

Behavioural ecology at the spatial–social interface

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ABSTRACT

Spatial and social behaviour are fundamental aspects of an animal's biology, and their social and spatial environments are indelibly linked through mutual causes and shared consequences. We define the 'spatial–social interface' as intersection of social and spatial aspects of individuals' phenotypes and environments. Behavioural variation at the spatial–social interface has implications for ecological and evolutionary processes including pathogen transmission, population dynamics, and the evolution of social systems. We link spatial and social processes through a foundation of shared theory, vocabulary, and methods. We provide examples and future directions for the integration of spatial and social behaviour and environments. We introduce key concepts and approaches that either implicitly or explicitly integrate social and spatial processes, for example, graph theory, density-dependent habitat selection, and niche specialization. Finally, we discuss how movement ecology helps link the spatial–social interface. Our review integrates social and spatial behavioural ecology and identifies testable hypotheses at the spatial–social interface.

Key words: behavioural ecology, collective movement, ecological niche, social environment, social niche, social phenotype, social network, spatial environment, spatial phenotype.

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I. INTRODUCTION

Animals constantly engage in spatial and social behaviours, for example, moving among preferred habitat types or foraging sites and switching social groups to associate with preferred social partners. Both spatial (i.e. habitat preference) and social (i.e. social preferences) behaviour inform movement, and movement generates patterns (e.g. the route the individual took across the landscape, and the conspecifics with whom the animal was associated, respectively) and consequences (e.g. seed dispersal or disease transmission, respectively) in both the spatial and social domains. In some cases, spatial behaviours can occur in the absence of a social change if social groups move from location to location together (or if individuals are solitary); and similarly, social context can change even while an individual's space use remains constant if other individuals depart from or join a focal animal's group. Often, however, spatial and social behaviours arise in tandem, with animals moving through social contexts and spatial locations simultaneously. Tests of hypotheses that explicitly quantify spatial behaviours and overlook social processes, or *vice versa*, may result in misallocation of effects that are interactive, limiting the predictive capacities of both domains. Yet, simultaneously accounting for spatial and social drivers of behaviour remains a challenge, due in part to simple miscommunication across the spatial and social ecological research boundary. Here, we propose a synthesis that explicitly integrates theory, methods, and vocabulary from social and spatial ecology. Ultimately, we aim to benefit empiricists and theoreticians who address increasingly complex questions requiring inter-disciplinary solutions.

At many levels, social and spatial behaviours are inherently intertwined. Despite being strongly interconnected through their origins, interactions, and emergent implications, spatial

and social processes have predominantly been considered independently for a variety of reasons. The study of sociality is rooted in ethology and the direct observation of social interactions (Tinbergen, 1963; Altmann, 1974), while the study of spatial ecology is rooted in the investigation of macroecological and landscape-scale patterns of animal space use (Vandermeer, 1972). Historical integrations of the two domains do exist, for instance, social behaviour (in the form of competition) has been incorporated implicitly into models of space use and habitat selection (MacArthur & Levins, 1964; Fretwell & Lucas, 1969). Meanwhile, spatial context has been incorporated implicitly into historical models of cooperation and altruism (Axelrod & Hamilton, 1981; Nowak, Bonhoeffer & May, 1994). However, in most cases these inclusions were implicit and relatively limited in scope.

Accounting for the inherent connection between social and spatial behaviour fundamentally advances the study of the mechanisms and consequences of behaviour across ecological scales. Spatial behaviours (e.g. dispersal), and social behaviours (e.g. network centrality), are influenced by similar mechanistic drivers like predation (Creel, Schuette & Christianson, 2014), foraging (Giraldeau & Dubois, 2008), mating (Maldonado-Chaparro *et al.*, 2018), or parasitism (Albery *et al.*, 2020a). For example, predation risk is a single mechanistic driver that manifests through both social aggregations of animals for shared vigilance (Lima, 1995), predator confusion (Krause & Godin, 1995), and space-use patterns that reflect an underlying 'landscape of fear' (Brown, Laundré & Gurung, 1999; Peers *et al.*, 2018). Additionally, spatial and social behaviours can influence each other (Spiegel *et al.*, 2016; Webber & Vander Wal, 2018). The spatial distribution of resources drives the spatial proximity patterns that are prerequisite for many forms of social interaction, for example, information about food sources

affects space-use decisions (Firth & Sheldon, 2016; Spiegel & Crofoot, 2016). Finally, social and spatial behaviours can have shared consequences. For example, spatial behaviours, such as habitat selection, are fundamental for resource acquisition and depletion (Duparc *et al.*, 2019), and animals often form social groups to gain access to certain resources or to improve foraging efficiency (Glück, 1987; Silk, 2007; Cantor *et al.*, 2021) both of which can alter ecological (i.e. spatial consequences) and population dynamics.

Empirical studies that incorporate both spatial and social components are beginning to emerge and span diverse fields. For example, social learning and cultural transmission have been identified as mechanisms by which ungulate migrations evolve (Jesmer *et al.*, 2018). Meanwhile, selection on social centrality differed significantly among subpopulations of forked fungus beetles (*Bolitotherus cornutus*) suggesting spatial variation in selection among discrete populations within a broader meta-population (Formica *et al.*, 2021). Empirical integration of concepts from spatial and social ecology can be attributed to advances in biologging technologies, which have historically informed spatial dimensions of behaviour (Kays *et al.*, 2015), and are now used to characterize diverse social dimensions of behaviour (Spiegel *et al.*, 2015; Smith & Pinter-Wollman, 2021), for example, the link between associations and kinship (Godfrey *et al.*, 2014), the mechanisms of collective decision-making (Strandburg-Peshkin *et al.*, 2015), and the spread of novel behaviours through populations (Aplin *et al.*, 2015). Despite their utility and increasing accessibility, core concepts at the interface between spatial and social ecology lack formal integration. We suggest four main causes for this disconnect. (i) Hypotheses or questions about spatial or social behaviours may only implicitly reference one another (e.g. spatial ecology may imply certain social processes, and *vice versa*). (ii) Semantic gaps impede the ability of practitioners to identify points for analogy or synergy that would improve unification. (iii) Differences in methods and sampling design may inhibit formal integration. (iv) Spatial and social behaviour are often quantified and studied at different temporal and spatial scales that preclude formal integration.

Mechanistic enquiries into animal movements offer an opportunity to integrate spatial and social processes and map them to corresponding spatial (i.e. movement) and social (i.e. dyadic interaction) patterns. To interact with conspecifics, animals must move with, or towards, one another. Meanwhile, patterns of space use emerge from animals moving and changing the environments in which they reside (Van Moorter *et al.*, 2016). Thus, both social and spatial behaviour produce movement, which has consequences that feed back into future movement decisions. Conveniently, movement ecology is a unifying paradigm that integrates animal space use with components of the social and spatial environments (Nathan *et al.*, 2008). The movement ecology paradigm is rooted in behavioural, cognitive, and spatial ecology (Nathan *et al.*, 2008) and the intuitive integration of space use, sociality, and movement is becoming more prevalent, for example through mechanistic movement modelling

(Schlägel *et al.*, 2019; Potts *et al.*, 2022) and quantification of dyadic movement interactions (Joo *et al.*, 2018; Noonan *et al.*, 2021).

Bridging theory and methods from social and spatial behaviour has several benefits: first, by uncovering how and why spatial and social behaviours influence one another in additive or synergistic ways; second, by sharing useful concepts and theory across disciplines; and third, by improving accuracy, breadth, and reliability of models of behaviour by incorporating drivers from one field into the other, and the tools we use for investigating these questions. To improve the integration of spatial and social behaviour, we present a synthetic framework that integrates theory and methods from these two fields. Our framework has five objectives: (i) to develop conceptual links between social and spatial behaviours and propose a series of testable hypotheses at the spatial–social interface; (ii) to identify shared concepts and vocabulary and reduce inconsistent terminology (Tables 1 and 2); (iii) to discuss the implicit and explicit integration of social and spatial phenotypes and environments (Section III); (iv) to highlight foundational ecological concepts in which the integration of social and spatial behaviours remains implicit (Section IV); and (v) to propose future directions of research at the spatial–social interface, with movement and network analysis as links (Section V).

