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昆虫滞育虫态及感应光周期的敏感阶段

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摘要：昆虫属变温动物，为度过不良环境条件，许多昆虫利用滞育特性适应环境的变化，通过对昆虫滞育及感应光周期的敏感阶段进行描述，拟让人们更清楚地了解昆虫滞育期及感应光周期敏感阶段昆虫生物学特性。

关键词：昆虫；滞育；滞育虫态；光周期；敏感阶段

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Characters of Insect Diapause Stage and Photoperiod Sensitive Stage

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Abstract: Insects are poikilothermal animal, in order to tide over serious environmental conditions, many insect use diapause characteristics to adapt to environment changes, through out describing diapause and photoperiod sensitive stage, in order to let people understand clearly about biology characteristics of insect diapause stage and photoperiod sensitive stage.

Key words: insect; diapause; diapause stage; photoperiod; sensitive stage

昆虫属变温动物，其生命活动受环境条件的制约，极端的环境条件(如高温、低温、干旱、食物缺乏等) 会影响其正常生活，也会威胁昆虫种群和个体生命的维持。为渡过不良环境条件，许多昆虫具有滞育的特性[1]。滞育不同于休眠，滞育常在不利环境还未到来之前就被诱导，昆虫一旦进入滞育，即使环境条件变得十分有利，滞育也不会很快消失，必须经历一段相当长的时期才能完成。本文就昆虫进入滞育虫态和感应光周期的敏感阶段进行介绍。

1　滞育虫态与分类单元

昆虫滞育虫态在亲缘关系相近的种类中常相同，如蜻蜓目(Odonata)中，大多数科的昆虫以幼虫滞育，少数以卵滞育[2]；竹节虫目(Cheleutoptera)大多数科以卵滞育[3]；直翅目(Orthoptera)蝗科(Acrididae)大多数以卵滞育[4]；半翅目(Heteroptera)黾蝽科(Gerridae)以成虫滞育[5]；鞘翅目(Coleptera)瓢虫科(Coccinellidae)以成虫滞育[6]；鳞翅目(Lepidoptera)天蚕蛾科(Saturniidae)以蛹滞育[7]；膜翅目(Hymenoptera)泥蜂科(Sphecidae)以幼虫或预蛹滞育[8]。然而也有少数亲缘关系十分密切的种类，滞育虫态也不一样，如日本柞蚕(*Antheraea yamamai*)以胚胎滞育，而柞蚕(*Antheraea pernyi*)以蛹滞育[9]；多化性的食蚜蝇(*Epistrophe baltea*)以成虫滞育，而一化性的食蚜蝇(*E.bifasciata*)以末龄幼虫滞育[10]。有些昆虫种类能以不同滞育虫态进入蛰伏，例如步甲主要以成虫或者幼虫进入滞育[11]；夜蛾科可以蛹，成虫或幼虫滞育；叶蜂可以卵或预蛹滞育；沼蝇可以卵、幼虫、蛹或成虫滞育。根据 Danks[12]统计资料，滞育虫态在各目中的分布，以卵、幼虫、蛹和成虫滞育的种类，分别占全部种类的 17%，35%，19%和 28%。在鳞翅目中，滞育虫态的比率

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依次为 3%，45%，48%和 4%。芬兰昆虫学家 Seppänen[13]曾报道了芬兰 875 种鳞翅目昆虫的越冬虫态，15%为卵，45%为幼虫，37%为蛹，3%为成虫。Scott[14]对北美 290 种蝴蝶的滞育虫态进行调查时发现，以卵滞育越冬的占 13%，以幼虫滞育越冬的占 58%，以蛹滞育越冬的占 24%，而以成虫滞育越冬的仅占 5%。Denlinger[15]报道了热带地区 73 种昆虫的滞育虫态，卵占 7%，幼虫占 32%，蛹占 30%，成虫占 31%。章士美[16]报道了我国夜蛾科 11 亚科 112 种的越冬虫态，卵占 8%，幼虫占 25.9%，蛹占 42%，成虫占 10.7%。另外我国半翅目 23 科 264 种昆虫的越冬虫态，卵占 6%，若虫占 8.3%，成虫占 82.6%，其中以两种或两种以上虫态越冬的占 3.1%[17]。

2 滞育虫态与地理分布

Johansen[18]指出在北极地区的昆虫中，占主导地位的越冬虫态是幼虫。Danks[19]报道在高寒北极地区的 90 种昆虫中，幼虫越冬占了 92%，而越冬的卵，蛹和成虫仅占 4%，1%和 3%，而到了温带地区幼虫越冬的比例明显减少。Holmquist[20]指出在冷温带森林地区除了卵没有取样之外，幼虫、蛹、成虫越冬的昆虫分别占所发现的 329 个物种的 25%，6%和 68%。成虫的优势在一定程度上是由于在这些资料中臭虫，蚂蚁还有甲虫的普遍存在。但是这些样本也显示了温带地区幼虫越冬的比例比北极高纬度地区更少[21]。

