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Colonization: Individual Traits of Colonists and Population Processes

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Abstract—Human activity generates new global processes, including range expansions caused by landscape transformations, climate change, and biological invasions. The study of the causes and processes that accompany the colonization of new areas, as well as the ecological and evolutionary consequences, has been developing rapidly in the last 20 years at the junction of such domains of biology as spatial ecology, ecology of movement, ecology of invasions, metapopulation theory, behavioral ecology, evolutionary ecology, population genetics, and personality research. In this review, we summarize theoretical ideas and empirical studies to answer two main questions: what distinguishes colonists from the residents of source populations and what specific demographic and genetic processes drive and accompany the wave of population expansion?

Keywords: range expansion, dispersal, genetic structure, demographics, personality

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INTRODUCTION

“The figure of the barbarian who adopted the cause of Ravenna, the figure of the European woman who opted for the desert; these two stories could appear antagonistic. However, within the two can be observed an impetuous secret, an impetus deeper than reason, and both obeyed this impetus which neither knew how to justify.”

(*The Story of the Warrior and the Captive*, J. Borges; translated by Daniel Beizsley)

Colonization, i.e., expansion into new areas (see Glossary), is an integral part of the evolutionary history of any biological species; in the rapidly changing modern world, we can observe it with our own eyes. All evolutionary or ecological changes and innovations in populations, be it morph formation, the emergence of new cultural traditions, or the colonization of new territories, begin with individuals. The questions arise: Do *colonists* (pioneers, first settlers, see Glossary) consistently differ from their conspecifics? And if so, then how? Or are colonists a random sample from the *maternal population* (see Glossary)? No less interesting and important are the consequences of colonization at the population level, namely: what specific processes occur in the *wave of expansion* (see Glossary) and in populations of colonists compared to resident populations? This review summarizes theoretical concepts and empirical studies aimed at answering these questions. It also discusses the methodological challenges of studying the colonization process.

Colonization research is an interdisciplinary field of biology with a wide range of topics and methodological approaches. In our review, we limit ourselves to two topics: (1) the phenotypic (individual) characteristics of colonists and (2) the consequences of colonization at the population level—demographic, genetic, and evolutionary. We ignore questions on the environmental consequences at the community, ecosystem, and landscape levels, referring the reader to relevant books and reviews (e.g., Clobert et al., 2012; Dgebuadze, 2014). We do not consider in detail the proximal (ecological) and distal (evolutionary) causes of emigration; the costs and benefits of dispersal to new territories, as well as the effects of external conditions on making a decision “to leave or stay” are special topics (see, e.g., Bowler and Benton, 2005; Matthysen, 2012; Edelaar et al., 2017). Although related to the study of colonization, they remain beyond the scope of our posed questions: here, we are not interested in external drivers but in individual phenotypic differences that may influence the decision to leave, migration success, and colonization of vacant areas, all else being equal. The hypothesis that different propensities for long-distance migrations are an intrinsic individual trait is justified both by the theory and empirical studies (Clobert et al., 2001; Ronce, 2007; Matthysen, 2012; Chuang and Peterson, 2016), and we limit the review to this aspect.

Colonization and related phenomena have been studied in a broad spectrum of organisms, even at the cellular level. In discussing specific examples, we focus mainly on vertebrates, which have been studied in this regard to a much lesser extent than invertebrates

(primarily arthropods): their fast life cycle and small size allow studying them in experimental populations (Miller and Inouye, 2013; Chuang and Peterson, 2016; Williams et al., 2019).

WHY STUDY COLONIZATION?

We live in a world rapidly changing mainly due to human activity, which gives rise to new processes, including changes in species ranges as a result of human-induced transformation of landscapes, biological invasions, and climate change (Formozov, 1959; Dinesman and Savinetsky, 2000; Alimov et al., 2004; Khlyap and Varshavsky, 2010; Kokko and López-Sepulcre, 2006; Dgebuadze, 2014; Markov et al., 2019; Sage, 2020). Range expansions at the species level as a subject of biogeography are inextricably linked with the processes at individual and population levels: the dispersal of individuals into vacant habitats, which can cause population expansion and the formation of colonies in new areas. Movements of individuals are a key process in the dynamics of metapopulations and include three stages: emigration, migration, and immigration (settlement in an already occupied habitat) or colonization (settlement in an unoccupied habitat) (Ims and Yoccoz, 1997) (see Glossary). The term *colonization* as dispersal in unoccupied habitats and the formation of new populations was first introduced explicitly by Levins in his metapopulation model (Levins, 1969) and became widespread in population biology following the understanding of the patchy structure of fragmented landscapes and populations (metapopulations) (Hanski, 1994; Hanski and Gaggiotti, 2004).

Research into the mechanisms and ecological and evolutionary consequences of colonization has become popular in the last 10–20 years; it continues to develop rapidly at the junction of such fields of biology as spatial ecology, movement ecology, the ecology of invasions, metapopulation theory, behavioral ecology, evolutionary ecology, population genetics, personality research, and pace-of-life theory (Ims and Yoccoz, 1997; Hanski and Gaggiotti, 2004; Pavlov et al., 2006; Réale et al., 2007; Clobert et al., 2009; Amundsen et al., 2012; Chuang and Peterson, 2016; Rajora, 2019). The study of colonization is not only of scientific interest; it is also of practical significance for managing, on the one hand, endangered species and, on the other, economically and medically important species (Welles and Dlugosch, 2019).

The colonization of new spaces by populations depends on the propensity and ability of individuals to move from one place to another, in other words, *dispersal* (see Glossary) (Holt, 2003; Kokko and López-Sepulcre, 2006; Welles and Dlugosch, 2019). Dispersal is one of the most fundamental features of the life cycle of any organism; it affects the dynamics and evolution of spatially structured populations, gene flow, species distribution, and the ability to adapt to new

favorable conditions (Naumov, 1955; Clobert et al., 2001, 2009; Bowler and Benton, 2005; Dobson, 2013). In the context of global change (climate change, landscape degradation and fragmentation, biological invasions), *long-distance dispersal* (see Glossary) is a key mechanism that allows species to react to changing environmental conditions (Cote et al., 2010). At the same time, range expansions and colonizations are expected to have important ecological and evolutionary consequences, in particular promoting spatial and genetic differentiation of populations, microevolutionary processes, and the development of adaptations (Nichols and Hewitt, 1994; Bowler and Benton, 2005; Le Galliard et al., 2012; Orsini et al., 2013; Welles and Dlugosch, 2019). Thus, colonization combines processes of different spatiotemporal scales at the individual and population levels: evolutionary processes leading to between-individual variation in their propensity to disperse and the ability to colonize new areas, processes of the annual and life cycles (dispersal as a seasonal phenomenon and as a stage of development), the formation of life tactics and strategies in new ecological and social conditions due to phenotypic plasticity or selection, and population dynamics.

Despite the well-developed theory, the mechanisms of colonization, as well as the processes occurring in colonist populations at the edges of expanding ranges, are poorly understood in comparison with the dynamics of resident *parent populations* (see Glossary), especially among vertebrates (Kokko and López-Sepulcre, 2006; Chuang and Peterson, 2016; Welles and Dlugosch, 2019). To understand, on the one hand, what phenotypic traits influence the propensity and ability of individuals to disperse and colonize new territories and, on the other, what demographic and genetic processes occur during the expansion wave, it is necessary to link theoretical concepts with empirical studies of the colonization process, which are lacking. Range shifts and invasions in today's rapidly changing environmental conditions offer such opportunities (Kokko and López-Sepulcre, 2006; Rajora, 2019).

