



进展与综述 REVIEWS

人为活动对野生动物体色适应的影响

赖馥茜¹, 卢思辰², 翟彬宇², 黄翠冰²,
廖宇浩², 汪海涛², 李旭^{1*}, 卜荣平^{2*}

(1. 云南省高校极小种群野生动物保育重点实验室, 西南林业大学, 昆明 650224;
2. 广西北部湾海洋生物多样性养护重点实验室, 北部湾大学海洋学院, 钦州 535011)

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摘要

在人类世,人类活动的不断扩展和加剧,使野生动物的生存环境发生了巨大变化。这些变化不仅影响了野生动物的生存和繁衍,还对其体色适应产生了深远影响。体色作为动物适应环境的重要特征之一,对野生动物的生存至关重要。栖息地破坏、全球气候变暖、城市化和环境污染等人为活动因素导致的环境快速变化,破坏了动物基于颜色的伪装、通讯和体温调节等能力。动物改变体色增强反捕食和体温调节适应能力,但环境变化的速度超过很多动物的体色适应速度,种群面临强大的生存压力。未来的研究应该综合考虑不同干扰类型的影响、人为活动造成的生态系统破坏、动物体色改变的适宜区间和体色改变的机理等,为理解人为活动对动物体色变化的影响提供更多的研究证据。本研究针对人为活动对动物体色适应的影响进行综述,为理解野生动物的体色适应和开展相关保护工作提供参考。

Body Color Adaptation of Wildlife Under Anthropogenic Influence

LAI Fuxi¹, LU Sichen², ZHAI Binyu², HUANG Cuibing²,
LIAO Yuhao², WANG Haitao², LI Xu^{1*}, BU Rongping^{2*}

(1. Laboratory of Colleges and Universities in Yunnan Province Tiny Populations of Wildlife Conservation, Southwest Forestry University, Kunming 650224, China;

2. College of Marine Science, Guangxi Key Laboratory of Beibu Gulf Biodiversity Conservation, Beibu Gulf University, Qinzhou 535011, China)

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第一作者简介: 赖馥茜(1997—),女,硕士研究生;主要从事动物多样性保护研究。E-mail:fuxilai47@163.com

*通信作者: 李旭, E-mail:lixu.swf@hotmail.com; 卜荣平, E-mail:rpbu@bbgu.edu.cn

Abstract: Body coloration, as one of the important strategies to adapt to environment, is crucial for the survival of wildlife. In the Anthropocene epoch, as human activities continue to expand and intensify, wildlife habitats have undergone significant changes. These changes not only impact the survival and reproduction of wildlife, but also make profound influences on their body color adaptation. Rapid environmental changes caused by anthropogenic factors such as habitat destruction, global climate warming, urbanization, and environmental pollution have impaired animals' color-based abilities including camouflage, communication, and thermoregulation. Animals alter body coloration to enhance anti-predation and thermoregulatory adaptations; however, the accelerating rate of environmental change now exceeds the adaptive capacity of coloration adjustments in many species, subjecting populations to intense survival pressures. Future studies should systematically integrate analyses of impacts from distinct disturbance types, ecosystem degradation caused by human activities, optimal thresholds for chromatic modifications, and molecular and physiological mechanisms driving coloration changes. Such multidisciplinary approaches are critical to deciphering anthropogenic impact on chromatic adaptation and generating robust empirical evidence. This study comprehensively reviews the effects of human activities on animal coloration adaptation, aiming to provide a reference for understanding wildlife body color adaptation and carrying out related protection work.

动物的体色是其最突出的形态特征,具有多种功能:伪装、惊吓、体温调节、威慑、性选择信号和作为视觉诱惑等^[1]。对动物颜色的研究有着悠久的历史,19世纪以前,科学家意识到动物的颜色与环境的相似性使它们不容易被捕食者发现和捕食,颜色多样性是动物适应不同环境自然选择压力的结果^[2],但因为缺乏体色量化的技术,该阶段的研究主要是描述观察的案例。20世纪,得益于光纤光谱在体色研究中的应用,颜色的量化分析得到快速发展,动物体色的适应进化得到大量的证据支持^[3]。21世纪以来,随着科技的进步,越来越多的新技术被应用到动物体色的研究中,包括数码摄影^[4]、深度神经网络^[5-7]、仿生学^[8]、扫描电镜^[9]和多组学技术^[10-11]等,促进了该领域的快速发展,动物体色的遗传特征得到验证,进一步增强了对动物发育、遗传学和进化的理解^[1,12]。

