Individual variation in perceived density and its impacts on the realization of ecological niches

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Key words: **local density**, **perceived density**, **niche choice**, **niche construction**, **niche conformance**

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Abstract:

Organisms gain information about their local environment using different senses. Variation in both reception and assessment of stimuli leads to differences among individuals in their perception of environments. Here, we highlight the importance of acknowledging and investigating such individual differences by focusing on perceived density, the individual's assessment of local density. We summarize how individuals sense their environment and identify factors shaping variation in sensory uptake and processing. We argue that differentially perceived environments likely affect relevant processes under selection, which contribute to the realization of individualized ecological niches. Ultimately, we provide practical guidelines for studying perceived density and present potential emergent consequences when considering individual differences, which will advance the in-depth understanding of individual and population-wide behavioural phenomena.

How do individuals perceive their environment?

Organisms gain information about their environment using different **sensory modalities** (see glossary), such as chemical, tactile, acoustic, visual, or electric cues (Table 1). This includes information about the social environment, such as the set of conspecifics that interact with and affect the individual (**local density**). As an incorrect interpretation of a **cue** can come with costs, selection favours individuals which interpret environmental cues more precisely [1]. Sensory multimodality can increase the robustness of the received **signal** as different channels may convey analogous, though not identical, cues and thus supplementary information [2,3]. Whether through one sensory modality or multiple sensory modalities, information must be received, transmitted and processed by the sensory receptors. Sensory receptors are sensitive to certain **stimuli** and convert them into an electrical signal, which in turn is passed on and processed by the nervous system. One reason for individual differences in the perception of environmental factors can result from differences in receptor density, functioning or sensitivity among individuals. For example, the presence or absence of certain receptor types leads to differences in taste perception [4]. Genetic variation and ontogeny have the potential to shape such differences [4,5]. In addition, individual differences in experiences, expectations and cognitive abilities can lead to individual differences in perception of environmental cues. Thus, differences in signal reception as well as in signal processing could shape dissimilarity in how individuals perceive their environments despite living under the same environmental conditions. Altogether, individual variation in perceived environmental conditions is key to the formation of individualized niches, and could lead to different ecological and evolutionary outcomes. Therefore, this concept determines a paradigm shift needed from the current population- or species-level framework towards the inclusion of differences among individuals in how they perceive and assess their local environments.

Density as a working example: individual differences in perception of local density

Population density plays an important role in the evolutionary dynamics of populations, life-histories, and in shaping individual behaviour. For example, when living at high densities individuals are more likely to disperse [6]. This pattern may be driven by negative impacts related to living at high density such as an increased risk of disease, resource depletion and heightened competition, whereas individuals living at low density may struggle to find mates or suffer from an increased predation risk. Thus, population density has both direct and indirect effects on an individual's fitness. Additionally, populations are rarely homogeneously distributed, due to the spatiotemporal heterogeneity of landscapes [7]. Given the individual variation in reception, processing and experience, each individual likely perceives local density differently. This difference in perception can have important consequences for density-dependent processes acting on individual decisions, which has rarely been accounted for in theoretical studies or assessed in empirical studies. In the following, we aim to develop in detail how individual differences in perception can have major consequences for the understanding of the ecological and evolutionary dynamics of populations. We will do so by explicitly focusing on the individual's assessment of local density, i.e. **perceived density**, as our working example (figure 1). However, other environmental factors could be similarly subjected to the same principles.

Across environmental context and time, individuals differ in their behavioural responses to population density [8]. Here we argue that it is not **absolute density**, i.e. the exact number of conspecifics per area *per se* that affects individual behaviour. Instead, behavioural responses ought to be influenced by perceived density, i.e. the number of conspecifics in an individual's immediate surroundings, detected directly and/or indirectly. These individuals most prominently determine an individual's competitive environment or its opportunities for cooperation. An individual's sensitivity to local density depends on morphological, physiological, life-history and behavioural traits [9]. The relative importance of these components is still poorly understood. Additionally, these factors interact and partly result from the competitive regime, the social system as well as the strength and fluctuation in resource availability, adding further layers of complexity [10]. Behavioural traits such as aggressiveness are often directly linked to an individual's competitiveness [11], which can modify the perception of competitor density, with a pronounced effect on perceived resource acquisition opportunities [12,13]. For example, in case of contest competition, a more aggressive individual will have higher competitiveness than a less aggressive one. Similarly, under scramble competition a more explorative individual might have higher competitiveness because it would find new resources more frequently than less explorative individuals. In both situations, the focal individual likely perceives its competitive environment through a lens of its own competitiveness, which in turn affects its sensitivity to local density. Internal factors, such as genetic make-up, ontogeny, or cognition, also have the potential to cause individual variation in density perception. Following Hamilton's rule, perceived relatedness can be a strong modifier of cooperation or competition, if there is variation in perceived relatedness within the local population [14,15]. When (perceived) kinship alters interaction proneness, it may also modify the perception of the density of conspecifics (e.g. [16]).

