The evolution of niche construction in social species

Mirjam J. Borger[1], Peter Czuppon[2,3], Melanie Dammhahn[4]

[1]Department of Evolutionary Biology, Bielefeld University, Germany
[2]Institut de Mathématiques de Marseille, Aix-Marseille Université, France
[3]Institute for Evolution and Biodiversity, Münster University, Germany
[4]Institute for Neuro- and Behavioural Biology, Münster University, Germany
Corresponding author: Mirjam Borger, mirjam.borger@uni-bielefeld.de

Abstract

Niche construction is a behaviour where the local environment is changed by individuals, often to improve reproductive success (e.g. nests or burrows). In social species, the niche construction behaviour of an individual also changes the local environment of others. In such cases, individuals could cheat and not contribute to the social behaviour, but instead make use of the efforts of others. While niche construction is often studied as a process that alters the environment also for future generations, there are also constructed niches that are not inherited (e.g. nests in many birds). Hence, we studied whether niche construction would evolve in social species without inherited environments, or if instead cheating would spread. To this end, we used an individual-based simulation and an adaptive dynamics approach. We found that niche construction can evolve in social species when the population is structured and multiple levels of selection arise, even when individuals disperse randomly. While cheating might result in higher fitness compared to others within the group, individuals from groups without cheaters ended up with even higher relative fitness, which consequently limits the spread of cheaters and allows for the evolution of cooperative behaviours like niche construction.

Introduction

Niche construction is a behaviour where individuals change their local environment (Odling-Smee et al., 1996). Often, niche construction has the goal of improving reproductive success (e.g. nest or burrow building), and it is a common behaviour in a plethora of species (e.g. burrow construction in African mole-rats, Šumbera et al., 2012, and mongooses, Schneider & Kappeler, 2014; nest building in passerine birds, Collias, 1997, in sticklebacks, Barber et al., 2001, in pufferfish, Mizuuchi et al., 2018, in Anuran frogs and toads, Fischer, 2023, in spittlebugs, Sahayaraj et al., 2025, and in bees Michener, 1964). Generally, it is expected that niche construction evolves when the benefits in improvement of reproductive success (e.g. higher survival rates of offspring) outweigh the costs of niche construction (e.g. energy spent on construction that could have otherwise gone to improving the survival or reproductive success of the individual).

In some species, individuals share their local environment, and for the purpose of this research we define these species as social species. In these cases, the niche construction efforts of one individual also influence the environment of the others in that local environment. For example, burrow building in meerkats can be beneficial for all genetic parents in the group, and the excavation of a nest can benefit all acorn woodpecker parents in a breeding group. In social species, one could argue that niche construction can evolve more easily as the load can be shared and therefore each individual has to invest less in niche construction. However, niche construction can also become a public goods game (Ostrom, 2000). In public goods games, beneficial behaviours often do not evolve, because, while it would be helpful to do something (e.g. construct a niche), it is even more beneficial if others show the behaviour, and a cheater (who does not show the behaviour) can make use of the efforts of others without having to bear any costs of the behaviour. Thus, in such situations the beneficial behaviour generally does not evolve, as cheaters often have higher fitness than cooperators (who do show the behaviour), unless there is policing behaviour (Singh & Boomsma, 2015), where cheaters get punished, or when there are ways for cooperators to only cooperate with other cooperators (e.g. Gardner & West, 2010; Hamilton, 1964, 1972; Nowak & Sigmund, 2005; West Eberhard, 1975).

Another aspect that is important to consider in niche construction, is that in some species the constructed environment will be reused and can even be inherited by following generations (burrows in social mammals), while other niche construction behaviours have to be repeated every generation (e.g. bumble queens build new colonies, Alford, 1969; burying beetles bury a carcass to deposit their eggs and die after reproduction, Pellissier Scott, 1998), or every breeding attempt or breeding season again (e.g. the nests of many songbirds, of anurans, pufferfish and sticklebacks), and hence the environmental change is not inherited by future generations. Whether the constructed environment gets inherited or not can change the long-term fitness consequences of niche construction strategies, and hence can have an impact on the evolution of niche construction. So far, most theoretical work on the evolution of nice construction has focussed on populations with inherited environments (e.g. Connelly et al., 2016; Fogarty & Wade, 2022; Laland et al., 1996, 1999; Lehmann, 2008; Mullon et al., 2024; Silver & Di Paolo, 2006; see e.g. Scheiner et al., 2022 for a model without inherited environments). Yet, in the wild niche construction without environmental inheritance is also common.

Therefore, in this study, we researched whether niche construction can adaptively evolve in social species without environmental inheritance, and what the effect of sociality is on the evolution of niche construction. To this end, we used individual-based simulations and an analytical model to validate the simulations. Our models were simplified for traceability, but were inspired by multiple niche constructing species and we suggest to keep one or some of these species in mind for a better understanding of the biological relevance. For example, burying beetles (*Nicrophorus spp.*) often breed communally and bury a (mouse) carcass in which they lay their eggs. Parasitic wasps (*Nasonia vitripennis*) inject a venomous mixture into the host they parasitise on before they deposit their eggs, and females do sometimes lay their eggs in the same host. Red flour beetles (*Tribolium castaneum*) produce a quinone-rich secretion as an external immune defence that also protects the larvae produced in the surrounding area, which can be offspring of their own or of others.

