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哺乳动物母性行为影响因素

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摘要:新生幼仔通常非常脆弱,需要亲代抚育才能成活,哺乳动物的亲代抚育主要由雌性完成。雌性在分娩前后所展现出的寻找分娩地点、筑造产房、分娩、舔仔、授乳、护仔等一系列动作称为母性行为,其对家养及野生动物幼仔的成活和发育均至关重要。母性行为受遗传、管理等因素影响,环境中残留的各类新型污染物也给正常母性行为的激发和维持带来了新挑战。此外,虽然母性行为是评判优良个体的重要参考,但由于母性行为性状遗传力低,这使得仅从遗传角度很难做出科学评价,而应结合行为表观遗传学综合分析上述因素对母性行为的整体影响。综述了遗传、营养、环境、管理以及疾病等因素对哺乳动物母性行为的影响,并重点指出塑化剂、重金属等残留在环境中的内分泌干扰物,以及电磁污染、光污染等是母性行为异常的新诱因。此外,还对动物生产及野生动物保护工作中如何在遗传学基础上,综合优化营养、环境、管理等措施来改善和培育优良母性行为性状提出了展望。可为下一步深入探究哺乳动物母性行为影响因素及调控机制提供参考,并为预防和改善动物母性行为异常以及提高动物母性照料能力提供依据,同时,还能为探索生态健康养殖、提高母幼福利提供一定的参考。

关键词:哺乳动物;母性行为;影响因素;研究进展;新诱因

Factors influencing maternal behavior in mammals

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Abstract: In mammals, newborn puppies are usually very delicate and their survival depends heavily on parental care. Parental care is primarily provided by the female mammal, who was found to exhibit a series of behaviors before and after giving birth, including searching for a suitable birthing site, constructing a birth chamber, giving birth, grooming, lactation, and nursing. These actions are referred to as maternal behaviors and are critical for the survival and development of newborns in both domesticated and wild animals. Previous studies by us and others have shown that maternal behavior is influenced by genetic and management factors. In addition, with the rapid development of industrialization and electrification in recent decades and changes in human lifestyles, the presence of various new types of pollutants in the environment poses new challenges for the elicitation and maintenance of normal maternal behavior. When disturbed by these undesirable factors, female animals often show abnormal maternal behavior such as not making nests, refusing to lactate, being reluctant to lick the cubs, unable to retrieve the cubs timely, attacking and cannibalizing newborns. Furthermore,

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while maternal behavior is an important criterion for assessing individuals, due to the low heritability of maternal behavioral traits, it is challenging to make an accurate scientific evaluation solely from a genetic perspective. Instead, when conducting maternal behavior assessment, the overall influence of management, environment, and other factors on maternal behavior should be analyzed in combination with behavioral epigenetics. Therefore, this paper systematically reviews the effects of genetics, nutrition level, environment status, daily management, and other factors such as disease on mammalian maternal behavior, and highlights endocrine disruptors such as plasticizers, heavy metals, and other residues in the environment, as well as electromagnetic and light pollution as new triggers of abnormal maternal behavior. What's more, the article also presents a new prospect on how to improve and breed excellent maternal behavioral traits in animal production and wildlife conservation based on genetics and integrated optimization of nutrition, environment, and management measures. The paper can provide a reference for the next in-depth investigation of the factors influencing and regulating mechanisms of mammalian maternal behavior, and provide a basis for the prevention and improvement of abnormal maternal behavior as well as the enhancement of maternal care of animals. At the same time, it can also provide a certain reference for the exploration of ecological and healthy breeding, and the improvement of the welfare of mothers and newborns.

Key Words: mammals; maternal behavior; influencing factors; research progress; new causative factors

动物幼仔在出生后通常比较脆弱,需要亲代抚育才能存活。对哺乳动物而言,亲代抚育通常由雌性个体提供,这与胚胎在雌性体内发育有关,相比父亲,母亲在控制后代出生地、出生时间等方面具有更高的自主权;此外,由于雌性个体进化出专门用于为幼仔提供营养物质的乳腺,这为其抚育后代提供了先天优势[1]。雌性的亲代抚育也被称为母性行为,主要包括选择分娩场所、建造和维护巢穴、分娩、舔仔、识仔、喂仔、护仔、教仔、亲仔等,是一种普遍存在于哺乳动物中的本能行为[2—3]。母性行为对后代的生存和发育具有重要的生物学意义,它可以提高幼仔的存活率、增强幼仔的免疫力、促进幼仔的神经发育、调节幼仔的应激反应等[4—5]。另外,母性行为对雌性动物自身的生理健康也十分重要,例如,羊水中含有多种激素,这些激素在母畜舔舐幼仔的过程中进入体内后,可改变母体的神经内分泌,从而促进母亲的子宫收缩、乳汁分泌、体重恢复等[6—7]。