动物的体色可以分为生物色^[13]和结构色^[14],前者是存在于动物皮肤、眼睛等部位不同色素细胞中极微小的色素而形成的体色,后者是动物体表细微的物理结构引起光波发生折射、衍射或干涉而产生的各种颜色。体色形成的主要机制是色素沉积,最常见的2种色素是黑色素和类胡萝卜素。黑色素的密度和分布会影响动物的体色外貌,产生对伪装和交流都很重要的可见颜色变化^[15]。黑色素有2种化学变体——真黑色素和褐黑素,真黑色素产生黑色或棕色,褐黑素产生淡黄色至红色^[16]。类胡萝卜素

不能自身合成,只能通过食物摄入,食物组成会影响类胡萝卜素的可获得性而影响黄色素细胞的形成,从而影响体色^[17-18]。生物体表现出的颜色和图案的多样性主要取决于体表各种色素的含量和分布^[15],色素选择性地吸收特定波长的光,同时允许其他波长的光被反射^[19],颜色的变化可以通过改变色素数量和色素聚集,或者通过含有色素的细胞器的分散或聚集而实现^[20]。色素通过一系列复杂的化学变化,被色素沉着机制中涉及的不同的酶催化^[21]。

动物的体色具有可塑性,可以随着温度、光线、栖息地特征、猎物和捕食者的视觉和行为等因素而改变^[1,22]。复杂多变的选择压力致使动物形成多态性体色。体色多态性是一个种群中相同年龄和性别的个体,在强烈的遗传控制下,存在2种或2种以上不同的颜色^[23-25]。人类活动对野生动物造成了强烈的生存压力^[26-27],已经成为动物进化适应的主要影响因素之一^[28-29]。体色是动物适应选择压力的重要特征,也受到了人为活动的影响^[30-32]。本研究针对栖息地破坏、全球气候变暖、城市化和环境污染等人为活动对动物体色适应的影响进行综述,为理解野生动物的体色适应和开展相关保护工作提供参考。

1 人为活动导致的生态影响

1.1 栖息地破坏

人为活动会破坏自然栖息地,生活在这些栖息

地的生物会面临与自然栖息地不同的干扰。生存在不同栖息地的动物种群通常表现出丰富的体色变异,栖息地破坏阻碍了动物融入环境的长期适应。在人类世,陆地和水生生态系统都受到人为活动的影响,森林、湿地和珊瑚礁等自然背景被人工或破碎的环境所取代,栖息地的变化速度超过了动物的适应速度^[33-34]。颜色的产生、感知和功能都受到栖息地破坏的影响,这可能造成捕食增加和繁殖成功率降低^[35]。栖息地破坏,迫使动物需要适应新的背景色和光照条件,从而可能发生体色进化适应。

对于水体栖息地来说,人为建设引发水体浑浊,水体富含泥沙等无机颗粒物,致使水下光量衰减^[36],影响水生动物的体色适应。光照度是动物生理颜色变化的常见刺激,促使动物变得更加隐蔽^[37-39],是降低潜在被捕食风险的适应。在浑浊的水域中,水下的光照环境发生改变,之前有效的适应性体色可能会变得无效^[40]。为了适应环境中光照度的变化,水生动物会改变颜色避免被捕食^[41-44]。另外,海洋酸化、海水温度上升和污染导致珊瑚礁白化,体色与明亮珊瑚相匹配的鱼类在白化或死亡珊瑚背景下会伪装失效^[45],降低它们对珊瑚礁栖息地的适应能力。

对于陆地生态系统来说,森林栖息地的破坏,阻碍了动物的反捕食适应^[46]。森林生态系统复杂多变的环境利于动物的伪装^[47],林下动物利用动态变化的栖息地来避免被捕食者发现^[48-49]。森林栖息地破坏还会使食物链改变,导致依赖于食物获得毒素的动物减少,相应的拟态动物也会改变颜色以适应模拟对象的减少,从而适应捕食压力^[50]。森林栖息地的破坏也会使动物失去林冠的遮盖,遭受更强的紫外线照射,影响林下动物维持其自然色素沉积的能力,更容易被捕食者发现,降低生存机会^[51]。