To make our model more ecologically relevant, we explored two more aspects in the model. First, we studied the effect of environmental heterogeneity on the evolution of niche construction. In other words, what if local environmental patches are not all exactly the same? For example, some mouse carcasses might already be partially covered due to wind, and therefore less effort might be necessary to bury the carcass. Second, we studied the effect of individual differences in the optimal niche. For example, burying beetles might differ in how deep they want to bury the carcass (deeper might be warmer, but might also be more difficult for offspring to leave), or red flour beetles might want to excrete different levels of secretion, as more secretion means better protection but could also increase mortality of larvae.

Methods

Simulation overview

Our individual-based simulation studies the effect of group size and environmental condition on the evolution of niche construction. The model is aimed to be conceptual, but is inspired by systems like the communally breeding burying beetles, parasitic wasp populations, or flour beetles, where multiple individuals lay their eggs in the same patch, to keep the model realistic. Each individual in the model has a certain amount of energy, which they can either spend on niche construction or on reproduction, and they have a gene *x* that determines which proportion of energy is spend on niche construction. Within each generation, individuals are first randomly distributed over the patches. Each patch has a value, and the closer this value is to the optimum value of individuals, the more efficient these individuals can convert their energy for reproduction into offspring. After arrival at the patch, individuals can change the value of the patch towards their optimum by investing energy in niche construction. After each individual in the patch had the opportunity to perform niche construction, the patch value gets updated. Next, reproduction takes place. Individuals reproduce asexually, and offspring inherit the gene *x* from their parent, with a small probability of mutation. Each individual obtains a fitness score, depending on the updated patch value and the remaining energy left for reproduction. The realised number of offspring produced by an individual is determined by its relative fitness score, relative to the scores of all the other individuals in the population, to keep the population size constant through time. As generations are non-overlapping, all adults die and the offspring are randomly distributed over all patches, starting a new generation. Over time, the niche construction behavioural strategy (*x*) can evolve due to a combination of natural selection, genetic drift and mutation, altering the frequency distribution of values for *x* in the population.

Simulation details

<u>Scenarios</u>

We looked at four scenarios in the simulation. In scenario 1, we assumed that all patches within and between generations had the same start value (before niche construction), and that all individuals in the population had the same optimal patch value. Patch values were not inherited between generations, as the model was based on situations where patches are only shortly available (e.g. mouse carcasses, fly pupae), and hence each generation has to restart niche construction. In the second scenario, we assumed a heterogeneous environment. Here, in every generation the start values of patches were drawn from a uniform distribution between 0 and 1, and all individuals had the same optimal patch value. Hence, individuals in some patches were closer to the optimal patch value than others already before niche construction. In the third scenario, every patch had the same start value (as in scenario 1), but individuals had different optimal patch values. Per individual an optimum was drawn from a uniform distribution between

0 and 1. This could cause conflict between individuals in niche construction, as for some the optimal value might be further away, or even in a different direction, than for others. These optima were not inherited, but instead reflect current environmental conditions. In the fourth scenario, the environment was heterogeneous and start patch values were again drawn from a uniform distribution between 0 and 1 (as in scenario 2). Moreover, individuals all had a different optimal patch value (as in scenario 3), again drawn from a uniform distribution between 0 and 1.

For the first scenario, we also made an analytical model to check the validity of the simulation model and to compare outcomes between the analytical and simulation model (e.g. in case polymorphisms arise). We did not do so for the other scenarios, as environmental heterogeneity and individual differences in optimal patch value make analytical understanding much more complex and less insightful.

Group and population size

We studied the evolution of niche construction for different group sizes within each patch. To keep the effect of evolutionary processes (stochasticity, mutation) comparable between these simulations, we kept the total population size *N* the same. In the results below, the total population size was 5000 individuals, and hence when the group size was 2 there were 2500 patches, while for the group size of 5 there were 1000 patches.

Niche construction

Each patch has a value *p* before niche construction. Niche construction changes the patch value to *p'* in the following way:

$$p' = p + \sum_{i=1}^{n} (a * \pm x_i),$$

where a is the maximum amount of niche construction one individual can perform (if a=1, one individual can change the patch value from 0 to 1 if it invests all its energy in niche construction, while if a=0.5 one individual can only change the patch value from 0 to 0.5 if it invests all its energy in niche construction). x_i is the value of *x* of individual *i* in the patch, and *n* represents the number of individuals within a patch. Individuals will perform niche construction towards their personal optimal patch value, hence in cases where the current patch value is higher than the personal optimal value, niche construction will decrease the patch value. Therefore, in scenarios 3 and 4, individuals might change the patch value in different directions.

Reproduction

The individual fitness score of individuals was calculated in the following way:

$$W_i = (1 - (p_i'(x_i) - \hat{p}_i)^2) * (1 - x_i{}^c).$$

Here, *p'* represents the patch value after niche construction (which depends on *x* of the individual and of that of its patch members) and $\hat{p}$ is the optimal patch value of the individual. In words, the closer *p'* is to the optimal patch value, the more efficient energy can be transformed into offspring and hence the higher the fitness score. The second part of the equation, $(1 - x_i{}^c)$., represents the energy left for reproduction. The c indicates the costs of niche construction. Here, we studied the scenario where *c = 1* (a very high cost) and *c = 2* (a milder cost). The realised number of offspring was then determined by:

$$\lambda(x)_i = \frac{W_i}{\overline{W} * N} * N = \frac{W_i}{\overline{W}},$$

where $\overline{W}$ is the average population fitness score and N is the total population size.

