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Ventral Tegmental Area Dopamine Neuron Dynamics During Postpartum Scarcity-Adversity Depend on Caregiving Quality and Pup Proximity

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7 **Ventral Tegmental Area Dopamine Neuron Dynamics During Postpartum Scarcity-**
8 **Adversity Depend on Caregiving Quality and Pup Proximity**

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Abstract

Maternal behaviors are evolutionarily conserved yet sensitive to environmental factors such as resource availability. Scarcity-adversity, modeled by providing dams with reduced bedding and nesting materials, reliably induces changes in sensitive and insensitive pup-directed maternal behaviors. Ventral tegmental area (VTA) dopamine (DA) neurons are activated by pup interactions and required for the expression of normal maternal behaviors. However, the effects of postpartum scarcity-adversity on dam VTA DA neuron activity during caregiving alterations remain unexplored. We conducted in vivo fiber photometry recordings of VTA DA neuron activity using Cre-dependent GCaMP7f in postpartum female TH-Cre rat dams in control or scarcity-adversity conditions. Dams were assigned to control or scarcity-adversity conditions on postpartum day (PD) 2 and underwent daily fiber photometry recordings during naturalistic maternal behavior observation sessions and a food pellet reward retrieval task through PD 5. Scarcity-adversity dams showed significantly elevated VTA DA neuron activity during insensitive caregiving, reflected by increased area under the curve, with no group differences during sensitive care. Additionally, scarcity-adversity dams exhibited a decrease in frequency of peaks when separated from their pups (i.e., out of nest), with no group differences during pup contact or nursing. Critically, alterations in VTA DA neuron activity in scarcity-adversity dams were not observed during food reward retrieval, suggesting that postpartum scarcity-adversity selectively disrupts VTA DA dynamics within the maternal caregiving context. These findings show that postpartum resource scarcity induces context-specific alterations in VTA DA neuron activity and provide a foundation for future investigation of projection-specific mechanisms underlying adversity-induced maternal behavior deficits.

Significance Statement

Postpartum adversity compromises maternal caregiving and increases risk for postpartum depression, but how it alters real-time maternal brain function during active caregiving is poorly understood. Using fiber photometry in TH-Cre dams exposed to resource scarcity, we

demonstrate that adversity alters ventral tegmental area (VTA) dopamine (DA) neuron activity during ongoing maternal behavior in a context-dependent manner. Adversity elevated VTA DA neuron activity during insensitive caregiving and reduced VTA DA activity during pup separation, without affecting VTA DA responses to food. These findings reveal that postpartum scarcity-adversity shapes the motivational architecture of maternal caregiving through context-specific alterations in VTA DA neuron dynamics, providing a neurobiological framework for understanding how adverse postpartum environments impair maternal care quality without broadly affecting reward processing.

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Introduction

Dopamine (DA) neurons in the ventral tegmental area (VTA) are critical for reward-related and motivated behavior, as they encode reward prediction errors (RPE) that drive associative learning and sustain goal-directed action (Schultz, 2002; Keiflin and Janak, 2015; Schultz, 2016; Lerner et al., 2021). During the postpartum period, VTA DA neurons become primed to respond to pup cues and pup interactions (Robinson et al., 2011; Rincón-Cortés and Grace, 2020; Day and Shea, 2025). Pup contact and pup-related cues activate VTA DA neurons and increase downstream DA release in the nucleus accumbens (NAc), reflecting the high incentive value of dam-pup interactions (Hansen et al., 1993; Champagne et al., 2004; Hernandez-Gonzalez et al., 2005; Afonso et al., 2009; Fang et al., 2018; Dai et al., 2022; Xie et al., 2023). Furthermore, disruptions in VTA DA signaling via lesions, receptor antagonists, or temporary suppression impair maternal care, pup retrieval, and pup-induced conditioned place preference learning (Hansen et al., 1991; Numan et al., 2009; Seip and Morrell, 2009). Altogether, these findings implicate VTA DA neuron integrity as essential for motivated maternal behavior.

Postpartum adversity, including environmental resource scarcity, is among the strongest predictors of both postpartum depression (PPD) and aberrant caregiving in humans (Goyal et al., 2010; Finegood et al., 2016; Ho et al., 2022; Szurek-Cabanas et al., 2024), and reliably impairs maternal caregiving in relevant rodent models (Ivy et al., 2008; Walker et al., 2017; Perry et al., 2019; Rincón-Cortés, 2025). In rodents, postpartum scarcity-adversity increases insensitive pup-directed behavior such as stepping, dragging, and shoving, and impairs maternal motivation, as indexed by pup retrieval deficits (Perry et al., 2019; Rincón-Cortés and Grace, 2022b; Nguyen et al., 2025; Porras et al., 2025; Jackson et al., 2026). We have previously demonstrated that rat dams exposed to postpartum scarcity-adversity exhibit attenuated baseline VTA DA neuron population activity, as indexed by fewer spontaneously active neurons, establishing a link between postpartum adversity, disrupted maternal behavior, and VTA DA hypofunction (Rincón-Cortés and Grace, 2022b, a).

While fiber photometry studies have begun characterizing real-time VTA DA dynamics during structured pup retrieval paradigms (Fang et al., 2018; Xie et al., 2023), VTA DA neuron activity during naturalistic home-cage mother-infant interactions, including how it may be modulated by postpartum adversity exposure, has not been characterized. Based on prior evidence indicating adversity-induced VTA DA downregulation and impaired maternal motivation (Rincón-Cortés and Grace, 2022b), we hypothesized that postpartum scarcity-adversity would reduce VTA DA activity during sensitive maternal caregiving, with the consequence of further disrupting the motivational drive underlying pup-directed care. We further hypothesized that scarcity-adversity dams would show reduced spontaneous VTA DA activity across maternal behavioral states, consistent with our prior electrophysiological evidence showing reduced baseline VTA DA activity in scarcity-adversity dams. To assess specificity of any observed effects within the postpartum context, we also examined VTA DA responses to a non-social reward (i.e., food) in the same animals immediately following naturalistic maternal behavior home cage observation sessions.

Here we used fiber photometry to record GCaMP7f fluorescence in VTA DA neurons of TH-Cre rat dams during naturalistic maternal behavior and food reward retrieval across PD 2-5 in control and scarcity-adversity conditions. We examined event-locked VTA DA neuron population responses during sensitive and insensitive caregiving behaviors, spontaneous frequency of peaks across behavioral states defined by pup proximity, and VTA DA neuron population responses to

food reward in the same animals. We report that postpartum scarcity-adversity does not alter event-locked VTA DA neuron population responses during sensitive caregiving or food reward retrieval but produces elevated population activity during insensitive caregiving and selectively reduces spontaneous VTA DA neuron frequency of peaks while the dam is away from pups (i.e., out of nest). These findings reveal context-specific alterations in VTA DA dynamics induced by postpartum scarcity-adversity, with food reward responses remaining intact in the same animals, suggesting adversity-induced disruptions are specific to maternal caregiving contexts.

Methods

Animals

All procedures were approved by the Institutional Animal Care and Use Committee (IACUC) at the University of Texas at Dallas (#22-02, #25-0178) and performed in accordance with the National Institutes of Health's Guide for Care and Use of Laboratory Animals. TH-Cre rats were maintained in ventilated cages on a 12h light/12h dark cycle with ad libitum access to food and water. All animals were born in-house and genotyped using a third-party genotyping company, Transnetyx (Cordova, TN). Only TH-Cre⁺ subjects were kept in the study. TH-Cre⁺ rats were weaned at postnatal day (PND) 23 and co-housed in same-sex pairs until adulthood (i.e., PND 70+) at which point they underwent surgery. Following a one-week recovery period, TH-Cre virgin females were bred with experienced TH-Cre males by cohousing an adult female with an adult male for a three-week period after which the pregnant female was separated and single-housed. Parturition was verified daily from gestational days 20-23 and the day of birth was designated as postpartum day (PD) 0. On PD 1, all litters were culled to 8-10 pups with equal sex distribution whenever possible, before the onset of scarcity-adversity exposure on PD 2 (see **Figure 1A, Timeline and Experimental Design**).

Scarcity Adversity

Dams were assigned to control or experimental (i.e., scarcity-adversity) conditions using simple randomization (i.e., coin flip). On PD 2, scarcity-adversity dams were placed in a cage containing 500mL of corncob bedding with no nesting material; control dams received 1800mL of corncob bedding with a nestlet (Lauraine et al., 2024; Nguyen et al., 2025; Porras et al., 2025; Salazar et al., 2025; Lauraine and Rincón-Cortés, 2026). This environmental manipulation (i.e., scarcity-adversity) produces aberrant pup-directed behaviors during the first week postpartum (Rincón-Cortés and Grace, 2022b; Lauraine et al., 2024; Porras et al., 2025; Jackson et al., 2026). Dam and pup body weights were recorded on PD 1, prior to the onset of scarcity-adversity exposure, and again on PD 6, to assess whether scarcity-adversity affected maternal or offspring weight. The dam and her litter remained in their respective conditions until PD 6, on which the dam was perfused and the litter was sacrificed.

