Trends in Ecology & Evolution

Cell Press REVIEWS

Opinion

The Power of Infochemicals in Mediating Individualized Niches

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Infochemicals, including hormones, pheromones, and allelochemicals, play a central role in mediating information and shaping interactions within and between individuals. Due to their high plasticity, infochemicals are predestined mediators in facilitating individualized niches of organisms. Only recently it has become clear that individual differences are essential to understand how and why individuals realize a tiny subset of the species' niche. Moreover, individual differences have a central role in both ecological adjustment and evolutionary adaptation in a rapidly changing world. Here we highlight that infochemicals act as key signals or cues and empower the realization of the individualized niche through three proposed processes: niche choice, niche conformance, and niche construction.

Highlights

Individual differences are central in behavior, ecology, and evolution, because they determine which selective factors are relevant for an individual in interaction with its environment; yet ecological niches have rarely been studied on an individual level.

The subset of the species' niche realized by an individual is called its individualized niche and is implemented by three major processes: choice, conformance, and construction.

Infochemicals can differ between individuals and empower the realization of the individualized niche. Combining hormones and semiochemicals under the term infochemicals highlights their common function in information transfer within or between organisms.

We give several examples how chemical mediators, including hormones, pheromones, and allelochemicals, are essential in the realization of an individualized niche across the animal kingdom.

Niche Realization Processes

Ecological **niches** (see Glossary) have long been considered as n-dimensional hypervolumes of populations or species [1], whereby the dimensions are environmental conditions or resources that are defined by the requirements of all individuals of a population or species. Recently it has been recognized that individual variation and plasticity should be integrated into an **individualized niche** concept [2]. Each individual realizes just a subset of a population's or species' niche [3]. Moreover, individuals within the same population might occupy multiple local fitness optima, leading to divergent selection [4]. Thus, for a comprehensive ecological niche concept, the concept of the individualized niche has to be included. For such integration we need to understand the ecological and physiological circumstances that modulate the resulting phenotypic and fitness differences [5].

The interaction of an individual with its environment results in individualized niches via three major processes, namely **niche choice**, **niche conformance**, and **niche construction** (Figures 1 and 2). When an individual chooses the environmental conditions that best match its phenotype, it shows niche choice. Niche conformance occurs when an individual adjusts its phenotype to a given environment. Niche construction is the process whereby an individual modifies its environment according to its individual needs, which can also affect other species [6]. All three processes have consequences for the individual and its offspring and facilitate a better match between the individual and its environment, enhancing the individual's fitness. For successful niche realization, appropriate communication both within and between individuals is crucial. The most ancient way of communication occurs via the use of chemicals and chemoreception. Such chemicals may be **hormones**, which convey information transfer within an individual, or **semiochemicals**, which mediate information between individuals. Whereas **infochemicals** have traditionally been seen as synonymous with semiochemicals [7], we propose to use the term infochemicals for both hormones and semiochemicals because of their unifying function in information transfer (Figure 2). Due to their evolutionary age, omnipresence, and high plasticity, infochemicals are predestined

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to be involved in processes leading to individualized niches, but this link has so far been neglected. We suggest that phenotypic adjustments via hormones and the information coded in semiochemicals are key factors mediating individualized niche realization. Integrating these factors into a comprehensive concept of the individualized niche will allow a deeper understanding of when, how, and why individual phenotypes are adaptively modulated by environmental factors or how and why individuals modulate their environment to meet their individual needs. Here, we focus on the role of infochemicals in the realization of individualized niches in the animal kingdom. Our conceptual approach may likewise apply to all living beings.

[7]https://www.uni-muenster.de/Evolution/molevolsocbio/juergengadau.shtml
[8]https://www.uni-muenster.de/Biologie.NeuroVer/Verhaltensbiologie/Team/sylviakaiser.shtml
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Hormones: Intraindividual Chemical Mediators of Individualized Niches

Hormones are ubiquitous and often structurally highly conserved [8,9], indicating their long phylogenetic history and essential role in development, survival, and reproduction. Based on genetic or environmental factors, an intriguing intraspecific variation occurs in hormone titers and hormone responses among individuals [10], which has drastic consequences, for example, on rank positions, mating success, or foraging. In most cases, endocrine cells respond quickly to environmental influences and thus change their secretion of hormones within seconds or minutes. However, the duration of behavioral responses to such hormonal changes can vary from seconds (e.g., fight and flight responses) to months or even years (e.g., organizational effects of hormones on sexual behavior) [11].