INDIVIDUAL LEVEL: PHENOTYPICAL CHARACTERISTICS OF COLONISTS

The propensity and ability to disperse and colonize new areas is supposed to be governed by individually consistent traits: behavioral, physiological, neurophysiological, and morphological, which are genetically determined and(or) formed during development. If these traits or some of them are correlated (which is not always possible to detect, see below), then they form a *dispersal syndrome* (see Glossary) (Clobert et al., 2001, 2009; Ronce, 2007; Cote et al., 2010; Matthysen, 2012; Ronce and Clobert, 2012; Chuang and Peterson, 2016).

These ideas began with a large experimental study by Myers and Krebs (1971). Based on the idea that

animal populations comprise individuals with different traits, Myers and Krebs compared resident voles and voles dispersing into artificially vacated areas in two species—*Microtus pennsylvanicus* and *Microtus ochrogaster*. The comparison of various characteristics such as body weight, sex, age, reproductive status, exploratory activity, open-field activity, and aggression showed significant differences between residents and dispersers. With the advent of animal *personality* research (see Glossary) over the past two decades and particularly in recent years, interest in this topic has rapidly increased. Theoretical considerations, models, and new data have emerged, asserting that, all else being equal, the success of dispersal is governed by individual characteristics, and successfully dispersing individuals that ensure population expansion are not a random subset of phenotypes of the maternal population (Bowler and Benton, 2005; Ronce, 2007; Clobert et al., 2009; Chuang and Peterson, 2016; Markov and Ivanko, 2022). Most empirical studies have been conducted under experimental conditions, while in natural populations, individual signs of dispersal syndrome have been demonstrated for only a small number of species (Duckworth and Badyaev, 2007; Sih et al., 2004; Bowler and Benton, 2005; Ronce, 2007; Cote et al., 2010; Debeffe et al., 2014).

Physical Characteristics

Dispersal and especially long-distance movements through the matrix, i.e. unsuitable habitats, followed by settlement in habitats already occupied or void of conspecifics (i.e. colonization) entail risks and significant energy costs. Therefore, good physical condition, particularly a large size and body weight, is considered a major phenotypic characteristic of migrants (Cote et al., 2010; Chuang and Peterson, 2016). Good physical condition is important both at the first stage of migration, emigration, to bear the hardships of further movement, and at the last stage, immigration into a competitive environment or colonization of an unfamiliar space. Clearly, the costs of movement, settlement, and colonization of a new site can weaken physical condition so much that it can end up worse than that of the residents remaining in the parent population, but sufficient to successfully settle in the new place. Therefore, strictly speaking, it is not always correct to compare the physical conditions of *immigrants* or *colonists with residents* (see Glossary). For example, in midday gerbils (*Meriones meridianus*), no differences in body weight were found between colonists and residents of the parent population with sex and age taken into account (Tchabovsky et al., 2023). However, it is unclear whether the lack of differences indicates that future colonists did not initially differ from residents.

However, because physical parameters are convenient and easily measurable individual characteristics, many comparative studies evaluate them correctly,

i.e., at different dispersal stages. For example, in ground squirrels *Spermophilus beldingi*, dispersing animals were heavier at the time of emigration than non-dispersing (Holekamp and Sherman, 1989). In an experimental study, green frogs (*Rana clamitans*) that colonized artificially vacated ponds differed by their larger size from residents inhabiting ponds that were sources of emigration. Moreover, body size increased with distance from the parent population, indicating that larger frogs are more successful at colonizing over long distances (Searcy et al., 2018). Another example is the invasion of cane toads (*Rhinella marina*) in Australia, where long-legged individuals were more abundant in the expansion wave (Phillips et al., 2006). Body and limb size may correlate with locomotor activity, in that larger individuals are likely more capable of travelling greater distances. Therefore, we can theoretically expect individuals to be larger in the wave of expansion than in core areas (Chuang and Peterson, 2016), which is confirmed by the empirical studies we have reviewed above.

Individual Behavioral Characteristics

Since the first studies on dispersal syndrome as a set of consistent phenotypic traits, primary attention has been paid to the behavioral characteristics of dispersing individuals (Myers and Krebs, 1971; Bekoff, 1977). With the advent of the theory of personality in animals and exponential growth of empirical data on this topic in various fields of biology over the last 20 years (Vasilieva, 2021; Laskowski et al., 2022), it has become one of the main concepts in studying dispersal and colonization, range expansions, and invasions (Clobert et al., 2001, 2009; Ronce, 2007; Ronce and Clobert, 2012; Carere and Gherardi, 2013; Chuang and Peterson, 2016; Duckworth et al., 2018).

The propensity to disperse and ability to colonize new areas in representatives of various taxa (invertebrates, fish, reptiles, birds, and mammals) are most often associated with general activity, exploratory activity, and boldness (or more broadly, risk-taking behavior) taken together (as “explorer syndrome”) or individually (Duckworth and Badyaev, 2007; Cote et al., 2010; Le Galliard et al., 2012; Debeffe et al., 2014; Chuang and Peterson, 2016; Duckworth et al., 2018). For example, in European roe deer (*Capreolus capreolus*), dispersers initially demonstrated higher levels of exploratory activity and energy metabolism than philopatric individuals (Debeffe et al., 2014). House mice (*Mus musculus*) with higher exploratory activity dispersed earlier than less active ones (Krascow, 2003). Colonizing bank voles (*Myodes glareolus*) showed higher mobility and activity levels than resident voles in parent populations (Ebenhard, 1987). However, the relationship between explorer syndrome and dispersal is not always confirmed. For example, in voles *Microtus pennsylvanicus* and *Microtus ochrogaster*, male dispersers demonstrated lower exploratory

activity than resident ones, even though the trait was highly consistent individually and repeatable in successive tests (Myers and Krebs, 1971). In western mosquitofish, *Gambusia affinis*, explorer syndrome, which combined correlated and temporally consistent individual traits (general activity, exploratory behavior, and boldness), was not associated with the dispersal distance (Cote et al., 2010a).

One well-known example is a series of studies based on long-term research on dispersal as a function of individual differences in the behavior of great tits (*Parus major*) in a natural population in the Netherlands (Verbeek et al., 1994; Dingemanse et al., 2003; van Oers et al., 2004; Fidler et al., 2007). First, the authors showed that exploratory activity and boldness (propensity for risk-taking behavior) were correlated. Moreover, both traits are consistent individual characteristics, varying in successive tests of one individual less than between individuals (Verbeek et al., 1994). The correlation of individually consistent behavioral traits is a reliable criterion for the behavioral syndrome (Sih et al., 2004). It was then shown that the initial level of exploratory activity of young individuals and their parents correlated with the distance of natal dispersal in a natural population and was higher among immigrants than residents (Dingemanse et al., 2003). Then, by selecting birds in a laboratory over four generations, the authors obtained two lines—bold birds with a high level of exploratory activity and timid birds with low—and proved that these traits were genetically related and heritable (van Oers et al., 2004). Finally, they revealed the genetic basis for interindividual variation in exploratory activity, demonstrating that its level is determined by a polymorphism in the dopamine receptor gene *Drd4*, in which some single-nucleotide substitutions correlate with a tendency to seek novelty and risky behavior (Fidler et al., 2007). However, even though a later study confirmed the relationship between the *Drd4* polymorphism and exploratory activity in the same tit population, it was not found in three other populations, which confuses the idea of a relationship between *Drd4* and the propensity to disperse (Korsten et al., 2010). Nevertheless, the migratory distance out of Africa in *Homo sapiens* is also associated with polymorphism of the dopamine receptor gene: the higher the frequency of alleles 2R and 7R in the polymorphic region of the gene in different human populations, the farther they dispersed outside Africa (Matthews and Butler, 2011). The same pattern was shown for human populations of South America, where the frequency of the novelty-seeking alleles of the *Drd4* gene correlated not only with the distance of migrations but also with the way of living in the recent past: it was higher among once hunter-gatherers than among agriculturalist populations (Tovo-Rodrigues et al., 2010).