Microinjections and Surgeries

Adult TH-Cre virgin females (PND 70-120) underwent VTA microinjection and fiber optic implantation surgery. Immediately prior to surgery, animals were anesthetized using gaseous isoflurane in an induction chamber (1.5L/min of O₂ and 0.5-5% isoflurane over five minutes). After induction, anesthesia was maintained at 0.8-1L/min of O₂ and 3-4% isoflurane. Animals received a 1 mL intraperitoneal (IP) injection of saline for hydration, a 1mg/kg IP dose of atropine for heart

rate stabilization, a 6mg/kg subcutaneous (SC) dose of bupivacaine as a local analgesic, and eye lubrication to prevent cornea dehydration. Animals were kept mounted on a stereotaxic apparatus (Kopf) and kept warm using a covered heating pad (Sunbeam, 40-43°C). An adeno-associated virus (AAV) carrying Cre-dependent jGCaMP7f (Addgene 104492-AAV9: syn-FLEX-jGCaMP7f-WPRE) was unilaterally injected (1000nL; 100nL/min, additional 10 min for diffusion) into the VTA (AP: -5.85, ML: +0.80, DV: -8.6mm from bregma). This TH-Cre-dependent viral targeting approach has been shown to yield high cell-type specificity for VTA DA neurons (Liu et al., 2016; Lohani et al., 2017). Mono fiber-optic cannulas (2.5mm, 400µm core and 0.48 NA; Doric Lenses) were implanted in the VTA at the same AP/ML coordinates (DV -8.5mm) (see **Figure 1B** for images of viral spread and fiber placements and **Table S1** for key resources). Histological verification confirmed that viral expression was centered medially and dorsally within the VTA and spanned approximately -5.20 to -5.80mm from bregma across subjects, encompassing much of the rostrocaudal extent of this structure. The fiber-optic cannulas were secured to the skull using bone screws and dental cement (C&B Metabond, Parkell, Brentwood, NY and Teets 'Cold Cure'). Animals were given one week to recover from surgery before breeding.

Fiber Photometry

All behavioral testing and fiber photometry recordings were conducted between 8:00AM and 2:00PM under standard light cycle (regular room lighting) conditions. To record jGCaMP7f activity in VTA DA neurons during behavior, the fiber-optic cannula implant was coupled to a rotary joint and mono fiber-optic patch cord (Doric Lenses, 2.5mm, 400µm core and 0.48 NA) via a mating sleeve (Doric Lenses, 2.5mm bronze). Two LED light sources (405nm and 465nm) were emitted and detected by a Tucker-Davis Technologies (TDT) RZ10X LUX-I/O Processor. Light power was adjusted using TDT's Synapse software to around 100 µW at the start of each recording session. Prior to behavioral recording, the dam's home cage was transported to the behavioral room for a 30-minute habituation. After habituation, the dam and litter were placed in a new, clean cage with either control or scarcity-adversity conditions. At this time, the dam's fiber-optic cannula was coupled to the patch cord, and the dam and litter were given 15 minutes to habituate to the new cage and tether. During these 15 minutes, the LED light power was turned on and adjusted to 100 µW.

Maternal Behavior Observations

From PD 2-5, after habituation to both the testing room and new cage/tether, a 30-minute maternal behavior observation period was recorded with simultaneous fiber photometry data collected using a TDT processor. A time-locked camera (TDT iCON and iV2 Video Capture Interface) was positioned to record the entire cage as the dam interacted with her pups. During this time, maternal behaviors were live scored to determine the number of occurrences of sensitive and insensitive caregiving behaviors, as well as the percentage of time dams spent engaging in these (Nguyen et al., 2025; Porras et al., 2025; Salazar et al., 2025). Sensitive caregiving behaviors (e.g., licking/grooming, anogenital licking, nursing) were defined as pup-directed behaviors that support normal maternal care, while insensitive caregiving behaviors (i.e., stepping, dragging, shoving) were defined as pup-directed behaviors that disrupt normal maternal care. We use the term "insensitive caregiving" for consistency with terminology used in our prior work characterizing pup-directed maternal behavior in this paradigm (Jackson et al., 2026; Lauraine and Rincón-Cortés, 2026).

Reward Retrieval Test

Immediately following the maternal behavior observation recording, the litter was removed from the recording cage, and the reward retrieval test was conducted. This entailed dropping a Cheerio in one corner of the recording cage and annotating when the dam retrieved (i.e., picked up with her mouth). This test included six trials of Cheerio rewards per day from PD 2-5. Similar food reward retrieval tasks reliably induce phasic increases in VTA DA activity and are commonly used for signal verification (Simpson et al., 2024). After the reward test, the dam was reunited with her litter in their home cage and returned to the animal housing facility.

Behavioral Scoring

All tests were video recorded and underwent both live- and post-hoc scoring using TDT's OpenScope software, which allows for time-locked note annotation of behavioral bouts. The maternal behavior observation recordings were scored live as previously described (Nguyen et al., 2025; Porras et al., 2025; Salazar et al., 2025). Briefly, each 30-minute observation session was divided into 5-minute segments during which behaviors were scored as occurring or not. Dams were spot-checked periodically during each 5-minute segment and if a behavior occurred during that segment, a tally mark was made. To represent behaviors as a percentage of time, we divided the number of segments in which the behavior was observed by the total number of observation segments on all days. We also quantified the total number of occurrences of sensitive and insensitive mother-pup interactions. Post-hoc scoring involved annotating the recorded videos at the precise moment when pup-directed sensitive or insensitive maternal behaviors occurred using TDT's OpenScope. Only these post-hoc annotations were aligned to the fiber photometry data collected through TDT's Synapse software. Reward retrieval tasks were similarly scored post-hoc using TDT's OpenScope.

Fiber Photometry Analysis

Data was analyzed with custom MATLAB (MathWorks) script. Briefly, the isosbestic control signal (405nm) was fitted to a least-squares linear regression model modeled by the GCaMP7f signal (465nm) to account for photobleaching (Simpson et al., 2024; Keevers and Jean-Richard-Dit-Bressel, 2025). Next the fitted isosbestic signal was subtracted from the GCaMP7f signal to account for autofluorescence (Simpson et al., 2024; Keevers and Jean-Richard-Dit-Bressel, 2025).

$$\text{Corrected Photochannel} = 465\text{nm} - \text{Fitted } 405\text{nm}$$

A $\Delta F/F$ for the whole recording was calculated using the following formula:

$$\frac{\Delta F}{F} = \frac{465\text{nm} - \text{Fitted } 405\text{nm}}{\text{Fitted } 405\text{nm}}$$

The z-score of this $\Delta F/F$ was calculated using the following formula (MATLAB z-score function):

$$zscore \Delta F/F = \frac{\frac{\Delta F}{F} - (\text{mean } \frac{\Delta F}{F})}{stdev \frac{\Delta F}{F}}$$

However, individual behavioral event $\Delta F/F$ s were calculated using the first two seconds of the event window (i.e., 5 seconds prior to the event and 10 seconds after).

$$\text{Event2sec baseline} = \text{mean of the first 2 seconds of the Corrected Photochannel}$$

241

$$\text{Event} \frac{\Delta F}{F} = \frac{(\text{Corrected Photochannel} - \text{Event2 sec baseline})}{\text{Event2 sec baseline}}$$

242 The z-score of the event $\Delta F/F$ was then calculated and used for further analysis and figure
 243 generation. Using event z-score $\Delta F/F$ ($Z\Delta F/F$), we found the mean $Z\Delta F/F$ before the event (i.e.,
 244 0-5 seconds before) and the maximum $Z\Delta F/F$ after the event (i.e., 0-10 seconds after) (MATLAB
 245 findpeaks function). We also found peri-event (i.e., -5-10 seconds), and after-event (0-10
 246 seconds) area under the curve (AUC) (MATLAB trapz function). For visualization purposes only,
 247 we display the average VTA DA neuron activity and heatmaps such that the highest $Z\Delta F/F$ peak
 248 within 5 seconds before and after the event are aligned. For behaviors such as time in nest, out
 249 of nest, and nursing, we found the number of peaks above 0.5 $Z\Delta F/F$ and divided this by the
 250 duration of the behavior to get peaks/second (Frequency of Peaks). This threshold was selected
 251 to capture discrete population-level activation events rather than continuous low-amplitude
 252 fluctuation in the signal.

253 *Transcardial Perfusion and Tissue Fixation*

254 On PD 6, dams were removed from their litter, weighed, and injected with 3-6mL of 30% urethane
 255 in saline. Once absence of the toe pinch reflex was confirmed, the dam was perfused by flushing
 256 the body with 0.1M phosphate buffer (PB) and 5% heparin before fixing the body with 4%
 257 paraformaldehyde (PFA) in 0.1M PB. Brain tissue was collected for histological verification of viral
 258 expression and fiber cannula placement. Brains were stored overnight at 4°C in a 30% sucrose/
 259 4% PFA solution before being switched to a 30% sucrose solution in 0.1M PB for long-term
 260 storage at -10°C.

261 *Histology*

262 Fixed brains were frozen at -20°C, sliced at 20µm, and immediately mounted on slides. Viral
 263 histology was conducted in the VTA to verify the microinjection and optic-fiber cannula
 264 implantation site. Slides underwent a 10-minute citrate acid buffer incubation, were washed in
 265 0.1M phosphate buffered saline (PBS), incubated for one hour in 10% normal donkey serum, and
 266 incubated overnight in a 1:1000 dilution of the primary anti-GFP antibody (Invitrogen Cat# A-
 267 11122, GFP Polyclonal Antibody). The following day, slides were washed in 0.1M PBS and
 268 incubated for two hours in the dark in a 1:1000 dilution of the secondary antibody (Invitrogen Cat#
 269 R37118, Donkey anti-Rabbit IgG (H+L) ReadyProbes, Alex Fluor 488). The slides were washed
 270 once more in 0.1M PBS and cover-slipped using a DAPI mounting medium (EMS Glycerol
 271 Mounting Medium with DAPI). The slides were stored in the dark at -10°C.