Hormones are important drivers of niche choice, conformance, and construction (Figure 2, Table 1). In insects, juvenile hormone titers entrain individual niche choices in dependence of the environment experienced during a certain developmental stage. For example, resource availability impacts hormone titers that determine horn size in dung beetles (*Podischnus agenor*) and horn size influences the behavioral niche choice of the individuals [12]. In locusts (e.g., *Schistocerca gregaria*), individual-specific information about the environment likewise affects juvenile hormone titers. These titers influence phase transition from solitary to gregarious behavior, which is accompanied by further behavioral, morphological, and physiological changes [13,14]. In vertebrates, individual hormone titers, especially of glucocorticoids, are central in niche choice. For example, in eider ducks (*Somateria mollissima*) the degree of corticosterone reactivity influences nest-site selection, with consequences for fitness [15].

Niche choice and conformance can be tightly linked; that is, immature stages may choose a certain niche, to which later stages have to conform, or adults choose a specific niche to which their offspring must adjust. Hormonal regulation of horn size in dung beetles influences the individual's behavioral niche choice, but could also be considered as niche conformance, because beetles adopt a mating strategy matching their horn size. The role of hormones in regulating niche conformance is well studied in guinea pigs (*Cavia aperea* f. *porcellus*). Living in different social environments during adolescence triggers different neuroendocrine responses in males that lead to adaptive shaping of their behavioral phenotypes [16]. The frequency and intensity of social interactions during adolescence modulate testosterone secretion, influencing cortisol responsiveness and thus aggression (Figure 1B). Individuals with high or low aggressiveness conform to different social situations and use either resource defense or queuing strategies, realizing thereby distinct individualized social niches.

An involvement of hormones in niche construction is observed, for example, in bees (*Megalopta genalis, Bombus impatiens*) to adjust their social organization. Dominant females can modulate changes in juvenile hormone levels in their daughters via social interactions or resource limitation of their offspring, leading to further physiological and behavioral changes in their daughters. These changes make the daughters more likely to become helpers or workers rather than reproductives [17]. In various vertebrate species nest-building behavior, often leading to niche construction, is regulated by different hormones [18–20]. Given that nest-building behavior varies among individuals [20], niche construction must be considered at the level of the individual.

In summary, in a rapidly changing environment and a world with dynamic global changes, the ability of an individual to respond quickly to such changes and thus the ability to realize individualized niches is crucial for survival and reproduction. Hormones are a key factor in the realization of individualized niches. Their crucial role is particularly evident in view of the current discussion that selection might act on the (endocrine) mechanisms of behavior rather than on the behavioral traits themselves [21].

Pheromones: Intraspecific Chemical Mediators of Individualized Niches

Pheromones are considered as a subgroup of semiochemicals that cause behavioral or physiological responses in conspecifics [22]. In some animal species the terms 'colony recognition cues' or 'signature odors' (or 'signature mixtures') are used instead of pheromones because these cues need to be learned and the behavior may not be instinctively altered by a (few) chemical(s) [23]. For simplicity, we refer here to such compounds as pheromones. Some pheromones signal over long distances, such as the first identified sex pheromone, bombykol, which is released by female silkworm moths (*Bombyx mori*) to attract males [24]. Others such as cuticular hydrocarbons (CHCs) act at short range, for example, as sex or recognition pheromones in insects [25,26]. Similar to hormones, pheromones are powerful infochemicals mediating niche realization processes (Figure 2, Table 1). For example, competition for resources between species can be avoided by responding to the species-specific aggregation pheromones, as found in bark beetles (*Ips duplicatus* and *I. typographus*) [27]. Thus, pheromones can influence niche choice, ensuring aggregation of different species at distinct areas of their host trees. Likewise, several species decide which territories or breeding sites to use based on the presence of infochemicals. For example, female sac-winged bats (*Saccopteryx bilineata*) prefer to be in the vicinity of the odors produced by conspecifics over heterospecifics [28] (Figure 1A). Poison frogs (*Ranitomeya variabilis*) choose water-filled cavities of plants for tadpole rearing based on the presence of chemical cues released by conspecifics [29].

