

Review

Social Barriers in Ecological Landscapes: The Social Resistance Hypothesis

Nicolette C. Armansin,^{1,2,9,*} Adam J. Stow,^{1,2,9} Mauricio Cantor,^{3,4,5,6,9} Stephan T. Leu,¹ James A. Klarevas-Irby,^{4,6,7} Anthony A. Chariton,¹ and Damien R. Farine^{3,4,6,8,9,@,*}

Across animal societies, individuals invest time and energy in social interactions. The social landscape that emerges from these interactions can then generate barriers that limit the ability of individuals to disperse to, and reproduce in, groups or populations. Therefore, social barriers can contribute to the difference between the physical capacity for movement through the habitat and subsequent gene flow. We call this contributing effect ‘social resistance’. We propose that social resistance can act as an agent of selection on key life-history strategies and promote the evolution of social strategies that facilitate effective dispersal. By linking landscape genetics and social behaviour, the social resistance hypothesis generates predictions integrating dispersal, connectivity, and life-history evolution.

The Social Resistance Hypothesis

A central process in ecology and evolution is the transfer of genes from one population to the next. **Gene flow** (see Glossary) depends on movement, typically the **dispersal** of individuals from their natal environment. Physical features of the environment (e.g., mountains, deep water, or lack of suitable habitat) generate barriers that limit the ability of individuals (and their genes) to disperse [1]. However, even after overcoming physical barriers, **effective dispersal** is only realised if an individual that moves to a new **patch** is successful in entering and reproducing in that patch [2]. For social species, the characteristics of the **social system**, such as the organisation of groups and the structure of the social relationships therein, can create additional barriers to movement and breeding [3]. Overcoming social barriers will require different adaptations and will entail different costs compared with those imposed by physical barriers [4].

In societies where individuals have to navigate a more complex **social landscape**, the social barriers they face will be more challenging to overcome. A dispersing individual will experience **social complexity** arising from how persistent social relationships are, how related group members are to one another, whether parents give extended care to their offspring, or how promiscuous the mating system is [5,6]. For example, in many animal populations, individuals can form enduring social bonds, with the number and quality of their relationships shaping survival and reproductive success [7]. The importance of maintaining fitness-enhancing social relationships, including coalitions [8], can create resistance towards immigrating dispersers [9], and the need to form new relationships can protract the social integration of immigrants [10–12]. In an extreme example of a social barrier, communities where members are highly related can be completely closed to immigrants and new breeders, as observed in many eusocial species.

The barriers introduced by social systems can contribute to differences between where individuals can physically move to and where they can breed. We name this effect ‘**social resistance**’. Social resistance includes the barriers individuals face when trying to enter a patch (**entry resistance**) and the barriers they face in forming the social relationships necessary to reproduce within that patch (**breeding resistance**). By affecting the transitions from one **life-history stage** to another (Figure 1), social resistance can act as an agent of selection on life-history strategies. Possible targets of selection include strategies that enhance lifetime fitness by increasing the chances of offspring to overcome entry and breeding resistance. We call this counter-effect ‘**social facilitation**’.

Here, we outline how social resistance emerges by integrating concepts from studies focussed on the landscape scale with concepts from studies focused on behaviour. We synthesise

Highlights

The social environment can impose many challenges for animals as they attempt to disperse and reproduce.

The barriers arising from the social environment can generate a difference between where animals can move and where they recruit. We define social resistance as the contribution of the social environment to the difference between physical connectivity and gene flow.

We hypothesise that social resistance will be greatest when animals have to navigate through social landscapes that have high functional organisation.

Social resistance can act as a driver of life-history evolution by selecting for strategies that allow individuals to overcome social barriers.

By bridging individual social behaviour and landscape genetics, the social resistance hypothesis allows a greater understanding of the feedback between landscape-level processes and individual-level social behaviour.

¹Department of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia

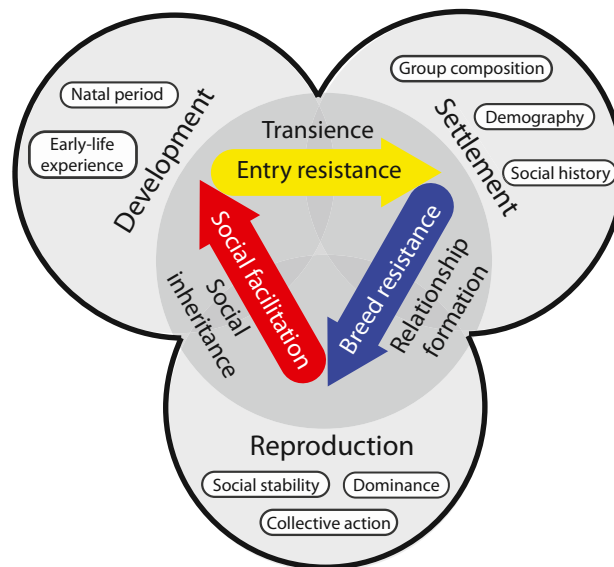
²Conservation Genetics Lab, Macquarie University, Sydney, NSW 2109, Australia