272 *Experimental Design and Statistical Analysis*

273 Sample sizes were determined a priori based on previously published behavioral and
 274 electrophysiological data from control and scarcity-adversity dams (Rincón-Cortés and Grace,
 275 2022b; Porras et al., 2025). Power analyses conducted in G*Power 3.1 (Faul et al., 2007) using
 276 published effect sizes for both adverse maternal behavior and VTA DA neuron activity ($d=1.71$ -
 277 2.18) indicated that a minimum of 6-7 animals per group was required to achieve > 80% power to
 278 detect significant group differences ($\alpha=0.05$, two-tailed). All groups in this study met or exceeded
 279 this minimum ($n=7$ -9 per group).

280 To compare the effects of scarcity-adversity exposure, two-tailed pairwise comparisons
 281 were utilized (i.e., Percentage of Time and Number of Occurrences of Maternal Care, Peri-Event
 282 AUC, After-Event AUC, and Frequency of Peaks). Normally distributed data sets were analyzed

using a Welch's t-test, whereas non-normally distributed data sets were analyzed using a Mann Whitney test. To compare the effects of scarcity-adversity exposure across time (i.e., peak ZΔF/F before and after the event), two-way analysis of variance (ANOVA) was utilized with the two factors being condition and time (**Figures 2, 4, 7**). To compare the effects of scarcity-adversity exposure across time (before/after event) and recording stage (i.e., PD 2-3 vs PD 4-5), a mixed-effects model was utilized with the factors being condition, time, and stage (**Figures 3, 5**). Effect sizes are reported as eta squared (η^2) for pairwise comparisons and partial eta squared (η^2_p) for ANOVA and mixed-effects model main effects and interactions. Statistics were calculated using GraphPad Prism 11.0.2 and significance was determined at $p < 0.05$. Statistical outliers were identified using a Grubb's test (GraphPad) and excluded from analysis. One control data point was excluded from Sensitive Care Peri-Event AUC (**Figure 2C**), and one adversity data point was excluded from Out of Nest Frequency of Peaks (**Figure 6G** and **Supplementary Figure S1H-I**).

Results

Postpartum scarcity-adversity induces alterations in sensitive and insensitive maternal caregiving

Scarcity-adversity exposure from PD 2-5 produced alterations in both sensitive and insensitive caregiving, consistent with prior reports (Rincón-Cortés and Grace, 2022b; Lauraine et al., 2024; Porras et al., 2025; Jackson et al., 2026). Scarcity-adversity dams spent a lower percentage of time licking/grooming pups compared to controls (CON: $n=9$, ADV: $n=8$, $t_{13.63}=2.63$, $p=0.02^*$, $\eta^2=0.34$; **Figure 1C**), although there were no differences in anogenital licking ($U=20$, $p=0.13$; **Figure 1D**). Scarcity-adversity dams also exhibited a reduction in the percentage of time spent nursing compared to control dams ($t_{10.95}=2.32$, $p=0.04^*$, $\eta^2=0.33$; **Figure 1E**). This adversity-induced decrease in sensitive pup-directed care remained even when comparing the total number of occurrences of licking/grooming and anogenital licking ($t_{14.22}=2.99$, $p=0.0097^*$, $\eta^2=0.38$) across all days (**Figure 1F**). With regards to insensitive caregiving behaviors, scarcity-adversity dams spent a greater percentage of time stepping on pups ($t_{13.53}=4.43$, $p=0.0006^{***}$, $\eta^2=0.59$; **Figure 1G**), with no differences in the percentage of time spent dragging ($U=18$, $p=0.07$; **Figure 1H**) or shoving pups ($U=35.50$, $p=0.99$; **Figure 1I**). When comparing the total number of insensitive caregiving events, scarcity-adversity dams displayed an increase in the total number of occurrences of insensitive pup-directed behaviors ($t_{14.78}=2.21$, $p=0.04^*$, $\eta^2=0.25$; **Figure 1J**). Despite these alterations in caregiving behavior, there were no significant between-group differences in dam or pup body weights on PD 1 (dam: $t_{15.99}=0.15$, $p=0.88$; pups $t_{13.78}=1.03$, $p=0.32$) or PD 6 (dam: $t_{11.90}=0.92$, $p=0.38$; pups: $t_{14.70}=0.50$, $p=0.62$). We have included examples of VTA DA neuron activity traces during a single bout of sensitive (licking) or insensitive care (stepping) in a control animal (**Figure 1K**). For complete statistics including means and standard error of the mean (SEM), please see **Table S2. Figure 1 Statistics**.

Postpartum scarcity-adversity does not alter VTA DA neuron activity during sensitive maternal care

Group-averaged peri-event VTA DA neuron activity during sensitive care is displayed for control and scarcity-adversity dams, aligned so that the highest peak occurring within 5 seconds before and after the event onset is centered (CON: $n=9$, ADV: $n=8$; **Figure 2A**). Likewise, heatmaps of

VTA DA neuron activity during sensitive care are shown for individual control and scarcity-adversity dams (each numbered line corresponds to one animal, **Figure 2B**). Scarcity-adversity dams exhibited comparable VTA DA neuron activity during sensitive maternal care (i.e., licking/grooming and anogenital licking) to control dams, as there were no between-group differences found for peri-event AUC ($t_{9.97}=0.68$, $p=0.51$; **Figure 2C**) or after-event AUC ($t_{13.97}=0.83$, $p=0.42$; **Figure 2D**). Two-way ANOVA revealed a main effect of time on $\Delta F/F$ peaks following the occurrence of sensitive care ($F_{(1,15)}=733.6$, $p<0.0001^{****}$, $\eta^2_p=0.96$; **Figure 2E**), as both control and scarcity-adversity dams displayed a higher $\Delta F/F$ peak following sensitive care events, but showed no main effect of condition ($F_{(1,15)}=1.77$, $p=0.20$) or an interaction between time and condition ($F_{(1,15)}=2.25$, $p=0.15$). This change in $\Delta F/F$ indicates that VTA DA neuron activity increased following licking/grooming and/or anogenital licking regardless of condition. For reference, we have included example traces of VTA DA neuron activity during a single bout of sensitive care (licking) in a control and scarcity-adversity dam (**Figure 2F**). For complete statistics including means and SEM, please see **Table S3. Figure 2 Statistics**.

VTA DA neuron activity during sensitive care is stable across the scarcity-adversity exposure period

To determine whether alterations in VTA DA neuron activity during sensitive pup-directed maternal behaviors emerge rapidly following adversity onset or reflect cumulative adaptation to repeated postpartum scarcity-adversity, we compared VTA DA neuron activity during sensitive care between the first (PD 2-3) and the second (PD 4-5) halves of the recording period in control and scarcity-adversity dams (**Figure 3**). Average VTA DA neuron responses during sensitive caregiving are shown for PD 2-3 and PD 4-5 in control dams (**Figure 3A**), alongside heatmaps of individual control dams during PD 2-3 (**Figure 3B**) and PD 4-5 (**Figure 3C**). The corresponding traces and heatmaps are shown for scarcity-adversity dams during PD 2-3 and PD 4-5 (**Figure 3D**), with individual heatmaps for PD 2-3 (**Figure 3E**) and PD 4-5 (**Figure 3F**). Peri-event AUC during sensitive caregiving did not differ between PD 2-3 and PD 4-5 in control ($U=27$, $p=0.68$) or adversity ($t_{10.86}=0.44$, $p=0.67$) dams, nor did it differ between control and adversity dams during PD 2-3 ($t_{12.74}=0.19$, $p=0.85$) or PD 4-5 ($U=19$, $p=0.88$; **Figure 3G**). Similarly, after-event AUC did not differ between PD 2-3 and PD 4-5 in control ($t_{13.74}=1.07$, $p=0.30$) or adversity dams ($t_{8.56}=1.57$, $p=0.15$), nor did it differ between control and adversity dams during PD 2-3 ($t_{14.12}=0.82$, $p=0.42$) or PD 4-5 ($t_{5.92}=0.26$, $p=0.80$; **Figure 3H**). A mixed model examining $\Delta F/F$ before and after the event across recording stage (PD 2-3, PD 4-5) and condition (control, adversity) revealed only a main effect of time ($F_{(1.27, 21.23)}=320.7$, $p<0.0001$) (**Figure 3I**). Together, these findings indicate that the absence of a scarcity-adversity effect on VTA DA neuron activity during sensitive pup-directed caregiving, reported for the full PD 2-5 dataset in **Figure 2**, is consistent across both halves of the exposure period, suggesting that this null effect does not emerge or resolve over the course of scarcity-adversity exposure. For complete statistics including means and SEM, please see **Table S3. Figure 3 Statistics**.

Postpartum scarcity-adversity alters VTA DA neuron activity during insensitive maternal care

Group-averaged peri-event VTA DA neuron activity during insensitive care is displayed for control and scarcity-adversity dams, aligned so that the highest peak occurring within 5 seconds before and after the event onset is centered (CON: $n=9$, ADV: $n=7$; **Figure 4A**). Likewise, heatmaps of VTA DA neuron activity during insensitive care are shown for individual control and scarcity-adversity dams (each numbered line corresponds to one animal, **Figure 4B**). Scarcity-adversity

dams exhibited differences in VTA DA neuron activity, as measured by increased AUC, associated with insensitive maternal care (i.e., stepping, dragging, and shoving pups). Specifically, scarcity-adversity dams exhibited increased peri-event AUC compared to controls ($t_{8.77}=2.58$, $p=0.03^*$, $\eta^2=0.43$; **Figure 4C**). No between-group differences were found for after-event AUC ($t_{13.96}=0.39$, $p=0.70$; **Figure 4D**). The increase in peri-event AUC but not after-event AUC suggests that adversity-induced alterations in VTA DA neuron activity occur before or coincide with the display of stepping, dragging, or shoving pups, but are not present after. Additionally, two-way ANOVA revealed a main effect of time ($F_{(1,14)}=367.7$, $p<0.0001^{****}$, $\eta^2_p=0.92$; **Figure 4E**) but not condition ($F_{(1,14)}=0.23$, $p=0.64$) or an interaction between time and condition ($F_{(1,14)}=0.48$, $p=0.50$) on $\Delta F/F$ peaks following the occurrence of insensitive care. Both control and scarcity-adversity dams displayed an increase in peak $\Delta F/F$ after insensitive care, indicating that VTA DA neuron activity peaked after insensitive pup-directed interactions in both control and scarcity-adversity dams. For reference, we have included example traces of VTA DA neuron activity during a single bout of insensitive care (stepping) in a control and scarcity-adversity dam (**Figure 4F**). For complete statistics including means and SEM, please see **Table S4. Figure 4 Statistics**.

