Performance-dependent movement: An alternative driver of adaptive divergence

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Abstract

It is a tenet of evolutionary biology that local adaptation is driven by natural selection, while it is hindered by gene flow. This is because random movements between populations disrupt the match between phenotype and the local environment. However, if individuals moved to the environments where they have higher ecological performance, movements between populations could facilitate local adaptation. Here we show that movements of individuals towards their phenotype-dependent optimal breeding areas rapidly result in adaptive population divergence. We manipulated local ecological performance in a wild population of Eurasian tree sparrows by creating an artificial ecological trait that gave differential access to a new food source. Individuals exhibited a very strong preference for the breeding sites where they had the highest ecological performance. This promoted higher reproductive success, local adaptation, assortative mating, and reproductive isolation with respect to the novel trait. Our results experimentally show how local adaptation can be achieved by directed movements of individuals, if they settle in the environment to which they are best adapted. Considering this mechanism of adaptation will improve our understanding of how populations and species adapt and diverge. This may be especially relevant for biodiversity management under global change, where organisms face rapid and novel environmental changes.

Main text

Population isolation is considered a beneficial, if not necessary, condition for adaptive divergence (1–3). This, however, may not generally be true if individuals do not move randomly between populations. If there is individual variation in local fitness and individuals move to areas where they have higher fitness, then adaptive population divergence will result from this process of spatial self-sorting (4, 5). This is especially likely if individuals can assess their local performance given their phenotype, and move to the area where they perform best. This process is called matching habitat choice (6–8). The best way to demonstrate this process is by manipulating a relevant phenotypic trait (6), since this changes ecological performance without changing potentially preexisting habitat preferences due to imprinting or genetic preference alleles (9–13). It has been shown that this phenotype-dependent movement may result in

ecological population divergence (6, 14). However, the fitness consequences of this process have not yet been quantified, and it is unknown whether this population divergence is transmitted to the next generation, thus leading to evolutionary divergence.

To test if performance-dependent movement can drive adaptive population divergence, we experimentally manipulated local performance of wild Eurasian tree sparrows (*Passer montanus*) by manipulating their ability to feed in different local habitats. We developed an experimental system that consisted of passive integrated transponder tags (Fig. 1a; rice-sized devices emitting unique codes that allow individual identification), representing a novel ecological trait, which operated programmable feeders (Fig. 1b) with transponder readers (15, 16), representing a new food source.

We placed these feeders in two subareas (area A and B; Fig. 1c) of our study site. Feeders provided supplementary food to those sparrows that were ringed with a plastic ring equipped with a transponder tag (Fig. 1a). We programmed the feeders in area A to provide access to food to half of the birds (type A), and the feeders in area B to provide access to the other half (type B). This mimics a situation found in natural populations, for example, in red crossbills (*Loxia curvirostra* complex), where birds exhibit variation in bill morphology (the ecological trait) that matches variation in cone morphologies of different tree species (the ecological resource); this resulting in differential access to seeds depending on bill morphology (17, 18). In our experiment, we created the strongest possible trade-off in local performance (19) by giving access to only one of the two locally available resources, depending on transponder type. Thereby, we maximized the costs of mismatch, and enhanced the probability of matching habitat choice to occur (20).

In addition, we placed nest boxes equipped with transponder readers in both areas (Fig. 1c). We predicted that if sparrows can assess spatial variation in their ecological performance (i.e., transponder-feeder match), and then choose to breed where their performance is highest, then adaptive population divergence would emerge (7, 12, 21).