³Department of Collective Behavior, Max Planck Institute of Animal Behavior, Konstanz, 78457, Germany

⁴Department of Biology, University of Konstanz, Konstanz, 78464, Germany

⁵Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, Florianópolis, 88048-970, Brazil

⁶Centre for the Advanced Study of Collective Behaviour, University of Konstanz, Konstanz, 78464, Germany



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Figure 1. Social Resistance Affects the Transition between Key Life-History Stages: Development, Settlement, and Reproduction.

Dispersers need to find and settle into new patches. The process of doing so, or transience, is shaped not only by the physical environment, but also by social characteristics of potential patches into which they attempt to enter (see [Box 1](#) in the main text). These social barriers to entry represent entry resistance (yellow arrow). Once individuals overcome entry resistance, whether they reproduce is determined by their ability to integrate into the social group, which is affected by the within-patch social environment (see [Box 2](#) in the main text). The barriers to reproduction represent breeding resistance (blue arrow). Selection arising from entry and breeding resistance should favour parental strategies, such as extended parental care or coalitionary support, that increase the ability of offspring to overcome entry and/or breeding resistance (see [Box 3](#) in the main text). The response to selection arising from social resistance is called social facilitation (red arrow). White boxes give examples of the social characteristics of patches.

knowledge on how social resistance emerges from aspects of social systems, revealing key areas where social resistance manifests, the transience phase of dispersal ([Box 1](#)), the formation of new relationships after settlement ([Box 2](#)), and strategies that facilitate the ability of offspring to overcome social resistance ([Box 3](#)). The social resistance hypothesis facilitates a greater understanding of how physical landscapes interact with social landscapes to shape effective dispersal.

Social Resistance Is a Missing Link between Models of Dispersal and Gene Flow

Dispersal has been investigated by population ecologists, landscape ecologists, and behavioural ecologists, each traditionally considering different spatial and temporal scales [13]. The three stages of dispersal (emigration, **transience**, and immigration [4]) can be evaluated using myriad demographic and genetic approaches to estimate movement of genes or individuals across space [14] ([Figure 2A,B](#)). Genetic-based analytical tools can be used to measure effective dispersal, while tracking individuals [9] or using mark-recapture methods [2] can provide data on dispersal movements [14]. Such methods have been successful at linking physical environmental features to dispersal, but have overlooked the additional contribution of the social environment in shaping movement outcomes ([Figure 2C,D](#)).

Dispersal models commonly use the resistance concept to map the propensity for an organism to move through a **physical landscape**. In these models, resistance reflects the physiological

⁷Department of Migration, Max Planck Institute of Animal Behavior, Radolfzell, 78315, Germany

⁸Edward Grey Institute of Ornithology, Department of Zoology, University of Oxford, Oxford, OX2 8QJ, UK

⁹These authors contributed equally to this work

@Twitter: @NicoArmansin (N.C. Armansin) and @DamienFarine (D.R. Farine)

*Correspondence: nicolette.armansin@hdr.mq.edu.au, dfarine@ab.mpg.de

Box 1. Transience: Dispersing through Social Landscapes

Dispersal is a major driver of population dynamics, connectivity, and gene flow [1,73,74]. Social resistance is likely to act strongly on dispersal. Local density [75], dominance rank [35], social cohesion [76,77], or differences in personality [78] can determine individual decisions to emigrate from the natal patch or about which patch to settle in. However, how transient individuals navigate through the social landscape during dispersal remains largely overlooked (reviewed in [4,79]). Transience is a crucial period because it represents the stage when individuals are most likely to gather and respond to new information and novel environments [79]. It is also when we can observe, in real time, how dispersing animals experience and respond to social resistance.

Social resistance could affect transience in two ways: by shaping where individuals can establish a new patch; or by determining entry into an existing patch. In Kalahari meerkats (*Suricata suricatta*), evicted cohorts of females that fail to rejoin their natal group (even when the strength of intragroup resistance is relaxed after the breeding period) must avoid territories of unrelated groups and find space free of conspecifics before they can establish a new group [9]. While successful dispersal in meerkats results in the formation of new groups, in many other species the transience phase involves having to penetrate an existing patch. The stronger and more long-lasting relationships are within a patch, the more challenging it is likely to be for an immigrant to enter. Observations from baboons suggest that the process of overcoming entry resistance can take months to years [80]. Prolonging the time individuals spend transitioning from one patch to another can translate to higher mortality (e.g., via predation) [81], thereby strengthening the potential for entry resistance to act as an agent of selection on dispersal strategies.

