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肉鸡木质肉和白条纹肉研究进展

孔富丽,刘冉冉,赵桂苹,文 杰*

(中国农业科学院北京畜牧兽医研究所,动物营养学国家重点实验室,
农业部动物遗传育种与繁殖(家禽)重点实验室,北京 100193)

摘 要:近年来,快大型白羽肉鸡木质肉(woody/wooden breast, WB)和白条纹肉(white striping, WS)等异质肉发生率不断提高,严重影响了鸡肉品质和肉鸡生产效率,受到业界的广泛关注。WS 是指肌肉表面出现平行于肌纤维的白色脂肪沉积条纹,WB 主要表现为胸肉明显硬化,WS 和 WB 组织病理学特征类似,常常共同出现。这两种肌肉缺陷严重影响了鸡胸肉的外观、营养价值以及加工特性,降低了消费者的购买意愿,造成了巨大的经济损失。目前,国外学者对 WS 和 WB 研究较多,国内报道很少。本文综述了 WS 和 WB 的病理学特征、对肉品质的影响、发生的影响因素和可能的形成机理,为未来进一步解析 WS 和 WB 形成机制,探究综合解决方案提供科学参考。

关键词:木质肉;白条纹肉;肉品质;发生机制

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Research Progress on Wooden Breast and White Striping Myopathies in Broilers

KONG Fuli, LIU Ranran, ZHAO Guiping, WEN Jie*

(*Key Laboratory of Animal (Poultry) Genetics, Breeding and Reproduction of Ministry of Agriculture, State Key Laboratory of Animal Nutrition, Institute of Animal Science, Chinese Academy of Agricultural Sciences, Beijing* 100193, *China*)

Abstract: Recently, wooden breast (WB) and white striping (WS), the newly reported myopathies attracted wide attention of global poultry industry for their increasing incidences and negative effects on meat quality and broiler performance. WS is characterized by the occurrence of white fat striations parallel to muscle fibers, while WB is mainly featured with obvious hardening of breast meat fillets. These two myopathies share similar histological lesions and often appear together. They can adversely affect breast fillet's appearance, nutrition value, ability for further processes and consumption intention, which result in huge economic loss to the industry. In recent years, most of the studies on WS and WB were reported by international research groups, few by Chinese research teams. In this review, we summarized the research progress of WS and WB from the aspect of pathological features, impacts on meat quality and nutrition value, the underlying causes and possible detailed mechanism in order to provide reference and theoretical basis for future studies.

Key words: wooden breast; white striping; meat quality; mechanism

* **Corresponding author**: WEN Jie, E-mail: wenjie@caas.cn

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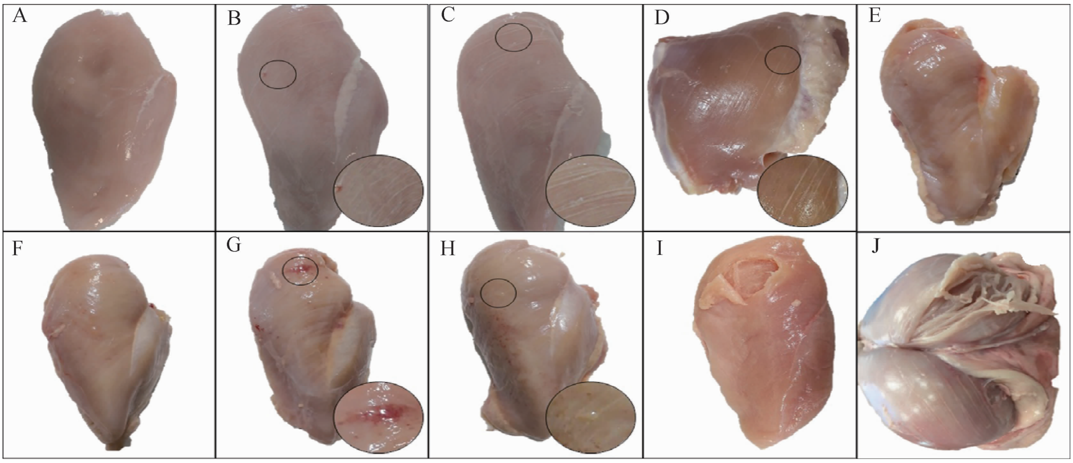
作者简介:孔富丽(1984-),女,河北邢台人,博士,主要从事鸡分子营养研究,E-mail:Kongfuli617@163.com