The relationship between dispersal and aggressiveness or sociability as personality traits has been studied less, and the research results are more heterogeneous

and contradictory (Le Galliard et al., 2012). On the one hand, less aggressive individuals are more likely to be displaced from a colony or population because of local competition for resources or mates. On the other hand, aggressiveness should contribute to successful settling in a new population or community, resulting in higher competitiveness at the intra- and interspecific levels (Clobert et al., 2009; Cote et al., 2010; Chuang and Peterson, 2016). Thus, in western bluebirds *Sialia mexicana*, aggressiveness and a tendency to disperse are consistent phenotypically and genetically correlated individual traits. As a result, in the wave of range expansion, more aggressive birds are found more often, facilitating subsequent colonization and displacement of a local closely related species (Duckworth and Badyaev, 2007; Duckworth and Kruuk, 2009). At the same time, the colonist phenotype is influenced by maternal effects, namely, the egg-laying order, which determines the variation of adult offspring in aggressiveness and propensity to disperse. Males that hatch from the first eggs laid by a female in a clutch (“early males”) are larger, more aggressive, and disperse farther, in contrast to the smaller, less aggressive and philopatric males that hatch last (“late males”).

Moreover, when resources are limited and competition for nesting sites is high, females produce more early males—potential emigrants and colonists—and, conversely, more philopatric late males when competition is low. This chain of sequential effects influencing the phenotype of the offspring is based on the mother’s hormonal background, set by external conditions (competition for resources); its consequence is emigration and colonization of new territories by aggressive birds with a subsequent decrease in aggressiveness in a series of generations of colonists with low competition in colonies (Duckworth, 2009; Duckworth et al., 2015). Higher aggressiveness in dispersing individuals was also found among voles of different species, although not in all (Le Galliard et al., 2012a). Several studies revealed a genetic basis for the correlation between aggression and dispersal (Zera and Brisson, 2012). In rhesus macaques (*Macaca mulatta*) and house mice, the tendency to disperse is associated with substitutions in the polymorphic noncoding region of the serotonin transporter gene *SLC6A4*, which controls aggressive behavior (Trefilov et al., 2000; Krackow and Konig, 2008).

Studies of the role of sociability as an individual behavioral trait in dispersal and colonization are rarer, and their results are even more contradictory. Bekoff (1977) proposed the social cohesion hypothesis, which predicted that more socialized, more socially integrated individuals would be less likely to disperse. This was confirmed in a study of yellow-bellied marmots (*Marmota flaviventris*), in which females more involved in social interactions in the group were less likely to leave the group than females avoiding group members (Blumstein et al., 2009). Female gray-sided

voles (*Myodes rufocanus*) that dispersed over greater distances more actively avoided conspecifics after dispersal than more philopatric females (Ims, 1990). Low sociability correlated with the distance of dispersal in western mosquitofish, so that in the expansion wave, there were more asocial individuals (Cote et al., 2010a). A recent review of scant available studies suggests that more social individuals are overall more likely to be philopatric (Taborsky, 2021), but exceptions are not uncommon (Clobert et al., 2009; Cote et al., 2010; Le Galliard et al., 2012).

In general, we can conclude that the empirical data confirm, though not always, that consistent genetically determined individual behavioral traits (personality traits) determine the propensity and ability of individuals to disperse and can play a role in the expansion of populations and colonization. These traits primarily include general activity, exploratory activity, and boldness, often forming a syndrome of correlated traits, which suggests the presence of a common basis (Sih et al., 2004). The role of sociability and aggressiveness in determining the propensity and ability to disperse remains unclear, perhaps due to the very different motivational bases of both behaviors, which vary depending on the situation. In addition, measurements of aggressiveness and sociability in tests and the tests themselves are much less standardized than estimates of activity, exploratory behavior, or boldness in the standard open field, novelty, startle, or emergence tests—common and fairly uniform procedures in personality research (Krebs et al., 2019; Lasowski et al., 2022). Variability in procedures and methods for assessing behavioral traits may contribute to the heterogeneity and inconsistency of the results.

Despite the considerable interest in this topic and its demand, there are still very few studies on the role of personality in dispersal, colonization, and range expansions, and this is mainly experimental data (Chuang and Peterson, 2016). The reason is clear: it is not easy to observe the dispersal of individuals and the spread of a population in nature and, at the same, time to assess the individual behavioral characteristics of residents and migrants. Moreover, it is necessary to be in the right place at the right time. A related problem is the need for repeated measurements of individuals before and after dispersal, or at least before. Otherwise, it is difficult, if possible, to relate the difference in behavior between colonists and residents of the parent population with the difference in their individual properties rather than in the conditions “at home” and “in the colony.” For example, in the above-mentioned study on great tits (Dingemanse et al., 2003), it remains unclear whether the greater exploratory activity shown in a standard test by immigrants compared to residents is due to their initial pre-dispersal curiosity or the result of increased motivation to explore in a new environment? In fairness, it should be noted that the authors in another study (van Oers et al., 2004) proved the heritability of curiosity in great tits. In a

review of 20 comparative studies on personalities in residents and migrants (Cote et al., 2010), the behavior of migrants before dispersal was assessed in 13 studies, after dispersal in 10 studies, and both before and after dispersal in only four studies. Thus, the heterogeneity and contradictory results of personality studies related to dispersal and colonization stem largely from a scarcity and methodological difficulties of observations, especially in natural populations.

Glucocorticoid Levels, Stress Reactivity, and Behavior

Interindividual differences in behavior—personality traits—may be associated at the proximal level with individual differences in the hormonal response to stress (Clobert et al., 2009; Ronce and Clobert, 2012). Several studies have tested how stress reactivity relates to behavioral traits such as boldness and exploratory activity, which in turn are associated with the propensity and ability to disperse and colonize (Koolhaas et al., 1999; Carere et al., 2003; Cote et al., 2010). For example, in bold and actively exploring great tits (*Parus major*), corticosterone levels increased less after social stress than in shy and low-exploring birds (Carere et al., 2003). Lower fecal glucocorticoid levels were reported in bold Richardson’s ground squirrels (*Urocitellus richardsonii*), while exploratory activity was unaffected by glucocorticoid concentrations (Clary et al., 2014).

Meanwhile, dispersing individuals may demonstrate higher stress reactivity. The relationship between the level of corticosterone rise in response to a stressor and exploratory activity was tested in a population of the house sparrow (*Parus domesticus*) in Kenya, where it is expanding into new areas. The level of exploratory activity and the strength of the stress response increased with the distance from the population core to the leading edge of expansion (Liebl and Martin, 2012). The authors believe the increased stress reactivity helps explore new spaces, allowing stressors to be better identified, differentiated and remembered in an unfamiliar environment.

