

Absence of inter-horn migration validates bilateral embryo transfer as a within-dam experimental design in mice*

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Embryo transfer (ET) is a foundational technique in mouse reproductive biology. Bilateral ET, in which embryos of different genotypes are placed in opposite uterine horns of a single recipient, offers strict control over maternal variables but requires that embryos remain in the horn to which they were transferred. Here, we tested this assumption directly by transferring BTBR T⁺Itpr3^u/J (BTBR) and C57BL/6J (B6) blastocysts into opposite horns and genotyping mid-gestation fetuses by strain-specific PCR. Across four experiments varying embryo load, recipient strain, and donor-recipient synchrony, no genotype-discordant fetus was detected contralaterally. These findings validate bilateral co-transfer of genotypically distinct embryos as a methodologically safe design that halves the number of recipient females while providing rigorous within-dam experimental control.

KEY WORDS: bilateral embryo transfer / transuterine migration / blastocyst implantation / 3Rs reduction, BTBR strain / C57BL/6J strain / ipsilateral implantation / within-dam experimental design

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Short summary for non-experts

Many experiments in mouse biology depend on transplanting embryos into surrogate mothers under tightly controlled conditions. We asked whether embryos surgically placed in one uterine horn can cross over to the opposite side, and found that they could not: every embryo developed exactly where it was placed. This means that embryos of different genetic backgrounds can be carried by a single mother in either uterine horn, thus reducing the number of animals required and strengthening control over experimental variables.

Introduction

Embryo transfer (ET) is one of the most widely used procedures in mouse reproductive biology, enabling the generation of offspring with defined genotypes in controlled maternal environments. Surgical ET can be performed unilaterally (embryos deposited in one uterine horn) or bilaterally (embryos deposited in both horns). Bilateral transfer has the advantage of allowing experimental and control embryos of different genotypes to develop in the same recipient, thereby eliminating inter-dam variability in hormonal environment, immune status, diet, and gestational stress. However, the validity of this within-dam design depends on a critical assumption: that embryos placed in one uterine horn remain in that horn and do not migrate to the contralateral side. If inter-horn migration occurs, the genotype-to-horn assignment is lost, and the experimental control is compromised.

After transfer to the uterine horn, preimplantation embryos undergo a stereotyped sequence of movements that culminates in their even distribution along the horn and attachment to the endometrium at the implantation site [Flores *et al.* 2020, Lufkin *et al.* 2023]. This process is driven by coordinated myometrial contractions, endometrial signaling, and embryo-uterine crosstalk, resulting in regularly spaced implantation sites within each horn. This intra-horn spacing is regulated in part by LPA3-mediated lysophosphatidic acid signaling and has been extensively characterized by Arora and colleagues [Hama *et al.* 2007, Flores *et al.* 2020, Lufkin *et al.* 2023, Dawson *et al.* 2024]. Importantly, all the described mechanisms of embryo spacing operate within a single horn and do not involve movement between horns.

Transuterine migration is well documented in species with a bicornuate uterus, including the dog [Tsutsui *et al.* 2002], cat [Tsutsui *et al.* 1989], pig [Dhindsa *et al.* 1967], horse [Pascoe 1982], and cattle [McMillan and Peterson 1999], where the continuous uterine lumen permits embryo movement between horns. Whether embryos can migrate from one uterine horn to the other in the mouse has received surprisingly little direct experimental attention. The anatomical basis for expecting that they cannot is the duplex structure of the mouse uterus: the two horns converge into a short uterine body divided by a septum that extends through the cervical-vaginal junction, creating two functionally separate luminal compartments. The only controlled study to directly

test this question is that of Rüllicke *et al.* [2006], who transferred two-cell embryos unilaterally and found no evidence of transuterine migration, with the exception of a single contralateral resorption. However, their study did not address whether inter-horn migration might occur under different conditions, such as blastocyst-stage transfer directly into the uterine lumen, variation in recipient genetic background, or differences in donor-recipient synchrony.

In the present study, we directly test whether surgically transferred blastocysts undergo inter-horn migration and contralateral implantation. We employ a bilateral genotype-coded transfer design in which BTBR T⁺Itpr3^{fl}/J (BTBR) and C57BL/6J (B6) blastocysts are placed in opposite horns of the same pseudopregnant recipient, and their horn of origin is resolved by strain-specific PCR genotyping of mid-gestation fetuses. This approach provides an unambiguous within-dam readout of migration. Our working hypothesis was that blastocysts would remain confined to the uterine horn to which they were transferred, with no viable contralateral migration detectable at mid-gestation.