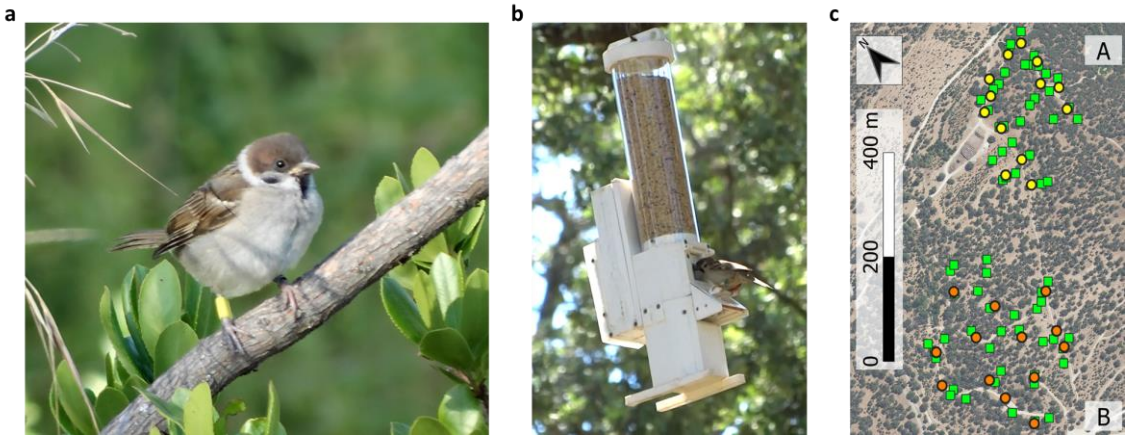

Figure 1. Local performance of wild tree sparrows was manipulated using transponder tags giving access to electronic feeders in only one area. ***a****, Wild tree sparrow with a plastic leg ring equipped with a transponder.* ***b****, Programmable electronic feeder that allows food access only to birds with a specific transponder-tag.* ***c****, Location of the electronic feeders (yellow and orange points) and of the nest boxes (green squares). Feeders in area A (yellow points) gave access to*

food to half of the tagged birds (type A); feeders in area B (orange points) gave access to the other half (type B).

Our results confirmed this prediction. Among those individuals that could compare local performance before selecting their breeding area (n = 41; see Methods), there was a positive association between the area of supplementary food access and the area of breeding. 85% of individuals bred in the area where feeders matched their transponder type (Fig. 2). An alternative explanation for this observed ecological population divergence could be divergent natural selection (21, 22): if home ranges were small, then individuals that coincidentally had feeders matching their transponder type within their home range may have had a higher probability of breeding. However, this explanation could be ruled out since we only considered birds that visited the feeders in both areas prior to selecting a site for breeding (see Methods), i.e., all individuals had access to supplementary food.

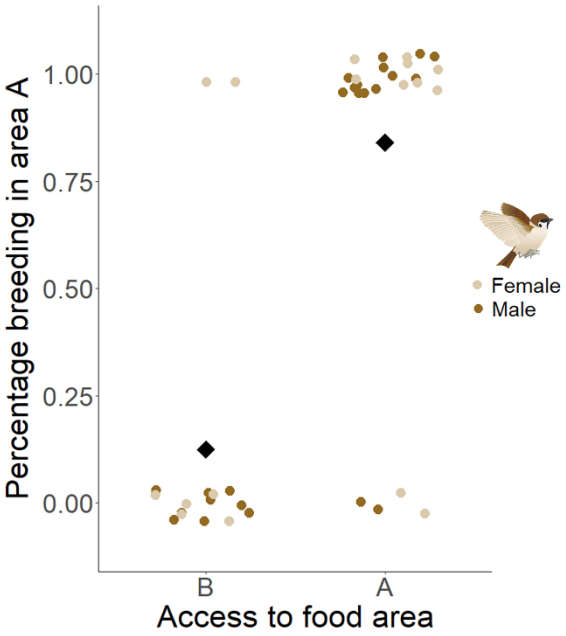

Figure 2. Performance-dependent movements generated ecological population divergence. *There was a positive association between the area where birds had access to supplementary food (A or B) and the breeding area (A or B) (two-tailed Fisher's exact test, P < 0.0001). Dots are raw data for breeding females (tan) and males (brown). Black diamonds represent the mean response given as percentage of individuals with supplementary food access in area B and A that bred in area A.*

To investigate whether this observed population divergence was adaptive, we conducted genetic parentage analyses (see, Methods). Individuals that bred in the area where they had access to supplementary food (i.e., feeder-matching individuals) produced more fledglings than those that were mismatched (Fig. 3a). Hypothetically, this higher number of fledglings could trade-off against lower fledgling quality or other fitness components (23, 24), ultimately affecting the parental contribution to the next generation. However, we found no indication

that the offspring produced by matching individuals were of lower quality (Fig. 3b). Thus, our results support that the movement towards a matching area for breeding resulted in local adaptation, despite the small spatial scale of the experimental setup.