During maturation of most organisms, sensory receptors develop leading to improved or altered perception [17]. The age of an individual can predict its behaviour, the area it uses, and the way it uses this area, thus potentially modifying the perceived density substantially [18,19]. The same applies to sex, which is a commonly studied modifier of resource overlap and competitive ability. However, sex can sometimes also lead to spatial segregation and thus, distorts the perception of the competitor-to-resource ratio (e.g. [20]). Additionally, seasonal variation interacts with both sex and age, as seasonal phenomena such as mating or variation in resource availability may modify the signals used by individuals. Therefore, changes in density can result in different requirements for the current or coming generation. For example, in red squirrels, *Sciurus vulgaris*, females which perceive higher density through social cues (manipulated with playback of territorial vocalization) have higher maternal glucocorticoid levels, which in turn increase the growth rate of their offspring [21], thus preparing them for a highly competitive environment.

Previous studies have provided evidence across a variety of taxa for individual variation in response to different levels of local density. Nest digging behaviour of queens of the harvester ant, *Messor semirufus*, varies considerably among individuals in the time spent before initiating digging, which is in part attributable to current and past experiences of conspecific queen density [22]. Individual field crickets, *Teleogryllus oceanicus*, are more phonotactic towards playbacks of conspecific calling songs when originating from a population where calling songs are rare [23]. These examples showcase that individual variation in experience and internal factors and variation in the reception and response to external factors will affect how individuals experience and respond to their environment and therefore the way they realize their ecological niche.

How are the concepts of individualized density perception and niche connected?

Population density is an important determinant of intraspecific competition and therefore often serves as its proxy (e.g., [24,25]). However, intraspecific competition may be reduced through niche complementarity, i.e. “the tendency for phenotypically divergent individuals to compete less strongly” ([26], p. 183), ultimately leading to higher carrying capacity and stability of populations [26]. Recent research has provided evidence on how intraspecific trait variation contributes to niche complementarity between individuals of the same population or species. In the framework of ecological niches, individual variation has been suggested as a shaping element of fundamental and realized niches [27], similarly it can also be utilized for disentangling within- and between-individual variation in niches [28]. Analogous to Hutchinson's niche concept, Takola and Schielzeth (2022) propose that the **individualized potential niche** represents the multi-dimensional environmental space in which a particular individual could be found with an expected lifetime reproductive success larger than or at least one, i.e. living to reproduce successfully [27]. However, the individual's phenotype and perception of local density affects the **individualized realized niche** for example mediated by differential resource use. In three-spined stickleback, *Gasterosteus aculeatus*, manipulating intraspecific competition via population density promotes niche variation within populations as phenotypically different individuals diverge in chosen prey items [29]. Moreover, intraspecific competition is altered by individual **niche specialization** [30] creating dynamic feedback between the behaviour of an individual and its social environment [31]. Due to such dynamics, individuals realize only a subset of their **potential niche**, as do populations and species in Hutchinson's framework [32]. This realized niche can be acquired through three key processes: niche choice, niche conformance and/or niche construction (**NC3 processes**)[33]. Each of these processes can be modified by individual variation in environmental perception.

Perceived density in relation to improving the phenotype-environment match

As individuals gauge local density through cues (see Table 1), when able, they respond to changes in **cue levels**, e.g. intensity of stimuli extracted from sensory input, to optimize their phenotype-environment match. Such optimization can occur via one or multiple of the following processes:

Through **niche choice**, individuals change which parts of the environment they interact with to improve the match with their present phenotype. In many species, dispersal is an optional key element of individual life histories. However, choosing whether to disperse or not rests on a trade-off between the cost of dispersal and the potential fitness gain, which is often density-dependent [34]. In group-living species, local density can be perceived directly as group size, and the decision to disperse relates to the individuals' tolerance to group size. For the common lizard, *Lacerta vivipara*, individuals display repeatable personalities, where at high density individuals with lower social tolerance disperse more readily than individuals with high social tolerance [35]. Here, different personalities are likely causal to the observed individual differences in perceived density. Other phenotypic traits can also interact with local density to shape an individual's behaviour. For example, in feral horses, *Equus ferus caballus*, the likelihood to disperse varies with age and sex, but also in accordance to individual perception of local density and group size [9].