costs of moving and/or the decrease in survival probability resulting from dispersal [15]. Resistance modelling involves selecting environmental variables, which are represented as GIS raster surfaces, where cells are assigned a resistance score that reflects the physical constraints to movements [16] (Figure 2E,F). Each layer can be parameterised using expert opinion, empirical methods informed by genetic data, habitat data, or species distribution models [17]. Correlating layers against demographic or genetic data [18] allows for the construction of models of physical connectivity (Figure 2G). Likely movement pathways can be estimated using methods

Box 2. Social Relationship Formation: Overcoming Social Resistance to Reproduction

Despite increasing evidence linking social relationships beyond mating partners to survival and reproduction (e.g., [7]), little is known about the process by which such functionally important social relationships are formed, especially after immigrants enter a new patch [82]. Forming social relationships can be a protracted process. Observations of chimpanzees (*Pan troglodytes*) suggest that relationships require weeks, if not years, to form [83]. A key hypothesis regarding relationship formation is that individuals initially avoid investing in costly affiliative behaviours, when reciprocity is not guaranteed, by 'testing the waters' [84]. That is, they can initially engage in less costly social interactions, and then 'raise the stakes' to more costly social behaviours over time as the relationship strengthens. Evidence from vampire bats supports this hypothesis, with individuals introduced into new social groups first establishing grooming relationships before switching to food-sharing relationships if the former are reciprocated [85].

A second key hypothesis comes from structural balance theory [86], which proposes that the ratio of positive to negative relationships among triads (every possible set of three individuals in a patch) is important in maintaining social stability at the patch level. For example, if individuals A and B have a strong social relationship and a third individual C develops a new relationship with A, but is rejected by B, then the triad will be unbalanced because A and B are not unanimous in their relationship towards C. In rock hyraxes (*Procavia capensis*), the presence of pre-existing balanced triadic relationships limits the ability of immigrants to form relationships and overcome breeding resistance [87].

Finally, linking structural balance theory to the raising-the-stakes hypothesis highlights a further challenge if immigrants are required to establish reciprocated social relationships not only with one individual, but also with the social associates of that individual. Given the investments needed to become integrated into a patch, both in terms of time and costly behaviours, immigrants are likely to face significant breeding resistance even after entering a new patch.

Glossary

Breeding resistance: extent to which social factors limit the ability of an individual to breed in a patch. This could be either in the natal patch (potentially forcing dispersal) or in the destination patch (after entry).

Dispersal: process of moving between patches; does not need to imply permanent or long-term establishment or successful reproduction in a destination patch; typically involves three phases: departure (emigration), transience (movement), and settlement (immigration).

Effective dispersal: successful entry of, and breeding by, individuals in a new patch; requires overcoming entry resistance and breeding resistance to contribute to gene flow.

Entry resistance: extent to which social factors prevent a disperser from joining a patch.

Functional connectivity: extent to which physical connectivity together with behavioural responses shape dispersal.

Gene flow: intergenerational transfer of genetic material from one patch to another.

Life-history stages: represent the major stages in the life of an organism as determined by function. We consider three life-history stages here: development, settlement, and reproduction.

Patch: discrete unit in the physical or social landscape. In a physical context, a patch represents a relatively homogeneous habitat area that is different from its surroundings. In a social context, a patch is a set of individuals that have a close functional link with each other. Habitat patches and social patches can scale independently; a social patch can encompass multiple habitat patches, or a habitat patch can contain multiple social patches.

Physical connectivity: structural configuration of landscape features that allow or restrict individual movement between patches.

Physical landscape: geographical areas that are heterogeneous in terms of resources, habitat types, physical features, and structural characteristics.

Social complexity: often viewed as the emergent properties of a

Box 3. Social Inheritance: Maximising Offspring Success

Navigating the social environment is challenging. Therefore, selection should favour mechanisms that facilitate the ability of offspring to overcome social resistance, such as increasing social competence [63] or via the inheritance of beneficial social traits, such as dominance rank [88]. 'Silver spoon' effects, by which individuals that develop under favourable circumstances receive fitness benefits later in life [89], can have far-reaching consequences in social species. Prenatal effects, through genetic inheritance [90] and maternal effects [91], can predispose offspring for success in a social landscape from the moment they are born. One example of non-genetic social inheritance is through the timing of breeding. If dominant individuals in seasonal systems can monopolise access to breeding resources (e.g., food, nesting sites, or mates) that allow them to reproduce earlier than subordinates, then their offspring can gain a developmental head-start over their peers. These early-life advantages have been shown to confer lifelong benefits for survival, reproduction, and adult dominance across many species, including crested ibis (*Nipponia nippon*) [92], pukeko (*Porphyrio melanotus*) [93], bison (*Bison bison*) [94], and primates [7]. Such advantages reducing breeding resistance can then generate a positive feedback by which dominant lineages are inherited and maintained [56,95].

