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火鸡疱疹病毒载体活疫苗助力白羽肉鸡“无人养殖”发展

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摘要 白羽肉鸡养殖是我国畜牧业中集约化和自动化程度最高的产业之一,目前已基本实现环境调控与饲养自动化,然而现行依赖灭活疫苗和减毒活疫苗的传统免疫策略,需进行反复、多次疫苗接种,致使疫苗免疫仍高度依赖人工,成为制约白羽肉鸡实现“无人养殖”的瓶颈。本综述分析当前肉鸡饲养模式,展望发展趋势,并解析了火鸡疱疹病毒(HVT)载体活疫苗的免疫机制及应用潜力,提出:1) HVT载体活疫苗诱导强效细胞免疫应答,可有效弥补因母源抗体导致的抗体保护“窗口期”,为雏鸡提供早期免疫保护。2) 其“一次免疫、终生保护”特性及孵化场接种方式,可显著降低免疫人工成本。3) 研发插入多个外源基因的多价HVT载体活疫苗,可实现“一针多防”,有助于进一步推动白羽肉鸡“无人养殖”发展。综上,HVT载体活疫苗的应用,为克服传统疫苗局限、推动白羽肉鸡“无人养殖”的发展提供了高效免疫方案。

关键词 HVT载体活疫苗;集约化养殖;白羽肉鸡;“无人养殖”

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HVT vectored vaccines facilitating the development of “human labor-free farming” in white-feathered broilers

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Abstract White-feathered broiler farming represents one of the most intensive and automated sectors in China's animal husbandry industry. Currently, environmental control and feeding operations have generally been realized. Nevertheless, traditional immunization strategies relying on inactivated vaccines and attenuated live vaccines require repeated inoculations, resulting in a high dependence on artificial vaccination, which has constituting a critical bottleneck hindering the realization of “human labor-free farming” for white-feathered broilers. This review analyzes the current white-feathered broiler breeding models, prospects the development trends, and elucidates the immune mechanism and application potential of HVT vectored vaccines, proposing that: 1) HVT vectored live vaccines can induce strong cellular immune responses, effectively compensate for the antibody protection “window period” caused by maternal antibodies, and provide early protection for chicks. 2) Its characteristics of “single immunization with lifelong protection” and the mode of hatchery inoculation can significantly reduce labor costs for immunization. 3) Developing multivalent HVT vector vaccines incorporating multiple exogenous genes to achieve “one-shot prevention against multiple diseases” will help further advance the development of “human labor-free farming”. In summary, the application of HVT vectored live vaccines provides an efficient immunological solution to overcome the limitations of traditional vaccines and promote the development of “human labor-free farming” in white-feathered broilers.

Keywords HVT vectored live vaccines; intensive farming; white-feathered broiler; “human labor-free farming”

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肉鸡按品种特性主要划分为白羽肉鸡和黄羽肉鸡。白羽肉鸡具有生长速度快、料肉比低、胸肉比高等特点,49日龄内出栏,适合规模化养殖和快餐加工。黄羽肉鸡是我国本土培育的优质特色鸡种,其生长周期相对较长,出栏日龄通常不低于55天,该品种肌间脂肪含量丰富,肉质细腻,风味鲜美等优点,适合清蒸、炖汤等传统烹饪方式。近年来,随着我国肉鸡规模化、集约化养殖模式的推进,以及快餐、团餐等消费模式的转变,白羽肉鸡产业结构占比呈现持续上升态势。2015年全国肉鸡出栏量90.44亿只,白羽肉鸡出栏量43.89亿只,占总出栏量48.53%;2024年统计数据显示,肉鸡出栏量148.42亿只,其中白羽肉鸡出栏量达90.31亿只,占总出栏量60.85%^[1]。相比之下,黄羽肉鸡受“活禽市场管制”、小型白羽肉鸡替代等因素冲击,产量持续萎缩。我国白羽肉鸡养殖是畜牧业中自动化程度最高的产业之一,其饲养管理已基本实现自动化。然而,目前白羽肉鸡养殖中广泛使用的灭活疫苗和减毒活疫苗,需要反复、多次接种,对人工需求量比较大。便捷、高效的疫苗免疫可大大减少免疫人工成本,降低免疫人员“串舍”导致的疫病传播风险,提高疫病防控效力,从而推动肉鸡养殖业向“无人养殖”发展。