II. WHAT IS THE SPATIAL–SOCIAL INTERFACE?

We define the spatial–social interface as the proximate and ultimate interactions between social and spatial phenotypes and environments and define this interface to operate as four interconnected components (Fig. 1). In this framework, individual social phenotypes and the social environment are linked to individual spatial phenotypes and to the underlying spatial environment (see Table 1 for a glossary of key terms). A phenotype is a suite of measurable characteristics that reflects underlying interactions between an individual's genotype and its environment. Social and spatial phenotypes are individually quantifiable traits, including mate preferences, social network centrality, home range size, and dispersal distance (Fig. 1). For a phenotype to evolve, it must differ between individuals, be heritable (and repeatable for behavioural phenotypes), and ultimately drive variation in fitness. Many social and spatial phenotypes have the potential to meet these criteria and be categorized as important evolved traits, although the assumptions are rarely confirmed *per se*. An environment is a set of spatial or social elements that an animal faces (Table 1) and can be characterized by risks, resources, and conditions (Manly *et al.*, 2002; Matthiopoulos, Fieberg & Aarts, 2020). The fitness outcomes associated with an environment can differ among individuals: for example, lifetime reproductive success (i.e. fitness) is the result of certain individual (predetermined) genotypes and their plastic phenotypes may be more or less optimal for a certain environment – for example, different habitat or social group configurations.

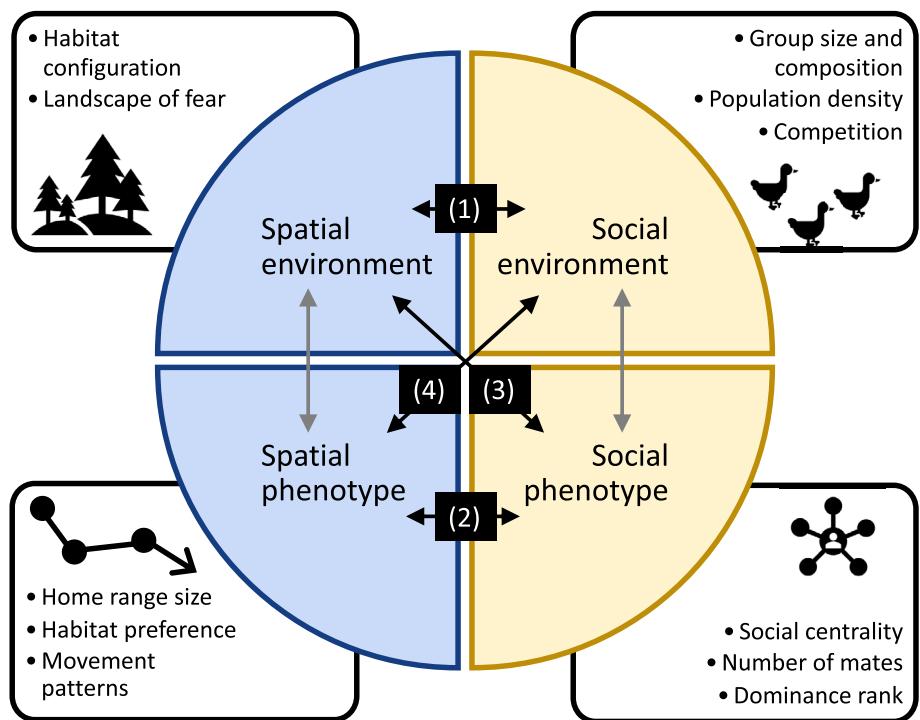


Fig. 1. Conceptual symmetry at the spatial–social interface, decomposed into (1) spatial *versus* social environment; (2) spatial *versus* social phenotype; (3) social phenotype *versus* spatial environment; (4) spatial phenotype *versus* social environment. Numbers for each pairwise interaction correspond to the detailed overviews of each interaction in Section III. Social phenotypes emerge from interactions among individuals, including social centrality, number of mates, and dominance rank, while the social environment comprises aggregative attributes of individuals, including group size and composition, population density, and competition. Similarly, spatial phenotypes comprise movement behaviours to, from, and within geographic and environmental space, including home range size, habitat preference, and movement patterns, while the spatial environment incorporates aspects of geographic and environmental space, including habitat configuration and the landscape of fear. The social phenotype–social environment and spatial phenotype–spatial environment arrows are shown in grey as these domains are well covered in existing literature and conceptual frameworks.

An individual's spatial environment involves two components: geographic and environmental space (Van Moorter *et al.*, 2016) (Table 1). Geographic space concerns the position, size, shape and location of animals' home ranges and the physical attributes of their ranges in two- or three-dimensional space (Moorcroft, 2012). Environmental space comprises abiotic and biotic factors like climatic conditions (e.g. temperature or humidity), risks (e.g. predators), resources (e.g. mates or food) and their spatial distributions (Manly *et al.*, 2002; Matthiopoulos *et al.*, 2020). An individual's fitness depends in part on its spatial environment, and the scale of the spatial environment is dependent on the ability of an animal to move: the fitness of long-distance migrants may depend on climatic conditions over whole wintering and breeding grounds, while fitness for small rodents is more likely to depend on responses to local weather conditions. Animals have physiological and energetic requirements that must be met by the surrounding biotic and abiotic conditions. Thus, environmental space limits geographic ranges to locations within the species' and an individual's ecological niche. Together, available geographic and environmental space dictate accessibility and the suite of resources, risks, and conditions that the animal must face to survive, grow, and reproduce.

The social environment is conventionally defined as the size and composition of a group and the type of interactions (e.g. affiliative, agnostic, etc.) among individuals within a group or population (Table 1). [Correction added on 2 February 2023, after first online publication: In the preceding sentence, changes have been made to the article content to improve clarity in this version.] Examples of the social environment include group size, group composition, fission–fusion dynamics, and the extent to which individuals compete with one another. We note that the social environment is not limited to species that are strictly social, as evidenced by social behaviours, such as the 'dear enemy effect' (Temeles, 1994), being expressed in territorial species. The social environment can differ among individuals within the same group, for example when different individuals have different interactions with one another. It can also be comprised of different types of relationships, such as to both conspecifics and heterospecifics (Goodale *et al.*, 2020), with the latter potentially also providing fitness benefits.

An individual's spatial phenotype incorporates aspects of space use and is defined as the movement within the spatial environment. Spatial phenotypes are context-dependent and emerge from the geographic space (i.e. latitude and longitude)

Table 1. Glossary of key terms.

Term	Definition
Animal personality or behavioural type	Consistent differences in behaviour among individuals over space or time (Sih <i>et al.</i> , 2004).
Behavioural syndrome	Covariation, or correlations, between consistent among-individual differences in behaviour over time and/or across situations (Sih <i>et al.</i> , 2004).
Behavioural reaction norm	The behavioural phenotypes that a single individual produces over a set of environments (Dingemanse <i>et al.</i> , 2010).
Environment	Set of spatial or social elements that an animal faces (see below for definitions of spatial and social environments).
Environmental space	The conditions (e.g. temperature or humidity), risks (e.g. predators), and resources (e.g. mates, food) and their spatial distributions within which an individual exists (Matthiopoulos <i>et al.</i> , 2020).
Geographic space	The position, size, shape, and location of home ranges and the physical attributes within the range of an animal (Moorecroft, 2012).
Phenotype	Suite of measurable and consistent characteristics that emerge from interactions between an individual's genotype and its environment.
Spatial proximity	Adjacency of individuals in space, which can be measured as Euclidean distance.
Social association	Animals' tendency to be in spatial proximity; usually a prerequisite for social interaction (Ginsberg & Young, 1992).
Social environment	The size and composition of a group and the type of interactions (e.g. affiliative, agonistic, etc.) among individuals within a group or population (Farine, 2015).
Social phenotype	The social position of an individual in a society that emerges from its social interactions (e.g. mating, grooming, etc.) with other individuals.
Spatial environment	The environment that concerns both geographic and environmental space.
Spatial phenotype	Spatial phenotypes incorporate aspects of space use and are defined as the movement within the spatial environment.