* **通信作者**:文 杰,主要从事鸡分子营养研究,E-mail:wenjie@caas.cn

鸡肉是除中国外的世界第一大肉类消费品。随着现代家禽育种技术的发展，肉鸡的生长速度和产肉量不断提高。2018年国内鸡肉产量为1 457.8万吨，约占国内肉类总产量(8 815.6万吨)的16.5%；世界鸡肉产量为1.14亿吨，约占世界肉类总产量(3.4亿吨)的33.4%[1]。近年来，一系列新的异质肉问题不断出现，如白条纹肉(white striping，WS)[2]、木质肉(woody/wooden breast，WB)[3]以及意大利面肉(spaghetti meat，SM)[4]等。这些异质肉问题可能单独出现，也可能两两或同时发生，其中以WB和WS报道最多。研究表明，WS和WB的发生率和严重程度在一定范围内与胸肌重呈正相关[5]。据报道，快大型白羽肉鸡中，重度WS和WB的发生率分别为10%和15%左右，并有逐年上升的趋势[6-10]。此外，一些报告显示，快速增长的大体重肉鸡(体重≥4.0 kg)WB出现率高达20%，据估计，仅对美国肉鸡养殖业造成的损失每年就超过了5亿美元，对全球肉鸡产业造成的损失更大[11]。因此，WB等异质肉问题引起了家禽学界的广泛关注，关于WS和WB的病理学特征、对肉品质的影响、发生机制及影响因素的研究日益增多。本文综述了近年来国内外WS和WB的研究进展，以期为进一步深入研究其形成机制、探究综合解决方案提供科学参考。

1　WS和WB的病理学特征

WS、WB和SM的命名与其特有的病理学特征相关。WS外观可见胸肌或腿肌有与肌纤维平行的数量不等的白色条纹[2]；WB胸肌木质化，触摸坚硬，出现脊状突起，严重的表面覆盖黏性液体[3]；SM可见肌纤维束有分离的倾向[4]。WS和WB共同出现时，肉眼可见弥漫性硬化的苍白区域和浅表的白色条纹。Kuttappan等[12]根据白条纹的数目和宽度对胸肌进行分类：正常胸肌无明显白条纹；中度WS有少量宽度小于1 mm的白条纹；重度WS有较多宽度大于1 mm的白条纹(图1)。Bowker等[5]以鸡胸肉的外观和坚硬程度为评分标准，对WB进行评分和分类：正常(0分)鸡胸肉整块柔软且具有弹性；轻度WB(1分)头端较坚硬，其余部位有弹性；中度WB(2分)胸肌坚硬，但中部至后部有弹性；重度WB(3分)整个胸肌严重坚硬、呈僵直状(图1)。



A. 正常胸肌；B. 胸肌，中度-WS(白条纹＜1 mm)；C. 胸肌，重度-WS(白条纹＞1 mm)；D. 腿肌，中度-WS(白条纹＜1 mm)；E. 胸肌，轻度-WB(苍白、局部硬化)；F. 胸肌，中度-WB(苍白、弥漫性区域硬化)；G. 胸肌，重度-WB(苍白、弥漫性硬化、瘀点、粘液渗出物)；H. 胸肌，WS和WB同时发生；I. 胸肌，SM；J. 胸肌，WS和SM同时发生

A. Normal breast muscle(without white striations or harden areas and hemorrhages); B. WS-moderate-2 breast muscle (with striation＜1 mm covering the breast surface extensively); C. WS-severe-3 breast muscle (with striation＞1 mm covering the breast surface extensively); D. WS-moderate-2 thigh muscle (with striation＜1 mm covering the thigh surface extensively); E. WB-mild breast muscle (with focal, hardened, and pale areas, without the hemorrhages); F. WB-moderate breast muscle(with diffused, hardened and pale areas, without the hemorrhages); G. WB-extremely severe breast muscle (with diffused, hardened and paleareas and hemorrhages); H. Simultaneous occurrence of WS and WB (WS/WB) breast muscle; I. SM-breast muscle (tendency towards separation of the berbundles composing the muscle tissue itself); J. Simultaneous occurrence of WS and SM (WS/SM) breast muscle

图1　胸肌病变分类[13]

Fig. 1　Classification of myopathies in chicken breast[13]