VTA DA neuron activity during insensitive care is elevated by adversity specifically during PD 4-5

To determine whether the scarcity-adversity induced elevation in VTA DA neuron activity during insensitive pup-directed maternal behaviors emerges rapidly following adversity onset or reflects cumulative adaptation to repeated postpartum scarcity-adversity, we compared VTA DA neuron activity during insensitive pup-directed maternal behaviors between the first (PD 2-3) and the second (PD 4-5) halves of the recording period in control and scarcity-adversity dams (**Figure 5**). Average VTA DA neuron responses during insensitive pup-directed behaviors are shown for PD 2-3 and PD 4-5 in control dams (**Figure 5A**), alongside heatmaps of individual control dams during PD 2-3 (**Figure 5B**) and PD 4-5 (**Figure 5C**). The corresponding traces and heatmaps are shown for scarcity-adversity dams during PD 2-3 and PD 4-5 (**Figure 5D**), with individual heatmaps for PD 2-3 (**Figure 5E**) and PD 4-5 (**Figure 5F**). Peri-event AUC during insensitive pup-directed behaviors did not differ between PD 2-3 and PD 4-5 in control dams ($t_{7.95}=1.20$, $p=0.26$), but was significantly elevated during PD 4-5 compared to PD 2-3 in scarcity-adversity dams ($t_{9.03}=2.54$, $p=0.03$, $\eta^2=0.42$). Peri-event AUC did not differ between control and adversity dams during PD 2-3 ($t_{11.95}=1.08$, $p=0.30$), but was significantly elevated in adversity dams compared to controls during PD 4-5 ($t_{10.00}=3.81$, $p=0.003$, $\eta^2=0.59$; **Figure 5G**). After-event AUC did not differ between PD 2-3 and PD 4-5 in control dams ($U=10$, $p=0.08$) or adversity dams ($t_{10.99}=0.77$, $p=0.45$), nor did it differ between control and adversity dams during PD 2-3 ($U=13$, $p=0.09$) or PD 4-5 ($t_{7.54}=1.52$, $p=0.17$; **Figure 5H**). A mixed model examining $\Delta F/F$ before and after the event across recording stage (PD 2-3, PD 4-5) and condition (control, adversity) revealed only a main effect of time ($F_{(1.75, 26.86)}=117.8$, $p<0.0001$) (**Figure 5I**). Together, these findings indicate that the scarcity-adversity-induced elevation in peri-event AUC during insensitive care, reported for the full PD 2-5 dataset (**Figure 4C**), is specifically driven by activity during PD 4-5 and is not present during PD 2-3, suggesting that this effect reflects a cumulative adaptation to repeated scarcity-adversity exposure rather than a rapid-onset response. For complete statistics including means and SEM, please see **Table S4. Figure 5 Statistics**.

VTA DA neuron activity is reduced in scarcity-adversity dams while away from pups

To assess patterns of VTA DA neuron activity while the dam was in the nest (In Nest, No Nursing), in nest and nursing (In Nest, Nursing) or not engaged with her pups (Out of Nest), we measured the peak $\Delta F/F$ and frequency of peaks during these behavioral windows (CON: n=9, ADV: n=8; **Figure 6A**). We did not find between-group differences in peak $\Delta F/F$ while in nest ($U=20$, $p=0.14$; **Figure 6B**), nursing ($t_{9.36}=0.25$, $p=0.81$; **Figure 6C**), or while out of nest ($t_{13.95}=1.20$, $p=0.25$; **Figure 6D**). Similarly, there were no between-group differences in spontaneous VTA DA frequency of peaks while dams were in the nest ($t_{14.65}=0.57$, $p=0.58$; **Figure 6E**) or during nursing ($t_{13}=1.01$, $p=0.33$; **Figure 6F**). However, scarcity-adversity dams exhibited significantly lower spontaneous VTA DA neuron activity (i.e., frequency of peaks) while out of the nest ($t_{13.40}=2.92$, $p=0.01^*$, $\eta^2=0.39$; **Figure 6G**) compared to control dams. For complete statistics including means and SEM, please see **Table S5. Figure 6 Statistics**.

To address whether differences in Out of Nest behaviors could explain the reduced frequency of peaks in scarcity-adversity dams compared to control dams (**Figure 6G**), we compared behaviors exhibited while dams were away from pups. Although we found an increase in the percentage of time scarcity-adversity dams spent self-grooming (CON: n=9, ADV: n=8, $t_{13.76}=2.65$, $p=0.02^*$, $\eta^2=0.34$; **Figure S1A**), there were no between-group differences in the percentage of time dams spent chewing bedding ($U=33$, $p=0.79$; **Figure S1B**), chasing/biting their tail ($U=22.50$, $p=0.08$; **Figure S1C**), exploring ($t_{12.40}=0.39$, $p=0.70$; **Figure S1D**), wall climbing ($t_{11.49}=1.31$, $p=0.21$; **Figure S1E**), or nest building ($U=20.50$, $p=0.19$; **Figure S1F**). Despite the increase in percentage of time spent self-grooming in scarcity-adversity dams, they still exhibited fewer peaks/second while out of the nest compared to control dams, suggesting that the between-group difference in **Figure 6G** is not attributable to differences in Out of Nest behavior. To further contextualize the between-group difference in Out of Nest frequency of peaks, we examined within-group patterns of VTA DA neuron activity across pup proximity states in control and scarcity-adversity dams separately (CON: n=9, ADV: n=7; **Figure S1G**). Within-group examination of VTA DA neuron activity across pup proximity states revealed that neither control ($t_{14.37}=1.92$, $p=0.07$) nor scarcity-adversity dams ($t_{12.99}=0.60$, $p=0.56$) displayed differences in peak frequency while In Nest (No Nursing) compared to Out of Nest (**Figure S1H**). However, control dams exhibited elevated frequency of peaks during pup separation (Out of Nest) relative to In Nest (Nursing) ($t_{15.74}=3.29$, $p=0.005^{**}$, $\eta^2=0.41$) but scarcity-adversity dams did not ($t_{10.91}=2.00$, $p=0.07$; **Figure S1I**). Scarcity-adversity dams had significantly lower frequency of peaks while In Nest (Nursing) compared to In Nest (No Nursing) ($t_{11.95}=2.49$, $p=0.03^*$, $\eta^2=0.34$), whereas control dams did not ($t_{15.28}=1.81$, $p=0.09$; **Figure S1J**).

VTA DA neuron activity is similar in control and scarcity-adversity dams during food pellet retrieval

To assess the specificity of adversity-induced effects on VTA DA neuron activity, control and scarcity-adversity dams underwent a food reward retrieval task immediately following each maternal behavior observation session on PD 2-5, enabling direct comparison of VTA DA neuron responses to socially rewarding (pups) and non-socially rewarding (food) stimuli in the same animal. Group-averaged peri-event VTA DA neuron activity during food reward retrieval is displayed for control and scarcity-adversity dams, aligned so the highest peak occurring within 5 seconds before and after the event are centered (CON: n=9, ADV: n=8; **Figure 7A**). Likewise, heatmaps of VTA DA neuron activity during food reward retrieval are shown for individual control and scarcity-adversity dams (each numbered line corresponds to one animal, **Figure 7B**). There were no between-group differences in peri-event AUC ($t_{14.77}=0.76$, $p=0.46$; **Figure 7C**) or after-

event AUC ($t_{14,48}=0.49$, $p=0.63$; **Figure 7D**). Two-way ANOVA revealed a main effect of time on $\Delta F/F$ after food reward retrieval, as both control and scarcity-adversity dams exhibited elevated $\Delta F/F$ peaks following reward retrieval ($F_{(1,15)}=1499$, $p<0.0001^{****}$, $\eta^2_p=0.98$; **Figure 7E**), but no main effect of condition ($F_{(1,15)}=0.006$, $p=0.94$) or an interaction between time and condition ($F_{(1,15)}=0.35$, $p=0.56$). The lack of between-group differences in VTA DA neuron activity during food reward retrieval suggests that while scarcity-adversity altered VTA DA neuron activity associated with insensitive care, this perturbation may be specific to stepping, dragging, and/or shoving pups and was not generalized to other rewarding stimuli. For reference, we have included example traces of VTA DA neuron activity during a single bout of reward retrieval in a control and scarcity-adversity dam (**Figure 7F**). For complete statistics including means and SEM, please see **Table S6. Figure 7 Statistics**.