The propensity to disperse may depend on the maternal stress hormone levels (Meylan and Clobert, 2005; Cote et al., 2010). For example, in viviparous lizards (*Lacerta vivipara*), chronically high maternal corticosterone levels negatively affected the dispersal of the offspring, worsening their physical condition (Meylan et al., 2002). Another recent study of rodents (Kameneva et al., 2022) found the opposite pattern. Stress experienced by the mother was shown to increase serotonin levels in the placenta and fetus, leading to a reduction in the size of the adrenal medulla, causing lasting and irreversible changes in behavior in the offspring. The offspring of such mothers showed lower levels of aggressiveness, territoriality, anxiety, and stress reactivity. Moreover, a reduction in the size of the medulla in migrants compared to residents was found in the natural population of northern

red-backed voles (*Clethrionomys rutilus*) against a population peak, i.e., a high level of intrapopulation stress.

Thus, glucocorticoids can influence both the behavioral profile (aggression, activity, sociability) and propensity to disperse and, therefore, potentially serve as a proximal mechanism linking personality to the propensity to disperse and colonize new areas (Cote et al., 2010). However, the relationship between glucocorticoid levels and behavioral dispersal syndrome is not always found (Roncè and Clobert, 2012). For example, in the white-collared flycatcher (*Ficedula albicollis*), corticosterone levels were not correlated with the response to novelty, aggressiveness, or boldness—correlated individual traits that are characteristic of dispersing individuals (Garamszegi et al., 2012a). Similar negative results were obtained in a natural population of Belding's ground squirrel (*Urocitellus beldingi*) (Dosmann et al., 2015). General activity, exploratory activity, and boldness demonstrated consistent interindividual differences and were correlated, forming a behavioral syndrome. The glucocorticoid levels were also individually consistent, repeatable and varied between individuals; however, they did not correlate with any behavioral trait. The authors conclude that individual behavioral traits are relatively conservative and independent of the internal state.

Studying stress reactivity, which may determine personality traits and dispersal tendencies, is quite a challenging objective; this may explain the inconsistency of the results. First, glucocorticoid levels are highly variable, and although they can vary between individuals (Dosmann et al., 2015), assessing their consistency as an individual trait is very difficult because they depend on numerous external and internal factors. This requires verified, highly standardized conditions, which is difficult to achieve not only in natural but also in experimental populations.

The question arises: how universal and rigid are the dispersal syndrome traits? How do they change, if they do, throughout life, and to what extent are they species-specific? A major part of characteristics, which determine the propensity and ability to disperse and colonize, was suggested a priori, based on theoretical considerations and common sense: large size, boldness, high activity and mobility, curiosity, aggressiveness, etc. Accordingly, they are considered quite universal for different taxa. Moreover, although not always, these traits can be detected in various organisms—from arthropods to mammals (Clobert et al., 2009, 2012; Roncè and Clobert, 2012; Chuang and Peterson, 2016), which reinforces the idea of their universality.

On the other hand, the results obtained from studies of different species are contradictory (see above), and a significant part of the work failed to show differences between dispersing individuals or colonists and residents (Chuang and Peterson, 2016). This questions the general universality of dispersal-related traits and

suggests they may be species specific. However, we are unaware of any special comparative studies on this topic. There are very few comparative studies of personality and behavioral syndromes in general, and a meta-analysis has shown that the strength of the syndromes is species-specific (Garamszegi et al., 2012). One may expect that while having universal features, the dispersal syndrome and colonist syndrome (see below) or their components will vary depending on the species' life history, particularly life strategy, sociality, the parameters of the annual cycle, and pace of life.

The existence of consistent genetically determined individual traits associated with the propensity to disperse and colonize new areas now raises little doubt, although they are not always possible to detect (Chuang and Peterson, 2016). Another question is to what extent they, like other personality traits, are plastic and can change depending on the developmental stage, the current state of the individual, context, and conditions (Clobert et al., 2009). The answer is they are plastic (e.g., interindividual variation explains less than 40% of the total variability in behavior (Bell et al., 2009)); however the degree of plasticity is also individual, so the consistency of behavior in combination with its plasticity forms the “behavioral reaction norms of individuals” (Dingemans et al., 2010; O’Dea et al., 2022).

POPULATION LEVEL

Demographic Aspects of Colonization

The theory and some empirical studies suggest that colonists are not a random sample from the parent population, and their characteristics can specifically influence the spatiotemporal dynamics of populations. The opposite is also true: population processes in colonies can cause changes in the life history parameters of the colonists (Roncè, 2007; Clobert et al., 2009; Amundsen et al., 2012; Chuang and Peterson, 2016). However, the dynamics of the demographic structure during the colonization process and consequences of a biased demographic composition of the colonist populations for their sustainability have been poorly studied, which is due to the lack of direct observations of the colonization process in real time (Welles and Dlugosch, 2019).

Sex and age structure. Young individuals are assumed to be more prone to disperse because they are less competitive than adults (Hamilton and May, 1977; Shilov, 1998), and by leaving their natal site, they lose less than adults with a permanent and long-established, “life-tested” home range (Clark, 1994). Therefore, we can expect that there will be more young individuals among colonists. However, the relationship between age and dispersal is not as clear-cut. For example, in different species of voles, neither the proportion of emigrants nor the distance of dispersal

has been shown to depend on age (Le Galliard et al., 2012a).

Sex-specific dispersal contributes to a biased composition of colonist populations. Thus, in mammals, males usually disperse more often and further, while females are more philopatric (Greenwood, 1980). Therefore, female philopatry theoretically will bias the sex ratio in colonist populations in favor of males (Bowler and Benton, 2005; Clobert et al., 2012; Li and Kokko, 2019). Strictly speaking, this expectation is not fully justified: the greater or lesser propensity of males and females to disperse will primarily determine the sex ratio among *emigrants*, i.e., at the first stage of dispersal, whereas the sex composition of colonists depends, in addition, on sex-differentiated success at subsequent stages (i.e. *transfer* and *settling* in a new habitat) (Bowler and Benton, 2009), which have been studied much less well (Le Galliard et al., 2012a).

In addition, the sex ratio among colonists may be governed by the different propensities of males and females to move short or long distances. Male dispersal in mammals has traditionally been associated with competition for mates and inbreeding avoidance: provided that females are philopatric, dispersal of males from the natal site increases access to unrelated females, reducing competition (Greenwood, 1980; Wolff, 1994). In this case, the availability of unrelated females will increase immediately with the distance from the natal site, minimizing the risk of inbreeding already at short distances even within the natal colony (Batova et al., 2021). Females, unlike males, compete to a greater extent not for mates but for resources (food and/or breeding sites, Andersson, 1994) and are more dependent on kinship ties (Wolff, 1994). Therefore, their tendency to disperse is less pronounced: departure from their natal home range breaks kinship ties but does not guarantee access to more resources than the amount already available. However, if local density and resource competition are very high, dispersal from natal site may be beneficial. Moreover, suitable conditions are more likely to be found at greater distances, in another colony or vacant habitat. Thus, the reasons for dispersal over short and long distances vary, determining differences between the sexes in dispersal distances (Ronce et al., 2001; Rousset and Gandon, 2002). Males should theoretically be more likely to disperse over short distances to avoid inbreeding, while females should be more likely to disperse over long distances to avoid overcrowding and competition for resources, thereby facilitating the colonization of new habitats (Ronce et al., 2001; Fontanillas et al., 2004; Lawson Handley and Perrin, 2007). Therefore, females are called the “colonizing sex” (Kerth and Petit, 2005; Gauffre et al., 2009).