3 滞育虫态与滞育类型

滞育分为夏季滞育和冬季滞育。Masaki[22]指出在夏季和冬季滞育中，主要滞育虫态往往是相似的，例如鞘翅目昆虫多以成虫进入越夏和越冬。他还指出了一些显著地区别：例如在鳞翅目中通常以蛹进入滞育，但除此之外更多的以幼虫越冬，以成虫进入夏蛰。这样的差别在大的目中很难解释，因为这些个体的生物学特性在属和科的级别上比较接近。然而相似的滞育要求，以及与之相关的改变，比越冬和越夏的差异更显著。

4 滞育虫态及感应光周期敏感阶段

昆虫滞育可出现在卵期、幼虫期、蛹期和成虫期，分别称为卵滞育、幼虫滞育、蛹滞育和成虫滞育。但卵滞育这个术语不够准确，因为至今还没有发现卵一产下就进入滞育的现象。事实上，卵一产下，胚胎发育立即开始，最早的胚胎滞育出现在卵裂前期[23]。因此，胚胎滞育是一个更好的词。大多数昆虫中，仅以生活史的某一固定虫态进入滞育，但昆虫的滞育虫态在种间存在差异，甚至在同一种内，滞育虫态可因昆虫栖息地的差异及滞育时间的不同而发生变化。

4.1 卵滞育

卵滞育可以发生在胚胎形成的各个时期，牧场大蚊(*Tipula simplex*)的卵在细胞核或卵裂前期进入滞育[23]。石蝇[24]和竹节虫[25]的卵滞育发生在胎盘形成前。大多数盲蝽[26]，石蝇[27]和玉米根叶甲(*Diabrotica virgifera*)[28]滞育发生在早期胚动期。豆长刺萤叶甲(*Atrachya menetriesi*)[29]，蜻蜓(*Lestes congener*)[30-31]和赤蜻(*Sympetrum danae*)[32]在“胚动”前不久以胚胎滞育。滞育发生在胚动早期的情况相对比较常见，直翅目[33]，稻飞虱 (*Muellerianella brevipennis*)[34]，蜉蝣(*Baetis vernus*)[35]和一些叶锋[36]在胚体下降完成前进入滞育。卵滞育似乎最常发生在胚胎后期。蜉蝣(*Ephemerella ignita*)滞育发生在背面愈合之前[37]。螽斯科滞育发生在胚胎后期的情况最普遍[38]。大多数伊蚊(*Aedes*)，许多蜻蜓[39]和一些盲蝽[40]的滞育胚胎完全形成。舞毒蛾(*Lymantria dispar*)[41]，天幕毛虫(*Malacosoma testacea*)[42]，欧洲弄蝶(*Thymelicus lineola*)[43]，麦地种蝇(*Delia coarctata*)[44]和沼蝇科[45]的一些昆虫以蜕裂幼虫进入滞育。胚胎滞育的昆虫，感应光周期的敏感阶段多出现在母性阶段，但有些种类，胚胎本身也对光周期敏感[46]。一些昆虫滞育发生在子代的卵期，母代成虫期是感受环境条件的敏感虫态。如二化性的飞蝗种群，成虫于短日条件下饲养，则诱导子代的卵进入滞育，长日条件下饲养，则子代的卵不进入滞育；而一化性的飞蝗种群，成虫不管是短日条件还是长日条件下饲养，子代的卵均为滞育卵[47]。一些蚊类的中期或后期胚胎对光周期敏感，包括三列伊蚊(*Aedes triseriatus*)[48-49]，(*A.campestris*)[50] 和(*A.canadensis*)[51]。(*A.dorsalis*)[52-53]，(*A.sollicitans*)[54]和 (*Psorophora ferox*)[51]的卵在胚胎发育的早期。