母性行为的启动、执行和维持是在复杂的神经内分泌系统调控下实现的[7],通常雌性动物在幼仔出生后会自然地展现出强烈的母性行为。但一部分雌性对怀孕、分娩、哺乳等过程反应过度[8],产生明显的病理性母性应激,引发情绪障碍,干扰母性行为的表达,使其对幼仔的照料质量下降而干扰行为增加[9—10],这对后代的认知能力、情绪稳定性、应激反应等产生长期负面效应[11]。此外,遗传、营养、饲养管理、环境等因素也会影响母性行为的表达[12—15]。除了这些传统的影响因素外,环境中残留的重金属及塑化剂等内分泌干扰物、电磁辐射、光污染等可诱发母体的神经内分泌及物质代谢紊乱,进而干扰动物的母性行为[16—18]。

现代育种技术使部分家养动物窝产仔数显著增加[19],这对母畜哺育能力提出了更高的要求,而环境、管理等因素对动物母性行为影响的程度也会因此被放大。因此,系统性归纳、总结现代化生活、饲养模式下的母性行为影响因素显得十分必要。本文系统性综述了当下影响哺乳动物母性行为的常见因素,从遗传、营养、环境、饲养管理、疾病以及环境内分泌干扰物等新挑战方面分析了各因素对母性行为的影响程度、作用方式和可能的调控机制。在明确现有研究不足的基础上,本文对未来可开展的研究方向和方法提出建议和展望,以期为深入探究动物母性行为影响因素及调控机制提供参考,为预防和改善动物母性行为异常以及提高动物母性照料能力提供依据。

1 母性行为概述及其对幼仔存活的重要性

母性行为早期的研究可追溯到 20 世纪中叶[20—21],它是一系列旨在为后代提供良好的照料和保护的自发行为。以分娩为节点,哺乳动物的母性行为可分为产前母性行为和产后母性行为。在分娩前几天,猪、兔、狗、狼等筑巢动物会利用树叶、茅草等搭建产窝[19],为新生幼仔提供温暖、舒适的环境,这属于产前母性行为。此

外,产前母性行为还包括分娩地点的选择、维护产窝等。分娩后,母亲对幼仔的舔舐、授乳等照料行为称为产后母性行为,产后母性行为在分娩后一周内最为强烈,且随着幼仔长大而逐渐减弱。

产前和产后母性行为构成了哺乳动物母性行为的总体内容,对野生动物及家养动物后代的存活及环境适应均至关重要[3]。在野外环境,合理的分娩地点可以为幼仔提供安全的生长环境,降低其被捕食风险[22]。而对家养动物而言,由于受限于养殖环境,其在分娩地点和产窝搭建材料方面的选择较少,产窝通常由主人直接提供,甚至在猪等家畜集约化养殖场中,产窝会被简易的分栏产床代替,这限制了相关母性行为的表达[23]。另一方面,家养动物通常无需考虑捕食者风险,这也降低了其选择分娩地点和搭建产窝方面的积极性[24]。以上分析表明,与野生动物相比,家养动物的产前母性行为常处于抑制状态,这降低了其对幼仔存活和发育的影响力。而人为干预导致的这种差异并未完全体现在产后母性行为上,对于野生动物和家养动物而言,产后母性行为（尤其是产后最初几天内的母性行为）对其新生幼仔的成活均十分重要。

新生幼仔常因失温而死[25],为了存活,幼仔需要减少热量散失并获得热量供应,而这均高度依赖及时的母性照料。出生后,母亲及时的舔舐有助于幼仔体表快速干燥,这能减少体表散热量;母畜持续的呼唤、轻推等动作可以幼仔尽快站立并靠近或爬向母亲腹部,这能减少其身体躯干部位与地面的接触时间,降低热量散失,有助于幼仔保持身体核心温度,提高生存几率[26—28]。随后,母畜通过侧躺、下蹲等姿势暴露乳房并完成授乳[29],幼仔通过初乳既获得生存所必需的营养物质并产生足够热量以维持体温,又通过乳汁中的免疫球蛋白获得被动免疫,提高免疫力[30]。在帮助幼仔渡过生命中最脆弱的时期后,母畜还会继续通过乳汁为幼仔提供生存和发育所必须的营养物质,同时,通过母子互动等,母畜还可为幼仔提供识别事物及采食或捕食的经验、以及必要的社交技巧等,增加幼仔的求生技能,提高其成活率[12,31—32]。此外,对一些圈养动物和大部分野生动物而言,母畜的护仔行为可在一定程度抵御捕食者风险,减少幼仔的死亡[33—34]。以上分析表明,无论在野外还是家养环境下,动物的母性行为性状,特别是产后母性行为都是一项用来评估后代存活几率的重要指标,是野生动物保护和家养动物繁育过程中的关键参考内容之一[35—36]。