By definition, pheromones are species specific but often differ in quantities or ratios between individuals [30]. These differences can convey important information about an individual, such as identity, genetic relatedness, or competitiveness [31,32]. Qualitative changes in the pheromones need to be accompanied by changes in their perception [33] and may provide some of the flexibility required to maintain functioning intraspecific communication. This may be particularly important when individuals adjust to new environmental conditions, that is, show niche conformance, potentially leading to niche-associated variation in pheromone signaling and perception [33]. If divergence in signals between populations increases, reproductive isolation may occur [34]. In social insects, differential production of and responses to infochemicals are an important mechanism for nestmate recognition and regulation of division of labor, resulting in task-specific niches. For example, CHC-based queen pheromones are crucial in regulating reproductive division of labor in colonies of ants, bees, wasps and termites [35]. Group-specific odors also carry important information in social vertebrates. For example, odors differ among groups in spotted hyenas (*Crocuta crocuta*) [36] or European badgers (*Meles meles*) [37], allowing maintenance and assessment of group affiliation by conspecifics. Immigrants need to acquire the group odor to conform to the social niche. In spotted hyenas, acquisition occurs during the active transfer of bacteria by overmarking [36].

Population densities can be modulated by aggression pheromones, for example, in *Drosophila melanogaster* [33,38]. The fine-tuned responses to different pheromone concentrations mediate

Glossary

Allelochemicals: infochemicals that mediate interspecific communication.
Hormones: molecules that are secreted and transported in an organism and regulate its physiology, development, and behavior.
Individualized niche: subset of the species' niche that results from the interaction of an individual with its abiotic and biotic environment and affects the individual-specific fitness function.
Infochemicals: chemical compounds that carry information either within an individual as hormones, between individuals of the same species as pheromones, or between individuals of different species as allelochemicals. (Please note that this term has traditionally only been used in reference to semiochemicals [7].)
Niche: n-dimensional hypervolume, where the dimensions are environmental conditions and resources that define the requirements of the individual, population, or species to persist and reproduce.
Niche choice: process by which an individual chooses a certain environment that matches its phenotype and thus increases its fitness.
Niche conformance: process by which an individual adjusts its phenotype to a given environment to better match this environment, enhancing its fitness.
Niche construction: process by which an individual modifies its environment with fitness consequences on the individual, its offspring, and potentially also other species.
Pheromones: signaling molecules that mediate intraspecific communication. In social animals often the terms 'colony recognition cues', 'signature odors', or 'signature mixtures' are used instead, because these chemicals, in contrast to pheromones, must be learned by conspecifics. In this paper, all these terms are subsumed under the term pheromone.
Semiochemicals: chemical cues that mediate information transfer between individuals of the same (see pheromones) or different species (see allelochemicals).