Through **niche construction**, an individual actively modifies its environment [33], such as by altering the physical properties of the substrate and territory. It can also involve contest competition and resource monopolization through territoriality. Availability of resources and local density can create a foundation for different behavioural strategies. For dung beetles, *Onthophagus taurus,* increased density negatively affects brood ball production. Here, females at high density are more likely to abandon their own brood balls and engage in kleptoparasitism, whereas solitary females continue constructing [36]. Females more adept at obtaining cues about local density are therefore more likely to switch strategy at increasing density. Individuals can also impact the absolute density, i.e. construct their **individualized social niche**, e.g. through infanticide. For example, male bank voles, *Myodes glareolus,* are responsible for > 25% of mortality in nestlings and exhibit infanticide more often towards female pups when density increases [37]. Here, differences in perceived density might be the driver behind individual variation in the occurrence of infanticide within the population.

In the case of **niche conformance**, individuals adjust their phenotype (reversibly or irreversibly) to match the present environment. In several species of mice and voles, communal breeding arises in high densities, in which younger, often related, females join older females, thereby adjusting their breeding strategy and space use [10]. For female house mice, *Mus musculus domesticus,* engaging in communal breeding is dependent both on body condition and population density [10]. Here, differences in when/which individuals conform to communal breeding may be driven by differences in perceived density, leading to differences in the perceived competitive environment. In addition, habitat niche or space use might be adjusted by individuals due to differences in perceived density. In Antarctic fur seals, *Arctocephalus gazella*, pups should conform to the breeding colony chosen by their mothers. This is expressed through differences in movement patterns in pups of the same age, where pups at a low-density breeding colony are more active and move into a more protected environment to avoid predators earlier than pups from a high-density breeding colony [38]. Here, pups that perceive a lower density likely anticipate an increased predation risk, culminating in a change of their spatial use.

To summarise, perceived density has the potential to drive many changes at the level of individual niche realization by mediating different NC3 processes to optimize the match between phenotype and environment.

Evolutionary mechanisms of perceived density

Differential response to density within and among populations offers variation on which evolutionary mechanisms can act. **Density-dependent selection** is a basic model of competition-driven selection used in theoretical biology, assuming a uniformly distributed panmictic population [39]. **Frequency-dependent selection** (FDS) is a subset of density-dependent selection models, which relates more closely to the perceived density concept, as it accounts for phenotypes under differential selection based on their relative frequencies. The phenotypes are likely modifiers of density perception, potentially affecting both the perceiving individual and the selection agents. A rich body of literature discusses the consequences of FDS bias [40]. FDS can be positive, e.g. in the case of Allee effects, where positive (or negative) interactions depend on the minimum density [41–43]. Under a positive Allee effect, behavioural phenotypes might be favoured to perceive density higher than average and therefore engage in reproduction at lower overall densities [44,45]. Another form of FDS are aposematic effects, where predators negatively associate prey conspicuousness with profitability [46]. While for the predators information about prey obnoxiousness is never perfect and mimicry may additionally complicate the interaction, biases in perception of the density of different prey types can lead to both maintenance of striking visibility in case of positive FDS or the fluctuation of several recognizable prey phenotypes in case of negative FDS [47]. Similar density-dependent variation of interactions as between predator and prey can occur between competitors and potential co-operators, where biases in the perception of different types can lead to unexpected distortions and complications of these systems [40,48].

Perceived density is an individualized metric. Individuals can differ both in reception and processing of local density cues. In addition, variation also arises in how each perceived conspecific contributes to an individual's perceived density. These differences can be underpinned by evolutionary mechanisms, such as genetic variation and differential selection pressures. Such evolutionary mechanisms are particularly evident in systems where competitors and non-competitors have genetically encoded phenotypic differences, leading to a competitive advantage of cryptic competitors. These individuals most likely do not contribute to the perceived density of competitors, but instead to that of potential mates, as in the case of the female-like male ruffs, *Calidris pugnax,*[49]. More broadly, phenotypic variation as a modifier of perceived density applies not only to competitive contexts but extends to any social context, for instance, to reduce mating-related harassment, as seen in andromorph females of the hummingbird, *Florisuga* spp. [50].