研究表明,可以通过测定血液中与肌肉损伤相关的酶含量来初步筛选胸肌病变个体[12,14-15]。此外,胸大肌是肱部的主要内收肌,退行性病变会抑制其延展性,限制肱部的活动范围,影响鸡的正常体征,通过测试鸡的翼举能力可以鉴别 WB 个体(图 2)[15-16]。1985 年,Siller[14]报道,通过测定鸡血液中肌酸激酶(creatine kinase,CK)含量可以鉴别深部胸肌病(deep pectoral myopathy, DPM);Kuttappan 等[12]发现,重度 WS 个体血清中 CK、谷丙转氨酶(alanine aminotransferase, ALT)、门冬氨酸氨基转移酶(aspartate aminotransferase, AST)和乳酸脱氢酶(lactate dehydrogenase, LDH)含量显著升高;Kawasaki 等[15-16]研究发现,胸肌损伤个体在失去翼举能力之前,血清中 CK 和 AST 值显著升高。

a、c. 正常鸡;b、d. WB 个体
a,c. Control birds; b、d. Affected birds(WB)
图 2　站立状态下正常鸡和 WB 个体[15]
Fig. 2　Standing positions of normal birds and the affected birds (WB)[15]

WS、WB 和 SM 病因可能不同,但对肌肉组织的损伤类似[17];这 3 种肌肉缺陷有各自特殊的组织病理学特征,但总体相似(表 1)。Sihvo 等[3]对 WB 进行病理学分析发现,多边形肌纤维减少,出现圆形肌纤维束、炎性细胞浸润以及肌纤维退化和坏死;退化的肌肉组织再生后被不断累积的胶原蛋白、结缔组织、肌间脂肪组织代替,逐渐纤维化。WB 组织病变程度从胸肌表面向内部逐渐降低[18]。

2　WS 和 WB 对肉品质和加工属性的影响

2.1　WS 和 WB 对肌肉组成成分的影响

鸡肉蛋白质含量高、脂肪含量低、营养丰富,加工方便、性价比高,是人们膳食中主要的蛋白来源之一,禽肉消费量有逐年递增的趋势,但 WS 和 WB 的

表 1　正常胸肌与 WS、WB 和 SM 之间的组织学差异
Table 1　The histological difference between normal and abnormal breast muscle(WS, WB and SM)

类别 Item	正常 Normal	白纹肉 White striping	木质肉 Wooden breast	意大利面肉 Spaghetti meat
外观病变 Appearance lesion	平整,肉色均匀,柔软	平行于肌肉纤维方向有白色条纹	区域硬化、突出,表面有瘀点和渗出物,触摸坚硬	肌纤维束有分离倾向
组织学特征 Histological characteristic	多边形肌纤维紧密排列、尺寸均匀	失去正常的肌肉结构。异常肌纤维呈圆形,核内化、变性、坏死,直至溶解,同时肌纤维再生;受损的肌周可见肌内结缔组织增生、脂肪和炎性细胞浸润		
特殊结构 Special structure		脂肪组织在肌周异常沉积(脂质沉积)	肌周网络的增殖和增厚(纤维化)	肌内和肌周结缔组织增加,肌纤维稀疏

发生对鸡肉营养成分造成了较大的影响。主要表现在水分含量增加、粗蛋白含量下降、胶原蛋白含量增加、脂肪含量增加[8,19-22]和肌糖原含量下降[23-24]。胶原蛋白是结缔组织主要的结构蛋白，含量较高时肌肉嫩度较低，WB比正常胸肌坚硬可能与此有关[20]。饱和脂肪酸含量显著降低，不饱和脂肪酸含量显著升高。而不饱和脂肪酸易被氧化，可能会对肌肉产品的存储产生不利影响[25]。此外，Soglia等[18,25]发现，WS和WB中总血红素含量显著下降，存在轻微的氨基酸成分变化、蛋白质和脂质氧化现象；WS和WB中钙、钠含量显著升高，细胞对钙的摄取增加，可能是造成肌肉损伤的原因之一。

2.2 WS和WB对肉品质的影响

近年来，消费者对肉品质的要求不断提高，而WS和WB引起肉外观、色泽、质地变化(表2)，极大地影响了消费者的购买意愿[26]。研究发现，不同程度WS的pH差异不显著，但随着WS严重程度增加而增加，同等程度的WB比WS对pH影响大，WS和WB共同出现对pH影响更大[7,27-31]。不同研究结果表明，WS和WB与正常胸肌相比，肉色(L*、a*、b*)3个值同时或其中的任意一个(L*或a*或b*)或两个(L*、b*和L*、a*)有显著性差异，且对胸肌皮肤侧的影响大于骨骼侧；其中WB和WS共同出现影响最大，WB次之，WS影响最小[7,27,31-32]。

表2 WS和WB对鸡肉品质性状的影响(n=48)[27]

Ttable 2 Effect of WS and WB on the meat quality traits of chicken(n=48)[27]