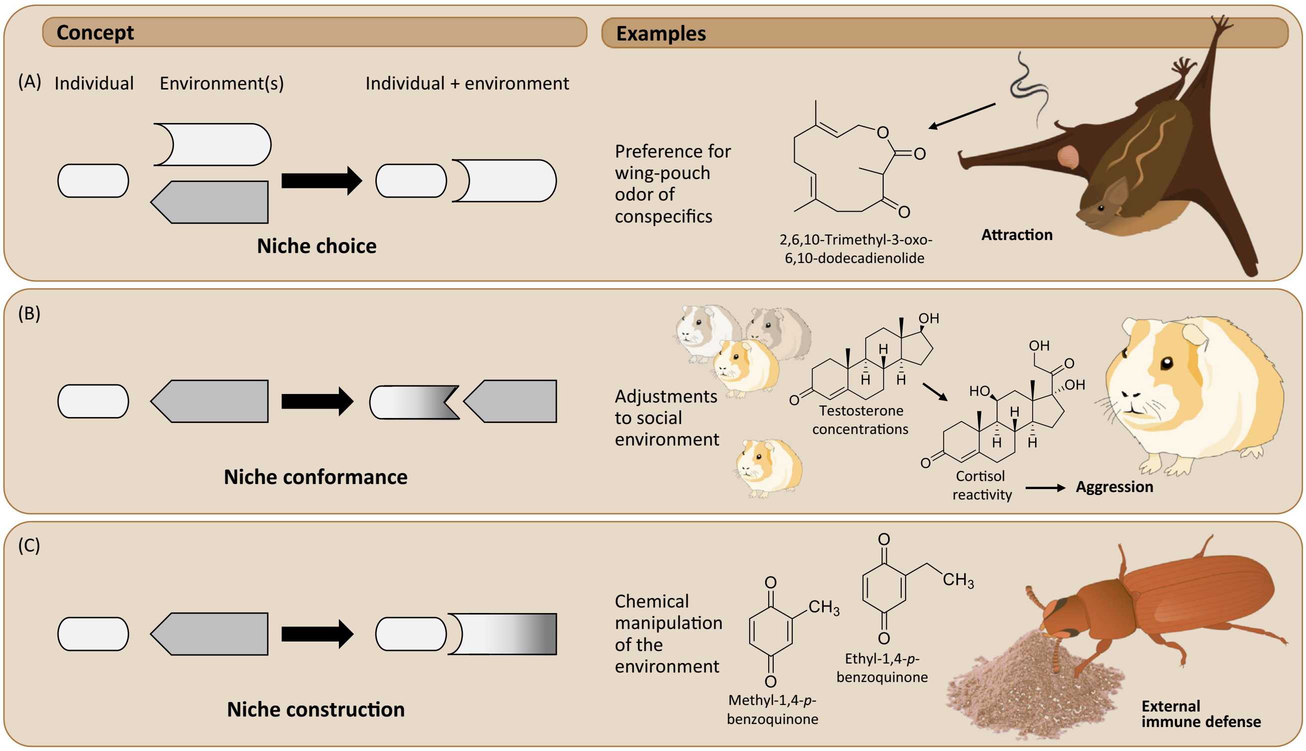

Figure 1. Three Main Processes That Lead to the Realization of Individualized Niches. Schematic depiction of the three processes involved in realizing an individualized niche (left) and examples (right). Individuals encounter environmental conditions and resources that either match or mismatch their phenotype. By the three processes niche choice (A), niche conformance (B), and niche construction (C), individuals reach a suitable match with their environment leading to realization of their individualized niche. For example, the greater sac-winged bat (*Saccopteryx bilineata*) uses pheromones of conspecifics for niche choice [28] (A), the social environment during adolescence influences hormone concentrations of domestic cavies (*Cavia aperea f. porcellus*) mediating their niche conformance [16] (B), and the red flour beetle (*Tribolium castaneum*) uses allelochemicals, released in its substrate and enhancing its external immune defense and defense against pathogens, for niche construction [50] (C). Drawings of animals by Marc Gilles.

social niche construction [38]. In mammals, scent marks are commonly used to define virtual borders, to deter potential intruders or to attract potential mates [31,39,40]. The odor-induced puberty delay in mice can be considered as another example for niche construction. Here, specific substances in the urine released by females in dense populations delay puberty in young mice, reducing competition [41].

Although invisible and therefore largely ‘overlooked’, pheromones are involved in all three processes of individualized niche realization. Across the animal kingdom and in numerous biological contexts, the same pheromones can mediate several processes simultaneously [39]. The evolution of these infochemicals is complex, involving biosynthesis of pheromones, signal perception, and exploitation of neural circuits that process these signals [22]. This complexity offers manifold sources for individual variation, which must be matched between the sender and the receiver. From an applied perspective, such variation on both sides needs consideration, for example, when using pheromones for biocontrol or in animal conservation programs.