1.2 全球气候变暖

葛洛格法则(Gloger's rule)认为,生活在温暖潮湿地区的动物(特别是鸟类和哺乳类)体色较深,而生活在寒冷干燥地区的动物体色较浅^[52]。因此,随着全球气候变暖,动物的颜色可能会变深^[53]。然而,综合分析表明动物体色与湿度相关,湿度越高体色越深,而与温度的相关性较差^[54]。全球气候变暖会引起干旱面积扩张^[55],动物体色变浅。全球气候变暖同时会招致寒冷地区暖湿化,如青藏高原北缘的暖湿化^[56],可能会造成当地动物体色发生适应性变深。尽管没有办法明确全球气候变暖对动物体色的

影响是否符合葛洛格法则,但对动物体色有影响是可以明确的,会加速动物体色的进化适应。

全球气候变暖严重影响依赖季节性变色生存的物种。动物的表型可塑性可能有助于某些物种应对气候变化,但这种适应性是有限的,特别是对于那些依赖于颜色季节性变化的物种^[35]。对于温带和北极环境中的物种,它们的皮毛、羽毛或皮肤会发生季节性变化,以融入雪或植物背景。由于气温升高,积雪减少,动物的体色与环境不匹配,致使动物被捕食风险增加和面临其他生存挑战^[57-60]。

进化速率假说(evolutionary speed hypothesis)认为,较高的温度会加快分子变异速度,特别是在变温动物中这种机制起主要作用^[61],气候变暖可能会加速变温动物的体色变异。另外,变温动物对温度变化特别敏感,由于过热或无法伪装以适应新的环境,它们面临着更高的死亡率,温度的变化直接影响它们的体温调节色素沉着和整体生理。热黑化假说(thermal melanism hypothesis)认为,深色的变温动物个体在吸收热量功能中有优势,在寒冷的气候中有益^[62]。两栖动物和爬行动物严重依赖环境温度进行体温调节,因此特别容易受温度变化的影响,温度变化会影响黑色素的合成,而黑色素对于伪装和抵御紫外线辐射至关重要^[63]。气候变暖在城市中形成热岛效应,不同颜色的蜥蜴利用不同的栖息地以抵御温度的快速升高,棕色的小脊阿诺利蜥(*Anolis cristatellus*)更多利用人造地面栖息地,而绿色的层纹阿诺利蜥(*A. stratulus*)会利用更高的树枝^[64]。

同样是变温动物的昆虫,也面临全球气候变暖带来的生存压力^[65]。在寒冷环境中的昆虫颜色更深,深色的身体比浅色的身体能吸收更多的太阳辐射,使深色的个体能够在较冷地区保持更长时间的活动,这可能会增加繁殖成功率和摄食率^[66-67]。随着温度的上升,深色个体在温暖的春季失去了体温调节优势,会调整为更浅的颜色^[68-71]。因此,全球气候变暖可能会导致昆虫的体色变浅,但仍需更多的研究案例支持。

1.3 城市化

城市化改变了自然生态系统的结构,迫使许多物种改变它们的颜色,以融入混凝土和玻璃等城市新环境^[72]。在城市环境中,栖息地背景从以草坪、灌木和树木为主的城市化程度最低地区的绿色变为以不透水表面为主的高度城市化地区的灰色^[73]。当

前,对于城市动物的体色适应存在两种观点,一种观点是“城市黑化”,为了适应城市栖息地的灰暗色调,生活在城市栖息地中的物种,往往表现出体色黑化模式,体色多态的物种在城市地区比非城市地区更倾向于颜色更深、黑化、暗沉和色彩减少^[74-76]。城市工业区内动物的黑色图案或条纹比自然栖息地的种群更多,以适应城市栖息地的变化^[77-78]。城市环境中动物颜色更暗的原因可能是城市饮食中含胡萝卜素的食物比非城市环境的更少,致使动物无法形成鲜艳体色^[79]。另一种观点是“城市保护盾”,城市动物面临的捕食者减少,显眼的颜色危险性降低,隐蔽色需求降低,城市动物颜色反而变得鲜艳^[80]。