参数 Parameter	胸肌类别 Breast meat category				标准误 S.E.M	P值 P value
	正常胸肌 Normal	白纹肉 WS	木质肉 WB	白纹肉/木质肉 WS/WB		
鲜生肉 Fresh meat						
pH	5.80^{c}	5.90^{b}	5.87^{bc}	6.04^{a}	0.01	<0.001
Lightness L*	56.0^{ab}	54.9^{b}	57.0^{a}	55.2^{b}	0.2	<0.001
Redness a*	1.76	1.72	1.67	1.70	0.05	ns
Yellowness b*	2.72^{b}	2.70^{b}	3.27^{a}	2.64^{b}	0.08	0.017
滴水损失/% Drip loss	0.93^{b}	0.72^{c}	1.19^{a}	1.03^{b}	0.03	<0.001
熟肉 Cooked meat						
蒸煮损失/% Cooking loss	1.6^{c}	24.7	28.0^{a}	29.5^{a}	0.4	<0.001
剪切力/kg Shearing force	2.37	2.35	2.19	2.21	0.04	ns
Lightness L*	4.0	83.7	84.0	83.5	0.1	0.037
Redness a*	1.64	1.81	1.79	1.85	0.03	ns
Yellowness b*	8.01^{b}	8.30^{ab}	8.43^{a}	8.47^{a}	0.05	0.001

同行数值肩标不同小写字母表示差异显著(P<0.05)，肩标不同大写字母表示差异极显著(P<0.01)，肩标相同字母或无字母表示差异不显著(P>0.05)。下同

In the same row, values with different small letter superscripts mean significant difference (P<0.05); and values with different capital letter superscripts mean extremely significant difference(P<0.01); while values with the same or no letter superscript mean no siginificant difference(P>0.05). The same as below

2.3 WS和WB对肉加工特性的影响

WS和WB具有较低的持水力和腌制吸收率，蒸煮损失较大[5,7,27,33]。陈宏强等[10]研究发现，与正常鸡胸肉肉糜相比，木质化鸡胸肉肉糜保水性显著降低，加热后得到的凝胶硬度、弹性、内聚性和咀嚼性均显著降低，观察发现其凝胶微观结构松散，空隙较大，具有较高的α-螺旋含量和较低的β-折叠、β-转角含量。Aguirre等[34]报道，正常肉类的腌制保留率为83.21%，重度WB为59.23%；在弹性、硬度、密度、黏合性、可碎性、纤维度、松脆度和咀嚼度方面，重度WB均显著高于正常肉；腌制和烹饪方法并不能改善WB的质量和质地。此外，解冻处理显著降低蛋白质氧化稳定性，WS、WB和SM的游离氨基酸含量显著降低[30]，而游离氨基酸是主要的

风味物质,这可能是 WS 和 WB 影响消费者口感的主要原因之一。

2.4　WS 和 WB 的无损检测

快大型白羽肉鸡主要是屠宰分割销售,分割后对劣质鸡胸肉进行分拣处理,耗费大量人力物力,实现生产线上无损检测可大幅提高工作效率。基于 WB 水分和蛋白含量与正常胸肌的差异性[19-21],在近红外(near-infrared spectroscopy,NIR)测量肌肉水分含量[35]基础上,Wold 等[7,36]建立了利用 NIR 技术检测蛋白和水分含量来鉴别 WB 的方法。根据 WS 的脂肪含量变化(从 0.5%上升到 10.1%)这一特点,Traffano-Schiffo 等[37]利用射频光谱传感器,建立了分光光度法来测定鸡胴体白条纹。此外,孙啸等[38]通过对各参数的测量发现,WB 评分与挤压力(compression force,CF)大小、胸肌厚度密切相关,随着 WB 评分增加,CF 显著增加,在此基础上建立了通过测定 CF 分拣 WB 的方法。