Allelochemicals: Interspecific Chemical Mediators of Individualized Niches

Allelochemicals are another group of semiochemicals that mediate communication between individuals of different species (Figure 2, Table 1). These can be infochemicals guiding an herbivore to its host plant, fending-off or manipulating a receiver, or acting beneficially for both partners in

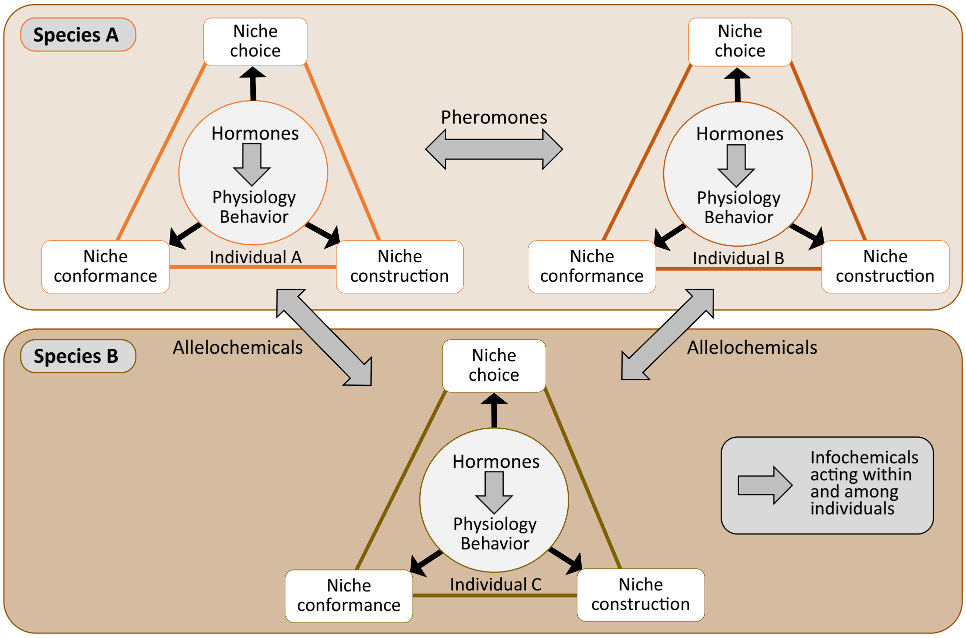

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Figure 2. Infochemicals That Mediate Information within and between Individuals. Different classes of infochemicals and their impacts on niche choice, conformance, and construction. In these processes, hormones mediate information within an individual, pheromones between conspecifics, and allelochemicals between individuals of different species. Each individual realizes its individualized niche.

mutualistic interactions. Numerous plant compounds have been identified that act as host-finding and host-acceptance cues, mediating niche choice. For example, many herbivorous insects specialized on Brassicaceae plants use glucosinolates as feeding and oviposition stimulants [42]. For prey or host selection, predators and parasitoids often use infochemicals that originate from their prey or hosts (sex pheromones, feces, etc.) or the food of their prey and hosts [43]. In the interplay between marine primary producers and vertebrate top predators, dimethyl sulfide plays a central role; it is produced by algae and other microorganisms during zooplankton grazing and is used by seabirds and marine mammals to find food [44]. Thus, allelochemicals can influence niche choice across various trophic levels.

Allelochemicals also allow species to co-exist based on distinct niche conformance. For example, different aphid species (*Macrosiphoniella tanacetaria* and *Uroleucon tanaceti*) inhabit different plant parts enabling them to live on the same plant without encountering direct competition [45]. For niche conformance, herbivores must be able to recognize their hosts as well as to tolerate, metabolize, or potentially detoxify (allelo)chemicals present in host tissues. Moreover, they have to plastically respond to slight modifications in chemical cues of their hosts caused by genetic and environmental factors. Furthermore, allelochemicals are used for niche conformance in induced defense responses against predators [46,47]. For example, water fleas (*Daphnia pulex*) form helmets when they perceive certain substances of low molecular weight of their predators [48].