Material and methods

Animals

BTBR T⁺Itpr3^{fl}/J (BTBR; JAX Cat# 002282; RRID: IMSR_JAX:002282) and C57BL/6J (B6; JAX Cat# 000664; RRID: IMSR_JAX:000664) mice were obtained from The Jackson Laboratory (Bar Harbor, ME, USA) and maintained by inbreeding at the animal facility of the Institute of Genetics and Animal Biotechnology, Polish Academy of Sciences, Jastrzębiec, Poland. B6 and BTBR females were used as either embryo donors or recipients. Animals were housed in transparent polycarbonate cages (265 × 207 × 140 mm), 3–5 mice per cage, under a 12 h light–dark cycle at 20–22°C and 40–60% relative humidity, with food (Labofeed H, Kcynia, Poland; 13 MJ/kg) and water *ad libitum*. Experimental procedures were performed in accordance with the European Directive 2010/63/EU and the Polish Governmental Act for Animal Care. All experimental procedures were approved by the II Local Ethics Committee for Experiments on Animals in Warsaw (approval no. 62/2015).

Embryo collection and transfer

Embryological methods were conducted as previously described [Sampino *et al.* 2014, Kotlarska *et al.* 2021, Ziętek and Sampino 2023]. Embryo donors were virgin BTBR or B6 females (3–4 months old) mated overnight with strain- and age-matched stud males. The morning of vaginal plug detection was designated 0.5 *days post coitum* (*dpc*). At 3.5 *dpc*, blastocysts were collected by flushing the uterus with pre-warmed M2 medium – prepared as previously described by Nagy *et al.* [2003]. Only morphologically normal blastocysts with no signs of fragmentation were selected for transfer. Recipients were pseudopregnant B6 or BTBR females (3–5 months old) mated 2 days earlier with vasectomized males. Recipients were anesthetized by intraperitoneal injection of xylazine and ketamine (10 and 80 mg/kg body weight, respectively). The ovary, oviduct, and proximal uterine horn were exteriorized through

a dorsal midline skin incision and a small incision in the abdominal wall above the ovary. The uterine wall was punctured with a dissecting needle, and blastocysts were transferred using a fire-polished borosilicate mouth-pipette. After transfer, females were kept on a warm plate (37°C) overnight and returned to the colony the following day.

Experimental design

Four experiments were performed to test whether blastocysts undergo inter-horn migration after surgical uterine transfer (Tab. 1-3).

Experiment 1: Unilateral transfer, standard embryo load. Fresh B6 or BTBR blastocysts (n = 5-7 per transfer) were transferred unilaterally into the left or right uterine horn of pseudopregnant B6 or BTBR female recipients. The contralateral horn received no embryos.

Experiment 2: Unilateral transfer, high embryo load. To test whether uterine overload promotes contralateral migration, n = 20 B6 or BTBR blastocysts were transferred unilaterally into the left or right uterine horn of strain-matched pseudopregnant female recipients. The contralateral horn received no embryos.

Experiment 3: Bilateral genotype-coded transfer across recipient strains. BTBR and B6 blastocysts (5-7 per horn) were transferred into opposite uterine horns of B6 or BTBR female recipients. This design provides an unambiguous test of inter-horn migration: any fetus whose genotype does not match the strain transferred to that horn is evidence of contralateral migration.

Experiment 4: Bilateral genotype-coded transfer with varied synchrony. The bilateral genotype-coded design was applied to BTBR recipients mated either 2.5 or 3.5 days before transfer, to test whether variation in uterine receptivity permits contralateral migration.

Assessment of implantation sites

At 12.5 *dpc*, recipients were euthanized by cervical dislocation. The reproductive tract was removed, and each uterine horn was dissected and opened longitudinally under a stereomicroscope. The number and position of viable fetuses and resorption sites were recorded separately for each horn. Viable implantation sites were identified by the presence of well-developed fetuses surrounded by extraembryonic tissue and with a visible heartbeat. Resorptions were distinguished by smaller, irregularly shaped implantation sites with a bloody and necrotic appearance.

Genotyping

Total DNA was extracted from fetal tissue samples using the GeneMATRIX Tissue DNA Purification Kit (Eurx, Gdańsk, Poland). DNA concentration and purity were assessed by NanoDrop spectrophotometry. Strain of origin was determined by PCR targeting two strain-specific mutations: (i) a 17,814 bp deletion spanning exons 6-12 of the *Nnt* gene in B6 mice, and (ii) a 12 bp deletion in exon 23 of the *Itpr3* gene in BTBR mice.