an individual occupies, which corresponds to environmental space (i.e. the biotic and abiotic components that make up conditions, risks, and resources). Spatial phenotypes can be either pattern-based or process-based. Pattern-based spatial phenotypes also emerge from geographic space and include those that directly relate to movement, e.g. daily movement distances

(Hertel *et al.*, 2020; Michelangeli *et al.*, 2022), dispersal (Cote *et al.*, 2017) or migration (Shaw, 2020), and spatial phenotypes that emerge from patterns of movement, such as home range size (Schirmer *et al.*, 2019). Process-based spatial phenotypes include habitat selection (Leclerc *et al.*, 2016), environmental niche specialization (Sheppard *et al.*, 2018; Carlson *et al.*, 2021), or foraging search performance (Webber *et al.*, 2020). These spatial phenotypes are processes whereby an individual uses a habitat component disproportionately more than that component's availability (Manly *et al.*, 2002; Matthiopoulos *et al.*, 2020). Regardless of whether a spatial phenotype is pattern- or process-based, they are predicted to exhibit within-individual plasticity while also demonstrating consistent within- and among-individual variation (Eggeman *et al.*, 2016; Webber *et al.*, 2020). Variation in movement phenotypes may also be learned (Nielsen *et al.*, 2013) or related to natal habitat preference (Stamps, Krishnan & Willits, 2009).

An individual's social phenotype is the social position of an individual in a society that emerges from its social interactions (e.g. mating, grooming, etc.) with other individuals (Table 1). An individual's social phenotype is therefore a reflection of its position in a society (Farine, Montiglio & Spiegel, 2015). For example, mating strategies (Fisher, Rodriguez-Muñoz & Tregenza, 2016), aggression level (Kilgour *et al.*, 2018), and cooperative behaviour (Dakin & Ryder, 2018) are quantifiable social phenotypes, all of which are impacted by the social environment. Notably, an animal cannot express their mating phenotype in the absence of potential mates. Social phenotypes can also be pattern-based and process-based (Cantor *et al.*, 2021). Pattern-based social phenotypes include those that affect who an individual associate with, such as mate choice (Wang *et al.*, 2022) or differences in the social rules that individuals use when moving in a group (del Mar Delgado *et al.*, 2018) and the social properties that emerge from differences in social behaviour, such as the social position of individuals in their group (Farine *et al.*, 2017). Process-based social phenotypes include decisions that arise in response to changes in the social environment, such as group dispersion in response to competition (e.g. the Ideal Free Distribution; Fretwell & Lucas, 1969), social niche specialization (Montiglio, Ferrari & Réale, 2013), or differences in the acquisition of information arising from social position (Aplin *et al.*, 2012).

III. RELATIONSHIPS BETWEEN SOCIAL AND SPATIAL PROCESSES

Despite a lack of formal synthesis, there is implicit integration embedded in the theory and methods used regularly to study social and spatial behaviour. For example, social associations are often defined using spatial thresholds (Spiegel *et al.*, 2016) and spatial sampling designs can be informed by social structure (Mladenoff, Sickley & Wydeven, 1999). Among the four combinations of phenotypes and environments, there are six possible pairwise interactions, each with unique implications

Table 2. Concepts that appear in studies of both spatial and social behaviour.

Spatial concept	Definition	Social concept	Definition
Ecological niche	A spatial distribution that is constrained based on the biophysical and environmental conditions across geographical space that permit an individual to survive and reproduce. Niche variation is predicted to affect fitness variation.	Social niche	A set of social interactions, which are constrained by the social environments. According to the definition by Saltz <i>et al.</i> (2016), a focal individual can have non-zero inclusive fitness in their social niche.
Spatial connectivity	Structural configuration of landscape features that allows or restricts animal movement between locations. For example, rivers, lakes, or mountain ranges may facilitate or restrict spatial connectivity among individuals.	Social connectivity	The frequency or tendency for animals in a population to interact or associate with one another. The structural configuration of social connections allows or restricts individuals from interacting. For example, competition or affiliative interactions may facilitate or restrict social connectivity among individuals.
Spatial density	The potential for a phenotype of species, population, or individual to change as a function of changes in population density. Population density is typically defined as the number of animals in a given area, measured, for example, as the intensity of a Poisson point process of animal occurrences over space.	Social density	The number and strength of social interactions among individuals within a given area; can be operationalized as graph density.

for an animal's ecology (Fig. 1). With reference to movement ecology, we highlight underlying mechanisms and ecological and evolutionary consequences and identify potential areas of future research and accompanying testable hypotheses for each link (Table 3).

(1) Social environment and spatial environment

(a) Mechanisms and consequences

The spatial environment provides the geographic space within which animals aggregate, interact, and form the social environment. Therefore, the spatial environment should affect the social environment on the basis of first principles alone: the ideal gas law predicts that individuals in a high-density population will be more socially connected simply by chance compared to individuals in lower-density populations (Hutchinson & Waser, 2007). The risks, resources, and conditions associated with the spatial environment change in the presence of multiple individuals because group size and composition are conditions unto themselves. Meanwhile, animals' propensity to form groups may depend on habitat (Barja & Rosellini, 2008), time of year (Peignier *et al.*, 2019), or physical constraints of the environment (Pinter-Wollman, Jelic & Wells, 2018). For example, wildfires alter habitat and resource availability in the spatial environment of red-backed fairy wrens (*Malurus melanocephalus*), with social connectivity increases as a result (Lantz & Karubian, 2017). Similarly, the collective (i.e. social) behaviour of harvester ants is influenced by the spatial structure

of the nest (Pinter-Wollman, 2015), and the available resources in the spatial environment can shape the social environment through resource specialization (Janson & Boinski, 1992; Cantor & Farine, 2018; Sheppard *et al.*, 2021).

Reciprocally, the social environment can determine the spatial environment through effects of population density, resource depletion, habitat selection, dispersal, or direct environmental engineering. For example, the environmental engineering hypothesis (Table 3) predicts that the group composition of *Veromessor pergandei* ants with polymorphic workers determines the structure of the nests they construct (Kwapich, Valentini & Hölldobler, 2018). These nests form the spatial environment in which the ants live and function as a colony. In addition, herbivore movements can determine seed dispersal patterns (Niell *et al.*, 2020) or food availability (Janson & Boinski, 1992), which drives the subsequent distribution of plants and food in the spatial environment. Density-dependent habitat selection is the mechanism through which competition acts to determine where individuals settle and therefore the spatial environment. For example, Allee effects, which are positive relationships between individual fitness and population size or density (Stephens, Sutherland & Freckleton, 1999), can influence the speed of species invasion into new habitats, thus influencing the spatial environment in which individuals encounter one another (Taylor & Hastings, 2005). In some cases, it is clear that temporal changes in the spatial environment lead to changes in the social environment (e.g. seasonal cycles), but at most scales whether, how, and when this principle operates is still poorly known.

Table 3. Summary of hypotheses presented in Section III.

Section	Hypothesis	Prediction(s)	Key references
(III.1) Social environment and spatial environment	Social resistance hypothesis	Genetic relatedness and gene flow could be influenced by the relationship between the social and spatial environments.	Armansin <i>et al.</i> (2020)
	Environmental engineering hypothesis	The social environment of animals that build their own shelter (e.g. dens, nests, or burrows) can influence the structure of the spatial environment, for example, nests of social insects, beaver dams, or spider webs.	Doody <i>et al.</i> (2021)
(III.2) Social phenotype and spatial phenotype	Pace-of-life syndrome hypothesis	Physiology (e.g. hormone production) or life history (e.g. senescence) may shape variation in spatial and social phenotypes. Specific predictions linking physiology and life history with spatial and social phenotypes are widespread.	Silk & Hodgson (2021)
	Habitat matching hypothesis	Population density may relate to settlement decisions with less-social individuals settling in lower-density patches, which may have lower-quality resources. Foraging in low-quality habitats requires individuals to move more to encounter resources, therefore resulting in covariance between spatial and social phenotypes with less-social individuals moving more than more-social individuals.	Fagen (1987); Morris (1999)
(III.3) Social phenotype and spatial environment	Social reaction norm hypothesis	The spatial environment is composed of both dynamic (e.g. predator presence) and static (e.g. local topography) components. Social phenotypes may change in response to the dynamic components of the spatial environment and changes might happen at different temporal scales, which relate to the rate of change in the spatial environment.	Martin & Jaeggi (2021); Strickland <i>et al.</i> (2021)
	Information centre hypothesis	Social living is advantageous because individuals may acquire information about resources by following cues from informed individuals at shared locations, such as roosts or nests, and follow informed individuals to new resources.	Ward & Zahavi (1973); Harel <i>et al.</i> (2017)
(III.4) Spatial phenotype and social environment	Density-dependent dispersal hypothesis	Individuals are more likely to leave a foraging patch or disperse when population density is high.	Matthysen (2005); Cote <i>et al.</i> (2017)
	Activity budget hypothesis	Given the social environment can be simplified as either the number of competitors or number of allies in a group, the proportion of competitors (individuals of differing size) or allies (individuals of similar size) is predicted to influence spatial phenotypes (e.g. movement or foraging behaviour).	Ruckstuhl (1998)