3　WS 和 WB 形成的影响因素

3.1　遗传和性别

研究表明,不同品种(系)、性别、胸肌产量鸡群的 WS 和 WB 发生率不同,对生长速度和胸肌产量的选育提高了异质肉的发生率[39]。2013 年,Kuttappan 等[40]评估 4 个不同品系肉鸡 WS 的影响因素发现,不同品系 WS 发生率不同,且公鸡发生率高于母鸡(表 3)。Petracci 等[8]发现,高胸肌产量与普通胸肌产量的鸡相比,前者 WS 发病率更高(15.2% *vs* 10.0%)。Chen 等[41]测定 3 个现代肉鸡品系和 ACRB 肉鸡(1950 年未选的肉鸡)WB 病变时发现,ACRB 肉鸡 WB 病变程度最低,3 个现代肉鸡品系之间 WB 的严重程度无显著差异。Zampiga 等[42-43]分别选择两个不同基因型的小型杂交肉鸡和火鸡,孵化和饲养环境相同、日粮相同、屠宰时生长性能相似,但严重 WS 和 WB 的发生率却差异显著。Trocino 等[44]发现,WB 在公鸡中出现的概率超过母鸡(8.0% *vs* 6.3%)。Brothers 等[45]通过分析 WB 样本的基因表达发现,公鸡有 189 个基因表达上调,其中 103 个(55%)位于 Z 染色体上,且与脂肪代谢、氧化应激、抗血管生成和结缔组织增生相关。刘一帆等[46]认为,未来可通过筛选与肌肉缺陷相关的分子标记物,利用遗传选育的方法降低 WS 和 WB 的发生率。

3.2　体重和胸肌重

研究表明,WS 和 WB 的发生与胸肌重密切相关,胸肌越重、尺寸越大,WS 和 WB 的发生率和压缩力越高[27-29,47](表 4)。Malila 等[48]基于 logistic 回归分析发现,胸肌重量每增加 1%,WS 和 WB 发生机会分别增加 50.9%和 61.0%。屠宰日龄从 6 周增加到 7 周,体重增加,WS 严重程度也随之增加(表 5)。由此可见,体重越大、胸肌重越大的个体发生 WS 和 WB 的几率越大。

3.3　营养

研究发现,改善生长性能、料重比会提高增重和胸肌产量,但同时会加重肌肉缺陷的发生[49-50];不同生长阶段的限饲措施,如限制采食量、采食时间或降低饲粮能量浓度等,会在一定程度上降低 WS 和 WB 的发生率,但会影响生产性能[44,51-53]。生长性能、胸肌产量与WS和WB的发生率似乎是不可调

表 3　不同品系和性别肉鸡的 WS 发生率[40]

Table 3　The incidence frequency of WS in broilers with different strains and sexes[40]

影响因素 Factor	发生数量/只(率/%) Frequency			
	正常胸肌 Normal	中度白纹肉 MOD-WS	重度白纹肉 SEV-WS	样本总量 Total
系别 Strain				
A	112 (59.3)	72 (38.1)	5 (2.6)	189
B	50 (27.2)	99 (53.8)	35 (19.0)	184
C	85 (49.1)	83 (48.0)	5 (2.9)	173
D	80 (41.5)	97 (50.2)	16 (8.3)	193
性别 Sex				
母鸡 Female	199 (53.2)	157 (42.0)	18 (4.8)	374
公鸡 Male	128 (35.1)	194 (53.1)	43 (11.8)	365

和的矛盾。但也有研究发现，调整生长前期赖氨酸和/或精氨酸比例，可在不影响生长性能、加工产量和胸肉品质的前提下对肌肉缺陷（主要是 WS 和 SM）发生率有积极影响[54-56]。此外，Livingston 等[57-58]研究表明，在种蛋储存时间较短的情况下，限时采食可降低 WS 和 WB 的发生率和病变程度；各饲养阶段中可利用磷水平固定，不同钾含量的日粮均显著降低 WB 发生率。Greene 等[22]发现，植酸酶可通过调节肉鸡体内氧稳态相关基因来降低 WB 的严重程度，而生长性能不受影响。谢谦等[59]认为，未来通过减缓肉鸡生长前期肌肉发育速度，同时通过营养调控促进血管生长、增加血红蛋白携氧量可在一定程度上缓解 WS 和 WB 的发生。谭权和孙德发[60]认为，添加抗氧化剂和有机微量元素能减少肉鸡 WS 和 WB 的发生。

4 WS 和 WB 的发生机制

4.1 WS 和 WB 的发生发展过程

研究表明，WS 和 WB 是一种进行性疾病，其发生与早期体重快速增加有关，从2周龄开始出现病

表 4 胸肌异常对生鸡胸重量、尺寸和质地的影响[27]

Table 4 Effect of breast muscle abnormalities on weight, dimension and texture of raw chicken fillets[27]