Each offspring inherited its gene x from its parent. However, genes could also mutate. For this, a Bernoulli distribution was used to determine the probability that a gene would mutate, with an average value of 0.01. If a mutation occurred, the size of the mutation was drawn from a normal distribution with mean 0 and standard deviation 0.001. The mutational step size had a limited standard deviation as *x* was bounded between 0 and 1 and we wanted to keep the occurrence of large mutational changes small. The drawn value was added to the old value. When this resulted in 0 > x or x > 1, a new mutational step size was drawn.

The analytical model for scenario 1

The above model could for scenario 1, assuming a monomorphic population, be summarised in a fitness function:

$$W(x) = (1 - x^c) * (1 - (p + anx - \hat{p})^2).$$

With this function we checked for optima, and, using adaptive dynamics, we checked whether these optima were evolutionary stable strategies. Please see Supplement XX for details on the mathematical calculations.

Results

Evolution of niche construction in non-social species

In non-social species where niche construction does not affect the environment of others (n=1 within a patch), niche construction did not evolve under most conditions in scenario 1 (homogeneous environment; everyone the same optimum) when the cost of niche construction was high (c=1). Only when the optimal value of the patch was far away from the current patch value, some level of niche construction could evolve adaptively (in our analytical model at least a difference Δ of 0.42 between p and $\hat{p}$ was necessary for any level of niche construction x>0.0 to evolve, and in the simulation Δ≥0.6 to visibly distinguish an adaptive x>0.0 from an adaptive level x=0 that is affected by mutation and drift).

Yet, niche construction evolved readily when the costs of niche construction were mild (c=2), see Fig. 1 (now Δ=0.01 was enough for x>0.0 to evolve in the analytical model). Interestingly, after a short period of rapid evolution on x to increase its value to a certain level, a wide variance of strategies evolved, and transient polymorphisms were present for distinct time periods, but were not stable and always disappeared after a while. When the population was followed for much longer (e.g. 5 million generations), the patterns stayed similar to what is shown in Fig. 1. These findings hint that natural selection is important early on until a certain level of niche construction is reached, and that afterwards selection becomes weaker, increasing the relative effects of drift and mutation.

Evolution of niche construction in social species

When multiple individuals shared a patch and niche construction affected others, niche construction still did not evolve under most conditions in scenario 1 when the cost of niche construction was high (c=1). These conditions were the same as when individuals were alone in a patch. Therefore, we decided to drop this parameter combination for our other questions, as the expectation was that no niche construction would evolve there either. Hence, from now on we will focus on niche construction with milder costs (c=2).

When the cost of niche construction was milder, niche construction again readily evolved in groups of different sizes, see Fig. 2. Transient polymorphisms were also present when groups were larger than one, but the total variance in niche construction strategies was smaller. Complete cheating (having a niche construction level of 0.0) did not evolve in any of the group sizes, and there were also no stable polymorphisms where one strategy had a much lower value for *x* than the other. Yet, there was variance in niche construction strategies, so some individuals did contribute more to niche construction than others. We expect that (strong) cheating behaviour did not evolve in this model due to the different selective pressures that individuals face. If individuals would only compete with others within their patch, then it seems likely that a cheating strategy would be most beneficial. However, individuals also compete with others from other patches, as their relative fitness score also depends on the individual fitness scores of others from other patches. The fitness scores of individuals from patches without cheaters were higher than