As outlined above, genetic modifiers of appearance can influence how individuals are perceived in terms of competitive ability or predation risk, thereby affecting perceived density. Importantly, while genetic factors play a pronounced role in this process, individual variation in behavioural plasticity has been recognized as another important contributor shaping individual variation (i.e., individual differences in plasticity and predictability), as outlined in the last decades personality research [51,52]. Similarly to genetic modifiers, behavioural plasticity can influence both perception and the processing of stimuli, introducing an additional dimension for selection for act upon. Therefore, perceived density is not solely determined by passive attributes of conspecifics but can also be shaped by active signalling, enabling some individuals to manipulate how they are perceived by other members of their population or community.

The concept ‘perceived density’ in ecology and beyond

We argue that perceived density is the measure of density relevant to an individual, as heterogeneity in the physical and social environment, along with variation in density cues, likely obscure the ‘absolute’ density. Therefore, establishing measures to evaluate density as it is perceived by the study organism is paramount for the application of perceived density as a tool in ecology and beyond (Box 1).

Once measures of density perception are established, it is crucial to disentangle within- and between individual variation to determine whether and to what extent it is under selection. In systems, where density perception proves to be a stable trait within individuals, selection acting on it can be more easily predicted. We identify two ways in which density perception could be under selection. Firstly, selection could act directly on sensory modalities which influence an individual’s perception of density, improving the accuracy of the perceived density relative to the actual local density. Secondly, selection could act on the response to perceived density, which – depending on modifiers such as social system, competitive regime, and spatio-temporal variation in resource availability – could be directional, fluctuating, disruptive, or stabilizing [53–56]. These selection pressures could shape how individuals respond to the density they perceive, with some behavioural strategies being more prevalent during certain environmental conditions compared to others.

In response to perceived changes in density, individuals should adjust the appropriate phenotypic traits. For example, following the concept of local resource competition, females should produce more dispersing offspring when they perceive higher density and thereby a more competitive environment for their offspring, also known as maternal effects [57]. Indeed, in great tits, *Parus major*, where females disperse further than males [58], experienced females nesting in a plot with experimentally elevated densities produce female-biased clutches and vice versa for low density plots. The females thereby showcase an adaptive response to changes in density, with variation dependent on female experience [59]. Determining the signals and cues each organism utilizes to assess its local density and quantifying them can therefore be used to establish a measure of perceived density or to experimentally manipulate it, without needing to translocate individuals.

Concluding remarks

Studying the causes and consequences of individual variation in perceived environmental conditions is critical to our understanding of how individuals engage with their environment and realize their ecological niche (Box 2). Here, we illustrate through the concept of 'perceived density' the importance of investigating both the measure relevant to the individual and the differences among individuals. The differences in reception and perception of cues can result in different responses, on which selection can act and thereby result in different evolutionary outcomes. Therefore, developing methods to investigate the individual differences in perceived environments is crucial to understand how they contribute to adaptation and evolution.

Box 1: How to study perceived density

Ecologists have established methods and reliability tests to estimate population density in a given area or volume [60]. Studies on the effects of density on population dynamics, life-histories and behaviour have applied this methodology to assess density. However, the presence of individuals alone does not allow us to investigate the effects of perceived density on an individual. The analysis of perceived density might allow researchers to evaluate the reliance of each individual on targeted aspects of perception. To do so, we need to substitute the physical presence of conspecifics with stimuli (visual, chemical or auditory etc, see Table 1), through which the individual can assess the number of individuals present. While a few studies have tested the behavioural effects of auditory cues of extraneous conspecifics on groups or individuals (e.g. [21,61,62]), little is known about either the effects of other types of cues and the effects of perceived density on the individual.

To analyse individual perceived density, the experimental methodology adopted needs to consider some important factors. First, it is important to maintain the identity of the individual exposed to the perceived density. This can be achieved by isolating the individual during exposure, or by using software and hardware that maintain the identity of the single individual within a population, such as GPS data collected from individual organisms in the wild [63,64] or multi-animal tracking software [65,66]. Second, measures need to be adjusted to the study organism and its life stage. In general, behavioural analysis is a suitable measurement across life-stages and species. In some species, parental perceived density can be estimated through the correlated offspring sex ratio, or by quantifying the resources allocated for egg or sperm production in some hermaphroditic species [67,68]. Furthermore, it is possible to experimentally modulate cue levels to increase or decrease the perceived density of an individual, for example, by changing the number of recorded conspecific calls, the number of visual cues, or by changing the intensity of chemical cue levels.