参数 Parameter	胸肌类别 Breast meat category				标准误 S. E. M	P 值 P value
	正常胸肌 Normal	白条纹肉 WS	木质肉 WB	白纹肉/木质肉 WS/WB		
重量/g Weight	244.7^b^	305.5^a^	298.7^a^	318.3^a^	3.4	<0.001
顶部高度(H1)/mm Top height	38.1^b^	45.7^a^	43.9^a^	45.7^a^	0.4	<0.001
中部高度(H2)/mm Middle height	24.7^c^	31.2^b^	30.5^b^	33.8^a^	0.4	<0.001
底部高度(H3)/mm Bottom height	8.2^b^	8.7^b^	11.0^a^	11.6^a^	0.2	<0.001
长/mm Length	195	196.5	196.8	196.5	0.9	ns
宽/mm Width	78.7	81.5	80.3	79.9	0.6	ns
压缩力/kg Compression force	2.02^b^	2.28^b^	4.02^a^	3.33^a^	0.15	<0.001

n=48/组；H1 在顶部最厚处测量；H2 在胸肌长度的一半处测量；H3 在距后端 1 cm 处测量

n = 48/group; H1 was measured at the thickest point in the cranial part; H2 was measured at half distance of the breast muscle length; H3 was measured far from the end of the caudal part by 1 cm towards adorsal direction

表 5 白色条纹和木质化胸肌的肉鸡胴体特征[48]

Table 5 Carcass characteristics of commercial broilers affected by white striping and wooden breast muscle[48]

日龄/胴体重 Age/Carcass weight	特征 Trait	肌肉缺陷类别 Defect level						
		正常胸肌 Normal	轻度白纹肉 Mild WS		中度白纹肉 Moderate WS		重度白纹肉 Severe WS	
			无木质肉 Non-WB	木质肉 WB	无木质肉 Non-WB	木质肉 WB	无木质肉 Non-WB	木质肉 WB
6周龄/≤2.5 kg	样本量	2	29	0	10	0	0	0
	胴体重/kg	2.3^b^	2.3^b^	nd	2.4^a^	nd	nd	nd
	胸肌重/g	165.5^b^	193.1^a^	nd	208.2^a^	nd	nd	nd
	胸肌产量/%	14.8^b^	16.9^a^	nd	17.5^a^	nd	nd	nd
6周龄/>2.5 kg	样本量	2	34	3	18	2	0	0
	胴体重/kg	2.9	2.8	2.7	2.9	2.9	nd	nd
	胸肌重/g	211.2^b^	228.5^b^	237.4^ab^	254.3^ab^	295.5^a^	nd	nd
	胸肌产量/%	14.6^c^	16.4^bc^	17.8^ab^	17.7^a^	20.4^a^	nd	nd
7周龄/>2.5 kg	样本量	0	34	2	38	3	4	2
	胴体重/kg	nd	3.2	3.3	3.3	3.4	3.4	3.1
	胸肌重/g	nd	286.8	327.5	304.5	312.2	318.6	311.4
	胸肌产量/%	nd	17.8	19.7	18.3	18.6	19.0	19.9

变，在 28 d 内显著增加，首先表现为急性炎症期的静脉炎，同时伴有脂质浸润，随后可见肌纤维变性、再生，最后逐渐发展为慢性纤维化[41,51,61]。Papah 等[62]证实，WB 组织学特征随着周龄递增而改变，第 1 周发生局限性静脉炎伴脂肪肉芽肿，第 2 周出现局灶性单肌纤维变性，第 3 周开始炎症反应，第 4 周出现多灶性弥漫性肌纤维变性、坏死、间质性水肿伴脂质增加和炎性细胞浸润，到最后的 5～7 周发生弥漫性肌肉变性、坏死、纤维化和脂肪浸润伴脂肪肉芽肿。

4.2　WS 和 WB 的发生机制

WS 和 WB 发生机理研究多是围绕组织缺氧、氧化应激、肌纤维类型转及代谢异常等方面展开。近几年来，陆续有学者利用蛋白组学、代谢组学、转录组学等方法从分子和基因水平来解析 WS 和 WB 的成因。Petracci 等[13]总结了肌肉缺陷的发生机制(图 3)。