2　母性行为的影响因素

母性行为属于确保动物繁衍的基础性状之一,家养动物即使在被驯养上万年之久后,仍保持与野生品种相似的母性性状,且经过人工选育,部分家养动物的母性要强于它们的祖先[37—38]。但不同于窝产仔数等性状在人工选育后可成倍增加,母性性状通常难以通过人工选育实现跨越式提升,这是因为评价母性行为性状时,需要综合考虑做窝、舔舐、呼唤、哺乳、护仔、攻击等多项行为的综合指标,这些行为性状的收集通常需要花费很长时间,并且需要将这些母性行为与幼崽的成活率、生长速度等生产性状相结合,评价过程繁琐且难以形成一个标准、统一的评价体系,尤其是考虑到不同品种单一母性行为性状（例如攻击幼崽）之间的差异性[39]。此外,如图 1 所示,母性行为性状还受饲养环境、营养状况、饲养管理、塑化剂及重金属等环境内分泌干扰物、电磁辐射、光污染等多种因素干扰[12—15]。因此,在家养动物研究上,为了将母性行为性状同动物生产性状更有效的结合,需要综合考虑上述因素对各母性行为性状的整体影响,而对于野生动物而言,探究这些因素对母性行为的影响有助于濒危野生动物的繁育和保护。

2.1　遗传因素对母性行为的影响

母性行为是动物的一种本能行为,年幼时无须学习,分娩前后自然出现,并随着后代独立生活能力增强逐渐减弱,直至消失[3]。这一系列本能行为受下丘脑-垂体-卵巢（HPO）轴、下丘脑-垂体-肾上腺（HPA）轴等调控[40—41]。HPO 及 HPA 轴中关键基因通过调控多巴胺、孕酮、雌激素、催产素、催乳素等神经递质及内分泌的合成和分泌,激活和维持母性行为[7],很显然,遗传因素是母性行为调控的基础。但因为母性照料过程中包含授乳、护仔等多种不同类型的行为,而单一基因或者某一基因组合很难对所有母性行为均发挥正向调控作用,例如,催乳素可以促进泌乳,但会抑制母亲的攻击行为[42],而适当的攻击行为是母亲的护仔行为的基础;肾上腺素可以促进母性的护仔行为,但又会抑制泌乳,影响母亲的授乳[43]。因此,仅依靠母性相关基因高

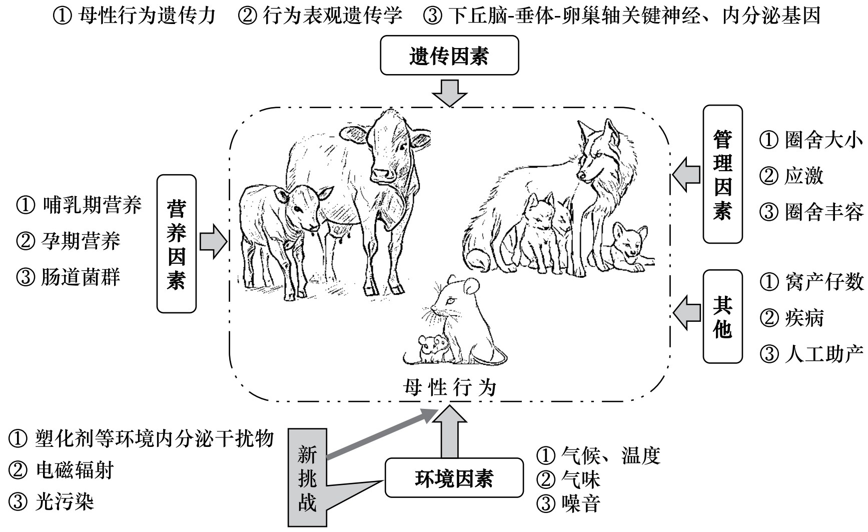

图 1 影响哺乳动物母性行为的因素

Fig.1 The factors that influence the maternal behavior of mammals

表达等基因型特征很难筛选出母性优良个体。并且,研究表明母性行为的遗传力较低,Gäde 等估测猪的母性行为的遗传力仅为 0.05—0.08[44—45],肉牛的母性遗传力为 0.11—0.13[46],绵羊为 0.09[47]。当然,由于母性遗传力研究的复杂性以及缺乏统一的标准,不同研究中母性遗传力存在明显差异,例如两项评估法国本土牛母性遗传力的研究中所记录的母性遗传力分别为 0.36 和 0.02[48—49]。