These theoretical considerations have been supported by empirical studies. For example, in the possum *Trichosurus vulpecula*, movements between colonies were more typical for males, while males and

females equally participated in colonizing vacant habitats (Ji et al., 2001). Among rodents, in species capable of quickly restoring numbers after depopulation, pregnant females significantly contribute to the colonization of depopulated habitats, in contrast to species unable to recover rapidly (Shchipanov, 2003). An experimental study of the common vole (*Microtus arvalis*) (Gauffre et al., 2009) showed that males, although dispersed significantly more often than females, moved mainly within colonies and less frequently between colonies (the average distance between colonies was 12.7 km). Dispersing females, on the contrary, changed the colony in the overwhelming majority of cases and very rarely dispersed within its boundaries. However, the tendency to move long distances is not always confirmed to be stronger in females than males. Thus, an analysis of sex-specific genetic markers in shrews (*Sorex antinorii*) showed an opposite relationship between dispersal distance and sex: dispersal over long distances was strongly biased in favor of males, while at the local level, females dispersed more often (Yannic et al., 2012). In the greater white-toothed shrew *Crocidura russula*, dispersal within a population was also biased towards females, but dispersal between populations was balanced between the sexes (Fontanillas et al., 2004).

Thus, because of sex-specific distance-dependent dispersal propensity, different dispersal success between males and females, and stochastic effects (Miller et al., 2011; Miller and Inouye, 2013), the sex ratio at the leading expansion edge may be strongly biased towards one sex or the other or approximately equal. Mathematical models have been proposed for population expansion depending on the degree of sexual dimorphism in dispersal, which determines the sex ratio of the expansion wave and, correspondingly, the speed of its movement (Miller et al., 2011; Shaw et al., 2018). These theoretical models were confirmed in a study of range expansion in butterflies simulated under experimental conditions. When dispersal was biased toward females, the rate of population spread increased, levelling out stochastic fluctuations in the sex ratio in the expansion zone (Miller and Inouye, 2013). According to the results of the above-mentioned experimental study of common voles, though females moved longer distances, there were still more males among immigrants because they dispersed more intensively (Gauffre et al., 2009). Most studies on sex ratios in the expansion wave are theoretical, more rarely experimental, and there are almost no direct observations in natural populations.

Reproduction and population dynamics during the expansion wave and life-history characteristics of colonists. A strong bias in the sex ratio in favor of one sex or another, combined with low density in the expansion wave, can negatively affect the intensity of reproduction, growth, and expansion of the colonist population due to the demographic Allee effect—a shortage

of mates of the opposite sex (Courchamp et al., 1999; Gascoigne et al., 2009; Miller et al., 2011; Li and Kokko, 2019). Difficulties in finding a mate can slow, delay, or stop population expansion. This effect is enhanced by the specifics of the mating system. In monogamous species, mate choice is limited, and, therefore, polygynandrous species have an advantage and are more successful in colonization, all else being equal (Shaw et al., 2018). Given that females are usually the limiting sex in animals with conventional sex roles (Andersson, 1994), a sex bias towards females in the colonist population accelerates population expansion (Miller and Inouye, 2013).

Low density, below the carrying capacity, is an integral feature of a population at the boundary of an expanding range, and, regardless of the biased sex ratio, it can itself limit expansion due to the Allee effect (Allee et al., 1949; Courchamp et al., 1999, 2008; Chuang and Peterson, 2016; Williams et al., 2019). According to the Allee principle, a drop in density below a critical threshold disrupts the negative feedback between density and population growth. In this case, low density does not lead to population growth but to a further decline in numbers through positive feedback loops, which can result in either a fixation of numbers at a very low level (weak Allee effect) or population collapse (strong Allee effect, (Courchamp et al., 1999)). If the density at the leading edge of the expansion wave is below a critical value, the Allee effect will limit population expansion (Chuang and Peterson, 2016). A simple rule here: population expansion indicates the absence of a strong Allee effect at its boundaries.

However, if the low density during the expansion wave does not fall below a certain threshold, we can expect the opposite effect— an intensive reproduction, growth, and further expansion of the population. This is because the negative effect of density on population growth, which is characteristic of a core population saturated with individuals, will be weakened (“escape from negative density dependence”). The positive effect of low density will remain in force until the population reaches the carrying capacity or other external factors (e.g. the pressure of competitors, predators, or parasites) stop the expansion (Burton et al., 2010; Chuang and Peterson, 2016; Williams et al., 2019).

For example, in midday gerbils (*Meriones meridianus*) currently expanding their range in Kalmykia due to a new desertification cycle (Surkova et al., 2022), the fertility of females in the expansion zone was higher and the population composition was younger than in the parent population (Tchabovsky et al., 2023). The higher productivity of colonizing gerbils may be due to more intensive reproduction and better survival of young due to decreased competition and less pressure from predators and parasites, which is considered one of the causes of emigration from parent populations (Chuang and Peterson, 2016). Indeed,

gerbils in colonies were almost free of fleas, in contrast to residents in the parent population, where the infestation rate was 20–30%, indicating not only a low parasitic load but also a low risk of epizootics. The high fertility of females and the young age of the colonist population in the expansion wave indicates that it does not experience the negative consequences of low numbers (the Allee effect) and well explains its rapid growth and expansion (Tchabovsky et al., 2023).

The density gradient in expanding populations (high density in saturated habitats in the core and low density in the colonization zone, which is below the carrying capacity) creates conditions favoring different life-history strategies, *r* or *K* (MacArthur and Wilson, 1967; Reznick et al., 2002), in different parts of the population: the *r*-strategy with a fast life cycle, high productivity, and low competitiveness in the expansion zone and the alternative *K*-strategy in the saturated core of the population (Burton et al., 2010; Amundsen et al., 2012). Thus, in theory, colonist syndrome (see Glossary) should combine, on the one hand, a tendency to disperse and, on the other, life-history traits associated with living in unsaturated habitats: early development and maturation, as well as high fertility, which determines the rapid growth of the colonist population (Ronce and Clobert, 2012). These theoretical considerations have been confirmed by some models and scant empirical studies.

Using an individual-based model, Burton et al. (2010) showed that the effect of low density in the expansion zone leads to selection for dispersal propensity and, at the same time, to the formation of *r*-strategy traits: an increase in the contribution to reproduction at the cost of decreased competitiveness. In the core of an expanding population or within a stationary range, the dispersal propensity and the intensity of reproduction decrease while competitiveness increases in accordance with the *K*-strategy.

A study of colonization of lakes by European cisco (*Coregonus albula*) in Norway over 20 years showed that the fish in the colonist population were smaller and younger; they grew more slowly, matured earlier, were more fertile, and had a higher mortality rate than in the source population (Amundsen et al., 2012). Moreover, with time, the size and growth rate of the colonists decreased, in contrast to the residents of the parent population. These results agree with theoretical models predicting that low density and low competition at the edge of an expanding range should favor the *r*-strategy and a fast life cycle: greater reproductive costs at the expense of lower somatic costs (Burton et al., 2010; Amundsen et al., 2012).

Genetic and Evolutionary Consequences of Colonization

The next important questions are: What genetic processes occur during range expansion and colonization of new areas? How does range expansion affect

the genetic structure of a population, its dynamics, and differentiation? Studying genetic processes during range expansions and invasions, which occur more and more often, allows us to understand their evolutionary consequences (Chuang and Peterson, 2016; Welles and Dlugosch, 2019).