Finally, allelochemicals act as powerful drivers in niche construction. Infestation of plants by phloem-feeding insects such as aphids can cause changes in the nutritional value of the phloem sap, which improves aphid performance [45,49]. Thus, aphids may make their host more suitable and construct their optimized niche. Flour beetles (*Tribolium castaneum*) excrete quinones, which

Table 1. Examples of Infochemicals That Mediate Niche Choice, Conformance, and Construction by Individuals

		Chemicals	Effects	Species		Refs
Niche choice[a]	Hormones	Juvenile hormones	Different horn size and behavior involved in reproductive strategies	*Onthophagus taurus*	Dung beetle	[12]
		Juvenile hormones	Hormone-mediated phase transition from solitary to gregarious lifestyle	*Locusta migratoria*	Migratory locust	[13,14]
		Corticosterone	Linking departure cues to the decision to migrate	*Turdus merula*	European blackbird	[59]
		Corticosterone	Nest-site selection	*Somateria mollissima*	Eider duck	[15]
	Pheromones	Unknown	Usage of different parts of the host plant	*Ips duplicatus* and *I. typographus*	Bark beetles	[27]
		2,6,10-trimethyl-3-oxo-6,10-dodecadienolide and unknown	Odor preference for conspecifics over heterospecifics	*Saccopteryx bilineata*, *S. leptura*	Sac-winged bats	[28]
		Unknown	Larval rearing site preference	*Ranitomeya variabilis*	Poison frog	[29]
		Unknown	Risk assessment of intrusion based on scent marks	*Mus domesticus*	House mice	[31]
	Allelochemicals	Glucosinolates	Feeding and oviposition stimulants of Brassicaceae plants		Feeding specialist herbivores	[42]
		Volatile and contact cues	Feeding preferences for certain plant chemotypes	*Macrosiphoniella tanacetaria, Uroleucon tanaceti*	Tansy aphids	[60]
		Indioside D	Induction of feeding preference for certain plants	*Manduca sexta*	Tobacco hornworm	[61]
		Dimethyl sulfide	Feeding preferences		Sea birds	[44]
Niche conformance[a]	Hormones	Juvenile hormone (JH), diapause hormone (DH)	JH regulates ovarian development depending on species and stage at which diapause is initiated, DH regulates egg diapause in silk moth	*Drosphila melanogaster, Leptinotarsa decemlineata, Bombyx mori*	Vinegar fly, Colorado potato beetle, silk moth	[62]
		Testosterone, cortisol	Social environments influence neuroendocrine responses during adolescence leading to different behavioral phenotypes	*Cavia aperea* f. *porcellus*	Guinea pig	[16]
		Glucocorticoids	Neuroendocrine changes during domestication	*Cavia aperea*, *Cavia aperea* f. *porcellus*	Wild cavy, guinea pig	[63]
	Pheromones	Unknown	Regulation in pheromone perception in males	*Spodoptera litura*	Cotton leafworm	[34]

Table 1. (continued)

		Chemicals	Effects	Species		Refs
		Unknown	Group odor production after transfer of group bacteria	*Crocuta crocuta*	Spotted hyena	[36]
	Allelochemicals	Unknown	Differential performance on different parts of the same host plant	*Macrosiphoniella tanacetaria, Uroleucon tanaceti*	Tansy aphids	[45]
		Low-molecular weight, non-olefinic hydroxy-carboxylic acid	Morphological changes due to the presence of predator cues	*Daphnia pulex*	Water flea	[48]
		Unknown	Induced predator defense in tadpoles	*Bufo bufo*	Common toad tadpole	[47]
Niche construction[a]	Hormones	Juvenile hormone	Caste determination	*Apis mellifera*	Honeybee	[64]
		Juvenile hormone	Decision between foraging and egg laying in foundress associations	*Pogonomyrmex californicus*	Californian harvester ant	[65]
		Estradiol, progesterone, testosterone, prolactin	Nest-building behavior	*Oryctolagus cuniculus*	Rabbit	[66]
		Mesotocinergic-vasotocinergic system	Nest-building behavior	*Taeniopygia guttata*	Zebra finch	[20]
	Pheromones	11-Cis-vaccenylacetate	Group size preferences and aggression, affecting social niche construction	*Drosophila melanogaster*	Fruit fly	[38]
		Unknown	Scent marking	*Mus domesticus*	House mice	[31]
		2,5-Dimethylpyrazine	Puberty delay	*Mus musculus domestica*	House mice	[41]
	Allelochemicals	Quinones	External immune defense, change in flour quality for offspring	*Tribolium castaneum*	Red flour beetle	[50]
		Unknown	Changes in phloem sap composition induced by aphid feeding	*Uroleucon tanaceti*	Aphids	[45]
		Unknown	Nest material selection	*Sturnus vulgaris*	Starling	[51]

[a]Note that the authors of the respective studies may not have named these processes niche choice, conformance or construction.

act as external immune defense and affect the microbiota community [50] (Figure 1C). These processes improve the quality of the flour, and in that way, parents construct a modified niche for their offspring. Some bird species (e.g., *Sturnus vulgaris*) actively collect parts of aromatic plants, which they add to their nests [51], thereby constructing an environment that protects the nestlings against ectoparasites [52]. The individual niches are thus chemically modified to improve fitness.