除了评估标准外,母性遗传力的差异还可能与品种有关,研究表明挪威和芬兰长白猪母性遗传力存在明显区别,母猪对仔猪尖叫反应的遗传力分别为 0.16 和 0.12[50];金色阿奎丹牛和利木赞牛的母性遗传力分别为 0.135 和 0.108[46]。不同品种间遗传力的差异可为生产中选择合适的品种选育策略提供参考,例如,对于母性遗传力高的物种或品种,可以尝试将母性优良的个体进行扩繁,从而实现群体母性性状的改良;而对于母性遗传力低的物种和品种,则可尝试通过杂交的方式提高母性性状。值得注意的是,以上选育策略的前提是筛选出母性优良个体,研究表明和母性性状遗传力一样,不同品种间母性行为表现也存在明显差异[51],约克夏母猪的母性行为表现明显优于长白母猪[45],而杜洛克母猪的表现则不如长白猪[52]。此外中国本土东北民猪的母性表现也要优于长白猪等国外引入品种并可通将民猪与引入品种杂交实现长白猪、大白猪母性的改良[53—54]。值得注意的是,即使同一品种,由于选育形成不同品系后,母性行为也可能存在明显差异,苏格兰黑脸绵羊胴体瘦肉率较高的品系产后开始舔舐羔羊的速度明显高于瘦肉率较低的品系,并且低瘦肉率品系会更频繁地离开羔羊[55]。当然鉴于母性行为遗传力总体较低的事实,若要实现种群母性改良,在充分发挥这些母性优良个体的遗传优势外,更多地还需借助饲养管理、营养及环境等策略的优化,这些因素虽不会改变遗传物质,但其可通过表观遗传修饰的方式影响母性行为。

表观遗传修饰是行为遗传学研究的重要组成部分[56],研究表明母性行为在雌性后代中传递与下丘脑雌激素受体的差异甲基化修饰有关[57]。此外,经产母畜的授乳、舔舐幼崽等母性行为明显优于初产个体[14,58],这说明分娩和育幼经历提高了母性行为表现。值得注意的是,这种改善不涉及个体遗传物质的改变,而是通过 DNA 甲基化、翻译后组蛋白修饰、非编码 RNA 活性等表观遗传修饰实现的,这种改变过程也被称为行为表观遗传学[59]。母性行为的这种表观遗传修饰调控方式,可以使母畜快速的响应内外环境的变化,使母体更容易的根据环境变化等及时地控制母性行为的激活、维持或抑制状态,增加母性行为的可塑性,提高了动物生存和繁衍的能力[5,60]。同时也需要认识到,表观遗传机制也是部分个体母性差的形成原因,研究表明,受到低水平母性照料的幼仔比受到高水平照料的个体的催产素受体(OTR)基因的启动子区域 DNA 甲基化水平更高,导致母鼠成年后 OTR 基因表达减少,母性行为变差[61]。由于表观遗传修饰是可逆的,那么,有理由相信由于

环境、营养等因素导致的母性不良可在后期通过提高动物福利等途径改善[62]。

除了从整体上探讨母性行为遗传机制外,寻找调控母性行为的关键基因也是母性研究领域的重点工作[63]。除了传统已知的 HPO 轴中催产素[64—65]、雌激素[66]、催乳素[67]、多巴胺[68]、γ-氨基丁酸[69]、5-羟色胺[70]、阿片肽[71]等关键神经内分泌基因,与表观修饰相关的组蛋白脱乙酰酶 HDAC[72]、与神经细胞间信号传导相关的酪氨酸激酶受体 RPTKs[73]、与胰岛素调节有关的胰岛素调节氨肽酶 IRAP[74]、与甲状腺激素调节有关的 3 型脱碘酶 Dio3[75]、与嗅觉信号传递相关的环核苷酸阳离子通道蛋白 α2 CNGA2[76]、与能量生成有关的 3 型腺苷酸环化酶 AC3[77]等均与母性行为的激活或维持有关。例如,敲除 AC3 基因可导致母性行为受损,母鼠对幼仔的照顾和保护减少,而攻击行为增加[77]。一项研究发现,给切除卵巢、接受雌激素治疗的母羊注射催产素后,可以激活其母性行为,母羊开始舔舐羔羊,并允许其吮乳[78]。值得注意的是,这些基因通常互相协调共同调控母性行为[79],并且常在大脑特定区域高表达,这些区域被认为是脑内调控母性行为的关键区域,特别是下丘脑内侧视前区(MPOA)[80]、终纹床核(BNSTpr)[81]、外侧隔核(LS)[69]以及中脑腹侧被盖区(VTA)[82]等。随着基因敲除、高通量测序、单核苷酸多态性(SNP)基因分型等技术的深入和优化,越来越多的母性相关基因将被揭示,这将为母性行为的遗传学研究提供最直接的材料[83]。基于此,在未来或许通过基因芯片技术便可以快速的评估某一个体的母性优劣,这可以大大提高母性优良种群的选育速度。