Range expansion can cause gradients in the allele frequencies, promote the spread of rare variants in colonized areas, shape the genetic structure, and lead to genetic admixture and new adaptations (Excoffier et al., 2009). Until now, most of our knowledge about changes in genetic structure over time and space during range expansions comes from models, simulations, and experiments in the micro- and mesocosm (Williams et al., 2019). To test the effects of these processes in natural populations, which are organized more complexly, we need empirical studies, which are still scarce (Graciá et al., 2013; Welles and Dlugosch, 2019).

Recent advances in population genomics and the need to understand and explain the processes of species range expansion and their consequences have stimulated the further development of a special research field—colonization genetics, which arose more than 50 years ago (Baker and Stebbins, 1965; Lewontin, 1965). Its main goal is to identify the mechanisms underlying the genetic differentiation of populations and evolutionary changes during colonization (Rajora, 2019; Welles and Dlugosch, 2019). Colonization genetics predicts that the spread of genotypes from source populations to new territories should often be associated with significant changes in genetic structure caused by drift (the founder and bottleneck effects, allele surfing), as well as adaptations to the new environment (Baker and Stebbins, 1965; Nei et al., 1975; Excoffier et al., 2009; Barrett, 2015). Understanding the genetic and evolutionary aspects of colonization is central to addressing many open questions in the biology of spreading and invasive species, particularly what factors may promote or hinder colonization success. These questions typically concern the role played by each of the major mechanisms of evolution (selection, gene flow, genetic drift, and mutation) in shaping the phenotypes of colonists in a new environment (McEachern et al., 2011; Welles and Dlugosch, 2019).

The theory of population genetics of colonization is well-developed and poses many important and still open questions at each stage of the colonization process (Welles and Dlugosch, 2019):

- What is the strength of the bottleneck, founder, and inbreeding effects in established colonist populations?

- Do genotypes from different sources mix, and is there gene flow between colonist demes?

- What adaptations arise in the wave of population expansion?

Drift. During the founding and expansion of a colony, a small effective population size, low genetic

diversity, and(or) inbreeding can cause strong genetic drift. Bottleneck effects during colonization and serial founder effects can reduce genetic diversity, promote inbreeding depression (Nei et al., 1975; Frankham, 1995; Williams et al., 2019), and hinder the ability of a population to adapt to environmental change (Frankham et al., 1999; Hale and Briskie, 2007). Therefore, the question of the strength of these effects and whether it is sufficient to prevent successful colonization and(or) adaptation of colonists to new conditions is one of the important issues of modern ecology and colonization genetics (Welles and Dlugosch, 2019).

Mathematical and simulation models suggest that range expansion can create gradients in allele frequencies caused by repeated founder effects when gene flow is limited and no genotype mixing occurs (Excoffier et al., 2009). These effects are usually studied by historical demographic methods based on their genetic traces in the past, modelling, or in experimental populations (Williams et al., 2019). Direct studies of the drift effects in natural populations before, during, and after a demographic bottleneck based on the detailed genetic and demographic characteristics of residents and immigrants are rare even for resident populations (McEachern et al., 2011).

In the study of human dispersal from Africa, Deshpande et al. (2009) found that the declining number of founders increases the cumulative bottleneck effect, depleting genetic diversity, which falls sharply along the range expansion axis. The expansion of bank voles (*Myodes glareolus*) in Northern Ireland was accompanied by a decrease in allele diversity and heterozygosity along the range expansion axis due to sequential founder effects and stochastic processes (White et al., 2013). Thus, a decrease in genetic diversity along the spatial axis is one of the signs of range expansion and an indicator of its direction. However, models show that a positive relationship between density and dispersal, which promotes a constant influx of immigrants from an overcrowded population core, can weaken the drift by increasing genetic diversity in the expansion wave (Birzu et al., 2019).

Another effect of genetic drift during colonization is allele surfing (see Glossary), in which the frequency of initially rare alleles (or mutations) that occurred by chance at the leading edge of the expansion wave increases in accordance with the strength of drift rather than selection. In this case, homozygosity will increase, and the loss of genetic diversity may cause genetic drift in the same direction as colonization. Then initially rare alleles, even deleterious mutations, will spread further and may be fixed, reducing the fitness of the colonist population and masking signatures of local adaptations (Hallatschek and Nelson, 2008; Excoffier et al., 2009; Chuang and Peterson, 2016; Williams et al., 2019). Different alleles can surf in different parts of the expansion wave, and then the

genetic differentiation at the leading edge will increase (Excoffier and Ray, 2008; Peischl et al., 2015). Correspondingly, as the range expands, the fixation index for the entire population should also increase (Excoffier et al., 2009).

Studying the effects of allele surfing is essential for understanding the patterns of genetic differentiation of populations and evolutionary processes during colonization, as well as the mechanisms underlying the sustainability and spread of invasive species populations (Welles and Dlugosch, 2019). Nevertheless, the theoretically well-founded effects of allele surfing during colonization have been studied in a few empirical works (Chuang and Peterson, 2016; Williams et al., 2019). In particular, allele surfing has been observed in bank vole (White et al., 2013, see above) and turtle (*Testudo graeca*) populations from Northern Africa that colonized northeastern Spain (Graciá et al., 2013). The authors found a decrease in genetic diversity along the range expansion axis in Spain, a clinal variation in allele frequencies, the spread of initially rare African alleles that became common in marginal populations, and the stronger spatial differentiation of the genetic structure in the expansion zone compared to the original range, the signatures of allele surfing.

The negative consequences of founder and bottleneck effects and allele surfing during colonization can be mitigated by gene flow between different genetically differentiated populations of colonists, influx of immigrants from the core population, and admixture of genotypes originating from different parent populations. All of them, taken together and individually, will contribute to the restoration of the genetic diversity lost at the expansion front due to drift (Blackburn et al., 2015; Welles and Dlugosch, 2019). Gene flow between colonizing populations originating from different source populations can significantly influence the genetics and success of colonists (Sakai et al., 2001; Kolbe et al., 2004; Lavergne and Molofsky, 2007). Moreover, theoretically, gene flow combined with genetic admixture between colonists from different source populations can provide very favorable genetic combinations (Welles and Dlugosch, 2019).

Selection. Dispersal to new habitats is an important condition for successful reproduction; therefore, the propensity and ability of individuals to disperse may be under strong selection at the edge of the range and evolve (Kokko and López-Sepulcre, 2006). One of the traits supposed to promote dispersal is large body size and longer limbs, which allow farther and faster movement. These theoretical considerations were supported by the few examples of the evolution of dispersal-related traits during the colonization of new areas. Thus, in the population of bush crickets at the front of the expanding range in the United Kingdom, there are more long-winged individuals capable of longer flight, which further contributes to population expansion (Simmons and Thomas, 2004). Common field mice

(*Microtus agrestis*) colonizing the islands of the Stockholm archipelago are larger, and their limbs are longer relative to body size than those of voles on the mainland. Both parameters increase with distance from the mainland and are genetically determined (Forsman et al., 2011). A study of the process of colonization of the islands of the Kerguelen Archipelago in the Indian Ocean by the brown trout (*Salmo trutta*, one of the world's most invasive species), which was traced back over 60 years, found that in colonized rivers, fish were larger than in parent populations; however, in subsequent generations, their size decreased. The large size of pioneer fish is attributed to their higher ability to disperse, and the subsequent decrease in size is likely due to selection under conditions of gradually increasing density (Aulus-Giacosa et al., 2021).