Primers: *Nnt* (B6): Forward 5'-GTAGGGCCAAGTGTCTTCTGCATGA-3';
Reverse 5'-GTGGAATTCCGCTGAGAGAACTCTT-3'. *Itpr3* (BTBR):
Forward 5'-TCCTGAACGTACGCATCTCC-3';
Reverse 5'-AGGGGTCAAGGCTTACTGGA-3'.

The amplification protocol consisted of 35 cycles with an annealing temperature of 58°C, yielding expected product sizes of 743 bp for B6 and 130 bp for BTBR. PCR products were then validated by gel electrophoresis on a 1.7% agarose gel prepared with 100 mL of 0.5× TBE buffer and 5 µl of SimplySafe stain (Eurx, Gdańsk, Poland) for visualization.

Statistical analysis

The primary endpoint was the occurrence of contralateral implantation. Because the expected event rate was zero or near-zero, the analysis was primarily descriptive. For each experiment, the number of ipsilateral and contralateral implantation sites was recorded for each recipient and each horn. Implantation efficiency (implantation sites/embryos transferred) was compared between groups using Fisher’s exact test. Data are presented as counts and proportions. All analyses were performed using GraphPad Prism 11.0 (GraphPad Software, San Diego, CA, USA). Statistical significance was set at $p<0.05$.

Results and discussion

Unilateral transfer yields strictly ipsilateral implantation

To determine whether embryos transferred into a single uterine horn can migrate and implant contralaterally, fresh blastocysts were transferred unilaterally into pseudopregnant B6 or BTBR recipients. In Experiment 1 (standard load, 5-7 embryos per transfer), 11 of 12 recipients became pregnant, yielding 59 ipsilateral implantation sites, all confined to the injected horn (Tab. 1). A single resorption site was observed in the contralateral (non-injected) horn of one B6 recipient. This isolated contralateral resorption site most likely represents a parthenogenetically activated oocyte or a spontaneous deciduoma rather than a migrated embryo, although no genotyping was

Table 1. Implantation outcomes after unilateral embryo transfer

Exp	Design	Recipient strain	n recipients (pregnant)	Embryos transferred	Ipsilateral implant.	Contralateral implant.	Implantation efficiency (%)
1a	unilateral (5-7 embryos)	B6	6/6	35 (18BT+17B6)	28	1 (resorption site)*	80.0
1b	unilateral (5-7 embryos)	BTBR	5/6	41 (20BT+21B6)	31	0	75.6
2a	unilateral (20 embryos)	B6	3/3	60 (B6)	28	0	46.7
2b	unilateral (20 embryos)	BTBR	3/3	60 (BT)	29	0	48.3

*Single contralateral resorption site.

performed in this experiment. Accordingly, the cellular origin of this structure cannot be formally established. No viable fetus was recovered from a contralateral horn in any of the four experiments. In Experiment 2 (high embryo load, 20 embryos per transfer, $n = 6$ recipients), all 57 implantation sites were again confined to the injected horn, with no contralateral implantations observed (Tab. 1). Thus, even under conditions of pronounced uterine crowding, blastocysts did not migrate to the contralateral horn.

Bilateral genotype-coded transfers confirm the absence of inter-horn migration across recipient strains

To obtain an unambiguous test of horn-of-origin, BTBR and B6 blastocysts were transferred into opposite uterine horns of B6 or BTBR recipients (Experiment 3; $n = 13$ recipients total; 130 embryos: 69 BTBR, 61 B6). Eleven of 13 recipients became pregnant. PCR genotyping of all conceptuses collected at 12.5 *dpc* confirmed that every fetus matched the strain assigned to its horn of implantation (Fig. 1). No genotype-discordant fetuses were detected in either recipient strain: 0/48 in B6 recipients (5/6 pregnant, 62 embryos transferred) and 0/43 in BTBR recipients (6/7 pregnant, 68 embryos transferred; Tab. 2). Implantation efficiency per horn was comparable across recipient backgrounds ($p = 0.0876$, Fisher's exact test), indicating that the recipient's genetic background does not affect the absence of contralateral migration.