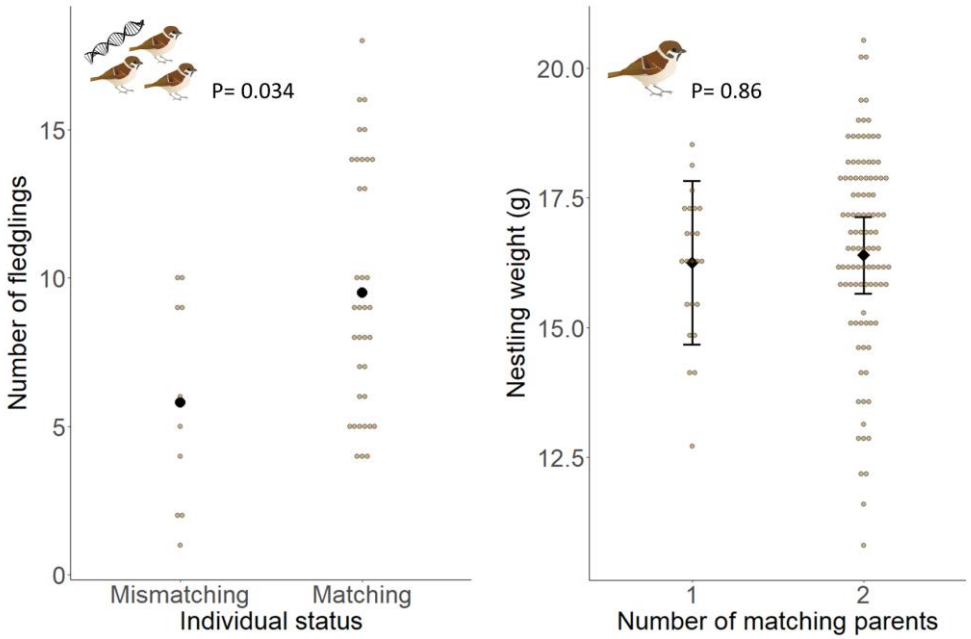

Figure 3. Tree sparrows that bred in the area where they had access to the feeders increased offspring number, while offspring quality was not reduced. ***a****, Number of fledglings (brown points) and population mean (black points) produced by matching versus mismatching individuals (two-tailed Mann–Whitney U-test, P = 0.034). Here, individuals that were only registered in one area prior to breeding are also included (see Methods)* ***b****, Model estimates for mean nestling weight (black diamonds) and raw data for each nestling (brown dots) (Generalized linear mixed model,* χ^2 *(1) = 0.032, P = 0.86; Extended Data Table 1); because of the strong effect of local performance on the selection of breeding area, there were no pairs composed of two mismatched individuals. Error bars represent the 95% CI of model estimates.*

If individuals that share similar ecological traits move to the same area to increase local performance and subsequently mate there, this should result in assortative mating for the ecological trait that drives this performance-dependent movement (25). As a consequence, reproductive isolation between individuals with distinct ecological traits is expected to emerge (8, 11, 12, 21, 26, 27). This prediction has hitherto not been tested. To do so, we used genetic parentage data and focused on biological pairs where both parents carried a transponder. We observed a total of 14 unique biological mother-father combinations. The majority of them (93%) mated assortatively for area of supplementary food access (one-tailed Exact binomial test, P = 0.0009). Five of those mother-father combinations were due to extra-pair copulations, which were all assortative. Hence, extra-pair copulations did not increase gene flow across areas A and B (28, 29). The I_{PSI} index describes overall reproductive isolation between groups and varies from -1 (maximum disassortative mating) to 1 (maximum assortative mating and complete

reproductive isolation) (30). Tree sparrows with different transponder types had an I_{PSI} value of 0.81, indicating a degree of reproductive isolation that is close to complete.

Reproducing within the habitat where local performance is higher, and with a partner with similar ecological traits, is predicted to result in the transmission of the achieved adaptive population divergence to the next generation if the traits are heritable (4, 27, 31). If we assume that the fledglings would inherit the transponder type of their parents (see Methods), then the vast majority of the offspring (90% of 85 fledglings) would have inherited the locally adaptive transponder type (two-tailed χ^2 (1) = 56.01, $P < 10^{-13}$).

To our knowledge, we provide the first experimental demonstration that non-random movement driven by differential perception of local performance can promote adaptive population divergence within and between generations. This created the same pattern of local adaptation as expected under divergent natural selection (4). However, here we demonstrate that this adaptive divergence results from selection of the breeding area *by* the sparrows rather than by current natural selection acting on the sparrows Thus, in our experiment the sparrows were selective agents rather than selective targets.