Both the spatial and social environments are composed of constant and time-varying components. For example, in temperate environments, the emergence of plants each spring can be quantified as the normalized difference vegetation index (NDVI), an index which uses remote sensing to quantify live green vegetation in the spatial environment (Pettorelli *et al.*, 2005). NDVI varies at a given location through time, while other spatial factors, like elevation, remain constant. Similarly, in the social environment, mate availability varies through time – e.g. as ranks and female oestrus status change (Hogg, 1988) – even when kinship within a given group is constant. Temporal fluctuations in the spatial environment (e.g. food resources) may generate fluctuations in the social environment [e.g. aggregation size (Sapolsky, 1986; Brown & Brown, 2014)], and *vice versa*. For example, pulsed births in some species lead to population-wide shifts in habitat selection while neonates are young and vulnerable to predation (Ims, 1990). In some cases, elements of the social environment related to competition may

vary spatially or temporally, e.g. influenced by spatial or temporal variation in resource availability (Bonnell, Henzi & Barrett, 2019).

(b) Key next steps and testable hypotheses

An understanding of the mechanisms driving relationships between social and spatial environments requires comparable descriptions of animal social structure – ideally along with life history, phenology, or physiology – across a range of systems and spatial environments. Most pressingly, there are relatively few known scenarios in which the social environment shapes the spatial environment. The roles an individual's (or population's) social and ecological niches play in the feedback between the two types of environments remain understudied. Fitness associated with a given social environment may depend on the spatial environment, and *vice versa*. For example, some species have spatially distinct mating grounds and the spatial distribution of the social environment may be

determined by the physical locations of mating sites (Maldonado-Chaparro *et al.*, 2018). The interactive effects of the spatial and social environments on fitness are an important area for future investigation, particularly where they complicate inference of either environment's selective influence.

Finally, the spatial environment may drive aspects of the social environment from the bottom up by shaping genetic relationships among individuals, groups, and populations. For example, spatially (and therefore possibly socially) connected groups are predicted to have higher inter-group relatedness and gene flow (Armansin *et al.*, 2020). Within the context of the genetic relationships among potentially spatially constrained groups, the social resistance hypothesis (Table 3) predicts that genetic relatedness and gene flow could be influenced by the relationship between the social and spatial environments (Armansin *et al.*, 2020). The effects of social and spatial environments on genetic interrelationships present opportunities to test hypotheses about their effects on fitness and consequences for the evolution of spatial and social behaviours.

(2) Social phenotype and spatial phenotype

(a) Mechanisms and consequences

Spatial and social phenotypes are related through a variety of mechanisms, and their covariance is relatively well studied across a wide range of systems. A number of complex mechanisms underlie covariance between social and spatial phenotypes. For example, the location where individuals forage (a spatial behaviour) can be socially learned (Page & Ryan, 2006; Keyman, Ridley & Lotem, 2015), and individuals with larger home ranges may encounter more potential social partners (Albery *et al.*, 2021). Conversely, territorial species may have restricted social encounters because they are spatially constrained by the location and size of their own territories and the territories of others (Wagner, Frank & Creel, 2008). Spatial phenotypes incorporate aspects of shared preference for a given site or territorial neighbours. Consequently, social phenotypes can be highly spatially autocorrelated.

An individual's social and spatial phenotypes may be correlated because the spatial phenotype determines the way an individual engages with its environment and the social phenotype is influenced by these environmental gradients. For example, an individual exposed to an environmental stressor, such as a predator, could transmit this 'stress' to its social associates (Brandl, Pruessner & Farine, 2022), and subsequently impact their choice to forage in risky habitat. Additionally, relationships between social and spatial phenotypes may be produced by shared intrinsic drivers, like reproductive state, that affect both (Saveer *et al.*, 2012). Importantly, such apparent links may arise spuriously due to methodological approaches. For example, spatial thresholds are commonly used to infer social interactions, with varying validity and success

(Castles *et al.*, 2014; Farine, 2015; Gilbertson, White & Craft, 2021). More generally, social network position is one measure of an individual's social phenotype, but both spatial phenotypes and environments play a role in driving social network position. As such, the interpretation of social position needs to be carefully validated against known spatial phenotypes, spatiotemporal confounding variables, and null models (Pinter-Wollman *et al.*, 2013; Spiegel *et al.*, 2016; Farine, 2017; Hobson *et al.*, 2021).

Covariance between social and spatial phenotypes may be interpreted within the context of consistent individual differences in behaviour (i.e. animal personality, or behavioural types). Empirical evidence supports the idea of individual differences (i.e. repeatability) in social phenotypes through space and time (Wolf & Krause, 2014), while social assortment is the repeated interaction among individuals that share a particular trait (Croft *et al.*, 2009). Similarly, animals display consistent individual differences in spatial phenotypes (Stuber, Carlson & Jesmer, 2022). The similarities and differences in the magnitude of repeatability in spatial and social phenotypes could influence the degree to which they covary. Furthermore, consistent individual differences in spatial and social phenotypes may be linked to traditional animal personality traits (Wolf & Krause, 2014; Spiegel *et al.*, 2017), such as exploration and boldness (Nomakuchi, Park & Bell, 2009; Aplin *et al.*, 2013; McCowan *et al.*, 2015; Spiegel *et al.*, 2017). Suites of traits that are correlated across time and contexts are known as behavioural syndromes (Sih *et al.*, 2004) and in the case of the spatial–social interface, correlations between these two types of phenotypes could be interpreted as a socio-spatial behavioural syndrome (Webber & Vander Wal, 2018).

(b) Key next steps and testable hypotheses

While spatial and social phenotypes are often known to covary, the causative mechanisms underlying these links – and their ecological consequences – remain an important research priority. Spatial and social phenotypes may covary when the spatial phenotype that optimizes fitness of one social phenotype is not optimal for a different social phenotype. In theory, the strength of the covariance will then increase with increasing divergence in the fitness outcomes across spatial and social phenotype combinations. However, there are relatively few empirical examples of this phenomenon, and the mechanisms underpinning and modifying this covariance remain unknown. For example, the correlation between social and spatial phenotypes could change according to food availability, being either more or less correlated in high-resource areas. Intrinsic drivers of the relationship between social and spatial phenotypes also remain relatively under-studied, for example, indirect genetic effects (Moore, Brodie III & Wolf, 1997; McGlothlin *et al.*, 2010), hormones (Newediuk, Mastromonaco & Vander Wal, 2022; Dantzer & Newman, 2022), endocrine systems (Kelly & Vitousek, 2017), or cognition (Beardsworth *et al.*, 2021). Examining how the effects of social phenotypes on fitness are modulated by

spatial phenotypes (and *vice versa*) is another important topic for future investigation.