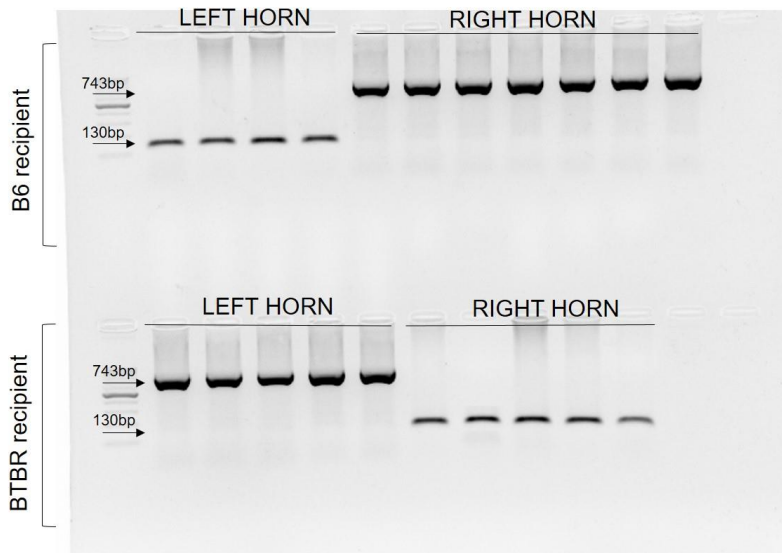


Fig. 1. Gel electrophoresis of strain-specific PCR products from fetuses recovered from the left and right uterine horns of B6 (top panels) or BTBR (bottom panels) recipients following bilateral genotype-coded transfer. Fetal strain was identified by amplification of strain-specific loci (BTBR: 130 bp; B6: 743 bp). Every fetus was genotyped to the strain deposited in its horn of recovery, with no genotype-discordant implantations detected.

Table 2. Implantation outcomes after bilateral genotype-coded transfer across recipient strains

Exp.	Design	Recipient strain	n recipients (pregnant)	Embryos transferred	Ipsilateral implant.	Contralateral implant.	Implantation efficiency (%)
3a	Bilateral (genotype-coded)	B6	5/6	62 (30BT+32B6)	48	0	77.4
3b	Bilateral (genotype-coded)	BTBR	6/7	68 (39BT+29B6)	43	0	63.2

Variation in embryo-recipient synchrony does not permit contralateral migration

To evaluate whether timing differences between donor embryos and recipient uterine receptivity create conditions permissive for contralateral migration, the bilateral genotype-coded design was applied to BTBR recipients mated 2.5 or 3.5 days before transfer (Experiment 4). No genotype-discordant fetuses were detected in either of the synchrony groups (Tab. 3). Implantation efficiency per horn was higher when embryos were transferred asynchronously at 2.5 *dpc* compared to synchronous transfer ($p = 0.0041$, Fisher's exact test).

Table 3. Implantation outcomes after bilateral genotype-coded transfer with varied synchrony

Exp.	Design	Recipient strain	n recipients (pregnant)	Embryos transferred	Ipsilateral implant.	Contralateral implant.	Implantation efficiency (%)
4a	Bilateral (genotype-coded)	BTBR (2.5 <i>dpc</i>)	3/3	22 (11BT+11B6)	20	0	90.9
4b	Bilateral (genotype-coded)	BTBR (3.5 <i>dpc</i>)	3/4	26 (15BT+11B6)	13	0	50.0

The present study provides robust experimental evidence that mouse blastocysts surgically transferred to one uterine horn do not undergo detectable contralateral migration under the experimental conditions tested, with no genotype-discordant implantation identified across four independent experiments. The key methodological advance is the bilateral genotype-coded transfer design, in which BTBR and B6 blastocysts are placed in opposite horns of the same recipient and their origin is resolved by strain-specific PCR genotyping at mid-gestation. This approach provides a definitive within-dam test that eliminates the ambiguity inherent in earlier studies relying on visual assessment alone. Our findings are consistent with Rüllicke et al. (2006), who reported no transuterine migration after unilateral transfer of two-cell embryos, except for a single contralateral resorption. By extending the analysis to the blastocyst stage, to both B6 and BTBR recipient strains, and to different synchrony conditions, our data strongly support the view that the absence of inter-horn migration is a consistent feature of the mouse uterus under standard surgical embryo transfer conditions.

The single contralateral resorption observed in Experiment 1 warrants careful interpretation. Because pseudopregnancy in recipients was induced by mating with vasectomized males, this event most likely represents a parthenogenetically

activated oocyte or a spontaneous decidualoma rather than a transferred embryo that migrated across the cervical canal. Rüllicke *et al.* [2006] reported an identical finding: one contralateral resorption among all their transfers, and reached a similar conclusion. We therefore interpret this event as unrelated to embryo migration. It must be acknowledged, however, that in the absence of genotypic characterization, this interpretation cannot be confirmed with certainty. No viable fetus was recovered from a contralateral horn in any of the four experiments.