4.2 幼虫滞育

在不同昆虫中，几乎所有龄期幼虫滞育的情况都有报道。云卷蛾属的一些昆虫在幼虫孵化后取食

之前立即以一龄幼虫滞育[55]，西伯利亚松毛虫(*Dendrolimus sibiricus*)[56]以二龄幼虫进入滞育，云杉卷叶蛾(*Choristoneura fumiferana*)[57]在蜕皮至二龄并在开始取食之前进入滞育。一些昆虫以中间龄期幼虫进入滞育，尤其是在鳞翅目昆虫中[58]，例如豹灯蛾(*Arctia caja*)[59]，梨黄卷蛾(*Archippus breviplicanus*)[60]，醋栗褐卷蛾(*Pandemis ribeana*)[59]和苹小卷叶蛾(*Adoxophyes orana*)[61]，落叶松鞘蛾(*Coleophora laricella*)[62]，红斑蝶(*Limenitis archippus*)[63-64]和斑点木蝶(*Pararge aegeria*)[65]。少数昆虫的滞育可以发生在幼虫的不同龄期。西伯利亚松毛虫(*Dendrolimus sibiricus*)和欧洲松毛虫(*D.pini*)[39]可以以除了一龄幼虫以外的任何龄期幼虫越冬。八字地老虎(*Xestia cnigrum*)可以以三龄和四龄幼虫进入滞育[59, 66]。在某些情况下滞育发生在不同幼虫期依赖于不同的刺激。例如，在中性温度下光周期诱导亮褐异针蛉(*Pteronemobius nitidus*)滞育发生低龄幼虫阶段，在高温下发生在老龄幼虫期[67]。以幼虫滞育的昆虫，大多数种类的幼虫本身对光周期敏感，敏感期可出现在整个幼虫期，也可出现在 1 至 2 个龄期；在极少数种类中，幼虫滞育与成虫或卵期接受的光周期有关[46]。梨小食心虫(*Grapholitha molesta*)[68]和苹果蠹蛾(*Cydia pomonella*)[39]在滞育前的早期最敏感。几种昆虫在滞育之前的整个阶段敏感，包括醋栗褐卷蛾(*Pandemis ribeana*)[59]，红铃虫(*Pectinophora malvella*)[69]和桃小食心虫(*Carposita niponensis*)[70]。然而在大多数昆虫中，在滞育发生之前的一到两个龄期最敏感。在全变态昆虫中这种界限非常明显，例如松叶蜂(*Neodiprion pini*)[71]的幼虫只在结茧前的最后一个龄期对光周期敏感，芜菁叶蜂(*Athalia rosae*)[72]只在取食的最后时期和结茧开始之间的这段时期对光周期敏感。在不全变态昆虫中界限并不那么精确，例如蟋蟀(*Gryllus campestris*)[73]在滞育发生前的最后三个龄期均对温度敏感。相当少的昆虫幼虫和卵均敏感，例如棉红铃虫(*Pectinophora gossypiella*)[39]二化螟(*Chilo suppressalis*)[74-75]和松黄叶蜂(*Neodiprion sertifer*)[76]。(*Lygaeonematus compressicornis*)[59]比较特别，因为它是在卵的最后胚胎阶段对光周期敏感，并不是幼虫阶段，尽管滞育发生在预蛹阶段。敏感期的持续时间依据实验条件的不同也可能不同。例如菜粉蝶(*Pieris brassicae*)如果光周期延长它的敏感期在第三次蜕皮之后持续 5 天，但是如果光周期缩短的话持续时间为 8 天[77]。

4.3 蛹滞育

曙夜蛾(*Adisura atkinsoni* Moore)以蛹进入滞育[39]，甘蓝地种蝇(*Delia radicum*)的夏眠发生在蛹显头期[78]。很少有昆虫的滞育发生在成虫蜕裂期。然而，Seppänen[13]曾报道 40 种以蛹滞育的荷兰鳞翅目昆虫以蜕裂的成虫越冬；这些占了以明显的蛹越冬昆虫的 13%。一些澳大利亚尺蠖以蜕裂的成虫夏眠[79]。道格拉斯冷杉球果蛾(*Barbara colfaxiana*)[80]和西方角蝇(*Haematobia irritans*)[81]也是以蜕裂的成虫越冬。以蛹滞育的昆虫，感应光周期的敏感阶段多出现在幼虫期，敏感性常随着幼虫龄期的增加而加强，也有些种类的敏感期出现在幼虫期的末龄阶段；在极少数种类中，敏感期可出现在胚胎期和部分幼虫期。甘蓝夜蛾(*Mamestra brassicae*)的敏感性随着龄期增加而增加[82]。欧洲粉蝶(*Pieris brassicae*)和菜粉蝶(*P.rapae*)在倒数第二龄最为敏感[83]。曙夜蛾(*Adisura atkinsoni Moore*)感应光周期的敏感阶段为一龄幼虫[84]。一些家蚕蛾，包括柞蚕(*Antheraea pernyi*)[85]，(*A.polyphemus*)[86]和惜古比天蚕蛾(*Hyalophoracecropia*)[85-86]在蛹化前的最后两个龄期最为敏感。甘蓝夜蛾(*Mamestra oleracea*)只在蛹羽化前的最后一次蜕皮期敏感[87]。已有报道，一些昆虫在幼虫发育早期敏感性更显著，例如棕尾别麻蝇(*Boettcherisca septentrionalis*)和肥须亚麻蝇(*Parasarcophaga similes*)[88]和(*Sarcophaga assipalpis*)[39]，这些昆虫的胚胎只在其生长发育的最后两天敏感[89]。葡萄小卷蛾(*Polychrosis botrana*)只在卵期和一龄幼虫期敏感[59]。美国白蛾(*Hyphantria cunea*)的幼虫期的前期最为敏感[90]。最后，一些昆虫在整个幼虫阶段均敏感，包括梨剑纹夜蛾(*Acronycta rumicis*)[91]，滞育是由在一个重要阶段积累的光周期信息所决定的。其他的例子包括(*Phalaenoides glycinae*)[92]，和夜蛾属的一些昆虫[39]。在一些昆虫中卵早期阶段也很敏感，例如葡萄小卷蛾(*Polychrosis botrana*)[59]，棉铃虫(*Heliothis punctigera*)[93]，(*H.zea*)[94]，烟草天蛾(*Manduca sexta*)[95]。在其他的昆虫中，蛹早期也很敏感，例如棉铃虫(*Heliothis punctigera*)[93]和(对温度敏感而不是光周期)苹果实蝇(*Rhagoletis pomonella*)[96]。麻蝇(*Sarcophaga argyrostom*a)和其他种的胚胎在母体时