There are established but infrequently tested hypotheses for the mechanisms that underlie the covariance between spatial and social phenotypes (Table 3). For example, the pace-of-life syndrome hypothesis (Table 3) predicts that aspects of physiology (e.g. hormone production) or life history (e.g. senescence) will shape variation in spatial and social phenotypes (Silk & Hodgson, 2021). Similarly, the habitat matching hypothesis (Table 3) predicts that less-social individuals will settle in low-density sites and more-social individuals will settle in high-density sites, while fitness outcomes for individuals in each habitat are predicted to be approximately equal (Fagen, 1987; Morris, 1999). In many cases, low-quality habitats host lower population densities, and thus will require more movement to encounter resources while supporting individuals that are less social and competitive, which could result in covariance between spatial and social phenotypes (Cote & Clobert, 2007; Spiegel *et al.*, 2015). Similarly, habitats with high-quality, but clumped, resources are predicted to be favoured by more-social and competitive individuals with reduced local movement since high-quality patches can support more-dense populations (Spiegel *et al.*, 2017). Validating or rejecting the predictions of these hypotheses will require regular joint examination of spatial and social phenotypes across ecological systems. The ongoing rapid technological improvements facilitate accurate and high-resolution tracking of growing numbers of concurrent individuals (Nathan *et al.*, 2022), thus improving the quality of data sets to test these links.

(3) Social phenotype and spatial environment

(a) Mechanisms and consequences

The expression, costs, and benefits of social phenotypes depend on variation in the resources, risks, and climatic conditions within the spatial environment. For example, animals may form larger groups in risky habitats (Lima, 1995), huddle to save energy through social thermoregulation (Gilbert *et al.*, 2010), and use social cues to find important resources (Harel *et al.*, 2017). The information centre hypothesis (Table 3) predicts that colonial living is advantageous because individuals that lack personal information about resources benefit from following cues from informed associates, whom they follow to previously visited resources (Ward & Zahavi, 1973). While resources, risks, and climatic conditions are spatiotemporally dynamic, other aspects of the spatial environment (e.g. topographic features) can generally be considered static within the lifetime of an individual. Some habitat features (e.g. water holes or dense vegetation) may promote or inhibit social interactions among animals (Leu *et al.*, 2016). Certain landscape features, such as barriers formed by rivers or mountains, may result in insular social communities (Armansin *et al.*, 2020) and influence collective movement (Pinter-Wollman, 2015; Strandburg-Peshkin *et al.*, 2017; Pinter-Wollman *et al.*, 2018). Social phenotypes

can therefore emerge from both dynamic and static aspects of the spatial environment, and both individuals and groups may match their social phenotypes to environmental conditions.

Phenotypic plasticity is the ability of a genotype to produce distinct phenotypes when exposed to different environments over time (Pigliucci, 2005), and social phenotypes often demonstrate such plasticity. For example, social ties in guppy (*Poecilia reticulata*) social networks diminish in strength as predation pressure declines (Kelley *et al.*, 2011). Similarly, individuals can express more-competitive social phenotypes in higher-quality habitats (for a review see Fokkema *et al.*, 2021). Phenotypic plasticity is adaptive when animals can match their phenotype to environmental conditions and maintain high performance across a large environmental gradient, but plasticity may be costly (either proximately, e.g. metabolically or ultimately, e.g. mismatch between phenotype and environment) and is therefore predicted to vary in direction and magnitude (Mathot *et al.*, 2012). As such, behavioural reaction norms (see Table 1), which we consider here as behavioural phenotypes (i.e. social) that a single individual produces over a set of environments (i.e. spatial), may themselves differ across environments. For example, an individual may change its number of contacts in response to a stimulus in one environment, but not in another. Importantly, certain individuals might express this plasticity, and others might not.

Reciprocally, social phenotypes can influence the spatial environment. For example, large social aggregations may deposit nutrients *via* faeces, urine, or other bodily excreta in a given area, elevating its nutrient quality (Ellis-Soto *et al.*, 2021). Social groups that build dens or nests may improve the environment for other species: for example, yellow-spotted monitor lizards (*Varanus panoptes*) dig nesting burrows that provide refugia, feeding, and nesting habitat for other burrowing species (Doody *et al.*, 2021). Such nests can influence both nutrients in the soil and vegetation structure through seed dispersal; for example, the nests of harvester ants and termites change the nitrogen composition of the soil, which facilitates the growth of plants in the environment (Bonachela *et al.*, 2015; Farji-Brener & Werenkraut, 2017).

(b) Key next steps and testable hypotheses

The relationship between social phenotypes and the spatial environment fits well within the existing theoretical and methodological frameworks used to test the social reaction norm hypothesis (Table 3; Martin & Jaeggi, 2021; Strickland *et al.*, 2021). Examining how social phenotypes change as a function of environmental features (e.g. risks, resources, and conditions) may reveal the causes and consequences of among-individual differences in social plasticity (Piza-Roca *et al.*, 2018; Strickland, Patterson & Frere, 2018; Strickland & Frere, 2019). Similarly, given that social phenotypes differ consistently among individuals (O'Brien, Webber & Vander Wal, 2018), can be heritable (Wice & Saltz, 2021), and change as a function of the spatial environment (see

Section III.3.a), an important next step is to assess the potential for the spatial environment to select for certain social phenotypes (Formica *et al.*, 2021; Vander Wal, 2021).

Uncovering the role of social phenotypes in shaping the configuration of the spatial environment will help interrogate dynamic feedbacks between social and spatial processes (Pinter-Wollman, 2015; He, Maldonado-Chaparro & Farine, 2019). The sociality of ecosystem engineers may affect the level to which they alter the spatial environment (Doody *et al.*, 2021), while environmental conditions may impact individuals' tendency to aggregate by social phenotypes (Jolles, King & Killen, 2020). Relating social phenotypes and the spatial environment within the context of multiple contagion processes (e.g. pathogen and information transmission) is another interesting frontier that could reveal how the spatial environment influences pathogen spread and socially learned behaviours simultaneously (He *et al.*, 2021).

(4) Spatial phenotype and social environment

(a) Mechanisms and consequences

Spatial phenotypes can determine the range of social environments that animals experience. If individuals share a spatial phenotype, they might interact and form or influence the social environment. For example, the social environment may be more expansive if home ranges are large (Albery *et al.*, 2021) and overlapping (Peignier *et al.*, 2019). Conversely, the social environment can influence spatial phenotypes. For example, at high densities, the movements of individuals might be constrained based on competition among conspecifics, influencing their possible spatial phenotypes.

The activity budget literature represents a potential framework to integrate spatial phenotypes and the social environment, where habitat use and foraging behaviour actively shape the social environment (Ruckstuhl, 1998; Ruckstuhl & Neuhaus, 2000; Pérez-Barbería, Shultz & Dunbar, 2007). For example, animals assort into social groups based on similarities in activity budgets and dietary requirements (Ruckstuhl & Neuhaus, 2000; Bon *et al.*, 2001). In addition, when the social environment changes, individuals may alter their spatial phenotypes. For example, culling badgers (*Meles meles*) disrupted their social environments, causing individuals to disperse and move further than they had previously (Ham *et al.*, 2019). In another case, brown bears (*Ursus arctos*) caused surviving individuals to alter patterns of habitat selection (Frank *et al.*, 2018). Such feedbacks highlight the relevance of the link between the social environment and spatial phenotypes for management; an explanation for why culling efforts often fail to reduce local densities.

As with social phenotypes and spatial environments, the relationship between spatial phenotypes and the social environment can be considered within a behavioural reaction norm framework, describing how spatial phenotypes (e.g. movement patterns or home range size) change as a function of the social environment (e.g. group size or

population density). Spatial phenotypes are often plastic because an individual's primary response to environmental heterogeneity involves altering its space use (Day *et al.*, 2019; Schmidt & Massol, 2019). A rich literature links spatial phenotypes with aspects of the social environment, such as local density. For example, positive density-dependent dispersal occurs when competition increases the likelihood of dispersing because individuals are predicted to have higher fitness at lower-density sites (for a review see Matthysen, 2005). Similarly, negative density-dependent habitat selection exists when consumer density increases and resources within preferred habitats become limited and it may be beneficial for individuals to become less selective in their habitat use (for a review, see Avgar, Betini & Fryxell, 2020).