1 白羽肉鸡养殖现状分析

1.1 白羽肉鸡养殖业发展概况

我国白羽肉鸡养殖当前基本实现规模化、集约化。早期从个体散户养殖为主,转向公司-农户、大集团养殖等规模化模式为主,当前规模化养殖(单场存栏 ≥ 5 万羽)占比已突破85%^[2];早期以地面散养为主,随后逐步发展为单层网上养殖,目前主要以3~5层叠式立体笼养模式为主。在节约土地资源的同时,更利于机械化养殖的实现。通过物联网技术的应用,利用温度、湿度、氨气、二氧化碳等传感器实时采集数据,联动通风、湿帘及加热设备,可精准调控鸡舍环境^[3]。此外,自动喂料、自动饮水、自动清粪设备的应用,大大降低了人力投入,节省成本的同时,极大推动了养殖业规模化、集约化发展。随着我国人口结构变化,劳动力短缺问题日益凸显,传统养殖模式对人力的依赖已难以适应未来产业需求。在此背景下养殖模式持续升级,单栋鸡舍饲养规模从早期的1万~2万羽跃升至当前主流

的5万~10万羽,单人饲养量从0.5万羽提升到约10万羽^[4]。未来,通过整合人工智能视觉和音频监测、智能环控系统、自动化饲养设备等技术以及新一代免疫防控策略,可实现从环境调控、饲料供给到疫病防控的全流程无人化管理^[5],为最终实现白羽肉鸡“无人养殖”奠定了基础。这种管理模式不仅能进一步提升养殖效率,还能通过数据化运营优化料肉比、降低疾病风险,是应对劳动力稀缺、推动产业升级的必然选择。白羽肉鸡养殖已通过机械化奠定基础,而“无人养殖”凭借技术集成与效率优势,正逐步成为引领未来养殖业的终极模式。然而,在当前养殖条件下,疫苗免疫仍需要大量人工,成为制约白羽肉鸡实现“无人养殖”的瓶颈。

1.2 白羽肉鸡疫病防控现状分析

生物安全防控是养殖场疾病防控的第一道防线。当前规模化养殖场在选址规划、设施配置、人员管理等方面,已基本满足生物安全防护要求。但仅靠生物安全体系无法完全阻断疫病的发生和传播,疫病仍是制约产业发展的主要因素。目前白羽肉鸡养殖场主要疫病按照防控方式可分为三类:一是净化防控类疾病,如禽白血病、鸡支原体感染、鸡传染性贫血病等垂直传播性疾病,该类疾病的防控主要通过种禽净化来实现;二是饲养管理防控类疾病,如大肠杆菌病、球虫病等条件致病性疾病,此类疾病主要通过饲养管理和药物干预等来控制;三是疫苗免疫防控类疾病,如禽流感、传染性法氏囊病、新城疫、禽腺病毒感染、传染性支气管炎等以水平传播为主的疾病,这些疾病主要依赖疫苗免疫来防控。对于上述疫苗免疫防控类疾病,当前白羽肉鸡一般在1日龄孵化场点眼或喷雾接种传染性支气管炎、新城疫活疫苗;7~10日龄颈部皮下注射接种包含新城疫、H9亚型禽流感(Avian influenza virus, AIV)、禽腺病毒等的多联多价灭活苗;14日龄滴鼻接种传染性法氏囊病活疫苗;20日龄点眼或饮水接种新城疫活疫苗。为应对雏鸡免疫的人工成本压力,部分养殖场尝试将灭活疫苗提前到1日龄接种,但受母源抗体影响,无法为雏鸡提供有效免疫保护。