The anatomical basis for the absence of inter-horn migration is the duplex structure of the mouse reproductive tract. The two uterine horns converge into a short uterine body that is divided by a septum extending through the cervico-vaginal junction, effectively creating two independent luminal compartments [Rüllicke *et al.* 2006]. For an embryo to migrate contralaterally, it would need to traverse this septum and ascend the opposite horn against the prevailing direction of myometrial activity, a path for which there is no anatomical or physiological support in the mouse. In contrast, in cattle, which possess a bicornuate uterus with a continuous lumen, transuterine migration after embryo transfer occurs in approximately 20% of recipients [McMillan and Peterson 1999], underscoring the role of the septum as the critical structural barrier in the mouse. Notably, even when intra-horn embryo spacing is genetically disrupted in *Lpa3*-deficient mice, embryos cluster at the cervical end of the horn but do not migrate contralaterally [Hama *et al.* 2007, consistent with the view that the septum acts as a highly effective functional barrier to inter-horn embryo movement under standard surgical transfer conditions. In species where transuterine migration occurs, it is driven by prostaglandin-mediated myometrial contractions and serves specific functions such as anti-luteolytic signaling in the horse [Stout and Allen 2001]. The mouse has no equivalent physiological requirement for inter-horn embryo movement. Consistent with this, unilateral ovariectomy studies in mice have shown that despite effective ovulatory compensation by the remaining ovary, all implantations are confined to the ipsilateral horn [McLaren 1966, Biggers *et al.* 1962], further confirming the functional independence of the two uterine compartments.

The practical implication of these findings is that bilateral co-transfer of embryos with different genotypes into opposite horns of a single recipient is a methodologically safe experimental design. This approach offers two advantages: first, it reduces the number of recipient females required, in accordance with the 3R principle of Reduction; second, it provides rigorous control over maternal variables, hormonal environment, immune status, diet, microbiota, and gestational stress, because experimental and control embryos develop in the same dam. This Reduction strategy complements other recent 3R innovations in the ET workflow, including the replacement of surgical vasectomy with naturally sterile hybrid males for pseudopregnancy induction [Preece *et al.* 2021]. Bilateral co-transfer is particularly valuable for studies in which the maternal environment represents a potential confound, such as prenatal programming, placental biology, or strain comparison experiments. Our laboratory has successfully used this approach to investigate the prenatal origins of placental and

neurodevelopmental phenotypes in BTBR mice [Viscomi *et al.* 2026]. Previous studies comparing unilateral and bilateral ET in mice have focused on optimizing pregnancy rates, embryo survival, and litter size as a function of transfer mode, embryo number, and recipient background [Mahabir *et al.* 2018, González-Jara *et al.* 2017, Lamas *et al.* 2020, Auer *et al.* 2023]. However, none of these studies addressed whether embryos deposited in one horn can migrate to the contralateral horn, a prerequisite for using bilateral transfer as a controlled within-dam experimental design. Our data fills this gap by providing genotype-level confirmation that horn assignment is maintained.

Several limitations should be noted. First, our experiments tested surgical uterine transfer of blastocysts only; whether the same conclusion holds for non-surgical transcervical transfer or for earlier embryonic stages (e.g., two-cell, morula) transferred to the oviduct requires separate investigation, although the Rüllicke *et al.* [2006] data at the two-cell stage are consistent with our findings. Second, all collections were performed at mid-term gestational age; therefore, we cannot exclude the possibility that migration occurs earlier at the blastocyst stage and is resolved by selective implantation failure, although no evidence for this has been reported previously. Despite these limitations, the consistent absence of contralateral migration across all experimental conditions, combined with genotype-level verification, provides a strong empirical foundation for the use of bilateral co-transfer in controlled murine experiments.

Conflict of interest

The authors have no conflict of interest to declare.

Data availability

The data that support this study will be shared upon reasonable request to the corresponding author.

Author contributions

MPV: Investigation, Writing – original draft; DZ: Investigation, Writing – original draft; JC: Investigation; AMK: Investigation; DW: Investigation; JAM: Conceptualization, Methodology, Resources, Supervision; MMZ: Investigation, Methodology, Data curation, Supervision, Validation, Writing – original draft, Writing – review and editing; SS: Conceptualization, Investigation, Formal analysis, Funding acquisition, Methodology, Data curation, Supervision, Validation, Writing – original draft, Writing – review and editing.

Declaration of use of AI

Generative AI was used to improve English grammar and readability. The authors reviewed and edited the content as needed and took full responsibility for the content of the published article.

Ethics statement

All experimental procedures were approved by the II Local Ethics Committee for Experiments on Animals in Warsaw (approval no. 62/2015).

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