(b) Key next steps and testable hypotheses

Linking spatial phenotypes and the social environment requires an understanding of density dependence because population density is a salient aspect of the social environment (Matthysen, 2005; Cote *et al.*, 2017; Gil *et al.*, 2018; Avgar *et al.*, 2020). For example, the density-dependent dispersal hypothesis (Table 3; Matthysen, 2005) predicts that individuals are more likely to leave a foraging patch or disperse when population density is high (Cote *et al.*, 2017). The expectations of density-dependent dispersal also depend on phenotypes. Some individuals are expected to be less social, to disperse at higher probability from high-density environments, and to settle preferably in low-density environments (Cote *et al.*, 2017). By contrast, more social individuals may leave low-density environments and settle in high-density ones. Dispersal theory therefore intuitively extends to the expectations of the habitat matching hypothesis (see Section III.2).

The activity budget hypothesis (Table 3) can help integrate spatial phenotypes and the social environment. Spatial phenotypes associated with activity budgets include movement and foraging. As animals of a similar size, sex, and age move and forage together based on their shared energetic requirements, the social environment is shaped accordingly (Ruckstuhl, 1998). So far, there are few tests of hypotheses linking activity budgets with group size or composition, and then with survival or reproductive success. Additionally, activity budgets could be useful for investigating partitioning of the social environment: for example, the social environment can be simplified as either the number of competitors or number of allies in a group; when incorporating activity budgets, allies could represent group-mates with similar activity schedules, and an individual's competitors are its group-mates with conflicting activity budgets.

IV. SHARED CONCEPTS AND TERMINOLOGIES DESCRIBING SPATIAL AND SOCIAL BEHAVIOUR

Our framework reveals overlap in concepts and terminology among spatial and social behaviours (Fig. 1), and highlights

that multiple analogous processes bridge the spatial–social interface. In Table 2, we present terms and concepts that have similarities in the study of spatial and social behaviour. Below, we highlight five examples of concepts (niche specialization, mating systems and sexual selection, Ideal Free Distribution and density-dependent habitat selection, optimal group size theory, and geometry of the selfish herd) that explicitly or implicitly bridge the spatial–social interface. The examples are theoretically, methodologically, and empirically disparate from one another, yet application of our framework reveals opportunities to expand them all. Each concept makes rich historical reference to social or spatial ecology. In some cases, the treatment of one field is implicit, while in other cases a concerted effort has been made explicitly to integrate social and spatial processes. For instance, social processes associated with competition are implicit within the spatial structure of the Ideal Free Distribution (Morris, 2003), while spatial and social behaviour are explicitly integrated within the niche specialization literature through socioecological niche theory (Bergmüller & Taborsky, 2010). In some cases, there is historical precedent to establish linkages between two or more of these concepts, while in other cases there exists potential for novel inference based on integration of concepts. Each case is considered in detail below.

(1) Ecological and social niche specialization

The niche is a foundational concept in the field of ecology (Van Valen, 1965; Vandermeer, 1972). An ecological niche comprises the environmental conditions across geographical space that a species can inhabit based on its biology and is therefore inherently a spatial feature (see Table 2). While the traditional concept of an ecological niche was meant to apply to species, individuals also occupy niches within their species' niche, ranging from resource specialists to generalists (Bolnick *et al.*, 2003; Woo *et al.*, 2008). Individual differences in ecological niches are predicted to drive variation among individuals in fitness (Van Valen, 1965; Costa-Pereira *et al.*, 2019). Social niches (see Table 2) extend the ecological niche concept by capturing the set of social environments in which a focal individual has positive inclusive fitness (Bergmüller & Taborsky, 2010; Montiglio *et al.*, 2013; Saltz *et al.*, 2016). An application of ecological niche theory to the development of social niche theory is equating an individual's realized niche with their 'social role' (Bergmüller & Taborsky, 2010). The realized niche is the fraction of potentially suitable niches that is used, and the difference is often reflected by social constraints. Meanwhile, a social role is the '*realised behaviour or tactic an individual uses in response to social challenges such as competing for food, space or mating partners*' (Bergmüller & Taborsky, 2010, p. 1) and is predicted to change over time (Montiglio *et al.*, 2013). Some individuals may specialize in their social roles, whereas others may be generalists (Pinter-Wollman *et al.*, 2012). While key concepts from ecological niche theory have been applied to social niche theory (Montiglio *et al.*, 2013), an important next step

is to integrate the study of both social and ecological niches to assess an individual's role simultaneously in the spatial and social environments.

(2) Mating systems and sexual selection

Animal mating systems are an important component of animal sociality (Kappeler, 2019). Most animals have a wide range of social and spatial behavioural strategies that result in the emergence of different mating systems (Clutton-Brock, 1989). Furthermore, sexual selection acts on behaviours that impact access to mates and reproductive success. Within the context of the spatial–social interface, sexual selection has the potential to change the ratio of males to females (Shuster, 2009). Furthermore, among-individual variation in social and spatial phenotypes can impact variation within and among species in mating systems, such as when environmental conditions determine the extent to which mates can be defended or monopolized (Emlen & Oring, 1977). Leks present a pertinent example: males in species that form leks defend small mating territories (spatial phenotype) in large aggregations (social environment), which do not contain any resources (spatial environment) other than placing them in a favourable spot for mating opportunities (social phenotype) (Isvaran, 2005). Furthermore, Emlen & Oring (1977) proposed the environmental potential for polygamy (EPP), which measures the extent to which the social and spatial environment can facilitate the monopolization of females by males in a mating context. While the EPP has been criticized for being difficult to quantify in a natural setting (Shuster, 2009), it has direct connections to the spatial–social interface. For example, the EPP is predicted to be highest when resources (including females) are spatially clumped and female receptivity is asynchronous, while it is predicted to be lowest when resources are uniformly distributed and female receptivity is synchronous (Emlen & Oring, 1977). Finally, a number of recent studies have linked the spatial distribution of individuals in breeding territories to the social relationships that they form prior to the establishment of territories or any reproductive behaviours (Farine & Sheldon, 2015; Firth & Sheldon, 2016; Beck, Farine & Kempemaers, 2020), thereby highlighting the link between social and spatial processes in mating systems. Testing hypotheses associated explicitly with the socio-spatial aspects of mating systems provides an opportunity to integrate evolutionary theory (i.e. natural and sexual selection) within the social–spatial interface framework.

(3) Ideal Free Distribution and density-dependent habitat selection

Classic habitat selection theory is based on the Ideal Free Distribution (IFD), which posits that habitat selection is density dependent and variation in density between habitats leads to a fitness equilibrium (Fretwell & Lucas, 1969; Bradbury, Vehrencamp & Clifton, 2015). The available resources within a habitat sustain a certain number of

individuals and in a finite world (and at high densities exceeding the above-mentioned Allee effect; see Section III.1.a), fitness in a habitat is predicted to decline as a function of density (Morris, 1987, 2011). Consumers are predicted to aggregate in high-quality habitats, but space apart to reduce competition (Sutherland, 1983). While the IFD explicitly predicts that animals should assort in space to equalize fitness, the Ideal Despotic Distribution (IDD) predicts heterogeneous fitness due to dominant individuals forcing others into lower quality habitats (Oro, 2008). The IDD often occurs in territorial systems where habitat selection of subordinate individuals is constrained by territoriality of dominant individuals (Oro, 2008; O’Neil *et al.*, 2020). While the IFD and IDD implicitly incorporate social processes, there has been little *explicit* consideration of the social processes underpinning the IFD and IDD. Despite the apparent contradiction between IFD and IDD the two mechanisms may complement each other, acting on different spatial or temporal scales, depending on the properties of the system in question (e.g. territory size, resource distribution, perceptual ranges, and social information). Notably, classic habitat selection theory has inherent and historical connections to niche theory (see Section IV.1). For example, many exciting opportunities exist to quantify the role of social phenotypes and the social environment within these foundational ecological concepts to help shed light on the mechanisms that influence the distribution of animals in space.