Offspring can also benefit from parental support via postnatal social interactions, especially in species with extended parental care [96]. Maternal and kin-based coalitionary support in dominance interactions can predict offspring acquisition of social rank. For example, in spotted hyenas (*Crocuta crocuta*), strong dominance hierarchies among females are maintained through maternal support of offspring, which allows young females to be dominant over other adults that are subordinate to their mother, irrespective of other traits such as body mass [97,98].

Social inheritance mechanisms can ultimately have a role in determining the dispersal and reproductive success of an individual. In spotted hyenas, male dominance rank is largely determined by asymmetries in social support, with immigrant males typically receiving less support compared with resident males [98]. Among dispersers, offspring of higher-ranking parents can maintain better condition [99], and individuals with better body condition are more likely to settle and breed in higher-quality patches [100]. As such, social resistance should drive the evolution of social strategies that allow individuals to facilitate the chances of their offspring overcoming entry and breeding resistance.

such as least-cost paths and circuit theory [19,20], representing a spatially explicit predictive framework.

By and large, the structural variables evaluated in resistance models are those that influence the capacity for animals to move between patches of habitat. The social resistance hypothesis captures how social factors within patches can further affect dispersal through entry resistance and effective dispersal through breeding resistance (Figure 2C,D), highlighting that **functional connectivity** is the product of both physical and social factors that influence how animals move through the landscape. Properties of the social environment can be represented as additional layers in resistance models. Layers can represent habitat suitability from a social perspective (Figure 2H), and how the social landscape acts as a filter, thereby altering effective dispersal (Figure 2H,I). For example, a social layer can describe resistance arising from territorial boundaries or patterns of kinship among individuals, and can change suitable habitat into part of the nonhabitat matrix. Correlations between layers could reveal whether the physical landscape, such as habitat boundaries, also correspond to social barriers, such as territorial boundaries.

Layers based on measured movements (e.g., generated from tracking or genetic data) capture realised movement after the combined effects of physical and social resistance. The difference between the actual transfer of immigrants among patches and the predicted transfer from models of physical connectivity (e.g., a movement cost surface) captures the effects of entry resistance, while the difference between the presence of immigrants in a patch and their contribution to gene flow captures the effects of breeding resistance. A study of the movement restriction and reproductive challenges faced by dispersing Florida snail kites (*Rostrhamus sociabilis plumbeus*) [2] is a good example of the application of the approaches described herein for quantifying entry resistance and breeding resistance.

system arising from repeated interactions among individuals, often the same ones, and across contexts. Complexity can come in the form of strongly differentiated relationships among typically unrelated individuals, or in the form of interactions typically taking place among kin. In the context of social resistance, social complexity can be viewed from the perspective of an individual, expressed in terms of how challenging it is for the individual to navigate social interactions, and to make appropriate social decisions throughout its lifetime.

Social facilitation: parental investments that increase the chances that offspring will overcome social resistance to join the breeding population.

Social inheritance: non-genetic mechanisms allowing the transmission of social traits from parent to offspring.