Directed movements based on local performance combined with subsequent reproduction after settlement can result in reproductive isolation between populations (7, 9, 27). Any ecological trait involved in this process could therefore be considered a 'magic trait' that promotes ecological divergence and reproductive isolation at the same time (32). We manipulated only one ecological trait (the transponder tag). However, if ecological performance, depends on multiple aspects of the phenotype, local reproduction after performance-dependent movement, as observed in this study, would also increase the probability that individuals with different locally adaptive traits mate, and produce offspring which combine several adaptive traits. This could increase variation in local performance across individuals, enhance performance-dependent movements (matching habitat choice) within each generation, reinforce adaptive population divergence across generations (33), and accelerate adaptation to multiple environmental challenges (34).

Our experiment demonstrates that performance-dependent movement can drive adaptive population divergence at very small spatial scales, where disruptive natural selection alone is unlikely to achieve the same due to the homogenizing effect of (random) gene flow (35). We observed nearly complete reproductive isolation among two populations of birds breeding just a few hundred meters apart (and in a single generation). This experimental result confirms that performance-dependent movement can be an important contributor to microgeographic adaptation and sympatric speciation (36–38). When preference depends on ecological performance, then all individuals have the same preference rule ('go to where you perform best'). This avoids the problematic coupled divergence of independent ecological traits and preferences (i.e., performance-dependent preference provides a favorable so-called one-allele mechanism of divergence) (11, 33, 36, 38).

Tree sparrows adaptively responded to a novel ecological trait (the transponder tag) and a novel environment (the feeders). Thus, matching habitat choice can be seen as a mechanism that evolved by natural selection (20), which allows individuals to rapidly (even in a single generation)

and adaptively adjust to novel ecological challenges, as long as they are able to evaluate the effects on their local performance (7, 21). Rapid local adaptation could also be achieved by natural selection (39). However, strong natural selection is intrinsically linked to high demographic costs (40), which can lead to a decline in population size and phenotypic and genetic variation. This, in turn, can reduce the adaptive potential of a population, increase sensitivity to stochastic events, and ultimately lead to extinction (41). In contrast, performance-dependent movements can reduce demographic costs, since pre-adapted individuals are using or colonizing different environments (7, 8, 12). Alternatively, if novel environments are too different and performance is poor, performance-dependent movement can help populations to avoid these suboptimal environments, contributing to population survival, niche tracking, and evolutionary stasis. As organisms are increasingly exposed to rapid and novel environmental challenges as part of global change (42, 43), recognizing the consequences of performance-dependent movement for the degree, speed, and spatial scale of adaptation will be important for the conservation and management of biodiversity.

Methods

Study population and site

The study was conducted in a population of tree sparrows breeding in nest boxes in the Encinar de San Pedro reserve in Madrid, Spain (40°25’34’’N 3°45’14’’W). Tree sparrows were captured in the area during 2020-2022 using three different methods: (i) mistnetting throughout the year, (ii) trapping nestlings and breeding adults in nest boxes during the breeding season, and (iii) trapping individuals in nest boxes while roosting at night in winter. Each bird was marked with a numbered metal leg ring and a plastic leg ring with a passive integrated transponder (PIT)-tag with a unique identification code (Eccel Technology Ltd.). Additionally, a small blood sample (<100 µl) was collected from the brachial vein in nestlings and the jugular vein in adults for molecular parentage analysis.

Ethics statement

The well-being of animals utilized in this study was ensured by adhering to all relevant international, national, and/or institutional guidelines and recommendations concerning the care and usage of animals. Capture, manipulation, transponder ringing, and blood sampling of birds were authorized by the Consejería de Medio Ambiente (Comunidad de Madrid, Spain) under license from the Spanish institutional authorities. Permit numbers: 10/003873.9/20, 10/446029.9/20, 10/569983.9/20, 10/507452.9/21, and 10/507452.9/21.

Programmable feeders and nest boxes equipped with transponder readers

We used programmable electronic PIT-operated feeders (NatureCounters; United Kingdom) to control access of individuals to supplementary food. These feeders were able to read the PIT-tag when a tagged bird perched on the feeder, and to respond according to 3 programmable modes. In mode 1, feeders were open by default, giving access to food to all birds (including other species). In mode 2, feeders were closed by default, and opened only when a PIT-tagged tree sparrow perched on it. In mode 3, feeders were closed by default and opened only when birds with feeder-matching PIT-tags (i.e., specific identification codes) perched on the feeder.