(4) Optimal group size and optimal foraging theory

Optimal group size theory posits that group size is shaped by balancing the costs (e.g. competition) and benefits (e.g. protection from predation) of group living (Sibly, 1983; Fryxell *et al.*, 2007). Optimal group size theory explicitly addresses group size (i.e. the social environment) while the underlying spatial processes are implicit. Nevertheless, the spatial environment plays a key role determining group size and its system-specific optimal range. For example, group size–fitness optima depend on resource availability and predation risk in the habitat (Webber & Vander Wal, 2018). As highlighted in Section II, the social and spatial environments are often correlated and living in a group may be beneficial only in certain environmental conditions. Animals are therefore predicted to balance the costs and benefits of grouping as a function of the spatial environment and form groups of optimal size where fitness is maximized (Higashi & Yamamura, 1993). Eurasian jackdaws (*Coloeus monedula*), for instance, change their group size according to the available resources at different ecological contexts such as food, shelter and nesting sites (Chen *et al.*, 2022). Indeed, species with fission–fusion dynamics and those that form multilevel societies offer substantial opportunities to study the relationship between optimal group size and the spatial environment. For example, within-group conflicts of interest – differences in the optimal decision, such as when to leave a food patch, among group members – drive group fission. Applying optimal foraging theory (Krebs, 1978) predicts that conflicts of interest decrease as environmental conditions

become harsh, an explanation for the paradox of why large aggregations of animals can be observed when resources are scarce (Davis, Crofoot & Farine, 2022).

(5) Geometry of the selfish herd

The geometry of the selfish herd (GSH) describes the spatial arrangement of gregarious animals in response to predation risk (Hamilton, 1971). An important benefit of group living is the reduced *per capita* cost of predation, i.e. the detection–dilution trade-off (Krause & Ruxton, 2002). However, the geometry of the selfish herd suggests that risk is not equal among individuals in a group. Although the concept was initially formulated based on an undetected predator randomly appearing at any location within a group of prey and attacking the nearest individual (Hamilton, 1971), the domain of danger (i.e. the area around an individual in which it is exposed to predation) is often smallest at the group’s centre, in which case individuals should seek to position themselves in both spatially and socially central positions to minimize their risk of predation and maximize fitness (Morrell, Ruxton & James, 2011; Dostie *et al.*, 2016; Bonar *et al.*, 2020). For example, sheep move towards the centre of the herd when herded by dogs (King *et al.*, 2012), and redshanks (*Tringa totanus*) at the edge of their flock are targeted by sparrowhawks (*Accipiter nisus*) (Quinn & Cresswell, 2006). The GSH provides an explicit integration of theory from social and spatial behavioural ecology that remains to be explored within our proposed spatial–social interface framework. Specifically, the GSH inherently relies on spatiotemporal uncertainty in risk within the spatial environment, typically at a relatively fine spatial scale (within the area occupied by an aggregation); for an individual to alter their domain of danger, they may change both social and spatial phenotypes, e.g. by becoming more central spatially or socially. Other forms of threat (e.g. from infectious pathogens) may offer countervailing selective pressures, often at a larger scale by reducing fitness of individuals with high social and/or spatial centrality (Ferrari *et al.*, 2006), and favouring approaches of social distancing (Stockmaier *et al.*, 2021).

V. UNIFYING THE SPATIAL–SOCIAL INTERFACE: FUTURE DIRECTIONS

To consider the causes and consequences of social interactions within a spatial context we suggest movement ecology (Nathan *et al.*, 2008) and network analysis (Newman, 2003) as existing tools with which to interrogate the spatial–social interface (Fig. 2). In this section, we present movement ecology and network analysis as unifying factors of the spatial–social interface.

(1) Movement ecology

Movement behaviour emerges from social and spatial processes, while the outcome of movement is spatial

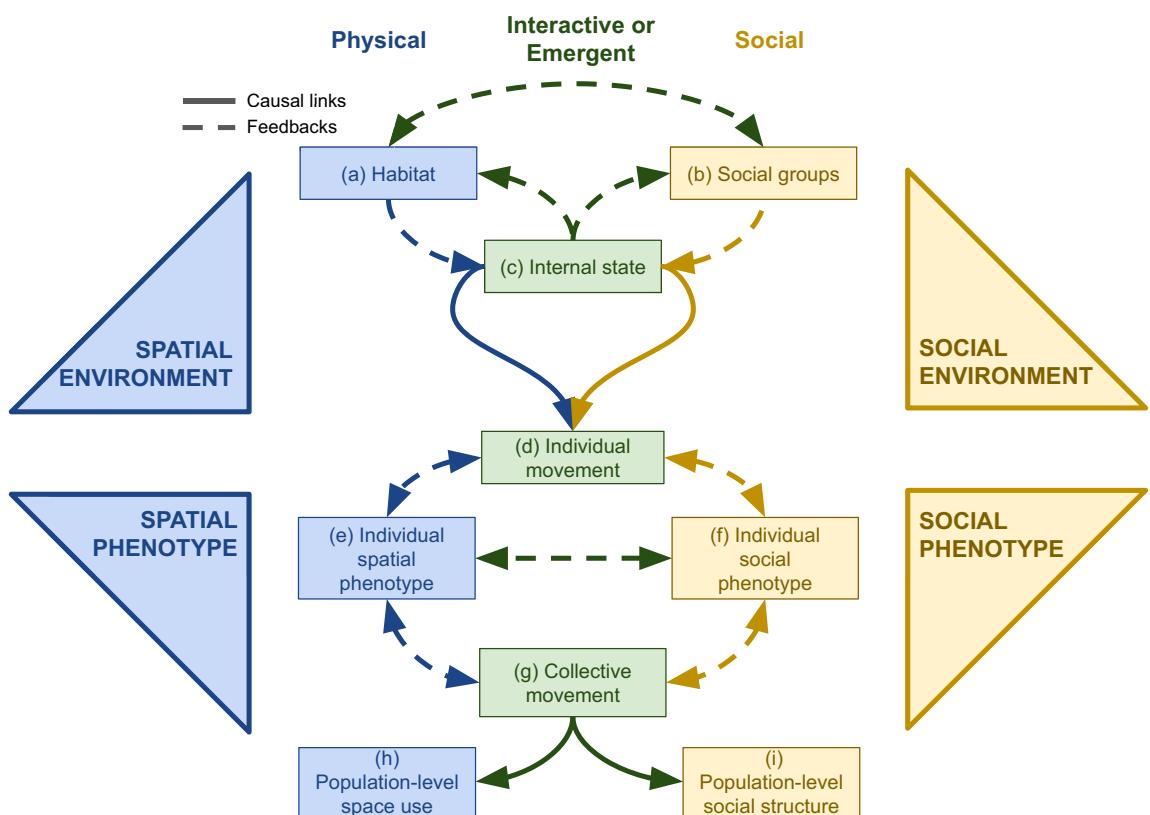


Fig. 2. Movement ecology as a framework to link the spatial–social interface. Aspects of the spatial environment (e.g. habitat, box a) and social environment (e.g. social groups, box b) are related to one another through feedbacks, but they also affect an individual's internal state (box c) as well as spatial and social navigational capacities. For example, the caloric intake an animal gains from a particular foraging patch in the spatial environment (box a) may depend on how many group mates it has who can help subsidize vigilance for predators (box b). Whether an animal should move to an alternative patch might therefore depend on how hungry it is (its internal state, box c) and how much it can satisfy that hunger in the spatial and social environments the new patch provides. Together, the habitat an individual occupies and the size and composition of their social group affects their movement (box d), which in turn has potential to enter a feedback loop. Within the feedback loop, individual movement can affect, and can be affected by, spatial (box e) and social (box f) phenotypes, which in turn can affect, and can be affected by, collective movement (box g). Finally, the feedback between individual movement ↔ spatial phenotypes ↔ social phenotypes ↔ collective movement leads to population-level space use (box h) and population-level social structure (box i). Individual movement is positioned at the centre of the spatial–social interface and represents the connection between social and spatial environments (top half of the figure) and social and spatial phenotypes (bottom half of the figure).

displacement of an animal. The *movement ecology* paradigm integrates animal space use, cognition, and behaviour with components of the social and spatial environments through the study of patterns arising in geographic space. The movement ecology paradigm is composed of three factors related to an individual – internal state, motion capacity, and navigation capacity – as well as a fourth component related to external factors – the social or spatial environment – affecting movement behaviour (Nathan *et al.*, 2008).