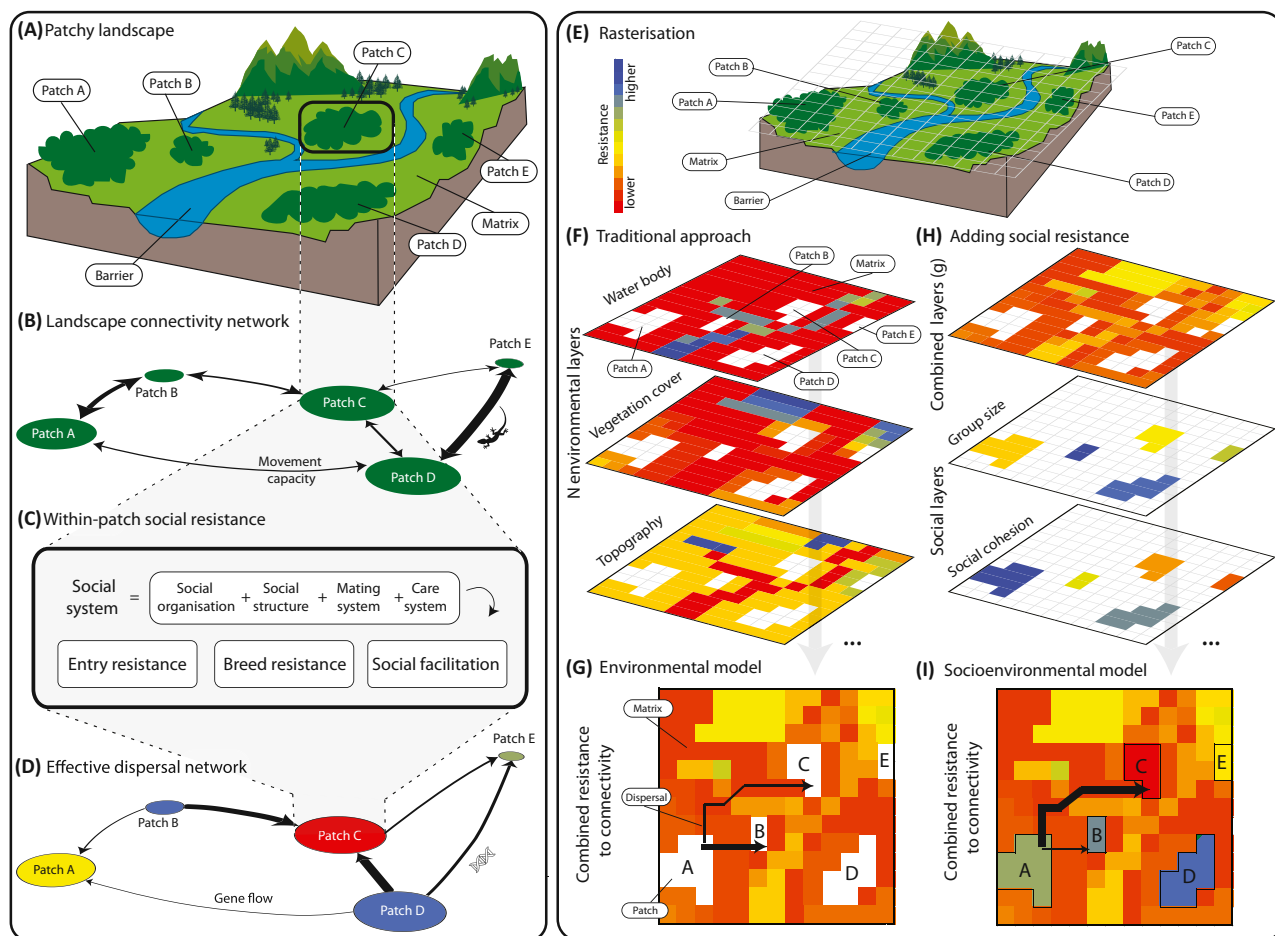
Social landscape: set of individuals, and the social relationships among them, in a given environment.

Social relationship formation: social integration into patches and development of affiliations essential for reproduction.

Social resistance: contribution of social processes to differences between the physical connectivity and the effective dispersal between patches.

Social system: social characteristics determined by four components: social organisation (referring to the size and composition of social units), social structure (referring to the content, strength, and temporal stability of interactions among individuals that result in social relationships), mating system (referring to the identity and number of sexual mates that individuals have), and care system (referring to who cares for, and how related they are to, the dependent young).

Transience: period between departure from the natal patch and settlement in the destination patch.



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Figure 2. Within-Patch Social Environments Affect Functional Connectivity Across Landscapes.

(A) Physical landscapes are patchy, here illustrated by a terrestrial environment containing patches within a matrix intersected by physical barriers (e.g., river or mountains). (B) The landscape can be represented as a weighted network of suitable patches, where some pairs of patches are strongly connected (thicker arrows) and others are more weakly connected (thinner arrows) due to physical barriers (e.g., Patch B to Patch A versus Patch B to Patch C). (C) Patches can also have higher or lower social resistance. Characteristics of social organisation and structure, and the mating and care systems can impose challenges for a disperser to penetrate (entry resistance) a patch and reproduce (breeding resistance) within it. (D) Accounting for social resistance can change the predicted effective dispersal (e.g., despite physical barriers, Patch C is the least-resistant patch to effective dispersal, whereas Patch D is the most resistant). Thus, when social resistance is strong, there is a greater disconnect between the ability for individuals to move across the nonhabitat matrix and their subsequent reproduction in patches. (E) In landscape resistance models, the physical landscape is rasterised. (F) Environmental layers (here, river stream, vegetation cover, and topography) can be parameterised, and (G) a physical connectivity model can be generated to describe the probability of dispersal (arrows) between patches due to environmental features alone. (H) Social layers representing the patch social environment (here, group size or social cohesion), either for an entire population, for a given class, or independently for each individual, can be added to resistance models. (I) Resistance can then be quantified from the combination of social and physical layers (see [9]).

How Do Social Systems Generate Social Resistance?