2.2 营养因素对母性行为的影响

母性照料虽然是母亲在分娩后的本能行为,但当自身基础营养需求无法满足时,母畜对幼仔的照料会变差,并表现出更多的攻击性,甚至可能引起杀幼、食仔现象[84]。当食物受限时,体重轻、体型瘦的仓鼠杀幼、食仔的比例明显多于更重、更胖的个体,这与后者能够更好地从储备的脂肪组织中获取能量供给有关。而当食物供给时,被允许囤积食物的个体的母性行为明显优于那些不能够囤积食物的个体[85]。营养不足的母羊对幼仔的照料减少,攻击性增强,营养不足的母鼠则在幼仔取回实验中效率明显下降并较少舔舐幼仔[86]。并且,当怀孕期间营养状况更好时,母羊较少动用体内脂肪,其所产的羔羊更快站立,这有助于母羊尽早完成哺乳,促进母性行为表达[87]。此外在饥饿状态时待产动物筑巢倾向明显减少甚至完全消失[88]。除了主要营养物质外,缺乏微量元素也会影响母性行为的表达,研究表明母亲缺铁可导致贫血并影响产后情绪和认知[89]。孕期营养不良导致母羊舔舐羔羊的时间明显减少,并且对羔羊更具攻击性,这除了可能与母羊能量储备不足有关外,还可能与孕期营养不足影响母羊 HPO 轴结构和功能有关。研究表明母鼠孕期缺乏硫胺素甚至会引起产后杀幼现象,这种攻击性增加可能与多巴胺神经元退化有关[90—91]。与营养不足相反,产羔前短期补充额外营养可改善母猪和母羊的母性行为,使其对后代的梳理更加频繁并更愿意授乳[92—93],孕期额外的营养补充同样会提高小鼠对幼仔的护理效果[94—95],这说明充足的营养供给有助于让母亲将更多的精力用于抚育后代。但要注意,孕期营养过剩容易导致代谢失衡,反而对母性行为产生负面影响[96]。此外,不能仅凭动物的胖瘦判定其是否营养不良,应结合营养指标检测等综合判断。

研究人员除了关注营养状况对成年雌性动物的直接影响外,还关注在胎儿期母体营养不足、过剩或失衡等对雌性后代成年后母性行为的跨代影响。母鼠高糖饮食导致雌性后代 N-甲基-D-天冬氨酸受体(NMDA)异常和认知障碍,对母性行为造成不利影响[97]。胎儿期微量元素缺乏的个体在成年后学习能力较差,对母性行为造成潜在干扰[98],研究表明胎儿期维生素 D 缺乏会影响母鼠在幼仔取回实验中的表现[99]。这是因为胎儿期是个体发育的关键时期,营养不足或过剩均会改变胎儿脑内的基因表达情况,进而影响其成年后的行为。

另外,为了更好的探究营养因素影响动物母性行为的机制,研究人员开始关注肠道菌群及脑-肠轴在其中发挥的作用。尽管目前将肠道菌群与母性行为直接关联的研究尚少,但已有研究将与母性行为密切相关的攻击行为同肠道微生物群落联系起来[100]。并且,益生菌已被证实可通过微生物菌落-肠-脑轴发挥抗焦虑和抗抑郁作用[101],这或许可以被用于治疗母亲的产后抑郁,改善动物的母性行为[102]。当然,肠道菌群在母性调控中的具体作用和机制尚需后续进一步探究。