Table 2. List of exemplary studies whose methodologies can be used to analyse perceived density at the individual level in different organisms.

289 **Table 1. Modalities for perception of presence and density of conspecifics**

Modality	Literature examples
Light sensing	● Plants perceive vegetation density through light signals reaching specific photoreceptors such as phytochromes, cryptochromes and phototropin [69]. ● *Datura ferox* seedlings adapt growth according to perceived canopy density detected from changes in red:far red ratio of the light [69].
Quorum sensing	● Density-dependent dispersal in freshwater protozoan *Paramecium caudatum* using physical cues [70]. ● Intracellular dynamical state encoding cell density information through glycolytic oscillations in cells of yeast (*Saccharomyces cerevisiae* X2180) [71].
Chemical sensing (olfactory, gustatory)	● Hermaphroditic polychaete (*Ophryotrocha diadema)* evaluate group size via water-borne chemicals resulting in shifts in sex allocation [67]. ● Dispersal behaviour in common lizards (*Lacerta vivipara*) is impacted by their social personality and perceived population density via odour cues [35].
Electric signalling	● Weakly electric fish (*Apteronotus* spp.) display grouping behaviour mediated through electrosensory signals to identify conspecifics [72].
Tactile	● Tactile stimulation of hind legs is a cue for conspecific density in desert locusts (*Schistocerca gregaria*) inducing change from solitary to gregarious behaviour [73]. ● Emigrating ants (*Temnothoray albipennis*) assess density of nest mates through encounter rates and tactile contact [73].
Visual	● Wood frog (*Rana sylvatica*) tadpoles adapt development/growth and activity levels to visually perceived changes in conspecific density [74]. ● Australian brush-turkey (*Alectura lathami*) chicks use visual cues to aggregate with conspecifics [74].
Acoustic	● Increased territorial calls lead to increased maternal hormone levels and offspring growth in North American red squirrels (*Tamiasciurus hudsonicus*) [75]. ● Conspecific acoustic cues lead to density-dependent attraction in least flycatchers (*Empidonax minimus)* during habitat selection [75].

Echolocation	• *Rhinopoma microphyllum* bats emit echolocation calls for detection of conspecifics in high-density foraging aggregations [76].

Table 2: Experimental designs that can be used to study perceived density at the individual level.

Stimulus type	**Animal model**	**Life stage**	**Experimental tools for density manipulation**	**Measurements**	**Location**	**Reference**
Visual	*Drosophila melanogaster*	Adult	Visual exposure to conspecific corpses	Aversive behaviour and lifespan	Lab	[77]
			Buridan paradigm	Numerical discrimination		[78]
	Apis mellifera		Y-maze			[79]
	Danio rerio	Larva	Dichotomous-choice test			[80]
		Adult	Habituation-dishabituation test			[81]
			Operant conditioning			[82]
	Poecilia reticulata	Newborn	Choice assay			[83]
		Adult				[84]
	Astatotilapia burtoni		Separated visual exposure	Behavioural annotation, mRNA and hormone level analysis		[85]
Chemical	*Ophryotrocha diadema*	Adult	Co-specific chemical cues	Sex allocation	Lab	[67]
	Drosophila melanogaster		Exposure to conspecific corpse odour	Aversive behaviour and lifespan		[77]
	Iberolacerta cyreni		Exposure to scent-marked area	Area choice		[86]
	Mus domesticus			Behavioural annotation		[87]

Auditory	*Teleogryllus oceanicus*	Adult	Conspecific playbacks	Sperm viability and paternity tests	Lab	[88]
				Emergence latency and mobility		[89]
	Mungos mungo			Behavioural annotation		[90]
	Panthera leo				Field	[61]
	Sciurus vulgaris					[91]
	Pan troglodytes					[62]
Other	*Nasonia vitripennis*	Adult	Host and social environment manipulation	Sex allocation	Lab	[68]
	Drosophila melanogaster		Conspecific corpses	Offspring production		[92]
		Egg	Egg density	Egg hatching and morphology		[93]

Box 2: Outstanding questions

In this paper, we address how individual differences in density perception and assessment can play an important role in an individuals' choice, conformance and/or construction of their own niches, with the subsequent fitness consequences. Although we focused on various aspects of perceived density as an exemplary case, the conceptual and methodological framework postulated here would be broadly applicable to the perception and evaluation of other environmental factors. Similarly, the challenges and outstanding questions about perceived density identified in the following section are likely to be relevant to future research on other environmental factors.