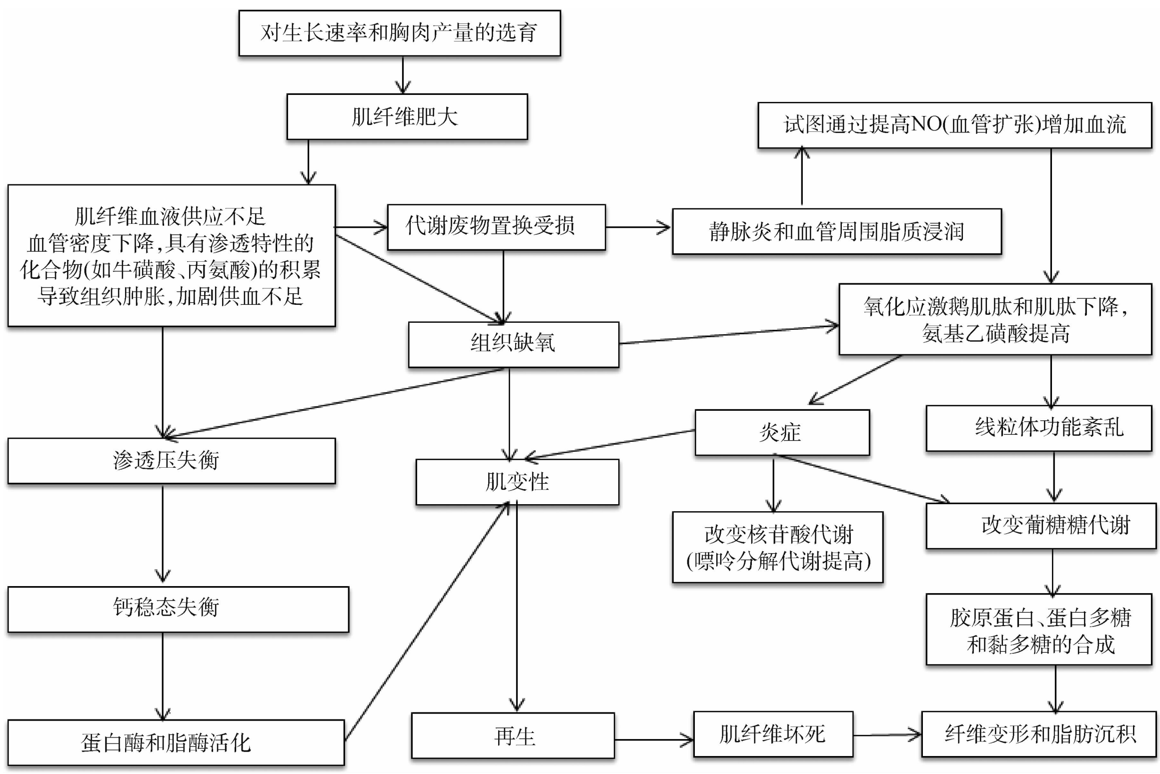


图 3　WS、WB 和 SM 可能的发生机制[13]

Fig. 3　Schematic representation of the possible etiologies and mechanisms leading to the development of white striping (WS), wooden breast (WB), and spaghetti meat (SM) abnormalities[13]

4.2.1　缺氧与氧化应激　　研究结果表明，肉鸡胸肌内部毛细血管密度小，血管化程度低，氧气供应不足，代谢废物的累积造成氧化应激增加[19,23,63-64]。肌肉快速生长可能导致类似筋膜室综合征的状态，从而致使 WS 和 WB 发生[65]。Malila 等[66]通过定量分析发现，缺氧诱导因子 1(HIF1A)的转录物在 WS 和 WB 样本中增加了约 1.7 倍；Mutryn 等[67]对 WB 进行 RNA-Seq，通过对超过 1 500 个不同的基因分析发现，部分基因与肌肉缺氧、细胞内钙量增加和肌肉纤维形态转变相关；Xing 等[68]研究表明，氧化应激诱导活性氧过量导致氧化损伤，进而改变动物体内 Ca^{2+} 的平衡状态，Ca^{2+} 平衡的紊乱会使肉质恶化，WB 尾部出现脊状突起及硬度增大可能与 Ca^{2+} 浓度增加导致的肌肉收缩有关。

4.2.2　肌纤维类型转换　　肌纤维分为Ⅰ型纤维(慢速收缩-红色肌纤维)和Ⅱ型纤维(快速收缩-白色肌纤维)两种，肉鸡胸肌纤维几乎完全由Ⅱ型纤维组成。畜禽出生后，肌纤维数量不再改变，而纤维类型持续转化[69]。纤维类型的转化次序为慢肌向快红肌转化，快红肌向中间型快肌转化，最终转化为快白肌，形态主要表现为肌纤维肥大[70]。研究人员从 WB 组织切片中观察到了肌纤维退化和再生[3]；WB 中肌红蛋白含量升高，而肌红蛋白主要分布在Ⅰ型纤维中，推测可能是Ⅱ型纤维细胞凋亡和Ⅰ型纤维

的再生导致的[67]；Zambonelli 等[71]发现，与肌纤维合成相关的部分基因在 WB 中上调，如富含半胱氨酸蛋白 2（*CSRP*2）、*FAM*64A 基因；Papah 和 Abasht[72]发现，WB 中慢肌纤维型基因的细胞定位表达增加。由此可见，WB 发生过程中存在Ⅱ型纤维向Ⅰ型纤维转换。