2.3 环境因素对母性行为的影响

环境因素是影响母性行为的重要因素,主要指天气状况、温度、光照、噪音、气味等外界刺激[103—104]。这

些环境因素可以通过影响神经内分泌系统、营养代谢和表观遗传等机制来影响母性行为。此外,近年来越来越多的研究开始关注塑化剂及重金属等环境内分泌干扰物、电磁辐射、光污染等新型环境因素对动物母性行为的影响[16—18]。

气候的变化和季节的长短可以影响植物的生长期,这会影响野生和放牧食草动物的饲草品质和数量,造成其过冬的能量储备不足或营养不良,母畜在这种环境恶化的条件下通常会改变幼仔抚育策略,授乳总时长显著减少,授乳中断频率明显增加[103]。当处于低温环境下,母狒狒通过腹侧接触为幼仔保温的行为明显增加;而在高温环境下,母狒狒与幼崽接触的单次时长变短,但接触频率增加,这样有利于热量的散失[105]。当然,当因温度过高或过低引起母亲热应激或冷应激时,动物母性通常会变差,热应激时,牛的直肠温度、心率、血清皮质醇、热休克蛋白显著升高,严重干扰牛的日常行为[106]。怀孕期经历热或冷应激使母鼠对幼仔的攻击行为明显增多或情绪反应更激烈[107—108]。

除了温度的影响,光照长短也会影响动物的母性行为,将光照时间从 8 h 延长至 16 h 时,母猪的产奶量明显增多,仔猪吮乳也更频繁,成活率更高[109],而光照时间缩短时,母鼠对幼仔的主动照料频率明显变少[110]。噪音也是一种环境干扰,妊娠期时受到随机噪声刺激的母鼠在幼仔取回实验中效率明显变差[111],在噪音环境中母猪变得警觉,并导致更多的仔猪被压死,表明噪音可以影响动物的母性行为,这可能与噪音干扰母畜同幼仔间的声音交流有关[112—113]。但类似的研究也存在差异,Owen 等的研究发现马来熊在嘈杂的噪音环境中反而会花费更多的时间照顾幼仔[114],这种差异可能与观测的实验条件、动物的种类及噪音种类等不同有关。气味是环境中常见的另一个母性行为影响因素,母亲对幼仔的识别需要借助嗅觉,嗅觉神经破坏时会导致母羊母性行为缺陷[115—116],而当环境中存在异味时会干扰母亲对幼仔的识别,影响其母性护理[117]。当环境中存在捕食者气味时,田鼠对幼仔的关怀减少[118]。但也有研究指出分娩当天接触猫气味的小鼠在随后五天内表现出更高水平的母性照料,其对幼崽的护理和舔舐行为明显增加,同时它们会采用更多的蹲伏姿势以便更好的隐藏自己和保护幼仔[119—120]。这种差异与接触捕食者气味的时间段、剂量、动物物种等都有关。值得注意的是,由于哺乳动物的母性行为的激活和维持通常需要嗅觉、听觉、触觉等多种感官协同发挥作用[121],那么我们在分析现实环境对母性行为影响时,也应将噪音、气味等因素协同考虑,综合评价环境的影响。

除了上述传统的环境因素,近年来,塑化剂、重金属以及电磁辐射等新型环境干扰因素对动物母性行为的影响也受到越来越多的关注。塑化剂等雌激素类似物以及汞、镉等重金属是现代工农业的重要原料,常被用于杀虫、灭鼠等[122]。人类及动物在日常生活及生产中常接触到其在环境中的残留物[123—125],这些环境污物属于环境内分泌干扰物,可以在体内充当雌激素等激素类似物,干扰动物的神经内分泌系统和生殖功能[126],影响动物的母性行为[17—18]。此外,这些环境污染物本身还具有毒性,可通过诱导氧化应激、炎症损伤、改变基因表观遗传修饰等方式影响与母性调节密切相关的 HPO、HPA 轴的结构和功能,进而威胁母性行为的正常表达[17,127—130]。值得注意的是,虽然环境中塑化剂、重金属等污染物的含量通常比较低,环境低剂量的此类干扰物一般不会引起成年个体的明显损伤,但它们对于胚胎期和胎儿期的生命来说却是巨大威胁,研究表明,在胎儿期接触塑化剂的小鼠在成年后表现出较差的子代照料行为,母鼠待在窝内的时间明显减少,取回离巢的幼仔所花费时间更久,并且这种母性异常还可持续数代[131—133]。成年期接触电子垃圾中的重金属可增高人类 HPA 轴中促肾上腺皮质激素释放激素（CRH）、促肾上腺皮质激素（ACTH）和皮质醇的浓度,并引起持续的氧化应激,而胎儿期接触镉等重金属会引起出生后的行为异常[134]。此外,除了直接影响母性行为外,以上污染物还会降低小鼠的空间记忆能力,并对母性行为产生明显威胁[135—136]。