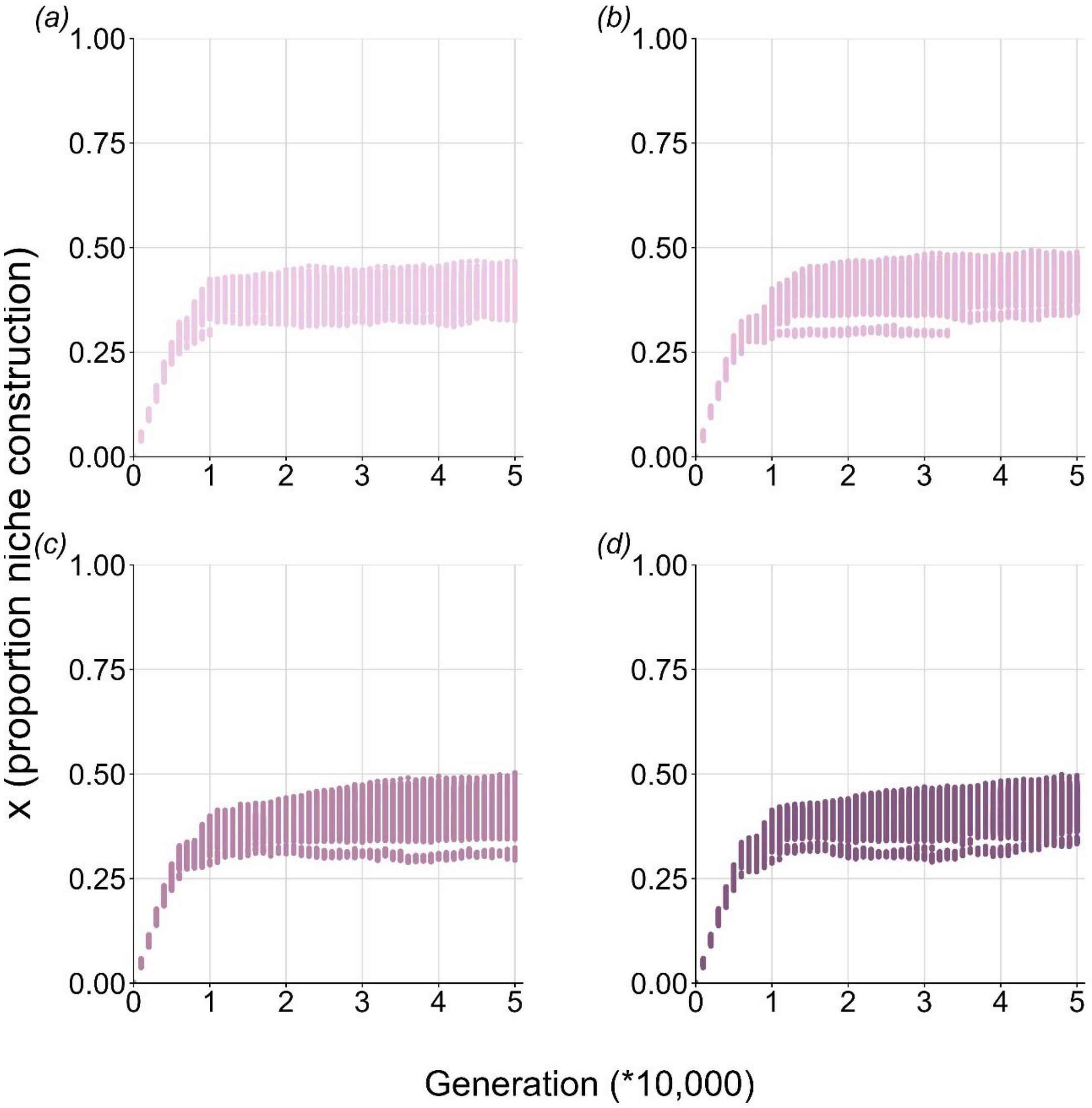

Figure 1: The evolution of niche construction strategy *x* in a non-social population. Four representative replicates of a simulation where individuals were alone in the patch (n=1), in a population of 5000 individuals in each generation. Each dot represents a single individual. The parameter combination used for these plots was p=0, $\hat{p}$ = 0.9, c=2, and a=1.

those of individuals from patches with cheaters, and therefore cheating did not spread in the population.

The total level of niche construction all individuals in a patch additively perform also changed with group size. While each individual separately spends less energy on niche construction, the total energy spent on niche construction increased with increased group size. In other words, there is not only load sharing when group size increases, but the total effort also increases.

