. the inhibition of one’s own competitive capability and instead making concessions to lower-ranking competitors to facilitate collective action like territory defense. Considering the opportunity to evict or at least peripheralize potential competitors under scramble competition, not only a dominance hierarchy but also social tolerance of group membership by dominants may occur under within-group scramble competition, at least if larger social groups provide benefits in e.g. between-group contest competition and resource defense (Isbell 2004; Port et al. 2017, 2020; Majolo et al. 2020). As the scramble costs for dominant individuals increase, also the benefits of evicting lower-ranking individuals increase. Group maintenance and cohesion then requires that dominant individuals do not insist on eviction and peripheralization, which represents a form of social tolerance in terms of granting group membership (Fig. 2)(Clutton-Brock and Huchard 2013).

Importantly, this does not challenge the notion that social tolerance requires contest competition. Generally, the SEM postulates that social tolerance requires a certain level of contest competition, because concession-making requires that the concession maker could do differently, i.e., could monopolize the resource (Sterck et al. 1997; DeTroy et al. 2022). Consequently, the relevance of social tolerance for group maintenance and cohesion decreases with a decreasing contest component and/or an increasing scramble component of competition, since subordinates are increasingly able to gain their share anyway ((Sterck et al. 1997; DeTroy et al. 2022); Fig. 2). However, the shift in perspective is that even under pure within-group scramble competition, competitive prospects can emerge from the opportunity to declare individuals as outcasts and excluding them from the group and the group-defended resources (Isbell 2004; Clutton-Brock and Huchard 2013; Port et al. 2017). Hence this aspect of social tolerance does not directly apply to local within-group scramble competition, but the opportunity to defend resources against outsiders and thus global between-group contest competition (Clutton-Brock and Huchard 2013; Teichroeb and Sicotte 2018; Leimar and Bshary 2022). Therefore, the argumentation that social tolerance requires contest competition remains valid. However, it also highlights that a categorical differentiation between within-group and between-group competition may underestimate the complexity and continuity in social organization and structure. In particular, this may explain why strong between-group contest competition is often not or only loosely related to social tolerance (Lu 2008; Grueter 2013; DeTroy et al. 2022): It may just loom as a thread into and thereby directly affect within-group social relationships.

Conclusions

We have shown how two major socioecological hypotheses can complement each other and can be integrated, and how such an integration of different hypotheses can advance our understanding of socioecological processes and particularly the potential impact of scramble competition. The SEM provides an ultimate framework for the evolution of sociality based on the fitness costs and benefits of living in groups, and how ecological conditions and particularly the spatiotemporal distribution of resources influences social organization, behavior and relationships. However, the SEM lacks an explanation of how groups form in the first place specifically in territorial species, which would be a prerequisite for directed selection on the costs and benefits of sociality. The RDH fills this gap, proposing a mechanism that allows group formation and to some degree also stable maintenance in territorial species even in the absence of direct benefits of sociality.

Integrating the two hypotheses and merging their terminology further reveals potential pitfalls in their current argumentations. Integrating the distinction between contest and scramble competition into the RDH reveals that its basic assumption of group formation without costs for the primary territory holder(s) is valid only under pure contest competition and strict PoA, whereas even a slight scramble competition component violates this assumption. Hence the occurrence of RDH-based group formation may be more limited than previously thought. On the other hand, the dynamic perspective on group membership that underlies the RDH may highlight a misconception about the role of scramble competition in the SEM that stems from the rather dichotomous distinction between within- and between-group competition. We outlined how pronounced dominance hierarchies and social tolerance by dominants may also be relevant under prevailing or even pure within-group scramble competition, due to rank-related control of group size and (thread of) eviction and peripheralization. Although this perspective is not particularly new (see e.g. Asensio et al. 2008; Berghänel et al. 2010; Clutton-Brock and Huchard 2013; Port et al. 2017; Riveros et al. 2017), it requires stronger consideration and implementation in socioecological hypotheses and research.

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Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

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