Much is known about how physical features of the landscape affect where individuals can disperse to and subsequently reproduce. In parallel, the study of behaviour is rich in hypotheses about how social behaviour operates within populations [21]. Less is known about how social systems can themselves shape dispersal and subsequent gene flow independently of the physical landscape. Early theoretical work considered links between social behaviour and dispersal movements [22], but focussed on population regulation and was limited by the contemporary understanding of social behaviour [23]. Here,

we outline predictions of how different components of social systems (social organisation, social structure, mating system, and care system [6]) can generate entry and breeding resistance, and modulate effective dispersal (Figure 2B–D).

Social Organisation

Social organisation considers patch properties, including the number of individuals, level of relatedness, phenotypic composition, demography, and cohesion [6]. Variation in these properties and, in particular, deviations from optimal values can alter the magnitude of the social resistance experienced by individuals

A well-established theory is that of an optimal group size, where the number of individuals in a patch should reflect the balance of social costs, social benefits, and resource availability [24]. We predict that social resistance will be higher for an individual attempting to enter a patch that is beyond the optimal group size than for one attempting to enter a patch that is currently below its optimal size, because doing so will further decrease the benefit:cost ratio for current members [25]. For example, highly territorial southern pied babblers (*Turdoides bicolor*) have an optimal group size of five–six individuals, and groups smaller than optimal are more inclined to accept immigrants [26]. Optimal group size is linked to resource richness, and the relationship between patch density and resource availability can modulate population regulatory processes by affecting dispersal between patches [22].

Patches can also have an optimal phenotypic or demographic composition [27]. Two predictions are that patch entry resistance will be greater if an immigrant would change the phenotypic composition by moving it away from the optimal [28], and that breeding resistance will be greater if the phenotype of an individual is mismatched to its patch (e.g., via social selection [29]). One such determinant of entry and breeding resistance is sex ratio [30]. Dispersing juvenile Siberian jays (*Perisoreus infaustus*) are more likely to enter groups containing fewer same-sex juveniles [10], potentially to reduce later breeding resistance arising from same-sex competition for reproductive positions. When patches contain fewer individuals, we predict that random fluctuations in sex ratio will increase the potential for sex-based asymmetry in the social resistance experienced by dispersers.

Relatedness can explain a variety of behaviours through processes such as kin selection and inbreeding avoidance, which, in turn, have consequences for social resistance. One prediction is that individuals with more same-sex relatives in a patch will experience reduced entry resistance into that patch. For instance, juvenile male brown jays (*Cyanocorax morio*) are more likely to immigrate into groups containing a familiar, related male [31]. If patches separated by larger distances are less likely to contain related or familiar same-sex individuals, then dispersers will experience greater social resistance the further they disperse. By contrast, being related to patch members of the opposite sex will result in greater entry resistance. For example, Cunningham's skinks (*Egernia cunninghami*) live in kin-based social groups that select nonrelated breeding partners [32]. Therefore, strong inbreeding avoidance coupled with high within-patch relatedness will lower breeding resistance for unrelated immigrants.

Finally, we predict that entry resistance will be modulated by social cohesion or the ability for patch members to express collective actions. For example, juvenile brown jays make more exploratory forays into other patches during nest building [31]; the reduced social cohesion during this period reflects lower entry resistance. An example of a collective action that can shape individual movement through the physical landscape is territory maintenance. The resulting territory boundaries can represent social barriers that determine where other conspecifics can range [9], thus rendering otherwise-suitable habitat unsuitable for dispersers.

Social Structure

Social structure refers to the content, quality, and emergent patterns of social relationships among patch members [6]. We identify four ways by which the entry and breeding resistance experienced by individuals will be determined by the extent to which social relationships modulate fitness.

First, we predict that entry resistance will be lower if there are existing social connections across patches. In social birds [31], primates [33–35], and other mammals [36,37], juveniles often disperse to groups with which they have previously had intergroup contact. Reduced entry resistance into familiar groups could be the outcome of a group-level process akin to the ‘Dear Enemy’ hypothesis [38], which postulates that aggression between neighbouring territory owners (here, groups) decreases with familiarity.

Second, because long-term social relationships can be crucial for survival and reproduction [7], establishing such relationships will represent a major component of breeding resistance. An example of how familiarity translates to reproductive performance is sleepy lizards (*Tiliqua rugosa*), where familiar pairs mate earlier than pairs formed among previously unfamiliar individuals [39]. We discuss the process of **social relationship formation** in Box 2. Reproducing earlier can then generate benefits for offspring, reinforcing the differences among integrated and non-integrated individuals via social facilitation (Box 3).