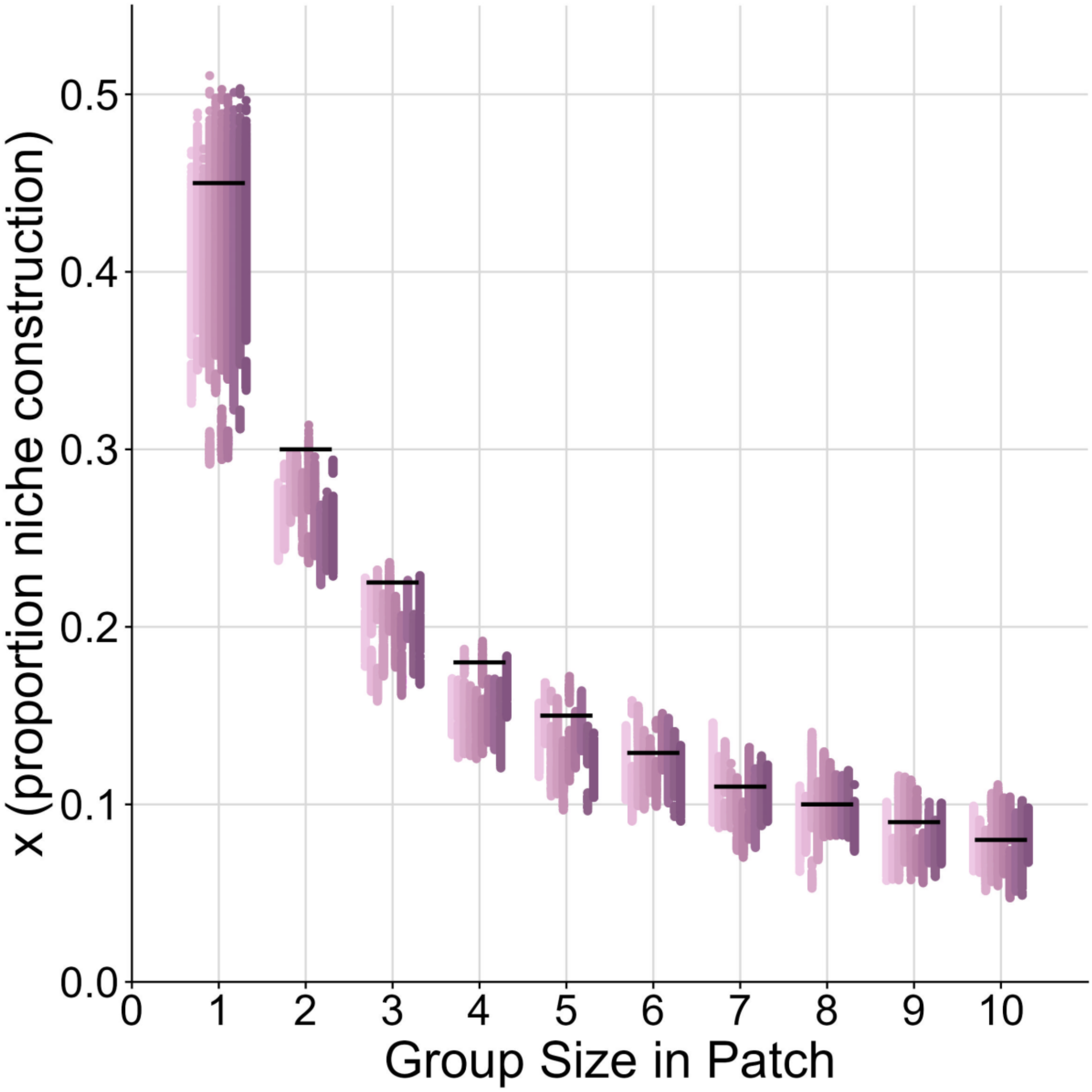

Figure 2: The proportion of niche construction of individuals in groups of different sizes. Each dot represents one individual in the population after 50,000 generations, and each shade of purple represent a different replicate (10 replicates are shown next to each other for each of the group sizes). The horizontal lines indicate the optimal level of niche construction according to the analytical model. The parameter combination used for this figure was the same as in figure 1, p=0, $\hat{p}$ = 0.9, c=2, and a=1.

The parameter *a* (the maximum amount of niche construction a single individual can perform) had somewhat an effect on the evolutionary outcomes, see supplement XX. When *a* was low, individuals in small groups (e.g. n=1 or 2) evolved low levels of niche construction as the benefits of niche construction were less pronounced. In larger groups (e.g. n = 4 or 5), niche construction did evolve to higher levels, as now the total group effort was enough to reach high benefits. Overall, after the initial increase in niche construction, the same decreasing pattern as Fig. 2 was found, where each individual invests less in niche construction with increasing group size.

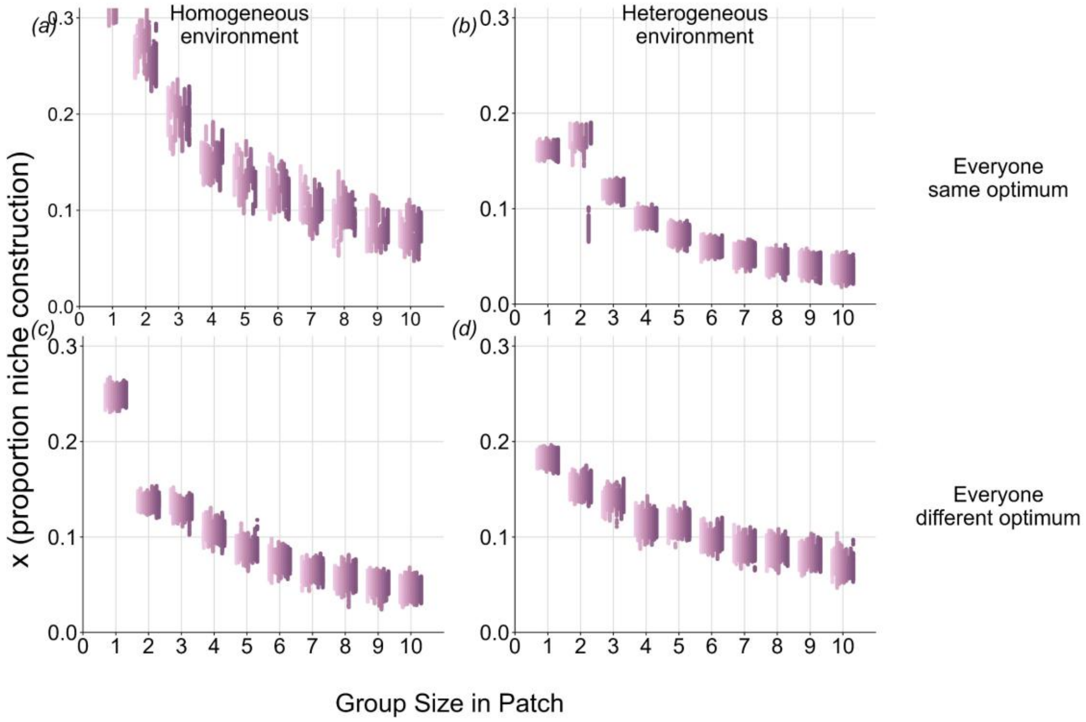

Figure 3: The proportion of niche construction in various environments. Each dot represents one individual in the population after 50,000 generations, and each shade of purple represent a different replicate (10 replicates are shown next to each other for each of the group sizes). a) is a cut-out of Fig. 2 (note difference in y-axis scale) and thus is scenario 1, b) is scenario 2, c) is scenario 3, and d) is scenario 4. The parameter combination used for this figure was the same as in Fig 1 and 2: p=0, $\hat{p}$ = 0.9, c=2, and a=1.