期获得了人工恒定的光照时，幼虫敏感期可能会延长[39]，而胚胎经过短光照处理后的幼虫敏感期会很短[97]。

4.4 成虫滞育

成虫滞育的特点是出现生殖延迟，特别是在雌成虫中。这可能与昆虫的静止情况一致或仅仅是生殖器官的功能性停止。这种类型的滞育在鞘翅目和鳞翅目昆虫中最常见，但在双翅目、直翅目、半翅目中也会出现。鞘翅目昆虫成虫在滞育期间表现为雌性卵巢小管不发育[98]，原卵区长度和宽度都只有非滞育个体原卵区长度和宽度的 60%~70%，雄性附腺纤细且短，精巢萎缩，呈黄色，无精子或含少量精子[99]。鳞翅目昆虫成虫滞育亦表现为生殖系统停止发育，雌蛾不交配或很少交配[100]，例如眼蝶卵巢发育不成熟，卵巢小管中含有畸形卵。苎麻赤蛱蝶(*Vanessa indica* Herhs)以成虫进入滞育[101]。东亚小花蝽[*Oriusauteri* (Poppius)]以雌成虫进入滞育，滞育个体的卵巢很小或者未发育[102]。以成虫滞育的昆虫，感应光周期的敏感期多出现在成虫阶段，羽化后的初期最敏感；有些种类的敏感期主要出现在幼虫期。例如秋家蝇 (*Musca autumnalis*)[103]成虫只在羽化后的两天敏感，一些甲虫，例如九纹瓢虫(*Coccinella novemnotata*)[104]在羽化后的一周内敏感。东亚小花蝽对光周期刺激反应的敏感虫态为若虫期，低龄或高龄若虫均能感受短光照对滞育的诱导作用。卵期和成虫期对短光照的滞育诱导作用不敏感[102]。一些昆虫的成虫的敏感性取决于生殖发育的一两个时期，每个时期要求不同的光周期。在一些其他昆虫中，幼虫也略微敏感，但通常对成虫滞育没有影响，除非成虫是在中间光照条件下饲养。很多昆虫只在幼虫的早期敏感（有时蛹期也敏感）。在这些昆虫中，刚羽化的成虫在早期条件下被诱导进入休眠，既使一直处于羽化时期的条件下，仍需要一段滞育发育的时期才能繁殖。有时候敏感性在幼虫期会有所变化，例如甘蓝 B 型烟粉虱(*Aleyrodes proletella*)在三龄幼虫期最为敏感[105]。通常，幼虫敏感性最强的时期是在末龄期，例如欧原花蝽(*Anthocoris nemorum*)[106]，马利筋长蝽(*Oncopeltus fasciatus*)[107]和草蛉(*Chrysoperla plorabunda*)[39]。最后，少数的昆虫在未成熟期和成虫期感应诱导信号。尖音库蚊(*Culex pipiens*)[108]的这种现象只包括蛹期和成虫期，盔唇瓢虫(*Chilocorus bipustulatus*)[108]的幼虫，蛹和成虫均敏感，但是大多数其他昆虫，只有幼虫和成虫阶段最敏感。在实验条件下，非诱导性的环境（例如长日照）对于刚羽化成虫的影响可以使更早阶段的诱导效果（例如短日照）无效，例如绿蝽(*Acrosternum hilare*)[109]。在正常条件下，幼虫的敏感性有助于加强诱导因素对成虫的影响。在一些情况下最大的诱导结果需要幼虫和成虫阶段条件的转变，例如斑须蝽(*Dolycoris baccarum*)。

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