Third, assortative mixing among behaviourally similar individuals can provide additional barriers. Assortative mixing represents the preference for forming social connections with individuals that have similar characteristics, thus increasing resistance to dispersers that are dissimilar. Particularly high entry resistance exists when behavioural variants, as opposed to space use, mark the social identity of patches [40,41]. To persist and reproduce after entering a behaviourally specialised patch, dispersers must adjust their behaviours, such as foraging tactics, dietary preferences, social norms, or communication repertoires, to match those of existing patch members [42]. For example, acoustic patterns are thought to identify social tiers in toothed whales [43], and individuals mostly interact with those that share the same markers, despite overlapping in space with others [44,45]. Social preferences for behavioural variants can also generate breeding resistance. For example, in songbirds where females display acoustic preferences [46], immigrant males will be less likely to acquire a mate. Assortative mating, and consequent resistance arising from mating preferences, can then shape genetic structure [40,47].

A fourth major aspect of social structure that can impact entry and breeding resistance is the dominance hierarchy. In highly stratified societies, individual progression to a higher dominance rank, and potentially a reproductive position, can require a protracted process of social integration. An example of a society with low entry resistance but high breeding resistance are the leks of *Chiroxiphia* manakins: males that enter can contribute to the cooperative dance that attracts females, but usually do so at the bottom of the lek hierarchy and must wait for years to rise to a reproductive position [48,49].

That individuals vary in their position within the social landscape suggests that how social resistance is distributed across the physical landscape can vary across individuals. For example, differences in the history of intergroup connectivity, or variation in social markers and social preferences, means that the entry resistance into a given patch could differ for individuals coming from different natal patches. Thus, models of landscape ecology that include social resistance could require individual-level social layers (Figure 2H).

Mating System

Mating systems are characterised by the number of mates per sex and their identity, representing varying levels of promiscuity (monogamy, polygyny, polyandry, and polygynandry [6]). The entry and breeding resistance that individuals face can be influenced by these levels of promiscuity.

Breeding resistance will be highest for the sex that experiences the greatest reproductive skew. By contrast, monogamous systems should generate higher entry resistance (e.g., having to establish a territory). The mating system can also influence which sex evolves to disperse [50] and, therefore, can determine which sex will experience entry resistance. Both sexes can experience breeding resistance if there are also barriers to reproducing in the natal patch. Furthermore, differences in mating

systems between patches could generate a mismatch between the sex of individuals trying to enter a patch and the patch sex ratio [51]. For example, by affecting mate availability, habitat fragmentation changed the mating system of mountain brushtail possums (*Tricosurus cunninghamia*) from monogamy to polygyny [52].

Breeding resistance can occur via reproductive suppression of patch members or mate choice. In the cooperative breeding system of some mammals, dominants rely on aggressive competition to suppress the reproduction of same-sex subordinates (including newcomers) [53–55]. Similarly, mate guarding can make it costly for newcomers to reproduce because access to mates is reliant on winning competitions [53–55]. Long-term studies reveal that competition can translate to large interindividual variation in lifetime reproductive success. Of 19 female spotted hyenas (*Crocuta crocuta*) present in a clan in 1979, only four had descendants 30 years later, and these were disproportionately represented by high-ranking females [56]. This highlights how breeding resistance can prevent some members of a patch from reproducing, resulting in the loss of their alleles from the patch. It further highlights the importance of longitudinal studies for providing data linking social processes with dispersal at intergenerational scales.

Care System

Care systems entail the number, identity, and relatedness of the individuals that care for the dependent young [6]. Care behaviour is inherently social, and can impact social resistance via direct and inclusive fitness routes; that is, through parental and alloparental investment.

The longer the parental care period, the more socially resistant a patch will be to dispersers. Extended care-giving makes parents more sensitive to dangers facing their offspring, as evident from female primates clustering with males to prevent new (potentially infanticidal) male immigrants [57]. Care behaviour can also generate breeding resistance. For example, a recently accepted male disperser would have proportionally fewer mating opportunities in a group where the females are caring for young (hence infanticide being a counter-strategy to increase the number of reproductively available females).

A strategy that can reduce entry resistance for dispersers is allocating. Protecting or provisioning the young of another patch member can strengthen the relationship of an immigrant with existing patch members, facilitating their social integration into the patch (e.g., [58]).

Social Resistance as an Agent of Selection on Life-History Strategies

Social resistance represents the social barriers faced by individuals as they transition from one life-history stage into another, over and above the physical barriers to movement. By altering connectivity between patches (Figure 2), social resistance can act as an agent of selection on both social and nonsocial traits that facilitate individuals navigating the social landscape [59]. Thus, social resistance is inherently linked to life-history evolution. Here, we highlight how social resistance can select for particular dispersal, delayed reproduction, and parental care strategies that modulate the extent to which connectivity is affected by social resistance.

The formation of long-term social relationships, or consistent social structures, will increase entry resistance into patches and, in turn, shape dispersal strategies. In particular, entry resistance should select for strategies that shorten the costly transience phase of dispersal [60], such as by exploiting intergroup contacts (e.g., [33,35]). By doing so, individuals can acquire information about interpatch connectivity (Figure 2) and, thus, make more strategic decisions during transience.