Additionally, for all birds equipped with a PIT-tag, the feeders registered each visit, including date and time, and individual identity. Feeders were filled throughout the experiment with a mixture of Prestige Tropical Finches seeds (Versele-Laga), so that that tree sparrows that had access to them could feed *ad libitum*. A small container below the feeder, and a wire grid on the soil underneath the feeder, largely prevented birds from feeding on spilled seeds.

We used nest boxes that were installed at the study site in previous years for population monitoring purposes. During the experiment, each nest box was equipped with a wooden frontal panel that allowed placement of an electronic PIT-reader (NatureCounters; United Kingdom). The electronic readers registered each bird visit to the nest box and individual identity if a bird was PIT-tagged.

Experimental procedures

In October 2020, we relocated the 68 boxes present in the study area, placing half of them in area A and the other half in area B (Extended data Fig. 2b), and installed wooden front panels with readers. In June 2021, before the end of the breeding season, we positioned 22 feeders in the study site, 11 in area A and 11 in area B (Fig. 1c). Feeders were set to mode 1 (open by default), so all adults and new fledglings were given access to food. In August 2021, after all chicks had fledged, we set all feeders to mode 2 (closed by default, and only opened when a PIT-tagged bird perched on them) In this way, the birds got used to the opening-and-closing mechanism (a small perspex plate moving up and down). At the same time, we started to gradually move all feeders towards the intermediate zone between both areas, to ensure that birds from both areas came together and were exposed to a single area with feeders. We moved the feeders every 2-3 days (7 times in total), for 37±20 m (value ± range) each time (Extended Document 1; Supplementary video 1). Once all the feeders were located in the central area, we checked the identity of every PIT-tagged bird that had used any of them and randomly assigned half of those tagged birds to type A, and the other half to type B (Supplementary video 1). Additionally, we randomly assigned all PIT-tagged birds that were not registered by the feeders to either type A or B. This was done in case they returned to the study site later in the season, ensuring that they were assigned to one of the two groups of transponder type. Thereafter, we set all feeders to mode 3, so that half of them (feeders A) only allowed access to birds with PIT-tag type A, and the other half (feeders B) to birds with PIT-tag type B. In this way, and from this moment on, we manipulated the feeding ability (local performance) of each bird for the two feeder groups. At this moment all feeders were located in a single area, thus birds were exposed to both types of feeders. After one week, we started moving the feeders to the experimental areas: feeders A to area A, and feeders B to area B. As before, we moved the feeders every 2-3 days (7 times in total) with each move being 37±20 m until they reached their final position (Extended Document 1; Supplementary video 1). We moved the feeders gradually to mimic a gradual change in the environment, and to allow the birds to follow the feeders. As a result, by September 2021, we had established two distinct areas (A and B), both with available nest boxes but with different feeders (A or B), where PIT-tagged tree sparrows had differential access to supplementary food (Fig. 1b). This movement of feeders was done directly after the breeding season because tree sparrows may select a nest box and start building their nests in autumn (44). We maintained the feeders in this mode and position for almost a year (until August 2022), when the breeding season had ended, and all experimental data had been collected.

Data collection

From February to August 2022, we checked nest boxes every week to monitor breeding activity. Once we found the first eggs, we placed an electronic reader inside the front panel of that nest box to identify the breeding individuals (however, data collection on chicks was performed blind with respect to parental treatment). When hatchlings were found, we estimated their age based on a validated identification key, with the hatching date set as day 0. At an age of 9-10 days, we counted the number of nestlings, ringed them individually, measured their weight, and took a blood sample for parentage analysis. We did not check the nest box for another 10 days to minimize disturbances and avoid early fledging. After this period, we determined the number of fledglings by checking the nest box for any dead individuals. We found no dead individuals or evidence of predation in any nest box, so we assumed that all ringed nestlings successfully fledged.

Genetic analysis

All DNA samples were genotyped at 9 microsatellite loci (Extended Data Table 2). DNA was extracted from blood samples using the QIAGEN DNeasy Blood & Tissue Kit according to the protocol purification of total DNA from Animal Blood (Qiagen), but lysing cells overnight, and digesting with RNase before the DNA purification. DNA elution was performed in 200 µl of AE buffer. The DNA was quantified using a NanoDrop™, obtaining a range between 6-78 ng/µl.