Discussion

This study characterized VTA DA neuron population dynamics during naturalistic maternal behavior in postpartum rat dams exposed to control or scarcity-adversity conditions. Contrary to our hypothesis, postpartum scarcity-adversity did not significantly reduce VTA DA neuron population activity during sensitive caregiving. Instead, we identified two distinct effects: elevated peri-event VTA DA population activity (i.e., AUC) during insensitive caregiving and reduced VTA DA neuron activity (i.e., frequency of peaks) while out of the nest. VTA DA neuron responses to food reward were unaffected in the same animals on the same recording days, suggesting that these effects are specific to maternal caregiving contexts rather than reflect a general feature of VTA DA neuron function during the early postpartum period.

Our hypothesis that scarcity-adversity would reduce VTA DA neuron activity during sensitive caregiving was not supported. Peri-event AUC, after-event AUC and peak $\Delta F/F$ during sensitive care were comparable between groups, indicating that VTA DA neuron population responses to licking/grooming, anogenital licking, and nursing are preserved under conditions of postpartum scarcity-adversity. Notably, both groups exhibited robust main effects of time on peak $\Delta F/F$ following sensitive care events, confirming adequate signal quality across conditions. These findings are consistent with published evidence of increased VTA DA neuron signaling during pup-directed maternal behavior (Fang et al., 2018; Xie et al., 2023) and suggest that scarcity-adversity does not globally blunt VTA DA neuron responses to pup contact. The null result during sensitive care is informative, as it focuses the adversity-induced effect specifically on insensitive caregiving interactions rather than pup-directed behavior broadly. These null effects remained stable when comparing the first (PD 2-3) and second (PD 4-5) halves of the exposure period, indicating that the absence of scarcity-adversity effects on VTA DA neuron activity during sensitive care are not attributable to insufficient exposure time and do not emerge or resolve over the course of scarcity-adversity exposure.

Scarcity-adversity dams exhibited significantly elevated peri-event AUC around insensitive caregiving events, while after-event AUC and peak $\Delta F/F$ did not differ between groups. This selective elevation in peri-event AUC without a corresponding change in after-event AUC or peak $\Delta F/F$ localizes the effect to the period immediately preceding and coinciding with insensitive pup-directed behavioral events, reflecting a prolonged rather than amplified VTA DA population response. Notably, this elevation in peri-event AUC was specifically driven by activity during the second half of the exposure period (PD 4-5), as no between-group difference was

found during the first half (PD 2-3), suggesting that this adversity-induced alteration may reflect cumulative adaptation to repeated scarcity-adversity exposure rather than a rapid-onset response. The absence of group differences in peak $\Delta F/F$ suggests that scarcity-adversity dams are not recruiting more DA neurons simultaneously, but that the population recruited remains active longer around insensitive pup-directed behavioral events. This pattern may reflect greater effort or uncertainty costs associated with caregiving interactions that are not resolving typically, consistent with proposed roles for VTA DA signaling in motivational vigor (Salamone and Correa, 2012; Hamid et al., 2016). Future work examining neuromodulatory contributions including oxytocin, which interacts with mesolimbic DA circuitry during maternal behavior (Pedersen et al., 1994; Shahrokh et al., 2010; Love, 2014; Olazabal, 2018), may help clarify the mechanisms underlying this finding in scarcity-adversity dams.

Scarcity-adversity dams exhibited a significantly lower frequency of peaks while out of the nest compared to control dams, while no between-group differences were observed while dams were in the nest or during nursing. Within-group comparisons revealed that control dams exhibited a significantly higher frequency of peaks while out of the nest compared to during nursing, an elevation that was not observed in scarcity-adversity dams. Scarcity-adversity dams also displayed a significantly lower frequency of peaks while nursing compared to in the nest without nursing, a within-group difference not observed in control dams. While the primary group difference in frequency of peaks was specific to the out of nest state, these within-group patterns suggest that scarcity-adversity may more broadly alter how spontaneous VTA DA neuron activity tracks pup proximity. The elevated frequency of peaks in control dams during pup separation relative to nursing may reflect VTA DA neuron responses to distal pup-associated sensory cues, consistent with prior evidence showing that pup cues alone evoke mesolimbic DA responses in postpartum dams even in the absence of direct pup contact (Afonso et al., 2013; Olazabal et al., 2013). These findings extend our prior electrophysiological finding of attenuated baseline VTA DA neuron population activity in scarcity-adversity dams (Rincón-Cortés and Grace, 2022b) by demonstrating that this suppression is present in awake-behaving dams and is specifically expressed during pup separation. This blunted pattern in scarcity-adversity dams may reflect reduced motivational drive associated with pup separation and a diminished response to distal pup-associated sensory cues, consistent with published deficits in pup-directed maternal motivation in scarcity-adversity dams (Rincón-Cortés and Grace, 2022b; Rincón-Cortés, 2024; Jackson et al., 2026).

No between-group differences were observed in VTA DA neuron population responses to food reward retrieval across any measure, and both groups exhibited robust main effects of time on peak $\Delta F/F$ following retrieval, confirming that VTA DA neurons in scarcity-adversity dams generate normal event-locked responses to non-social rewarding stimuli. Scarcity-adversity dams displayed these responses on the same recording days as the maternal behavior observations, ruling out a generalized postpartum deficit in VTA DA responsiveness as an explanation for the observed caregiving effects. This interpretation is further supported by two considerations regarding the sensitivity of our food reward task. First, the robust, highly significant increase in peak $\Delta F/F$ following food reward retrieval in both groups indicates that the task reliably evoked strong, time-locked phasic VTA DA responses, arguing against a floor effect that might otherwise obscure a group difference. Second, food is a highly salient reward during the postpartum period, with lactating rodents exhibiting enhanced food-seeking behavior and heightened VTA-NAc DA signaling during feeding that is causally required for increased food intake and motivation in this state (Pattnaik et al., 2026). Together, these findings suggest that postpartum scarcity-adversity

selectively reshapes VTA DA neuron population dynamics depending on caregiving quality and pup proximity without broadly disrupting DA-mediated reward processing. This is consistent with clinical and preclinical observations that postpartum adversity can impair caregiving responsiveness without producing global anhedonia (Brummelte and Galea, 2016; Post and Leuner, 2019).

The present findings should be considered in light of several limitations. First, fiber photometry measures bulk fluorescence from a population of GCaMP7f-expressing VTA DA neurons and cannot resolve the contributions of specific downstream projection targets. VTA DA neurons project to distinct forebrain and limbic regions including the medial prefrontal cortex, the NAc core and shell, and the basolateral amygdala, all of which can serve dissociable functions in maternal motivation and reward processing (Mattson and Morrell, 2005; Martel et al., 2008; Pereira and Morrell, 2011, 2020; Rincón-Cortés and Grace, 2020; Navarro-Moreno et al., 2022; Day and Shea, 2025). The relative contributions of these projections to the caregiving effects observed here remain unknown. Second, viral expression in this study spanned a broad rostrocaudal extent of the VTA. Prior work has identified the anterior VTA as a site of Fos activation induced by pup-interaction, although this activation was not specific to dopaminergic cells (Caba et al., 2019), suggesting that VTA subregional and cell-type heterogeneity in responsiveness to infant cues remains incompletely understood. Given this and other evidence indicating anatomical and functional heterogeneity within the VTA (Walsh and Han, 2014; Morales and Margolis, 2017), subregional differences in our viral spread could influence interpretation of our current findings. Future work incorporating subregion-specific targeting will be needed to determine whether the effects reported here are uniform across VTA or driven by a specific anterior-posterior subpopulation. Finally, whether the reduced frequency of peaks observed during pup separation in scarcity-adversity dams reflects a broader impairment in VTA DA responses during pup-directed motivated approach, or is specific to the spontaneous activity measured here, remains an important open question. Future projection-specific approaches using pathway-selective photometry or optogenetics will be necessary to identify which VTA DA circuits mediate adversity-induced alterations in caregiving quality and pup separation responses, and whether targeted manipulation of these circuits can rescue deficits in maternal motivation. We also considered whether a lower spontaneous baseline rate in scarcity-adversity dams could exaggerate event-induced activity by creating a larger signal differential. However, peak $\Delta F/F$ following behavioral events did not differ between groups during sensitive or insensitive pup-directed behaviors, arguing against this possibility. Additionally, because fiber photometry measures of population calcium activity, such as frequency of peaks, cannot directly establish whether observed changes reflect altered DA release, future work incorporating DA sensors (e.g., dLight, GRAB-DA) alongside calcium imaging will be important for linking population-level activity patterns to downstream neurotransmitter release and provide important insights into the functional consequences of adversity-induced alterations in VTA DA neuron dynamics.

Taken together, these results provide a neurobiological framework for understanding how adverse postpartum environments selectively disrupt the motivational architecture of maternal caregiving. Identifying the precise circuit mechanisms by which postpartum adversity reshapes VTA DA dynamics during mother-infant interactions may ultimately reveal tractable targets for interventions aimed at improving caregiving quality in postpartum mood disorders.