Individual variation in perceived density.

- How do species vary in their individual differences in density perception?
- How do species vary in their density perception and which sensory modalities they prioritize? Are these two components correlated?
- Do individuals vary in their density perception across time (i.e. lifetime, life stage, seasonal changes)?
- Which biotic and abiotic factors influence individual perception of density?

Consequences of among-individual variation in perceived density:

- How do differences in perceived density among-individuals affect dispersal decisions, foraging under risk, social foraging, mate choice, and sex roles?
- How can individual variation in perception of competition be implemented in classical competition models (e.g. Lotka-Volterra models)?
- Does perceived density shape the individualized social niche and should the concepts of density-dependent selection and social niche be merged?

Perceived density in conservation and welfare:

- What are the consequences and implications of perceived density for conservation and welfare?
- How can among-individual variation in perceived density be acknowledged in conservation to design and to improve animal welfare conditions?
- How do individuals differ in their perception of density under different human-induced environmental changes?

Glossary

Absolute density: The exact number of conspecific individuals per area, e.g. in experimental settings.

Cue: A trait that is produced by a sender that unintentionally convey information to a receiver.

Cue level: Intensity of a stimuli that the perceiving organism can extract from a sensory input.

Density-dependent selection: “Density-dependent selection occurs when the fitnesses of genotypes within a population respond differently to changes in total population size or density.” [94]

Frequency-dependent selection: “Frequency-dependent selection occurs when genotypic fitnesses are functions of their frequencies”. (Wright 1949, 1969; Crow & Kimura 1970).

Individualized potential niche: The hypervolume in environmental space in which a particular individual could be found with an expected lifetime reproductive success of ≥ 1. The individualized potential niche cannot directly be quantified, but significant parts of the niche space can usually be statistically inferred [27].

Individualized realized niche: The place in environmental space in which a particular individual is found and has an expected lifetime reproductive success of ≥ 1. The realized individualized niche can be quantified empirically [27].

Individualized social niche: The unit consisting of a focal individual and only those social interactions with other conspecific individuals that influence the focal individual’s inclusive fitness. [95].

Local density: The absolute number of conspecific individuals in an individual’s immediate surroundings, which affects its fitness.

NC3 processes: “NC3 processes consist of entities and activities that are spatially, temporally, and hierarchically organized in specific ways and produce a phenomenon” [33].

Niche choice: A NC3 process where the individual actively selects its environment or parts of the environment with which it interacts, e.g. through changes in location, resource use or social group.

Niche conformance: A NC3 process where the individual actively changing its phenotype to match the environment. Niche conformance involves phenotypic plasticity and “includes how phenotypic adjustments leads to change in the phenotype-environment match, fitness and the individualized niche of the focal individual” [33].

Niche construction: A NC3 process where the individual individually or as part of a group actively makes changes to its abiotic, biotic or social environment [33].

Niche specialization: The natural selection process by which a species becomes better adapted to specific characteristics of its environment.

Perceived density: The individual's assessment of its local density through its senses.

Perception bias: A type of cognitive bias where, based on prior experiences or expectations individuals receiving a signal might perceive it differently than the measured physical properties of the environment.

Population density: The number of individuals per area, counted or estimated by researchers.

Potential niche: The hypervolume in environmental space in which a species could survive and reproduce.

Sensory modalities: Sensory modalities are channels through which organisms perceive sensory stimuli.

Signal: A trait that is produced by a sender to intentionally convey information to a receiver. A signal has evolved specifically to influence the receiver and must have a benefit for the sender.

Stimulus: Any change in the environment that an organism can detect and respond to. Stimuli can be intentional (**signal**) or unintentional (**cue** or environmental factor e.g. sunlight).