PCR amplifications were performed by two multiplex PCRs sets, previously designed in silico using the software Multiplex manager (45) and Autodimer (46). Multiplex PCR reactions were performed in a Veriti™ thermal cycler (Applied Biosystems). PCR cycling conditions were as follows: an initial denaturation step at 95 °C for 5 min, followed by 30 cycles of denaturation at 95 °C for 30 s, annealing at 56 °C for 45 s and extension at 72 °C for 30 s, and a final extension at 60 °C for 30 min. Multiplex PCRs contained 1× Qiagen Multiplex PCR Master Mix, a final primer concentration between 0.3-0.8 µM of both forward and reverse primers (Extended Data Table 2), 3 µl of template DNA diluted 1/10 and nuclease-free water to a final volume of 10 µl. The forward primers were fluorescently labelled at the 5'-end with HEX, TAMRA, ROX and 6-FAM dyes (Extended Data Table 2), and the reverse primers were 5'-end tagged (5'-GTTTCTT-3') (47). PCR products were separated on an ABI 3730 DNA Analyser, adding a GS500-LIZ size standard. Electropherograms were automatically scored using GENEMAPPER software v 4.0 (Applied Biosystems) with the created bins, and posteriorly reviewed by eye.

Parentage analysis

We used 8 of the genotyped microsatellites (discarding Pamo1 due to amplification errors) for parentage analysis. We used the software CERVUS version 3.0.7 (48), which uses a likelihood approach to infer parentage. Parents were assigned on the basis of the highest log-likelihood ratio score using the "parent pair-sex known" option. We considered all genotyped individuals that were registered at the feeders during the breeding season as potential candidate parents. We also included individuals not registered in our nest boxes, to potentially account for extra-pair copulations. Nonetheless, the biological parents of all the observed extra-pair offspring had been recorded breeding in our nest boxes.

The simulation was run with the following settings: 10,000 offspring with a candidate number of parents equal to the total number of adult individuals genotyped and registered by the feeders and/or the readers during the breeding season (39 males and 43 females); the proportion of sampled candidate parents was set to 0.8; the rate loci mistyped was set to 0.01. We ran the analysis without specifying known parents, including all males and females as potential candidate parents.

In this way, we identified the biological parents of all fledglings that had both parents tagged and with the experimental treatment successfully applied.

Data analysis

All statistical analyses were conducted with R 3.4.1 (R Core Team). Generalized linear mixed models were fitted with the glmer function of the 'lme4' package (49). Model predictions and 95% confidence intervals were obtained with the function 'get_model_data' from the package (50).

We first determined which PIT-tagged individuals with differential food-access restrictions had bred in our nest boxes by checking the readers' registers. Next, we identified the individuals to which the experimental treatment was successfully applied. Matching habitat choice (i.e., performance-dependent movement) requires individuals to assess and compare their local performance across different habitats. To test whether this essential prerequisite was fulfilled for each bird, we checked the registers of all feeders and determined if the focal individual had attempted to access supplementary food at feeders located in both areas (i.e., both types of feeders) in the period between the day the feeders had been set in their final position in September 2021 and 30 days before its nestlings hatched. We considered the treatment successful when a PIT-tagged bird was registered at feeders in both areas during this time period. When birds were not registered by any feeder, or when they were registered by feeders from one area only, we considered the treatment as unsuccessful. This criterion ensured that all birds considered had the opportunity to assess their local performance in both areas before choosing their breeding area. Note that individuals that had already evaluated their local performance before the feeders were in their final position, and, as a consequence, avoided the feeders that did not provide access, were excluded. Excluding these fast-choosing individuals has a conservative effect on the results.

To test for the effect of transponder type on the selection of breeding area (i.e., for performance-dependent movement) and on ecological population divergence, we considered only individuals where the treatment was successful. To test for performance-dependent movement, we used Fisher's exact test to determine if there was an association between transponder type and breeding area. Individuals often had multiple broods (up to four), and sometimes change nest box between broods. However, virtually all individuals with multiple broods bred in the same area throughout the season, and therefore were assigned a single breeding area. A single individual (out of 42) that bred in both areas was omitted to simplify the analysis; this makes our analysis slightly anti-conservative but the effect is expected to be negligible, given the strength of the association ($P < 0.0001$; Fig. 2).