A well-known example of rapid evolution associated with range expansion is cane toads (*Bufo marinus*), which were introduced to Australia and quickly spread across the continent. At the leading edge of the expansion wave, long-legged toads are more abundant and disperse more successfully (Phillips et al., 2006). Moreover, toads of subsequent generations following the pioneers have shorter legs (Hudson et al., 2016). Such spatial sorting (see Glossary) of phenotypes should result in that prone to dispersal individuals, finding themselves at the leading edge of expansion, will mate with each other. As a result, the frequency of colonist phenotypes increases at the leading edge, which increases the rate of population expansion (Shine et al., 2011) and promotes further evolution of traits associated with the ability to disperse through the positive feedback loops (Chuang and Peterson, 2016; Williams et al., 2019). Indeed, from the 1940s to the early 2000s, the rate of spread of cane toads increased fivefold, and the leg length of toad descendants at the leading edge increased (Phillips et al., 2007; Phillips, 2009), producing next generations with even greater ability for dispersal and enhancing spatial sorting of phenotypes. This example demonstrates the so-called “Olympic Village effect,” suggesting that high-performing athletes who find themselves together in the same space just because of their outstanding abilities will produce offspring with even higher abilities (Chuang and Peterson, 2016).

Thus, at the edge of an expanding range, both the strength of drift and selection can increase or decrease, and their balance determines the variability of the shape (steep/flat) and speed of the expansion wave (Williams et al., 2019).

CONCLUSIONS: METHODOLOGICAL ISSUES

Studying the mechanisms and consequences of colonization of new areas by populations is a very interesting, important, and popular topic in various fields of biology. Colonizations are natural, albeit often human-driven, experiments occurring more and more frequently before our eyes. The expansion zone

is a natural laboratory, which provides an opportunity to test theoretical considerations and discover new patterns and mechanisms of the population dynamics and the evolution of adaptations. However, this is a very difficult line of research in terms of effort, time, methodology, and scientific luck. It is unsurprising that, despite enormous interest and demand, this area remains largely theoretical, and the main research tools are still models and experiments, with very little research in nature (Chuang and Peterson, 2016; Rajora, 2019; Welles and Dlugosch, 2019; Williams et al., 2019). In conclusion, let us dwell on the methodological problems of studying colonization in natural populations.

Repeated Measurements

The first, hard-to-solve, problem complicating the interpretation of the results is the need for repeated measurements of the assessed parameters (individual or population), which should be obtained at different stages of the dispersal/colonization process (before, during, and after) on relatively large spatial scales.

The conditions (ecological and social) in the parent population and colonies are different. Correspondingly, the requirements for phenotypic characteristics of residents and colonists differ; in fact, we want to evaluate this difference. However, dispersal involves three stages, and at each stage (emigration, transfer, immigration/colonization), these requirements, as well as the costs to individuals, are different, although interrelated (Bonte et al., 2012; Cote et al., 2017). In other words, the emigrant phenotype (the tendency to leave rather than stay) does not necessarily correspond to the immigrant/colonist phenotype (the ability to travel a distance and eventually settle in a new place); nevertheless, many models mistakenly equate an emigrant with an immigrant (Cote et al., 2017). An immigrant is, of course, an emigrant, but not every emigrant becomes an immigrant or colonist, and the characteristics of colonists are not equal to those of emigrants. For example, low aggressiveness (low competitiveness) promotes departure (emigration) but hinders settlement (immigration) and the colonization of a new environment. Therefore, strictly speaking, one should not compare the phenotype of established colonists with the phenotype of residents of the parent population for their propensity to disperse, which is one of the approaches in empirical colonization studies: colonists are emigrants that have reached a place, and, initially, emigrants could have been a random sample of residents.

In addition, the individual characteristics required at different stages of the dispersal process may be intricately interrelated. For example, the selection for the reduced movement costs (i.e., better ability to overcome distance) favors a greater propensity to emigrate and vice versa. However, this relationship is nonlinear (Travis et al., 2012). The different nature of costs and

risks at different dispersal stages may lead to the evolution of alternative strategies, i.e. short- or long-distance dispersal, depending on the degree of landscape fragmentation. Moreover, in the highly fragmented landscape, both strategies can be efficient and coexist (Cote et al., 2017). By comparing the characteristics of the colonists with the “control” sample of sedentary residents of the parent population, we obtain the phenotype of a successful migrant with an unknown strategy without being able to identify the features that are important at each of the three stages of the dispersal process and which may conflict with each other. In other words, knowing only the characteristics of the colonists, we cannot predict in advance, before emigration or during transfer, which individual will become a colonist and which will not.

Another problem is the actual difference in conditions in the parent population and in the new place. The phenotype is a product of the interaction of the genotype with the environment, so we cannot say whether colonists differ from residents (if they do) because they are different or because the conditions are different. For example, the curiosity of colonists may be caused by an unfamiliar environment rather than by their intrinsic inclination to explore, which prompted them to emigrate and helped them move and settle in a new place.

The third problem concerns the recognizing personality as individual behavioral characteristics consistent in different contexts and repeatable over time. Testing for personality traits necessarily requires repeated measurements to show the variation in behavior between individuals exceeds the intra-individual variation (Dingemanse and Dochtermann, 2013)—then and only then can this behavior be considered individually consistent and reflective of personality (Dingemanse and Wright, 2020). In other words, a more curious and(or) bolder or more stress-reactive individual in the parent population should retain these traits in the colony, and their consistency must be demonstrated. Otherwise, it would be impossible to attribute differences in the phenotypes of residents and colonists to individual personality traits.

To solve all three problems, it is necessary and likely sufficient to compare samples of phenotypes at all dispersal stages, at least at the initial stage, i.e. before emigration, and at the end stage—settling in the colony. To do so, first, we need to observe colonization in real time and, second, to carry out mass individual tagging, which is extremely difficult, although feasible. An example is the study on the dispersal of great tits, in which, over seven years of observations, 227 dispersed chicks were located as adults—5% of all marked chicks (Dingemanse et al., 2003). It is unsurprising that hardly any such studies exist.

Real-Time Observations

Observing colonization in real time solves other problems, although such observations, as we have seen, are rare. More often, researchers use reconstructions, by comparing the past and present state of the population, or the core and edge populations after colonization over some time. If we want to understand how colonists differ from residents, then when comparing the core population with the zone of expansion that has already occurred, we face two problems. The first is that in this case, we cannot distinguish between the pioneer colonists, i.e., those ready and able to colonize areas vacant of their conspecifics, from immigrants that follow the first colonists (see Glossary). The second problem is that, after colonization has already occurred, it is impossible to distinguish the first generation of colonists from their descendants. The mixing of colonists and immigrants, as well as different generations of colonists, confounds assessments. To solve these problems, one needs to be at the very leading edge of the colonization wave, ideally foreseeing its possible paths in advance. This will provide an opportunity not to reconstruct colonizing events (which is not always possible) but to observe and record them while simultaneously collecting the required set of parameters. It is clear that this requires some luck or subtle calculation, as well as long-term monitoring: there are many examples of ongoing expansions, colonizations, and invasions; one merely needs to choose the right place and time. We were able to do this by observing the population dynamics of midday gerbils in Kalmykia for almost 30 years, which gave us a chance to study colonist syndrome (Surkova et al., 2022; Tchabovsky et al., 2023).