594 **Conflict of Interest**

595 The authors have no conflict of interest to disclose.

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749 Figure Legends

750 **Fig. 1. Postpartum scarcity-adversity induces alterations in both sensitive and insensitive**
 751 **pup-directed maternal behaviors from PD 2-5.** A) Timeline and experimental design. B) VTA
 752 fiber optic placement and Cre-dependent GCaMP7f virus expression. C) Scarcity-adversity
 753 reduced percentage of time spent on pup licking/grooming (t-test, $p=0.02$) but not D) anogenital
 754 licking of pups (Mann-Whitney, $p=0.13$). E) Scarcity-adversity reduced percentage of time spent
 755 nursing (t-test, $p=0.04$). F) Total number of sensitive care occurrences was reduced in scarcity-
 756 adversity dams (t-test, $p=0.0097$). G) Scarcity-adversity increased the percentage of time spent
 757 stepping on pups (t-test, $p=0.0006$), but not the percentage of time spent H) dragging (Mann-
 758 Whitney, $p=0.07$) or I) shoving pups (Mann-Whitney, $p=0.99$). J) Total number of insensitive care
 759 occurrences was increased in scarcity-adversity dams (t-test, $p=0.04$). K) Example fiber
 760 photometry traces of sensitive (licking) and insensitive (stepping) maternal care in a control
 761 animal. Control (CON) group depicted by black circles, scarcity-adversity (ADV) group depicted
 762 by colored triangles. Error bars represent mean $\pm$ SEM. $n=8-9$ rats per group. * $p<0.05$, ** $p<0.01$
 763 *** $p<0.005$

764 **Fig. 2. No effect of postpartum scarcity-adversity on VTA DA neuron responses around**
 765 **sensitive pup-directed behaviors.** A) Average fiber photometry $\Delta F/F$ of sensitive care bouts
 766 (i.e., licking, grooming, anogenital licking) in control and scarcity-adversity dams. Individual traces
 767 are offset by up to 5 seconds so that each animal's peak $\Delta F/F$ response is aligned prior to
 768 averaging; the x-axis therefore reflects time relative to each animal's aligned peak rather than
 769 strict event onset. B) GCaMP7f heatmaps. C) No effect of scarcity-adversity on AUC around the
 770 entire event window (5 seconds before to 10 seconds after; t-test, $p=0.51$). D) No effect of
 771 scarcity-adversity on AUC after the event (start of event to 10 seconds after; t-test, $p=0.42$). E)
 772 Average $\Delta F/F$ before the event (5 seconds before to start of the event) compared to the peak
 773 $\Delta F/F$ after the event (start of event to 10 seconds after) was increased in both control and
 774 scarcity-adversity dams (two-way ANOVA, main effect of time, $p<0.0001$). F) Example sensitive
 775 care (licking) fiber photometry $\Delta F/F$ in a control and scarcity-adversity animal. CON group
 776 depicted by black circles, ADV group depicted by colored triangles. Error bars represent mean $\pm$
 777 SEM. $n=8-9$ rats per group. **** $p<0.0001$

778 **Fig. 3. VTA DA neuron responses around sensitive pup-directed maternal behaviors did**
 779 **not differ in PD 2-3 vs PD 4-5.** A) Average of PD 2-3 and PD 4-5 traces of VTA DA neuron
 780 responses during sensitive caregiving in control dams. B-C) Heatmap of VTA DA neuron
 781 responses during sensitive pup-directed behaviors on B) PD 2-3 and C) PD 4-5 in control dams.
 782 D) Average of PD 2-3 and PD 4-5 traces of VTA DA neuron responses during sensitive caregiving
 783 in adversity dams. E-F) Heatmap of VTA DA neuron responses during sensitive pup-directed
 784 behaviors on E) PD 2-3 and F) PD 4-5 in adversity dams. G) Peri-event AUC during sensitive
 785 care did not differ between PD 2-3 and PD 4-5 in control (Mann-Whitney, $p=0.68$) or adversity
 786 dams (t-test, $p=0.67$). Peri-event AUC did not differ between control and adversity dams during
 787 PD 2-3 (t-test, $p=0.85$) or PD 4-5 (Mann-Whitney, $p=0.88$). H) After-event AUC did not differ
 788 between PD 2-3 and PD 4-5 in control (t-test, $p=0.30$) or adversity (t-test, $p=0.15$) dams. After-
 789 event AUC did not differ between control and adversity dams during PD 2-3 (t-test, $p=0.42$) or PD
 790 4-5 (t-test, $p=0.80$). I) Mixed model of $\Delta F/F$ before and after the event during PD 2-3 and PD 4-
 791 5 recording in control and adversity dams (i.e., stage and time). Only a main effect of time was
 792 found for $\Delta F/F$ before and after the event ($F_{(1.27, 21.23)}=320.7$, $p<0.0001$). CON group depicted by

black circles, ADV group depicted by colored triangles. Error bars represent mean $\pm$ SEM. n=5-9 rats per group. **** p<0.0001

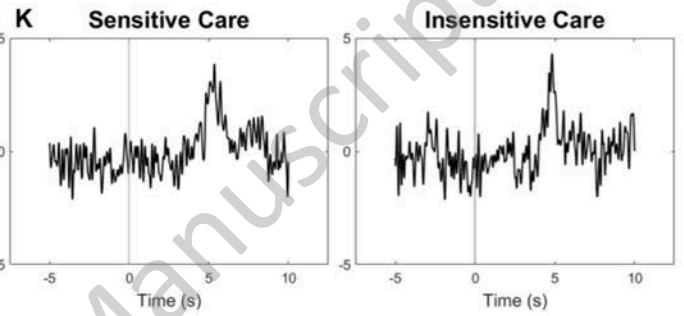
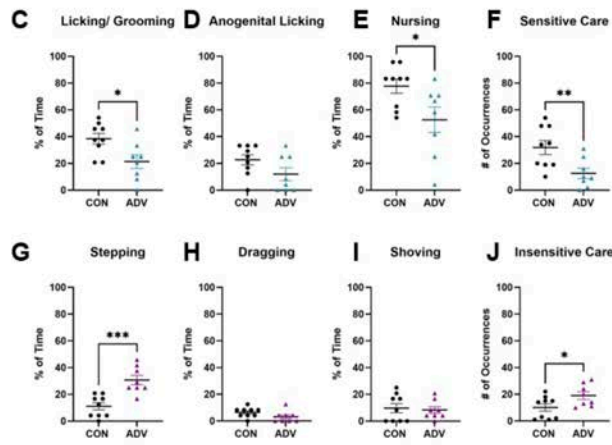
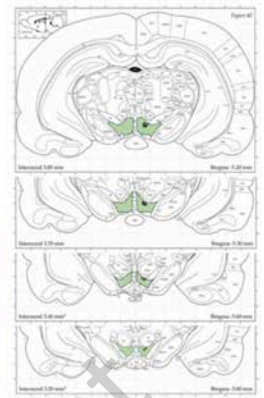
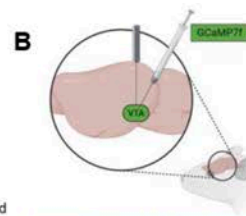
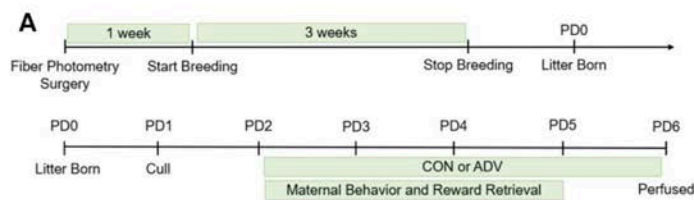
Fig. 4. Postpartum scarcity-adversity alters VTA DA neuron responses around insensitive pup-directed behaviors. A) Average fiber photometry $\Delta F/F$ of insensitive care bouts (i.e., stepping, dragging, and shoving pups) in control and scarcity-adversity animals. Individual traces are offset by up to 5 seconds so that each animal's peak $\Delta F/F$ response is aligned prior to averaging; the x-axis therefore reflects time relative to each animal's aligned peak rather than strict event onset. B) GCaMP7f heatmaps. C) AUC around the entire event window (5 seconds before to 10 seconds after) was increased in scarcity-adversity dams (t-test, p=0.03). D) No effect of scarcity-adversity on AUC after the event (start of event to 10 seconds after; t-test, p=0.70). E) Average $\Delta F/F$ before the event (5 seconds before to start of the event) compared to the peak $\Delta F/F$ after the event (start of event to 10 seconds after) was increased in both control and scarcity-adversity dams (two-way ANOVA, main effect of time, p<0.0001). F) Example insensitive care (stepping) fiber photometry $\Delta F/F$ in a control and ADV animal. CON group depicted by black circles, ADV group depicted by colored triangles. Error bars represent mean $\pm$ SEM. n=7-9 rats per group. * p<0.05, **** p<0.0001