In conclusion, allelochemicals provide important information about the environment of an individual. It is becoming increasingly evident that the chemical composition varies drastically among individuals within species and thus carries highly specific information [53]. Future research is needed to elucidate how this variation is genetically determined and maintained and what the consequences of this individual variation are on species interactions and their individualized niches.

Interactions Between Infochemical Functions and Infochemical Flexibility

Intriguingly, the same infochemicals often function in different ways. For example, hormones of female goldfish (*Carassius auratus*) released into the water act as pheromones for males [54]. In fact, 'any molecule can evolve into a pheromone' [22]. Furthermore, pheromones and allelochemicals act synergistically or antagonistically, enhancing or interrupting the response of the receiver [55]. A large proportion of infochemicals are modulated by the individual itself, allowing it to respond plastically to environmental changes. In contrast to acoustic or visual communication, chemical information processes cover an enormously broad spectrum, being either highly stable or incredibly variable and short-term adaptable. Hence, individuals can flexibly respond to choose, conform to, or even construct their individualized niche, using variation in their own and other individuals' infochemicals and enabling the optimization of their phenotypes in a dynamic world [10,22]. Ultimately, various traits determine the individualized niche, whereby trade-offs between these traits may be crucial to understand niche specialization [56]. Such understanding offers insights in the opportunities and constraints of organisms in evolutionary ecology and the otherwise often hard-to-explain intraspecific variation of infochemicals both in quality and quantity.

Concluding Remarks

Individual differences in infochemical composition and in responses to infochemicals should be studied in depth to understand their roles in individualized niche realization processes and the evolution of the underlying proximate mechanisms (see Outstanding Questions). Individualization has been a hot topic in different research areas, spanning from ecology and behavior to evolution of individuals, populations, and species. Focusing on the individual is also applied in other fields such as precision (personalized) medicine [57] and individual-tailored welfare assessment [58]. Modulation of infochemicals may likewise drive these individual differences and their investigation may help the society in understanding causes and consequences of individualized niches. More knowledge about individual variation in the ability to adjust and react to a rapidly changing world is essential as it has implications for both ecological adjustment and evolutionary adaptation.

Acknowledgments

This research was funded by the German Research Foundation (DFG: https://www.dfg.de/) as part of the SFB TRR 212 (NC[3]), Project numbers 396777467, 396777092, 396780988 and 396777165. B.A.C. is currently funded through a Freigeist Fellowship of the Volkswagen Foundation. We thank Marc Gilles for the drawings of the animals in Figure 1 and our colleagues of the SFB as well as Fritz Trillmich for discussing and clarifying our ideas on the individualized niche. Moreover, we thank two anonymous reviewers for their helpful comments.

Outstanding Questions

To better understand how infochemicals influence niche choice, conformance, and construction, we need an integration of ecological, behavioral, physiological, and evolutionary approaches, which will eventually lead to a comprehensive concept of the individualized niche.

How widespread is individual variation of infochemicals?

How important is individual variation in infochemicals for the realization of the individualized niche and thus fitness?

During different ontogenetic stages, an individual's niche can shift. Are the three types of infochemicals (i.e., hormones, pheromones, and allelochemicals), similarly involved in the adaptive modulation of the individual phenotypes *via* environmental factors during different ontogenetic stages?

Do infochemicals differ mechanistically in how they mediate the realization of individualized niches across phyla, and if so, how do they differ? Can these processes be generalized across phyla?

How do the different infochemicals interact and how important is this interaction for mediating individualized niche realization? How will global change affect these interactions?

What does the concept of the individualized niche, mediated by individual differences of infochemicals, mean for various disciplines, such as precision medicine or animal welfare?

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