Long-term, real-time observations of colonization from its onset to the foundation of a sustainable, established population provide an additional benefit of separating the effects of processes occurring on different time scales, varying from individual life cycles to the evolution of adaptations. Operating with a one-time snapshot, i.e. comparing the colonists with residents and finding some differences, how can we distinguish between phenotypic plasticity and genetically determined individual variability? How do we come to know whether a colonist's high fertility is an intrinsic individual characteristic, a consequence of low density in the colony, or due to changes in the life-history strategy caused by rapid evolution in conditions of low competition? Genomic studies can help but the possibilities for retrospective analysis are limited (Welles and Dlugosch, 2019). The ability to observe the emergence, formation, expansion, and development of colonies over a series of generations allows tracking changes in individual and population indicators, the dynamics of the demographic and genetic structure, microevolutionary processes, and adaptations, as in long-term studies of colonization in cane toads (Phillips et al., 2007; Phillips, 2009), western bluebirds

(Duckworth et al., 2018), or brown trout (Aulus-Giacosa et al., 2021), as well as some other species we considered. Then it will be possible to separate individual traits from the influence of the environment and assess if these traits are consistent or dependent on conditions. For example, if the level of glucocorticoids in colonists drops with the increasing age of the colony, then the high level of stress in the first settlers is determined by the novelty of the situation rather than by their intrinsically inherent high stress reactivity.

Tracing the history of colonies over a series of generations allows addressing questions about the heritability of traits specific to colonists. As the colony age (and, therefore, density) increases, the frequency of colonist phenotypes should decrease, as in brown trout (Aulus-Giacosa et al., 2021). Another example is western bluebirds, in which aggressive birds are more likely to disperse, and they are the ones that colonize new areas. With dispersal within old, long-established populations, the reproductive success of aggressive birds is lower than that of less aggressive philopatric individuals, while in new populations, their success is higher. However, as the colony age increases, the reproductive success of aggressive birds, i.e. the phenotype that founded the colony, decreases. Correspondingly, the frequency of the colonist's aggressive phenotype falls, and the overall aggressiveness within the population decreases, favoring non-aggressive philopatric birds (Duckworth, 2012). To obtain such striking results, we need long-term studies or a wide range of populations with known ages.

Studying colonization is a fascinating topic, interesting and important for both scientific and applied purposes. Until now, it has mainly been studied in theoretical models or experimental settings. Nevertheless, there are amazing examples of observations of natural populations that open new perspectives in understanding the mechanisms and consequences of dispersal, species expansion, colonization, and invasions. The methodological difficulties of highly sought-after studies of natural populations are great but can be overcome. Real-time observations of colonization are advantageous but require long-term monitoring. In addition, it is often impossible to trace the history of the colonies, and it is a serious methodological problem. At the same time, observations of the development of established colonies compared to parent populations are very productive for understanding colonist syndrome, as along with demographic, genetic, and evolutionary processes in the wave of population expansion.

GLOSSARY

Colonization is expansion into new areas vacant of conspecifics and the foundation of new colonies. The emergence of colonies can occur both within and outside the species' range or population boundaries. In the latter case, colonization leads to *range expansion* of the species or,

accordingly, *population expansion* within the range. The process of colonization occurs at the individual and population levels and on different time scales. **The dispersal** of individuals (see Glossary) promotes colonization, while population processes in the **expansion wave** (see Glossary) and in established colonies affect the demographic and genetic structure and can lead to phenotypic variability and/or specific adaptations.

Dispersal is movement resulting in the flow of genes in space, often from the place of birth to the place of reproduction (natal dispersal) or from the place of breeding to the place of the next reproduction (breeding dispersal). The dispersal process involves a change of “place of residence” and includes three stages: *departure*, or *transience (transfer)*, and *settlement* (Ronce, 2007; Clobert et al., 2009). The new place of residence can be located within the same population and then the individual remains its **resident**, in another population (**immigrant**), or in a habitat void of conspecifics (**colonist**).

Long-distance dispersal involves the dispersal of an individual beyond the *geographic range* and/or *genetic neighborhood*—an area that is proportional to the distance of dispersal of the offspring, within which interbreeding can be random within one generation (Jordano, 2017). The size of the genetic neighborhood may be larger than the size of the geographic range and vice versa. Long-distance dispersal is a relatively rare phenomenon and often involves crossing a matrix—unsuitable habitats (Baguette et al., 2013). **Short-distance dispersal** occurs within the genetic neighborhood (Jordano, 2017). Long-distance dispersal is usually a necessary condition for colonization (Ronce et al., 2001).

The maternal (or parent) population is the source population of emigration in metapopulation theory (Hanski and Gaggiotti, 2004).

Colonists in the narrow sense are first settlers or pioneers, emigrants from the core or periphery of a population that settled in habitats vacant of conspecifics; they are the founders of colonies. **Immigrants** in the context of colonization are emigrants that moved to habitats already colonized by their conspecifics, i.e., emigrants that joined the founders of the colonies (Clobert et al., 2009). **Colonists** in the broad sense are all the inhabitants of colonies, including pioneers (colonists in the narrow sense) and immigrants, as well as the descendants of both. In practice, it is very difficult to distinguish colonists in the narrow sense from the population of the colony (see text). **Residents** are the inhabitants of the parental population.

An expansion wave is a flow of individuals moving from the core or periphery of a population beyond its borders to new territories. The expansion wave includes *the leading edge (front)*; *the edge*, i.e., the front and demes adjacent to it behind; and *the intermediate region*, the area behind the edge of the wave to the core of the population (Chuang and Peterson, 2016). The shape of the wave (high and steep or shallow and flat), influencing the balance of drift and selection, determines the nature and rate of genetic processes in the colonization zone (Williams et al., 2019). If **long-distance dispersal** occurs quite often, then the population will

not spread in a continuous wave, but in “jumps,” forming separate, more or less isolated colonies, foci of further spread (Nichols and Hewitt, 1994; Markov and Ivanko, 2022).

Personality is a set of individual behavioral traits *consistent over time and in different contexts*; the intra-individual variation of personality traits is less than between individuals. The main characteristics of personality include boldness, curiosity (exploration), aggressiveness, activity, and sociability (Réale et al., 2007).

Behavioral syndrome is a set of individual personal behavioral characteristics *correlated* with each other. For example, boldness is often correlated with curiosity and aggressiveness.

Dispersal syndrome is a set of correlated phenotypic traits (morphological, behavioral, physiological, etc.), which are specific to dispersing individuals and distinguish them from residents (Ronce and Clobert, 2012). The **personality** research (see Glossary) suggests and in some cases demonstrate the individual consistency and genetic determination of a set of behavioral traits associated with the propensity and ability to disperse (Chuang and Peterson, 2016) (see text).

Colonist syndrome combines, on the one hand, the signatures of **dispersal syndrome** (see Glossary) and, on the other, specific life-history traits that arose as a result of phenotypic plasticity or adaptations in unsaturated habitats: early development and maturation, as well as high fecundity and other signs of *r*-strategy (Ronce and Clobert, 2012).

Allele surfing occurs when a population expands; the frequency of initially rare alleles or mutations that are at the leading edge can increase as a result of drift. Then rare alleles will spread further with the wave and can become fixed, which would not happen in the core of the population, where their frequency is extremely low. In different parts of the wave, different alleles can surf, and, thus, enhancing the genetic differentiation of the colonist population and the whole population.

Spatial sorting is the spatially ordered distribution of colonist phenotypes along the population spread axis, with the predominance of such phenotypes at the edge of the expansion wave, which leads to preferential mating of colonists with each other, promoting the further evolution of dispersal-related traits and spread of the population at an accelerating rate.

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ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This work does not contain any studies involving human or animal subjects.

CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

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