1.3 白羽肉鸡疫病防控“痛点”分析

疫苗免疫是防控传染病流行的最重要、最有效的手段。近年来,动物保健品行业快速发展,新型疫苗、多联多价疫苗等加速研发,整体疫病防控形

势良好。当前肉鸡用疫苗可分为灭活疫苗、亚单位疫苗等“死”疫苗,以及减毒活疫苗、载体活疫苗等“活”疫苗。“死”疫苗由于其安全性好,研制相对容易,应用广泛,占据疫苗主要市场。然而,这类疫苗受母源抗体干扰,最小接种日龄为2~3周龄,导致在2~4周龄出现抗体保护“窗口期”,此期间鸡群易感染并发病^[6-7]。此外,该类疫苗免疫主要在养殖场进行,人工成本高;需要逐只抓鸡,进行皮下或肌肉注射,易造成免疫应激,降低生产效益;在当前白羽肉鸡高度集约化养殖模式下,往往需要配备专职免疫人员进行免疫,这些免疫人员在不同鸡舍免疫时,增加了病原通过人员在鸡舍间传播的风险。更重要的是,“死”疫苗通过诱导中和抗体来提供免疫保护,难以对抗原性持续变异的流行毒株的感染提供有效保护^[8]。减毒活疫苗免疫雏鸡后,受母源抗体干扰更为严重,影响免疫效果的发挥,并且还存在着毒力返强、与流行毒株重组和残存毒力过高等安全风险。创新性研制能够孵化场免疫,“一针多防”、“一次免疫,终生保护”的高效、便捷疫苗是推动白羽肉鸡“无人养殖”发展的关键。

2 火鸡疱疹病毒(Herpesvirus of Turkey, HVT)载体活疫苗发展及应用

相对于目前广泛使用的灭活疫苗和减毒活疫苗,HVT载体活疫苗具有诸多优势:受母源抗体干扰小,能够孵化场免疫,且“一次免疫,终生保护”,显著降低免疫人工成本;可诱导强烈的细胞应答,弥补抗体保护“窗口期”,提供更好的交叉免疫保护;有多个外源基因插入位点,可研发多价载体活疫苗,实现“一针多防”^[9]。因此,HVT可作为当前白羽肉鸡养殖模式下理想的疫苗载体,将极大助力白羽肉鸡“无人养殖”发展。

2.1 HVT载体活疫苗重组病毒构建技术发展现状

作为马立克病病毒(Marek's disease virus, MDV)血清III型成员,HVT最早被用于MD的防控^[10]。1992年,HVT首次被用作病毒载体,在短独特区插入了新城疫病毒的F蛋白,构建了HVT-ND载体活疫苗^[11]。自此,HVT被广泛用于载体活疫苗的构建。HVT载体活疫苗毒株构建技术历经了三代革新。第一代基于同源重组,通过带同源臂的转移载体将外源基因插入HVT基因组,该技术易操作,但重组概率低、重组病毒纯化十分耗时^[12];第

二代借助粘粒或细菌人工染色体(Bacteria artificial chromosome, BAC)等大容量克隆载体构建感染性克隆,在大肠杆菌中完成外源基因插入后再拯救病毒,该方法中感染性克隆构建难度大,但构建成功后后续重组病毒构建和筛选相对容易,然而有研究显示构建的感染性克隆存在基因缺失现象^[13];第三代以CRISPR/Cas9系统为核心,结合荧光筛选与Cre-LoxP系统,将报告基因和外源基因插入HVT基因组后再删除报告基因,此方法大幅提升了重组病毒构建效率,但需要正向和反向筛选重组病毒,往往需多次传代,易导致重组病毒突变,尤其在构建插入多个外源基因的多价活载体疫苗时,传代次数进一步叠加,提升了非预期突变风险^[14-15]。因此,将BAC系统与CRISPR/Cas9技术结合,即借助BAC系统插入外源基因,再运用CRISPR/Cas9技术构建HVT-BAC并剔除BAC序列,能够显著减少重组病毒拯救中的传代次数,减轻非预期突变的风险,这或许是当前的最优方案。但要完全解决非预期突变的问题,还需要开发新构建技术的开发。尽管如此,HVT载体活疫苗的研发目前方兴未艾,该疫苗载体已经在禽病疫苗开发中广泛应用。