Entry and breeding resistance could also drive the evolution of delayed reproduction if interpatch connectivity varies according to age or status of the disperser. If there are few opportunities for entry (either into an existing patch or to establish a new patch), which therefore precludes reproducing, then individuals could remain on the natal territory to help their parents raise offspring while waiting for better dispersal opportunities [61]. Thus, gaining indirect fitness is an alternative strategy that can

Outstanding Questions

What traits of animals (e.g., living in a stable group) are likely to be associated with high levels of social resistance?

Does social complexity arising from strongly differentiated social relationships among nonkin versus complexity arising from relatedness among patch members generate different social barriers?

Does social resistance promote cooperation? For example, species with high entry resistance often feature same-sex dispersing coalitions or bachelor groups, or have delayed dispersal that promotes helping to raise siblings.

What is the importance of breeding resistance in determining whether selection arises via pre- versus postcopulatory traits? For example, do differing mating strategies reflect an energetic trade-off between maintaining social dominance and maintaining sperm quality?

Does the strength and expression of social resistance differ between males and females? For example, if the dispersing sex experiences greater juvenile mortality, then it could also become more favoured (rarer) and, therefore, experience lower breeding resistance.

Do heterospecific social interactions reduce the costs of social resistance? For example, heterospecifics can reduce risks during transience by benefiting individuals through group augmentation without incurring greater competition for entry into patches.

Can environmental changes render previously optimised dispersal strategies maladaptive by modifying the social landscape?

How does habitat change, in particular habitat fragmentation, affect the expression of social resistance? For example, as physical patches get smaller, they could generate more 'social patch'-like dynamics in otherwise open societies.

Can we represent social and physical layers using the same spatial resolution (e.g., Figure 2F,H in the

be selected for by social resistance. Further evidence that links social resistance to a later age of reproduction comes from Tasmanian devils (*Sarcophilus harrisii*). The large-scale death of adults from devil facial tumour disease reduced competition at food resources (carriion). Increased per capita resources then allowed for earlier sexual maturity and increased rates of precocial breeding [62].

Finally, social resistance could underpin the evolution of extended parental care. Successfully overcoming social resistance could require the development of social competence [63]. Empirical evidence suggests that early-life social experiences are important for developing social skills. For example, male zebra finches (*Taeniopygia guttata*) that grew up in richer social environments were better at socially integrating into a new group [64]. Remaining in the natal patch can provide opportunities to experience different types of social interaction. The skills accrued from early-life experiences could select for extended parental care.

As the social component of an individual's life becomes more strongly linked to its fitness (i.e., layers of social resistance are better at predicting effective dispersal than are layers of physical resistance), selection will favour strategies to effectively navigate the social landscape. Such strategies include the ability of the individual to overcome social resistance (e.g., dispersal ability) as well as parental strategies that facilitate the ability of offspring to overcome social resistance (Box 3).

Concluding Remarks and Implications

Social resistance is a prevalent natural phenomenon that is largely overlooked in landscape ecology (see Outstanding Questions). The social resistance hypothesis will improve our understanding of the differences between the physical connectivity among patches and gene flow. Addressing social resistance requires integrating research that spans in scale from the landscape (i.e., how the physical environment affects the ability for individuals to move) to the patch (i.e., how social factors affect the tendencies of individuals to enter a patch and breed). Such integration is possible by adding social layers to landscape models of connectivity (Figure 2E–I). A first step to identifying the importance of social resistance in a system is to study the difference between the predicted movements of individuals, given the physical features of a landscape, and the actual movement of individuals. Long-term studies are likely to be rich resources for characterising the social factors that explain this difference, and whether it can be attributed to social resistance.

Studying social resistance will benefit behaviourists by providing landscape perspectives on theoretical models of behaviour [65] and landscape ecologists by making models of landscape genetics [4,13,66] more predictive. For example, studying social resistance will be critical in an increasingly changing and fragmented natural world. Changes in habitat characteristics impact connectivity and resource distribution, which in turn can alter movements [67] and social interactions among individuals [68], with consequences for parameters of social systems (including territoriality, mating systems, and sex-biases in dispersal [51,67,69,70]). Further effects could arise from the dispersal process itself. For example, immigration can generate social instability within a patch [71] and affect the function of its members [72]. An extreme outcome could involve forcing juveniles that would otherwise remain within the natal patch to disperse [12], which could manifest as an increased intensity of movement through the nonhabitat matrix. Altering the state of social systems can present new and unexpected levels of social resistance, resulting in dynamic interactions between the physical and the social landscapes.

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main text)? How do we incorporate temporal scales into connectivity models if social features change over time?

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