另外,除了上述环境污染物,电磁辐射、核辐射等也会给动物带来巨大影响,来自电机、器械、手机等的电磁辐射可以通过诱导氧化应激、凋亡等途径破坏血脑屏障完整性、改变海马体结构及神经胶质细胞的信号通路等方式,影响动物的学习、记忆、探索、焦虑等行为模式,威胁动物的母性行为表达[16,137—138]。相比常规电磁辐射,核辐射对动物的影响更为严重,一项研究表明福岛核灾难幸存者在事故发生后 8 年内情绪、行为等仍受影响,并且核污染一旦出现,其对当地环境的危害可长达数十年[139—140]。不过,限于实验安全等角度考虑,目

前关于核辐射影响动物母性行为的研究尚少。值得注意的是,同塑化剂等环境污染物一样,电磁辐射等的危害对胚胎发育期的个体影响同样更大[141]。

2.4 管理因素对母性行为的影响

对家养动物而言,圈舍大小、分群、剪毛、隔离、运输、圈舍环境丰富度等日常管理措施也是干扰其母性行为的因素之一。日常管理策略会影响家养动物的环境和营养分配,例如,前期的研究表明当饲养密度过大时,小尾寒羊的母性行为变差,其跟随及舔舐幼仔的时间下降,授乳的持续时间减少[13]。在日常管理中,由于疾病治疗等需要母子分离或隔离时,母羊在隔离时反应非常强烈,待幼仔同母亲团聚后,短暂的隔离反而增加了母亲对幼仔的舔舐时间[142—143]。但这并非意味着母子隔离会增加母亲的母性行为,当隔离时间延长时(例如出生后短暂接触 5 min 后立即隔离 24 h),重聚后,母鼠对幼仔的照料行为会丧失,视觉、嗅觉、听觉等刺激均无法重新启动母鼠的母性行为[144]。这可能是因为出生后的几小时是母子建立联系的关键时期,而 5 min 不足以使它们建立嗅觉或听觉联系[145],影响了母亲对幼仔的识别,同时,由于听不到幼仔的叫声,母亲的母性激活也缺乏持续的刺激,这均不利于母性的激活和维持。但是育幼经历似乎能部分抵消这种影响,研究表明,在羔羊出生后立即被取走 2 h 的情况下,在团聚后,经产母羊接受羔羊并表现出良好的母性行为,而初产母羊则拒绝羔羊[146]。

此外,运输、混群、转圈及剪毛等日常管理也会引起动物不同程度应激[147—149],并且孕期动物及哺乳期母幼对此更为敏感。但出乎意料的是,对一些动物而言,妊娠期遭遇一定的应激并不会对产后母性产生明显干扰效应,有时反而会提高其产后的母性行为。例如,妊娠中期剪毛并不会对母羊的产后行为产生明显影响[150],小鼠妊娠期遭遇不同程度的应激(高温、光照、声音)处理后,反而表现出更为强烈的母性,但他们的攻击性有所增加[107]。然而,大鼠在遭遇类似的产前应激后却表现出较差的母性行为,它们在幼崽取回实验中成功率明显降低[111]。母猪在妊娠期经历应激处理后,其在授乳、对仔猪叫声反应速度上的表现评分均不及对照组[151]。雌性黑线仓鼠经历重复遭遇战刺激并未抑制性腺轴活性,不会明显影响母鼠的潜在繁殖能力[152]。这种差异可能与物种不同有关,还可能与应激源和刺激程度不同有关。

生产中,为了降低各种管理对家养动物的应激,操作应尽可能轻柔并尽量缩短处理时间,此外还可通过增加圈舍的环境丰富度来部分抵消日常管理带来的负面影响,改善动物福利[153—154]。研究表明,在圈舍中增加秸秆、稻草等可改善妊娠期遭遇应激处理的母猪的母性行为,但其并不能完全抵消此类应激对母性行为造成的负面效应[151]。另有研究指出,增加环境的丰富度还可改善产后抑郁[155]。但也有研究指出环境富集并不能改善圈养水貂的母性行为[156],甚至还会延迟大鼠幼崽诱导的母性行为的启动时间[157],因此,环境富集对母性行为的改善效果还有待深入观察。