To investigate the adaptive component of performance-dependent movement, we analyzed all PIT-tagged individuals with differential food access in both areas. While some of these

individuals did not compare their local performance between the two areas prior to breeding (i.e., the treatment was not applicable for their selection of breeding area), they did have access to the feeders and used them while breeding, so we included them to test if breeding in the feeder-matching area had effects on fitness. We compared the number of fledglings produced by matching individuals (i.e., those that bred in the area where they had access to supplementary food) and mismatching individuals (i.e., those that bred in an area where they did not have access to supplementary food). We accounted for extra-pair fertilizations in estimates of total offspring production by using the genetic parentage data. This allowed us to estimate the number of intra-pair and extra-pair fledglings from each individual. We then used a non-parametric Mann-Whitney U-test (since the distribution of the data was multi-modal) to test for differences in the number of fledglings produced by matching and mismatching individuals. We again omitted the individual that bred in both areas, as well as a male that bred in one area and had extra-pair fledglings in the other area, to simplify the analysis.

An increase in the number of fledglings could have negatively affected their quality by reducing their weight and subsequent survival. To investigate this, we used a general linear mixed model to compare the weight of nestlings raised by matching and mismatching individuals. Nestling weight was the response variable, and the number of matching parents in the parents' pair was the predictor variable. Due to the strong effect of matching habitat choice, we observed no pairs with two mismatching parents. We fitted the age of the nestling (as a deviation from the mean) as a fixed effect to account for differences in weight due to difference of age and Brood ID as a random effect to account for potential variation between them and for pseudoreplication.

We investigated assortative mating using genetic parentage data by focusing on nestlings for which both parents successfully received the experimental treatment (see above). We excluded pairs (biological father and mother) involving non-tagged individuals, as they were not part of the experiment. We also excluded biological parent pairs with individuals who did not undergo the experimental treatment, as any observed assortative mating in such pairs could not be unequivocally attributed to the effects of spatial sorting due to performance-dependent movement. This approach is conservative, but it ensured that any observed assortative mating resulted from performance-dependent movement. We defined a biological parent pair as assortative when both individuals had the same transponder type, and as disassortative when they had different transponder types. We then used a Chi-square test of expected frequencies to determine if the proportion of assortatively mated biological parent pairs differed from that expected if mating occurred randomly (i.e., 50% assortative).

We tested for reproductive isolation between birds with different transponder type (A and B) using the same subset of individuals as for estimating assortative mating. We calculated the I_{PSI} index that is based on Pair-Sexual isolation index (PSI) coefficients. It describes overall sexual isolation and varies from -1 to 1, with -1 reflecting fully disassortative mating, 0 random mating, and 1 fully assortative mating and complete sexual isolation. This statistic takes into account the proportion of each type of observed mating pair combination (maleA-femaleA, maleA-femaleB, maleB-femaleA and maleB-femaleB) relative to the total number of mating pairs.

We used the parentage data to identify the fledglings that were produced by pairs of adults that both successfully received the experimental treatment to study the inheritance of ecological population divergence. To this aim, we assumed that transponder type was inherited. We

assumed that if both biological parents were of the same type (i.e., assortative mating (25)), their offspring would virtually inherit the same transponder type. If parents were from different types (i.e., disassortative mating), a fledgling would inherit one of the two types randomly. There were just 10 fledglings from disassortative parents that were born in area A, so 5 of them inherited type A and 5 type B. We then compared the virtual transponder type of offspring with the area where they were born, to check if they would have been born in the area where they would have had access to supplementary food (locally adapted) or not (not adapted). We used a chi-square test of expected frequencies to determine if the proportion of offspring that is locally adapted differed from what was expected if location of breeding and subsequent mating occurred randomly (i.e., 50% of adapted offspring).

Data availability

The data that support the findings of this study are in Zenodo repository with the identifier https://doi.org/10.5281/zenodo.8016797. The code used to analyze and visualize the data is available in Zenodo repository with the identifier https://doi.org/10.5281/zenodo.8017752.

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Investigation: GMD, FP, PE

Software: GMD

Data curation: GMD

Formal analysis: GMD, PE

Visualization: GMD

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Resources: PE

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Supervision: FP, PE

Writing – original draft: GMD

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