Figure

Schematic depiction of perceived density

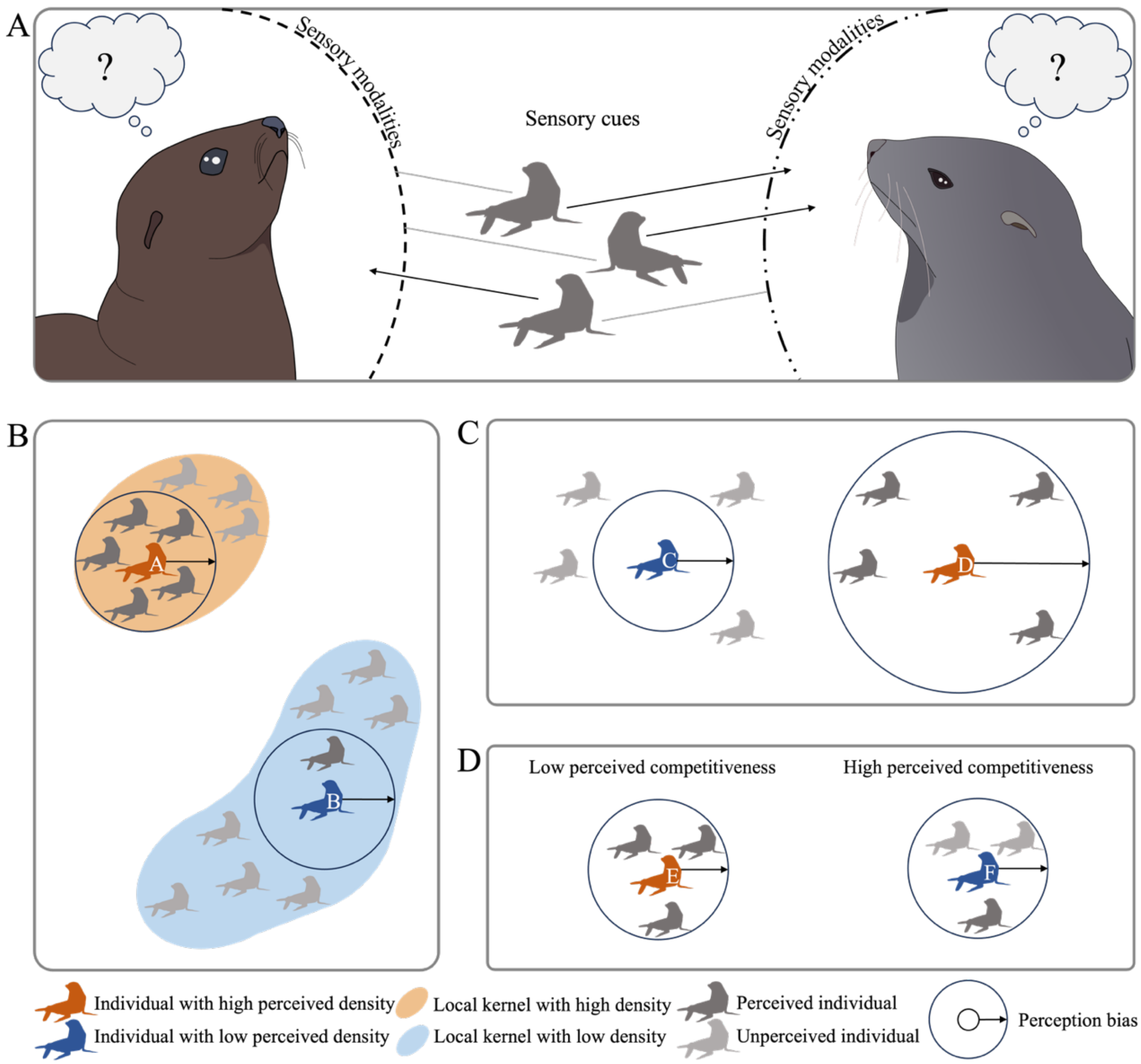

Figure 1: A: Two individuals of the same species differ in their sensory modalities and therefore they perceive density differently. B: The population density for the individuals "A" and "B" is measured equally within a given study plot (indicated by margins of panel B); their local and perceived densities differ. Local kernels can reflect discrete social groups, aggregations or spatial variation in density of continuous populations. C: Individuals may vary in their sensing and perception of local density. Individuals "C" and "D" perceive local density differently because their **perception bias** differ. D: Perceived density may be context dependent with individuals "E" and "F" having the same perception bias but interpret the same local density differently due to their respective perceived competitiveness.

Acknowledgments

This work was inspired by discussions with the members of the CRC TRR 212 (NC^3) – Project number 316099922.

Declaration of interests

The authors declare no conflict of interest.

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