2.2 HVT载体活疫苗国内外应用现状

目前对于HVT载体活疫苗的研究和应用已十分成熟,传染性法氏囊病病毒^[16-18]、H5/H7/H9亚型AIV^[19-24]、艾美耳球虫^[25]、新城疫病毒^[26]和传染性喉气管炎病毒^[27-28]等重组HVT载体活疫苗均已成功构建,并在实验室研究中取得了良好保护效果^[25,28-32]。自2006年勃林格殷格翰公司研发的VAXXITEK® HVT+IBD在巴西上市以来,国外现已有多款疫苗上市,包括Vectormune® AI、Innovax® ND、Procerta® HVT-ND、VAXXITEK® HVT+IBD、Innovax® ND-IBD和VAXXITEK® HVT+IBD+ND等,已上市的疫苗最多含2种外源病毒基因。然而受限于HVT重组病毒构建技术壁垒,目前国内仅有VAXXITEK® HVT+IBD这一款进口产品国内注册上市,尚无由我国自主研发的类似产品获批。近年来,随着国内研发实力的提升,国内多个科研团队围绕HVT载体活疫苗开展了大量实验室研究工作。截至目前,中国农业大学等单位研发的禽流感病毒(H9亚型)火鸡疱疹病毒载体活疫苗(HVT-H9-308株)以及中国农业科学院哈尔滨兽医研究所等单位研发的鸡传染性法氏囊重组火鸡疱疹病毒载体活疫苗(rHVT-VP2株)已获得临

床试验批件(国家兽药基础数据库),其他研究尚处于实验室研发阶段^[19-20,26,33]。

3 HVT 载体活疫苗的免疫保护机制解析

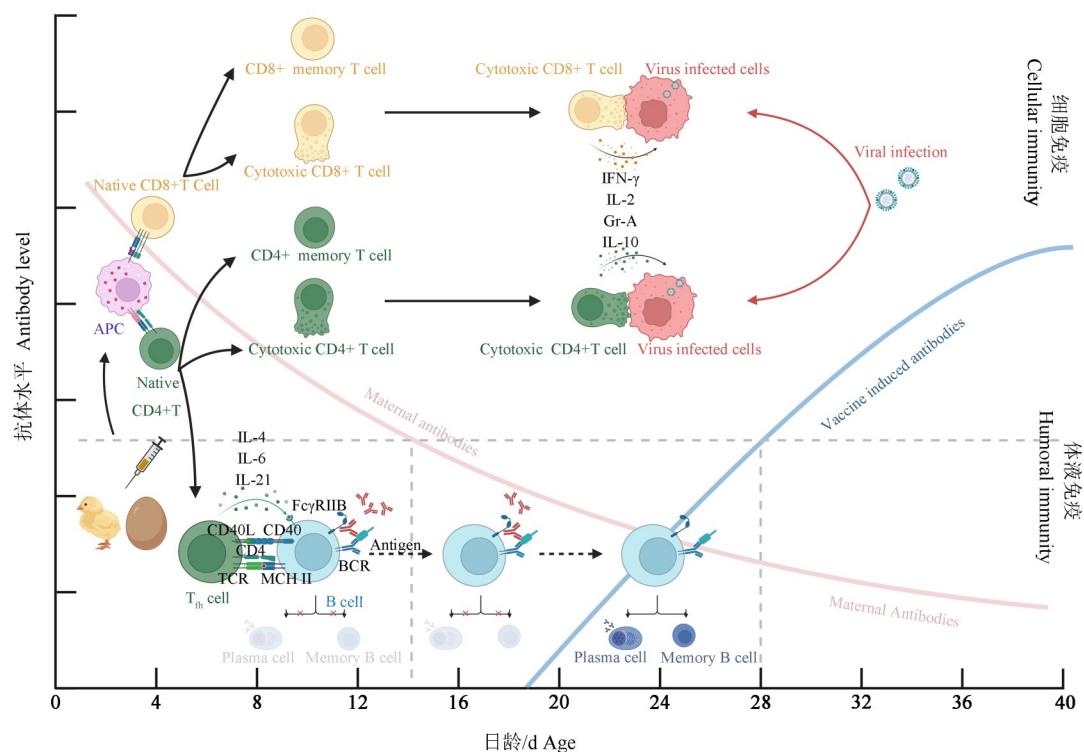
HVT 载体活疫苗与其亲本病毒 HVT(火鸡疱疹病毒)具有相同的生物学特性,需在孵化场进行免疫接种^[34]。HVT 感染后,末端重复序列促进其基因整合至淋巴细胞染色体端粒,使病毒基因组以类似宿主染色体端粒的方式被保护,避免被宿主核酸酶降解或沉默^[35-36]。因此,HVT 载体活疫苗能够在宿主细胞建立潜伏感染,实现“一次免疫,终生保护”^[36-37]。Vectormune® ND 疫苗免疫商品蛋鸡 72 周后仍维持高水平血清抗体,且保护率达 100%^[38]。除了体液免疫,HVT 载体活疫苗还能诱导强大的细胞免疫应答,特别是细胞毒性 T 淋巴细胞免疫应答,对不同血清型的病原提供交叉保护。HVT-H5 疫苗免疫鸡的脾脏 T 淋巴细胞可通过 MHC I 类分子限制性途径,有效裂解被 H5/H6/H7/H9 亚型 AIV 感染的靶细胞^[39];接种表达 H9N2 AIV 血凝素蛋白的 HVT-H9 疫苗的鸡肺部淋巴细胞 IFN- γ 表达量显著上升^[19],外周血淋巴细胞 IL-2、IL-6、IL-4、颗粒酶 A 和 IFN- γ 的表达量显著上升^[20]。