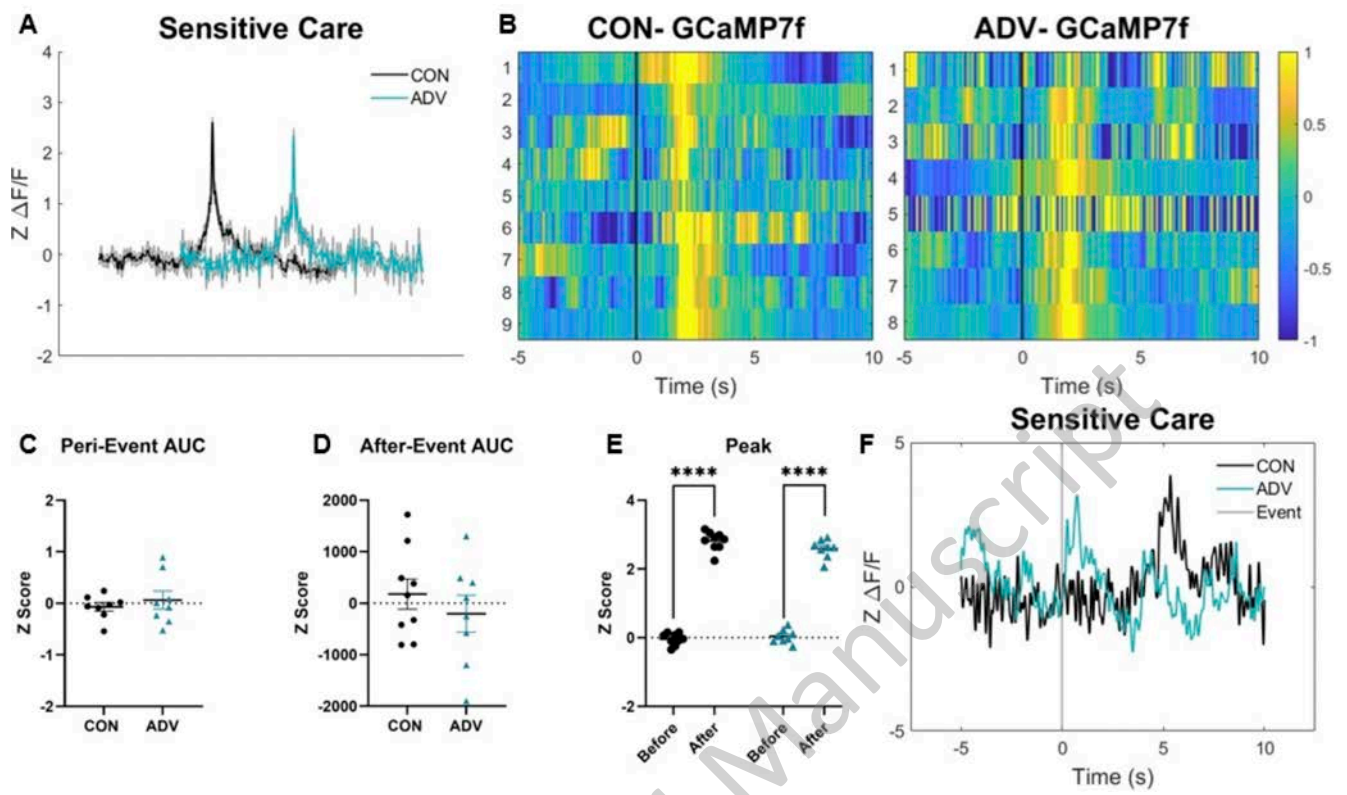
Fig. 5. VTA DA neuron responses around insensitive pup-directed maternal behaviors differ in PD 2-3 vs PD 4-5. A) Average of PD 2-3 and PD 4-5 traces of VTA DA neuron responses during insensitive caregiving in control dams. B-C) Heatmap of VTA DA neuron responses during insensitive pup-directed behaviors on B) PD 2-3 and C) PD 4-5 in control dams. D) Average of PD 2-3 and PD 4-5 traces of VTA DA neuron responses during insensitive caregiving in adversity dams. E-F) Heatmap of VTA DA neuron responses during insensitive pup-directed behaviors on E) PD 2-3 and F) PD 4-5 in adversity dams. G) Peri-event AUC during insensitive pup-directed behaviors did not differ between PD 2-3 and PD 4-5 in control dams (t-test, p=0.26) but was significantly increased during PD 4-5 compared to PD 2-3 in adversity dams (t-test, p=0.03). Peri-event AUC did not differ between control and adversity dams during PD 2-3 (t-test, p=0.30) but was significantly increased in adversity dams compared to controls during PD 4-5 (t-test, p=0.003). H) After-event AUC did not differ between PD 2-3 and PD 4-5 in control (Mann-Whitney, p=0.08) or adversity (t-test, p=0.45) dams. After-event AUC did not differ between control and adversity dams during PD 2-3 (Mann-Whitney, p=0.09) or PD 4-5 (t-test, p=0.17). I) Mixed model of $\Delta F/F$ before and after the event during PD 2-3 and PD 4-5 recording in control and adversity dams (i.e., stage and time) revealed only a main effect of time on $\Delta F/F$ before and after the event ($F_{(1.75, 26.86)}=117.8$, p<0.0001). CON group depicted by black circles, ADV group depicted by colored triangles. Error bars represent mean $\pm$ SEM. n=6-9 rats per group. *p<0.05, **p<0.01, **** p<0.0001

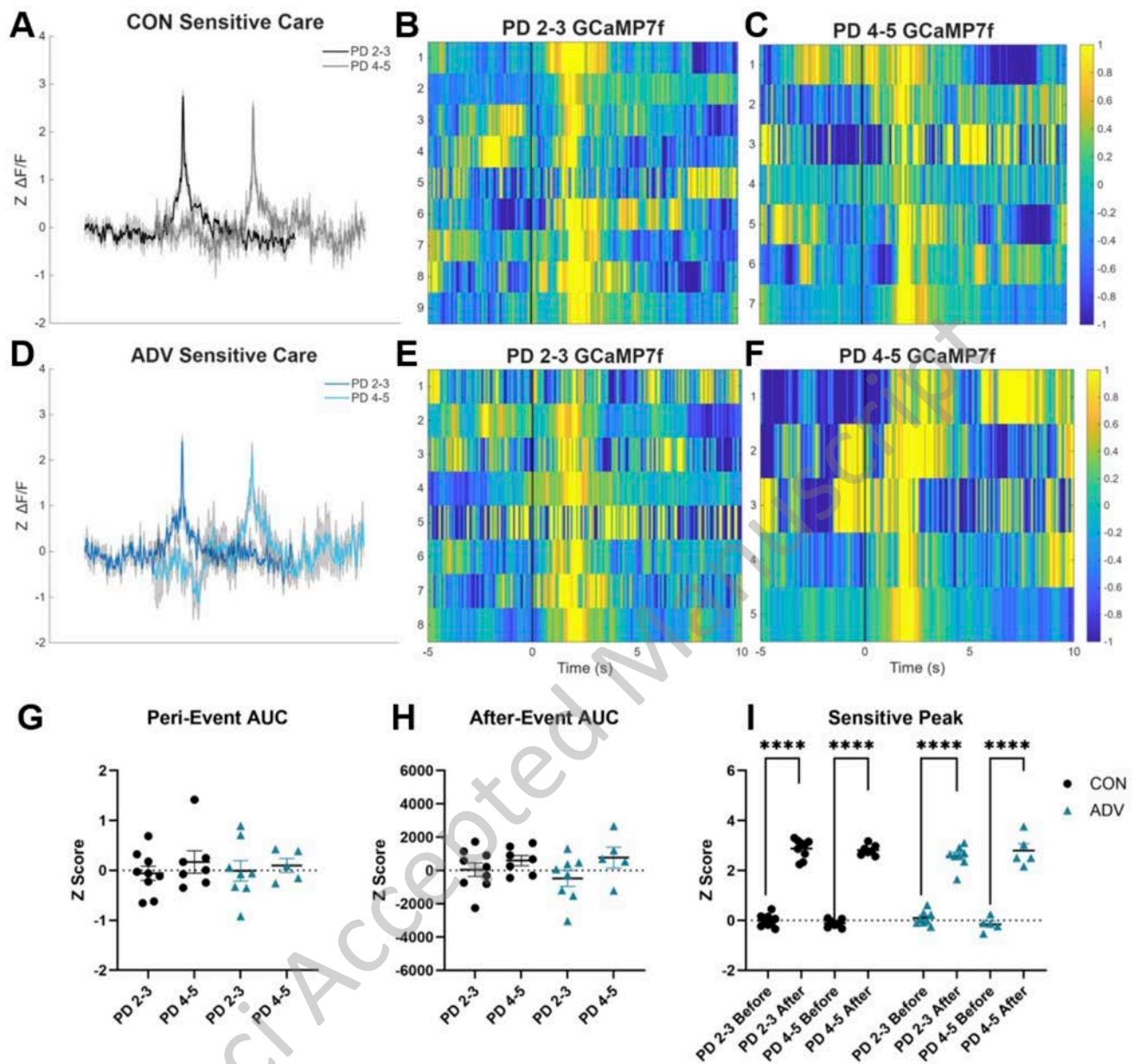
Fig. 6. VTA DA neuron activity is reduced in scarcity-adversity dams while away from pups. A) Behavioral states analyzed included In Nest (No Nursing), In Nest (Nursing), and Out of Nest. B) No effect of scarcity-adversity on peak $\Delta F/F$ while In Nest (No Nursing) (Mann-Whitney, p=0.14). C) No effect of scarcity-adversity on peak $\Delta F/F$ while In Nest (Nursing) (t-test, p=0.81). D) No effect of scarcity-adversity on peak $\Delta F/F$ while Out of Nest (t-test, p=0.25). E) No effect of scarcity-adversity on frequency of peaks per second while In Nest (No Nursing) (t-test, p=0.58). F) No effect of scarcity-adversity on frequency of peaks per second while In Nest (Nursing) (t-test, p=0.33). G) Scarcity-adversity dams displayed reduced frequency of peaks per second while Out of Nest (t-test, p=0.01). CON group depicted by black circles, ADV group depicted by colored triangles. Error bars represent mean $\pm$ SEM. n=7-9 rats per group. * p<0.05