Differences in the environment and between individuals

Next, we explored scenarios 2-4. Interestingly, all these three scenarios led to similar results, see Fig. 3. A similar pattern as in Fig. 2 evolved, where with increasing group size the individual level of niche construction decreased but the total level of niche construction of the entire group increased. The value of x evolved to a lower level than in scenario 1, which we expect is caused by a lower average distance from the current patch value to the optimal value. For instance, when all individuals have a different optimum and the patches have a starting value of 0, the average distance to an optimum will be 0.5, instead of the 0.9 in the case where everyone has the same optimum.

Interestingly, the variance between individuals in niche construction strategies was lower in scenarios 2-4 compared to scenario 1. Transient polymorphisms also evolved less often. We expect this is caused because in situations like scenario 2-4, fitness is a geometric mean over all conditions, and therefore more strategies had a low fitness (the fitness curve over all values of x became steeper, and only bet-hedging strategies could survive). In other words, when a strategy ends up in different conditions over time, fitness of these different conditions interact. For example, when a strategy has a fitness of 0 in one condition and ends up in that condition, it will not persist, no matter how good or bad the strategy performs in different conditions.

The analytical model of scenario 1

In the analytical model, we found similar conclusions as in the simulation, although the analytical optimal value of niche construction was on the higher end of the distributions found in the simulations, see Fig. 2. In other words, in the simulation selection against investing more than optimal was stronger than selection against investing less than optimal.

The analytical model was quite complex, and therefore we solved it numerically instead of producing a general solution. Moreover, we produced pairwise invasability plots (PIPs) to check if the equilibria were evolutionary stable (the strategy cannot be invaded) and convergence stable (the population moves towards this optimum), see Fig. 4 for an example of n = 3 and Supplement xx for PIPs of the other group sizes. By doing so, we found for all populations where the group size within a patch *n* was larger than one, that there was a second equilibrium. However, this second equilibrium was not convergence stable and instead was a repellor, hence populations tended to evolve towards the first equilibrium.

Discussion

We found that niche construction for groups of any size (also *n* = 1) evolved when the costs of niche construction were mild, or when the difference between the local environment and the optimal local environment was large. When the costs of niche construction were high and the difference between the local and optimal environment was intermediate to small, the proportion of energy spent on niche construction stayed around zero.

Niche construction did evolve in social species, where the local environment was shared by multiple individuals, even without policing (Singh & Boomsma, 2015), kin selection benefits (Hamilton, 1964; West Eberhard, 1975), green beards (Gardner & West, 2010) or reciprocity (Nowak & Sigmund, 2005). There was some variance in strategies between individuals, which could be interpreted as very mild cheating, but no stable polymorphisms in strategies or strong cheating evolved. In spatially structured models the absence of cheaters is often explained by viscosity (Hamilton, 1972; Kümmerli & Brown, 2010; Wakano et al., 2009), where through limited dispersal individuals tend to interact mostly with relatives, and hence cooperators tend to be surrounded by other cooperators, while cheaters are surrounded by other cheaters. However, in our model there is random dispersal, as we assumed this would best represent burying beetle and

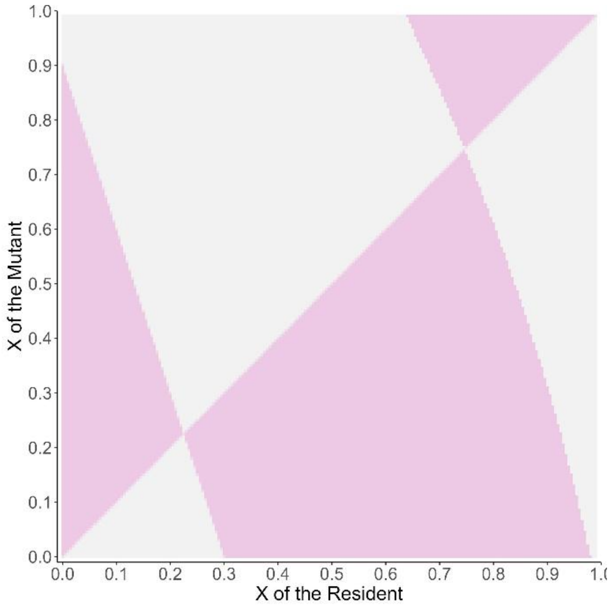

Figure 4: The pairwise invasability plot for individuals in groups of 3. The x-axis shows the potential values of the niche construction strategies for the resident population. The y-axis shows the potential values of a niche construction strategy for a rare, invading mutant. The diagonal shows all cases where the mutant is the same as the resident and hence mutants and residents will always be able to co-exist. When a point is pink, the mutant has a higher fitness than the resident and can invade, changing the value of the resident population to that value. When a point is white, a mutant cannot invade. Here, the left equilibrium (at 0.23) is evolutionary stable as no mutant can invade a population with that value of *x*. It is also convergent stable as resident populations with lower strategy values than the equilibrium will be invaded by mutants with higher values, and resident populations with higher values of x than the equilibrium will be invaded by mutants with lower values, and hence the population will evolve towards the equilibrium. The right equilibrium (0.75) is not evolutionary stable as every strategy can invade, and is not convergent stable as mutant strategies will invade that take the population away from the equilibrium.