临床研究表明,雏鸡早期体内高滴度的母源抗体可显著干扰低日龄阶段接种疫苗后同类抗体的产生。其机制在于,母源抗体能够通过交联 B 细胞受体与 Fc γ RIIB,抑制生发中心内经疫苗抗原激活的 B 细胞向浆细胞和记忆 B 细胞的分化^[41],从而削弱灭活疫苗、减毒活疫苗及载体疫苗所诱导的体液免疫应答。值得注意的是,大多数减毒活疫苗和载体疫苗以游离形式存在,还会受到针对病原或载体本身的母源抗体的干扰;这类抗体可特异性识别并中和病原或载体表面抗原,导致疫苗免疫失败^[40]。然而,母源抗体并不影响疫苗诱导的 T 细胞免疫应答^[41](图 1),因此 T 细胞免疫在早期抗感染过程中发挥关键作用。HVT 载体疫苗能够诱导针对 MDV 和外源基因供体病原的高水平细胞免疫和体液免疫应答。作为细胞结合型病毒,HVT 可通过细胞间连接直接感染新的宿主细胞^[42],避免其表面抗原暴露于体液中的母源抗体,从而有效逃避针对载体本身的抗体中和作用,降低免疫失败的风险^[41](图 1)。田间试验证实,含有母源抗体的商品雏鸡免疫 HVT-H9 疫苗或 H9N2 灭活疫苗后,母源抗体

水平持续下降,在 17 日龄左右时,母源抗体衰减至最低点,而疫苗诱导的抗体由于母源抗体抑制效应未能及时产生,导致此时血清抗体水平降至最低。灭活疫苗免疫鸡后主要诱导体液免疫应答,细胞免疫应答能力弱,在抗体保护“窗口期”内极易感染 H9N2 AIV 并发病;HVT-H9 免疫鸡群后体液免疫应答虽然也受到母源抗体的干扰,但其诱导的 T 细胞免疫应答可有效抵抗 H9N2 AIV 流行株自然感染^[42]。相比仅免疫 H9N2 灭活疫苗的商品肉鸡,不感染 H9N2 AIV 情况下,在 42 日龄时 HVT-H9 免疫组平均体重比对照组高 60 g;自然感染 H9N2 AIV 流行株情况下,免疫 HVT-H9 疫苗的鸡群死淘率下降 7.49%,在 42 日龄时,各每组饲养 12 000 只鸡的条件下,HVT-H9 组总重量较对照组增加 6 253.2 kg^[44]。因此,在母源抗体延后 HVT 载体活疫苗诱导的抗体产生情况下,HVT 载体活疫苗诱导的 T 细胞免疫应答,能够在抗体保护“窗口期”为商品鸡提供良好免疫保护,显著降低病原(如 H9N2 AIV)感染造成的损失,最终在规模化养殖场中转化为可观的经济效益^[43-44]。在墨西哥和哥伦比亚农场使用 VAXXITEK® HVT+IBD 进行的现场大型对照试验也证实了 HVT 载体活疫苗的优越性。在 IBD 高风险区 HVT+IBD 组日增重增加 2 g,饲料转化率从 1.881 改善至 1.831,屠龄缩短 1 d,临床 IBD 发生率从 4.33% 降至 0.19%,经济增益约 0.08 美元/羽,每 kg 增益 0.033 美元;IBD 低风险区每只增益约 0.035 美元/羽,每 kg 增益 0.014 美元^[45]。