The internal state accounts for the physiological and psychological state of the focal individual and asks and answers the question: ‘*why move?*’ (Nathan *et al.*, 2008). Animals move because the marginal value of a patch has been depleted. Movement therefore happens when animals are searching for resources (e.g. food and water), following the dynamic distributions of resources (e.g. seasonal migration), attempting

to gain new breeding opportunities (e.g. dispersal), or seeking to remain with specific other individuals. Individuals may differ in their needs or preferences, depending on short-term state (e.g. hunger; Spiegel *et al.*, 2013) or long-term traits (e.g. perceived risk reflecting both their boldness and their environment; Stuber *et al.*, 2022). In many species an individual's foraging reflects both exploratory tendency (a spatial phenotype), specific level of attention to social information (social phenotype), and the distribution of conspecifics and resources.

An individual's motion capacity accounts for its ability to move and asks and answers the question: ‘*How to move?*’ (Nathan *et al.*, 2008). At its core, motion capacity is an organism's biomechanical and physiological ability to move. Although fixed for most species, motion capacity can still depend on the spatial–social interface. For example,

movement capacity can be restricted by the spatial environment (e.g. deep snow; Pedersen *et al.*, 2021). Motion capacity could also incorporate an individual's capacity to move long distances. For migratory animals, social barriers associated with information transfer during migration can drive how individuals obtain cues about the environment, and therefore how they move, with potential to promote the evolution of collective migration (Guttal & Couzin, 2010). We posit that aspects of the spatial–social interface, e.g. deep snow in the spatial environment or social barriers during migration, can promote or inhibit *how* animals move within certain contexts.

Navigational capacity accounts for the ability of an individual to orient in space and/or time and addresses the question: ‘*when and where to move?*’ (Nathan *et al.*, 2008). An individual's movements are often guided by when and where the individual can pursue a goal – for example, move towards food or away from a threat. Importantly, navigation requires an ability to sense and respond to information about the spatial *and* social environments. When navigating, animals inevitably rely on the integration of spatial and social information to decide *when and where to move* and social foraging presents a clear case where the decisions on movement goals reflect the social environment (e.g. Ward & Zahavi, 1973; Harel *et al.*, 2017). For example, individuals moving in high-density populations can directly influence one another (Reynolds, 1987; Couzin *et al.*, 2002). These influences – called interaction rules (Couzin *et al.*, 2002) – can underpin a range of beneficial emergent properties of groups. For example, schools of fish are better at detecting shaded (preferred) *versus* unshaded (less preferred) microhabitats than single fish, a process also known as ‘collective sensing’ (Berdahl *et al.*, 2013). Navigational capacity and the questions of *when and where to move* are key mechanisms when considering the spatial–social interface since they reflect both the external environments and the ability of an individual or species to process this information (i.e. its phenotype).

(2) Networks as tools to describe social and spatial processes

Networks are often used for visualizing and analysing interactions among biological properties, including individuals, species, or physical locations. Networks as a tool and graph theory as a concept allow exploration of complex association patterns, and the emergent properties of different hierarchical phenomena (Newman, 2003). Indices at the individual level (e.g. degree: number of unique connections an individual has) and population level (e.g. network density: the number of connections within a given network) can describe systems in great detail and test various relevant hypotheses (Croft, James & Krause, 2008; Whitehead, 2008), for instance, testing hypotheses on scale-free degree distribution patterns of social structure (Lusseau, 2003), or measuring individual centrality in its group (Ripperger, Stockmaier & Carter, 2020). Accordingly, networks have been applied in diverse contexts in evolutionary biology. First, ecological networks are used to predict interactions among species, presenting nodes as species and

edges as their interactions, such as host–parasitoid, plant–pollinator, predator–prey, or spatial co-occurrence interactions (Ings *et al.*, 2009). Second, for the last two decades social networks have been becoming increasingly popular in the field of animal behaviour. Social networks depict individual animals as nodes and pairwise interactions or associations between individuals as edges (Croft *et al.*, 2008). Since observed associations reflect both social and spatial constraints, social networks allow the study of both social phenotypes and environments (Webber & Vander Wal, 2019) and the spatial behaviour of animals has been explicitly incorporated into the study of social preferences (Spiegel *et al.*, 2016). Third, ‘movement networks’ describe animals’ movements with discrete physical locations as nodes and animal movements between the locations as edges (Mourier, Ledee & Jacoby, 2019). Fourth, spatial networks represent features of the spatial environment, including habitats or resource patches (Silk *et al.*, 2018b; He *et al.*, 2021). Despite their similarities and common reliance on graph theory, social, ecological, movement, and spatial networks are largely applied distinctly from one another, and allow testing of different hypotheses on the social and spatial interface.

Recently, multilayer networks (Kivelä *et al.*, 2014) have been proposed as a novel analytic tool to examine multiple layers of spatial and social processes, presenting both methodological and conceptual advances over prior methods (Silk *et al.*, 2018b). For example, partitioning spatial or social behaviours across network layers may enable fine-scale assessment of the behaviours’ context dependence (Barrett, Henzi & Lusseau, 2012; Finn *et al.*, 2019). Future work could apply multilayer networks to integrate the spatial–social interface with ecological theory by linking social, ecological and spatial networks in a unified framework. For example, networks describing the social structure of predator and prey species could be linked in a multilayer network to test hypotheses about how social processes at one trophic level might influence social patterns at another (Finn *et al.*, 2019). In this example, the implicit aspects of social network analysis (i.e. interactions or associations among members of the same species) are integrated with inherent aspects of ecological networks (e.g. predator–prey dynamics) and would require that processes that are being examined at social and ecological levels occur on a similar timescale (Montiglio *et al.*, 2020). Multilayer networks could be useful to describe how social and spatial phenotypes influence contact processes and thereby pathogen transmission (Albery *et al.*, 2020b; Silk & Fefferman, 2021). For example, Silk *et al.* (2018a) used multilayer networks to link badger–cow interactions with a spatial network of the badgers’ latrines to study the transmission of bovine tuberculosis. Multi-host multi-pathogen networks represent a more complicated variation on this theme (Fountain-Jones *et al.*, 2018).

VI. CONCLUSIONS

(1) The spatial–social interface emerges from the interactions between social and spatial phenotypes and

environments. Our framework conceptualizes these interactions by highlighting theoretical and empirical links between components of the spatial–social interface and by proposing new questions and testable hypotheses within the context of each pairwise interaction at the interface (Fig. 1; Table 3). (2) We propose the spatial–social interface as a conceptual framework and a roadmap for future studies to integrate social and spatial behaviour, while situating the interface in the context of existing theory and empirical examples. Our framework relies on understanding social and spatial aspects of an animal's life, integrating these aspects and their interactions, and conceptualizing these interactions within the context of individual fitness and population dynamics. (3) We also introduce the idea that movement ecology serves to link the spatial–social interface in that spatial and social phenotypes almost always require movement to, from, or within the spatial and social environments. Although the questions of *why, how, when, and where to move* were first proposed to explain movement ecology, there is a natural extension between the spatial–social interface and the movement ecology paradigm. We hope our synthesis and framework helps integrate these often disparate subdisciplines and that future work will begin to share common vocabulary, theory, and methods to motivate broad impactful advances.

VII. ACKNOWLEDGEMENTS

Q. M. R. W. was supported by Natural Sciences and Engineering Research Council (NSERC) Canada Banting Postdoctoral Fellowship; G. F. A. was supported by a College for Life Sciences Fellowship from the Wissenschaftskolleg zu Berlin, and by NSF grant number 1414296; D. R. F. was funded by a grant from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (grant agreement number 850859) and an Eccellenza Professorship Grant of the Swiss National Science Foundation (Grant Number PCEFP3_187058); N. P.-W., O. S., and N. S. were funded by the NSF-BSF grant (2015662/2019822); O. S. was funded by the Israeli National Science Foundation (ISF 396/20), and the Bi-national Foundation (822/2019); E. V. W. was supported by a NSERC Canada Discovery Grant; and K. M. was supported by Utah Agricultural Experiment Station Project UTA01427 and new faculty start-up funds from Utah State University.

VIII. REFERENCES

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(Received 11 February 2022; revised 9 January 2023; accepted 10 January 2023; published online 23 January 2023)