parasitic wasp populations, and hence kin selection benefits are very weak. Instead, we expect that cheating does not evolve in this model due to multilevel selection effects (Okasha, 2007). That is, when individuals compete with others within their local environment, cheaters will have higher fitness relative to others within the local environment. However, in our model, individuals also compete with other individuals from different patches, and individuals from patches without cheaters have a higher relative fitness than individuals from patches with cheaters (both the cooperating and cheating individuals in those patches). Therefore, in populations with a spatial structure, cheating strategies cannot spread, and hence niche construction can evolve even when cheating is a potential option. While others did reach similar conclusions about the importance of multilevel selection on the evolution of cooperative behaviour like niche construction (e.g., Traulsen & Nowak, 2006; Wakano et al., 2009), these models did include viscousity/limited dispersal. We show here that this is not a requirement for the evolution of niche construction or similar cooperative behaviour.

Interestingly, we found more variance in niche construction strategies when the environment was homogeneous and all individuals had the same optimal patch value, compared to when the environment was heterogeneous and/or individuals had different optimal patch values. While some may believe that variance in the environment always increases variance between individuals, this is not always true and highly depends on ecological circumstances. When individuals can choose their local environment (niche choice) and can specialise on the local conditions, variance in environmental conditions can lead to more variance between individuals. However, when individuals have to deal with all, or part of, the environmental conditions (as in our model) over space or time (e.g. seasons), bet hedging strategies will have higher fitness than specialising strategies (Autzen, 2024; Starrfelt & Kokko, 2012; Yasui, 2022), and hence variance in environmental conditions can also decrease variance between individuals.

We also found a dramatic decrease in variance in scenario 1 between populations where the local population size n was 1 compared to social species (where $n \geq 2$). We hypothesise that this is again caused by multilevel selective pressures. In non-social species there is only between-patch competition, while in social species there is both competition between and within patches for a high relative fitness score. We expect that this changes the fitness function to become much steeper in social species and hence that the relative effects of selection and drift change between non-social and social species.

In conclusion, niche construction can evolve, also in social species, and purely due to multilevel selective pressures in spatially structured populations even without kin selection. Individual-based simulations are a great way of studying this, as it not only gives insights in optimal strategies, but also about variances between strategies and the relative effects of selection and drift.

Data Availability

Data will be publicly available on Zenodo repository XXX once the paper is published. The code of the simulation will also be publicly available, on github XXX.

Funding

M.J.B. was funded by the German Research Foundation (DFG Project no. 316099922) as part of the CRC NC^3 (SFB TRR 212).

Acknowledgements

We would like to thank Klaus Reinhold for his help with the development of this project.

References

Alford, D. V. (1969). A study of the hibernation of bumblebees (Hymenoptera:Bombidae) in Southern England. *The Journal of Animal Ecology*, *38*(1), 149. https://doi.org/10.2307/2743

Autzen, B. (2024). The foundations of bet hedging. *Biology & Philosophy*, *39*(6), 31. https://doi.org/10.1007/s10539-024-09970-0

Barber, I., Nairn, D., & Huntingford, F. A. (2001). Nests as ornaments: Revealing construction by male sticklebacks. *Behavioral Ecology*, *12*(4), 390–396. https://doi.org/10.1093/beheco/12.4.390

Collias, N. E. (1997). On the origin and evolution of nest building by passerine birds. *The Condor*, *99*(2), 253–270. https://doi.org/10.2307/1369932

Connelly, B. D., Dickinson, K. J., Hammarlund, S. P., & Kerr, B. (2016). Negative niche construction favors the evolution of cooperation. *Evolutionary Ecology*, *30*(2), 267–283. https://doi.org/10.1007/s10682-015-9803-6

Fischer, E. K. (2023). Form, function, foam: Evolutionary ecology of anuran nests and nesting behaviour. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *378*(1884), 20220141. https://doi.org/10.1098/rstb.2022.0141

Fogarty, L., & Wade, M. J. (2022). Niche construction in quantitative traits: Heritability and response to selection. *Proceedings of the Royal Society B: Biological Sciences*, *289*(1976), 20220401. https://doi.org/10.1098/rspb.2022.0401

Gardner, A., & West, S. A. (2010). Greenbeards. *Evolution*, *64*(1), 25–38. https://doi.org/10.1111/j.1558-5646.2009.00842.x

Hamilton, W. D. (1964). The genetical evolution of social behaviour. I. *Journal of Theoretical Biology*, *7*(1), 1–16. https://doi.org/10.1016/0022-5193(64)90038-4

Hamilton, W. D. (1972). Altruism and related phenomena, mainly in social insects. *Annual Review of Ecology and Systematics*, *3*(1), 193–232. https://doi.org/10.1146/annurev.es.03.110172.001205

Kümmerli, R., & Brown, S. P. (2010). Molecular and regulatory properties of a public good shape the evolution of cooperation. *Proceedings of the National Academy of Sciences*, *107*(44), 18921–18926. https://doi.org/10.1073/pnas.1011154107