4 HVT 载体活疫苗研制挑战与展望

HVT 在 MD 防控中不可或缺,近年来 MDV 抗原性不断变异^[46],单价 MDV 疫苗已无法提供良好保护,但 HVT 和血清 I 型 MDV 疫苗联合免疫时,免疫效果显著优于单价疫苗^[47-48]。将 HVT-ND 与 MDV-IBD 联合注射后,对 MDV、IBDV 和 NDV 的保护率分别为 94%、100% 和 94%,不仅无显著免疫干扰,还实现“三重保护”,体现了联合策略在多病原防控中的潜力^[49]。因此,除了白羽肉鸡外,通过与 MDV 血清 I 型疫苗联合应用,HVT 载体活疫苗在黄羽肉鸡、蛋鸡和种鸡中也具有巨大的应用前景。在提高 MDV 免疫保护效力的同时,为其他疫病提供免疫保护,避免多次免疫带来的生产性能下降。考虑到相同亚型的 MDV 疫苗同



商品雏鸡出壳后,母源抗体(红色实线)随日龄增长逐渐衰减。孵化场免疫疫苗后,雏鸡体内的母源抗体不影响T细胞免疫应答,但可抑制疫苗致敏的B细胞分化为浆细胞,从而阻断疫苗诱导的抗体产生。当母源抗体完全衰减后,疫苗致敏的B细胞重启分化程序,并产生抗体(蓝色实线)。母源抗体下降至低于保护阈值到疫苗诱导的抗体达到有效保护水平的时间间隔,称为抗体保护“窗口期”(2条竖虚线间,2~4周)。

After hatching, maternal antibodies (red solid line) in commercial broiler chicks gradually decline with increasing age. Maternal antibodies in chicks in hatcheries do not affect the T-cell immune response to vaccination. However, they inhibit the differentiation of vaccine-sensitized B cells into plasma cells, thereby blocking the vaccine-induced antibody production. Once maternal antibodies are completely depleted, vaccine - sensitized B cells restart their differentiation process and produce antibodies (blue solid line). The time interval between maternal antibodies dropping below the protective threshold and vaccine - induced antibodies reaching the effective protective level is referred to as the “window period” of antibody protection (between the two vertical dashed lines, indicating 2-4 weeks).

图1 商品雏鸡孵化场免疫疫苗诱导的免疫应答模式图

Fig. 1 Schematic diagram of immune response induced by vaccination in commercial broiler hatcheries

时免疫时可能造成干扰^[50],并且在MDV I型中插入外源基因可能降低其对MDV的保护效果^[9],未来可以聚焦开发更多类型的、免疫效果更好的MDV II型和MDV III型疫苗载体毒株,与MDV I型毒株联合应用。值得注意的是,2种不同HVT载体活疫苗同时接种鸡时,会导致疫苗免疫保护效果下降^[50],因此,为实现“一针多防”,需要研制在一个HVT基因组中插入多个外源基因的多价HVT载体活疫苗。当前HVT病毒中插入单个基因,构建单价HVT载体活疫苗技术和手段已经成熟。然而在HVT基因组中插入多个外源基因时,如何选择合适的插入位点,以及优化基因表达盒,以保证多价载体活疫苗免疫保护效果,仍需深入开展HVT病毒复制和免疫机制等基础研究。此外,通过在HVT载体活疫苗中整合佐剂基因与细胞因子,

增强局部免疫微环境,以提高HVT载体活疫苗的免疫效力也是重要的研究手段^[51-54]。

目前疫病免疫防控以传统的灭活疫苗和减毒活疫苗为主,需要养殖场多次免疫接种,劳动力成本高;疫苗免疫后受母源抗体干扰,免疫效力低,且疾病引入风险大。当前肉鸡养殖模式下,高效、便捷的多价HVT载体活疫苗免疫策略,实现了孵化场免疫,“一次免疫、终身保护”,“一针多防”,可降低疾病发生率,降低人力成本,提高生产效益,是实现“降本增效”的重要突破点,也是推动白羽肉鸡“无人养殖”饲养模式实现的关键,具有广阔的应用前景。

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