2.5 其他因素对母性行为的影响

除以上因素外,疾病因素是影响动物的母性行为的另一因素,产后抑郁、乳房炎、产后瘫痪、弓形虫等寄生虫感染等疾病会影响或者彻底终止母畜的授乳、舔舐等行为,使母亲对幼仔的照料品质下降或失去照料幼仔的意愿和能力[158—160]。另外,分娩持续持续时间、分娩过程中是否难产,以及难产时人工助产的方式等也会影响后期的母性行为[161]。最近的一项研究表明,在母羊分娩时提供人工助产,可以缩短产程并显著提高母羊的母性行为[162]。此外,母亲在育幼的过程中通常警惕性比较强,应当努力维持育幼环境稳定,减少陌生人的干扰,当母猫等察觉到危险时,便会频繁地更换幼仔的巢穴地点,这也可能影响母性行为的表达[163]。母亲年龄也是影响其母性行为的重要因素[164],但年龄小通常和缺乏育幼经验重叠,因此,不太好确定年龄对动物母性行为的具体影响,但人类上的研究表明年龄大的产妇比早产产妇母性照料表现更好[165]。母畜的性格也可以影响其母性表现,性格平稳的母羊母性行为表现更优,其对幼仔的舔舐更加频繁[166]。在同猪群内,性格温顺的个体等级地位通常较低,这也对母猪的母性行为造成一定干扰[167]。

另外,除了母羊自身因素外,羔羊性别、状态等也是影响母性行为的重要因素,们前期的研究表明窝产仔数、幼仔性别也会影响母羊的母性行为,具体来说,产 2—3 羔的母羊授乳、跟随等行为明显更多,产母羔的母

羊母性行为也优于产公羔个体[14—15]。当幼仔受伤并表现出疼痛相关表现时,母羊对受伤个体的关注度明显上升,并表现出更多的舔、嗅反应[168]。以上分析表明,母性行为既有基于遗传的本能表现,又会受到周围环境、营养、管理、疾病等因素影响,同时还与母亲和幼仔的体况、性格等密切相关,因此在生产中分析母性行为影响因素时,应结合实际情况综合分析。

3 展望

哺乳动物的母性行为受遗传、营养、环境、管理和疾病等多种因素影响,并且母性行为的激活和维持正面临塑化剂、重金属、电磁辐射等新型挑战。通过对这些因素的归纳、总结,本综述为后续深入探究哺乳动物母性行为、分析母性行为异常的潜在干扰因素及挖掘改善母性行为的措施等提供参考。同时,也需要认识到,无论是在野外还是家养环境,这些因素通常是共同影响母性行为的,且这些影响可能是基因突变、表观遗传、营养失衡、情绪失控等多种机制相互作用的复杂产物。另外,鉴于母性行为总体性状遗传力较低,通过遗传选育高品质母性种群的难度较大,且大部分现有以提高产仔数、提高产奶量等为导向的种群选育模式反而可能会降低动物母性行为,因此,在动物生产中,应当在照顾生产性状的同时,在遗传学的基础上,综合优化营养、环境、管理等措施,改善动物的母性行为并尝试培育具有优良母性性状的高产种群。

当然,要实现这一目标尚需大量工作,未来可通过建立更细化、更符合不同动物生活环境下的母性行为评价系统,以便更精确地捕捉群体中的优良母性性状,为改良种群的母性行为提供遗传基础。同时,要深入分析营养、环境、管理等因素影响动物母性行为的详细机制,以便更明确地区分不同自然和人为干扰下的母性优劣,为改良种群的母性行为提供可行的人为干预措施。另外,要密切关注塑化剂、重金属等环境内分泌干扰物及电磁辐射等影响母性行为的新型干扰因素,以便更清晰地认识这些新挑战影响母性行为的机制,为改良种群的母性行为提供符合现代生活和饲养模式的与时俱进的灵活方案。此外,在分析母性行为异常表现时,还应积极将其与其他反常行为相结合[169],评估类似异常行为对母性的影响。最后,在未来的研究中,应结合 SNP 基因分型、高通量测序、基因敲除、基因芯片、DNA 指纹图谱[170]等技术继续深入挖掘调控母性行为的关键基因,并利用免疫共沉淀等技术分析各关键基因间的相互作用,进一步探索影响母性行为的遗传和表观遗传各因素的分子机制、调控网络、动态变化及跨代传递规律等,以期揭示母性行为的本质和规律,为母性行为的评估和干预提供理论依据和实践指导。当然,在探索改善家养动物母性行为的研究中,应当更多地遵循动物母性调节的自身规律,更好地服务于生态健康养殖理念。同时,动物模型上关于母性行为的这些研究,还可为解读人类母婴关系、提高母婴身心健康提供有价值的参考。

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