Laland, K. N., Odling-Smee, F. J., & Feldman, M. W. (1996). The evolutionary consequences of niche construction: A theoretical investigation using two-locus theory. *Journal of Evolutionary Biology*, *9*(3), 293–316. https://doi.org/10.1046/j.1420-9101.1996.9030293.x

Laland, K. N., Odling-Smee, F. J., & Feldman, M. W. (1999). Evolutionary consequences of niche construction and their implications for ecology. *Proceedings of the National Academy of Sciences*, *96*(18), 10242–10247. https://doi.org/10.1073/pnas.96.18.10242

Lehmann, L. (2008). The adaptive dynamics of niche constructing traits in spatially subdivided populations: Evolving posthumous extended phenotypes. *Evolution*, *62*(3), 549–566. https://doi.org/10.1111/j.1558-5646.2007.00291.x

Michener, C. D. (1964). Evolution of the nests of bees. *American Zoologist*, *4*(2), 227–239. https://doi.org/10.1093/icb/4.2.227

Mizuuchi, R., Kawase, H., Shin, H., Iwai, D., & Kondo, S. (2018). Simple rules for construction of a geometric nest structure by pufferfish. *Scientific Reports*, *8*(1), 12366. https://doi.org/10.1038/s41598-018-30857-0

Mullon, C., Peña, J., & Lehmann, L. (2024). The evolution of environmentally mediated social interactions and posthumous spite under isolation by distance. *PLOS Computational Biology*, *20*(5), e1012071. https://doi.org/10.1371/journal.pcbi.1012071

Nowak, M. A., & Sigmund, K. (2005). Evolution of indirect reciprocity. *Nature*, *437*(7063), 1291–1298. https://doi.org/10.1038/nature04131

Odling-Smee, F. J., Laland, K. N., & Feldman, M. W. (1996). Niche Construction. *The American Naturalist*, *147*(4), 641–648.

Okasha, S. (2007). *Evolution and the Levels of Selection*. Oxford University Press.

Ostrom, E. (2000). Collective action and the evolution of social norms. *Journal of Economic Perspectives*, *14*(3), 137–158.

Pellissier Scott, M. (1998). The ecology and behavior of burying beetles. *Annual Review of Entomology*, *43*(1), 595–618. https://doi.org/10.1146/annurev.ento.43.1.595

Sahayaraj, K., Princess, A. A. G., Alkherb, W. A. H., Alshehri, M. A., Alkeridis, L. A., Estelle, L. Y. L., Srinivasan, M., Sundar, S., Petchidurai, G., & Sayed, S. (2025). Preferential host plants and nesting sites for foam building by the spittlebug, *Poophilus costalis* Walker (Hemiptera: Aphrophoridae). *Phytoparasitica*, *53*(2), 27. https://doi.org/10.1007/s12600-025-01249-8

Scheiner, S. M., Barfield, M., & Holt, R. D. (2022). Do I build or do I move? Adaptation by habitat construction versus habitat choice*. *Evolution*, *76*(3), 414–428. https://doi.org/10.1111/evo.14355

Schneider, T. C., & Kappeler, P. M. (2014). Social systems and life-history characteristics of mongooses. *Biological Reviews*, *89*(1), 173–198. https://doi.org/10.1111/brv.12050

Silver, M., & Di Paolo, E. (2006). Spatial effects favour the evolution of niche construction. *Theoretical Population Biology*, *70*(4), 387–400. https://doi.org/10.1016/j.tpb.2006.08.003

Singh, M., & Boomsma, J. J. (2015). Policing and punishment across the domains of social evolution. *Oikos*, *124*(8), 971–982. https://doi.org/10.1111/oik.02064

Starrfelt, J., & Kokko, H. (2012). Bet-hedging—A triple trade-off between means, variances and correlations. *Biological Reviews*, *87*(3), 742–755. https://doi.org/10.1111/j.1469-185X.2012.00225.x

Šumbera, R., Mazoch, V., Patzenhauerová, H., Lövy, M., Šklíba, J., Bryja, J., & Burda, H. (2012). Burrow architecture, family composition and habitat characteristics of the largest social African mole-rat: The giant mole-rat constructs really giant burrow systems. *Acta Theriologica*, *57*(2), 121–130. https://doi.org/10.1007/s13364-011-0059-4

Traulsen, A., & Nowak, M. A. (2006). Evolution of cooperation by multilevel selection. *Proceedings of the National Academy of Sciences*, *103*(29), 10952–10955. https://doi.org/10.1073/pnas.0602530103

Wakano, J. Y., Nowak, M. A., & Hauert, C. (2009). Spatial dynamics of ecological public goods. *Proceedings of the National Academy of Sciences*, *106*(19), 7910–7914. https://doi.org/10.1073/pnas.0812644106

West Eberhard, M. J. (1975). The evolution of social behavior by kin selection. *The Quarterly Review of Biology*, *50*(1), 1–33.

Yasui, Y. (2022). Evolutionary bet-hedging reconsidered: What is the mean–variance trade-off of fitness? *Ecological Research*, *37*(3), 406–420. https://doi.org/10.1111/1440-1703.12303