4.2.3 胸肌卫星细胞 骨骼肌卫星细胞具有干细胞的潜力，有自我更新、修复和再生的作用，在肌肉损伤修复中发挥着重要作用。据报道，骨骼肌卫星细胞可通过诱导增殖和分化，形成成熟的成肌细胞，这些肌细胞与损伤周围幸存的肌纤维相结合，生成新的肌纤维或修复损伤的肌纤维[73]。Harding 等[74]研究发现，当受到热刺激时，厌氧型胸肌卫星细胞比好氧型股二头肌卫星细胞更容易发生脂肪转化。已有研究表明，胸肌内的脂肪并非来源于肝合成，可能在胸肌损伤修复过程中产生[12]。提示，WS 和 WB 内脂肪可能来源于自身卫星细胞转化。Meloche 等[75]发现，重度 WB 可改变 Myf-5＋和 Pax7＋肌源性干细胞的异质性和有丝分裂活性。Powell 等[76]研究发现，不同浓度 Met/Cys 比影响鸡胸肌和骨骼肌卫星细胞激活、增殖和分化，同时影响生长因子和信号转导关键基因（如肌源性调控因子 1（MyoD）、转录因子配对盒基因 7 等）的表达。未来有可能筛选出有效调控胸肌卫星细胞增殖分化的营养方案以达到缓解 WS 和 WB 的作用。

4.2.4 代谢异常 WS 和 WB 的组成成分变化，主要表现为脂肪含量升高，蛋白含量下降，代谢相关研究也集中在这两个方面。Papah 和 Abasht[72]利用 RNA 原位杂交技术分析 WB 样品发现，脂蛋白脂肪酶（LPL）在鸡毛细血管内皮细胞和小口径静脉中均有表达，RNA-seq 分析显示，第 3 周时与脂质相关的基因表达上调，第 7 周时与脂质相关的基因表达下调。Zhao 等[77]研究发现，WB 通过上调乳酸脱氢酶（LDHB）和一元羧酸转运蛋白（MCT4）水平来降低乳酸含量。De Almeida Mallmann 等[78]发现，与正常鸡相比，WB 鸡骨髓内脂肪沉积增加、骨矿化降低。代谢组学研究结果显示，WS 代谢紊乱影响了肉鸡的脂肪酸氧化、TCA 循环、精氨酸代谢、牛磺酸代谢，导致细胞肿胀、渗透压改变[79]；WB 的糖酵解活性减弱，己糖胺途径、葡萄糖醛酸途径活性增强，透明质酸合成酶 2 基因的表达水平增高[23]。蛋白组学分析显示，肌病的发生与蛋白质代谢上调和翻译增加密切相关，蛋白代谢的增加可能与较高的生长速度和/或退行性肌病的修复再生有关；重度肌病碳水化合物代谢水平降低，pH 升高[80]。

4.2.5 分子机制 应用分子生物学技术从分子水平解析 WS 和 WB 的发生机理，取得了显著进展。Fare 等[81]比较 WB 与正常胸肌基因表达，发现 113 个差异表达，其中 71 个表达上调，42 个表达下调，密切相关的生物学途径包括跨膜、代谢、细胞外基质受体相互作用。Vignale 等[82]分析发现，重度 WS 的 MuRF1 相对表达水平显著升高，atrogin-1 表达水平略有升高。Zambonelli 等[71]发现了 WS 和 WB 中与肌肉发育、多糖代谢过程、蛋白多糖合成、炎症和钙信号通路相关的 204 个差异表达基因（DEGs）（102 个表达上调，102 个表达下调）。Marchesi 等[83]通过转录组学富集到与 WS 相关的 36 个显著高表达，密切相关的生物学过程为免疫系统激活、血管生成、缺氧、细胞死亡和横纹肌收缩等。后续研究需要在这些结果基础上深入分析才能阐明 WS 和 WB 发生的分子机制。

5 小 结

综上所述，WS 和 WB 给肉鸡养殖业造成了巨大的经济损失，是目前亟待解决的难题之一。现有研究已经揭示了异质肉的发生与遗传、体重、胸肌重、生长速度以及饲料营养等因素存在相关，也利用生物学技术陆续从细胞、分子水平，缺氧、代谢、肌纤维类型转换等多角度探究了肌病的成因，但具体的发生机理仍不明确。后续研究应当在已有报道的基础上，一方面继续探究精准营养等环境改善措施，选择最佳饲养管理方案；另一方面深入探究胸肌内代谢异常机制及相关的分子遗传基因挖掘，从源头找出 WS 和 WB 的发生原因，以期利用遗传选育的方法降低其发生率。

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