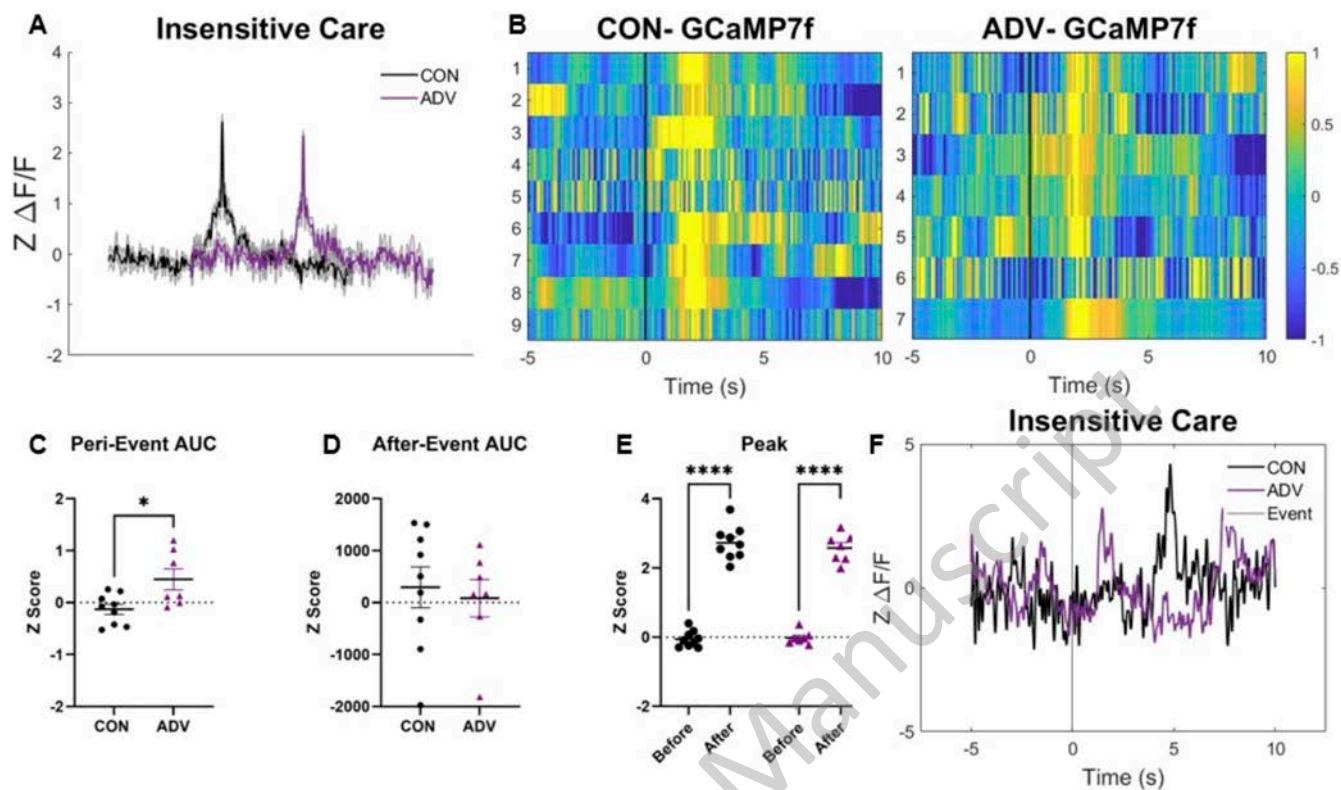
Fig. 7. No effect of postpartum scarcity-adversity on VTA DA neuron responses during food reward retrieval. A) Average fiber photometry $Z\Delta F/F$ of reward retrievals in control and scarcity-adversity animals. Individual traces are offset by up to 5 seconds so that each animal's peak $Z\Delta F/F$ response is aligned prior to averaging; the x-axis therefore reflects time relative to each animal's aligned peak rather than strict event onset. B) GCaMP7f heatmaps. C) No effect of scarcity-adversity on AUC around the entire event window (5 seconds before to 10 seconds after; t-test, $p=0.46$). D) No effect of scarcity-adversity on AUC after the event (start of event to 10 seconds after; t-test, $p=0.63$). E) Average $Z\Delta F/F$ before the event (5 seconds before to start of the event) compared to the peak $Z\Delta F/F$ after the event (start of event to 10 seconds after) was increased in both control and scarcity-adversity dams (two-way ANOVA, main effect of time, $p<0.0001$). F) Example reward retrieval fiber photometry $Z\Delta F/F$ in a control and ADV animal. CON group depicted by black circles, ADV group depicted by colored triangles. Error bars represent mean $\pm$ SEM. $n=8-9$ rats per group. **** $p<0.0001$

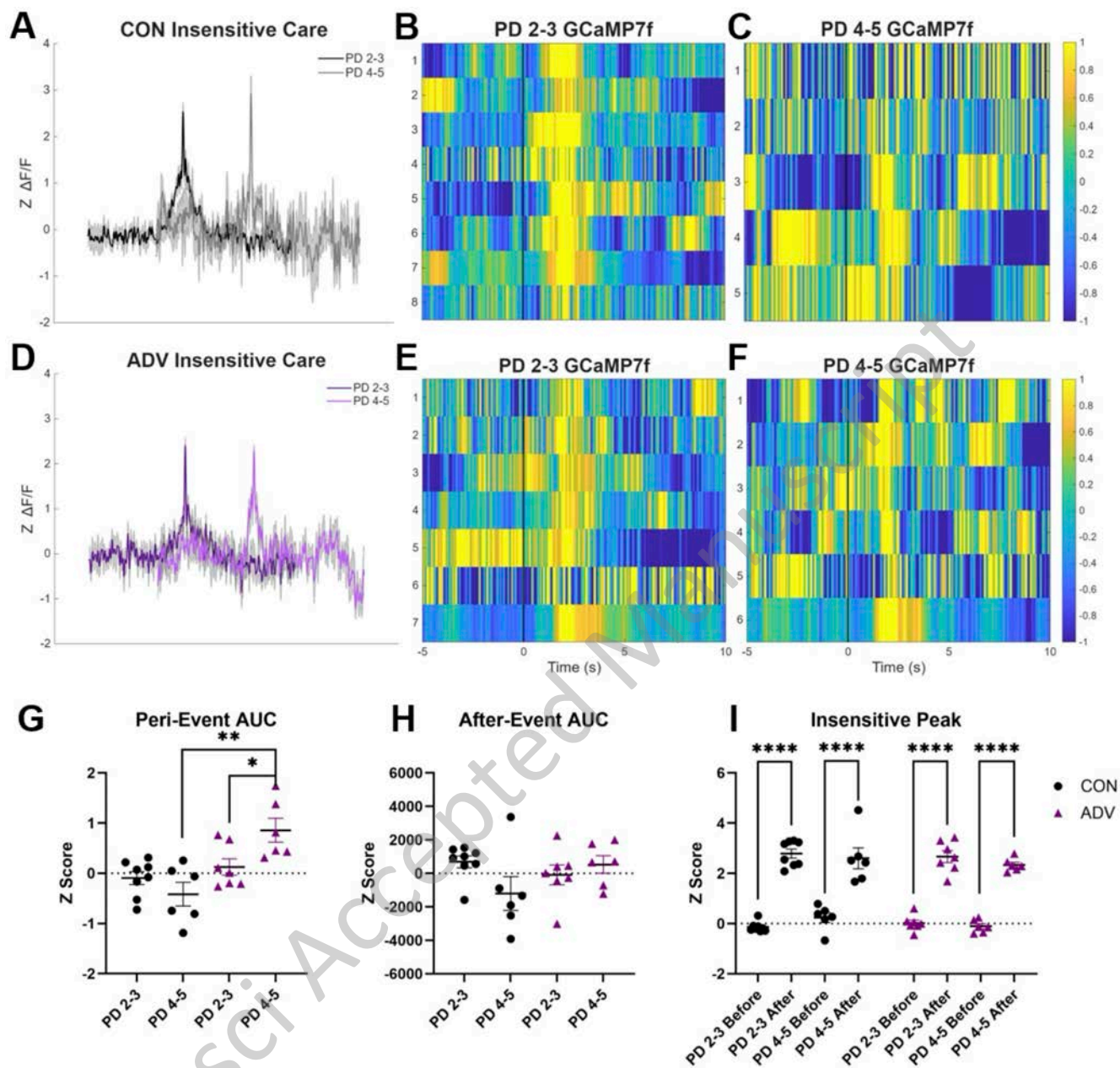
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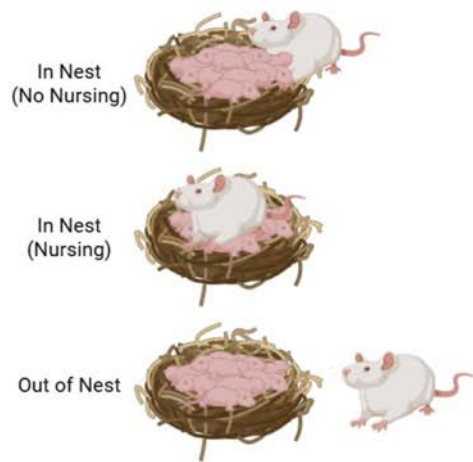
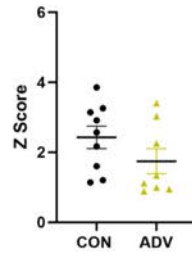
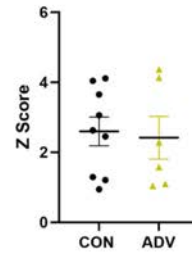
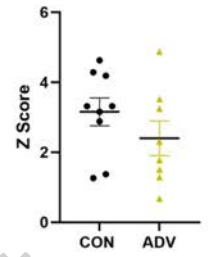
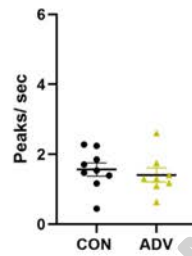
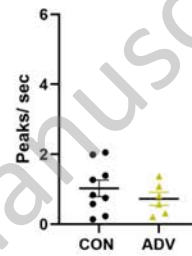










A**B** In Nest (No Nursing) Peak**C** In Nest (Nursing) Peak**D** Out of Nest Peak**E** In Nest (No Nursing) Frequency of Peaks**F** In Nest (Nursing) Frequency of Peaks**G** Out of Nest Frequency of Peaks