鸟类是适应城市化最成功的物种之一,从形态和行为都快速地作出改变,快速改变体色融入人为景观^[32,81]。城市环境颜色为暗色调,为了减少反捕食压力,鸟类减少羽毛的鲜艳色调以适应栖息地颜色的变化,减少了性选择特征^[82-83]。性选择特征是性二态鸟类繁殖的重要特征,在城市地区的性选择羽毛显著性降低^[84-87],可能会影响鸟类的交配和繁殖^[32],造成城市鸟类种群的长期存续压力。最近的Meta分析表明,在物种层面,城市鸟类种群表现为蓝色、深灰色和黑色,棕色和黄色减少,支持“城市黑化”观点;在群落层面,考虑物种丰富度的变化,城市鸟类体色多样性更高,支持“城市保护盾”观点^[12]。

无脊椎动物在城市中的颜色支持“城市黑化”观点,灰色调的城市环境中暗色的物种比鲜艳的物种更多,捕食压力是颜色黑化最主要的驱动因子^[88-89]。城市化会影响蝴蝶的栖息地利用特征,彩虹色的蝴蝶会避开城市地区,选择农村环境,而翅膀上有虎斑的个体在城市地区更常见^[90]。这些发现表明,城市动物正在进化,以应对视觉和热环境压力,但城市化的速度可能超过了一些物种的适应速度。

1.4 环境污染

污染可以通过改变栖息地背景颜色创造新的环境,对具有颜色多态性的动物产生间接影响。工业污染,特别是金属污染物和化学径流(如除草剂和杀虫剂)的释放,对动物的色素合成产生重大影响。如重金属(铅、汞和镉)等污染物和除草剂等化学物质会干扰动物的色素沉着,特别是类胡萝卜素的获得,造成颜色受损,进而影响动物交流、吸引配偶或融入环境的能力。工业污染还会改变环境颜色,使动物体色发生适应性改变,例如,桦尺蠖(*Biston betu-*

laria)黑化个体增加,但这种黑化可以随着栖息地的恢复而恢复^[89]。另外,工业颗粒污染造成的污垢可以通过降低鸟类羽毛的反射率直接影响其体色^[74]。

鸟类体色受污染影响严重,污染造成富含类胡萝卜素的食物可得性变化会引起鸟类体色变化^[91]。铅和汞等重金属减少了鸟类类胡萝卜素的摄入和沉积,使其羽毛颜色暗淡,这可能会阻碍交配展示和削弱社会信号^[85,92]。污染物不仅直接影响鸟类体色,而且作为应激源还可导致其氧化应激,降低其产生色素的生理能力^[93-94]。黑色的个体更能适应重金属污染,它们可以从血液中排除重金属,减少污染的潜在负面影响^[95]。农业中使用的除草剂和杀虫剂也被证明会干扰色素的产生,影响鸟类的类胡萝卜素代谢^[96-97],降低鸟类羽毛的活力,从而影响配偶选择和繁殖成功率。

环境污染能破坏水生动物对藻类和浮游生物等关键食物成分的获得,而藻类和浮游生物是类胡萝卜素和其他色素的主要来源。依靠富含类胡萝卜素的藻类和浮游生物获得鲜艳色彩的物种,特别容易受到水污染造成的食物短缺的影响,致使物种颜色暗淡,增加被捕食的风险^[46,98]。接触杀虫剂会损害两栖动物黑色素的合成,而黑色素对提供伪装的颜色至关重要,生活在农药污染水中的两栖动物皮肤更苍白,伪装能力降低,增加了被捕食的风险^[99]。微塑料的积累破坏了鱼类对色素细胞的神经控制^[100],引发其延迟或不完全的体色变化,损害了它们根据社会信号或环境线索调整体色的能力。

海洋酸化会干扰包括头足类动物在内的海洋物种的神经元功能,使其无法控制体色变化。在酸性越来越强的环境中,头足类动物对捕食者和环境线索的快速变色能力受损。这在很大程度上是由于控制色素体的神经信号通路被破坏,而色素体是头足类动物用来控制皮肤图案的。在海洋酸化造成的较低pH环境中,莱氏拟乌贼(*Sepioteuthis lessoniana*)对环境刺激的反应变慢,产生复杂颜色图案的能力降低,反捕食能力下降^[101]。

噪音和光源污染也会影响动物的体色适应。城市噪音和光污染会干扰两栖动物利用颜色信号进行有效交流的能力。在人为噪音环境中,视觉提示的效果较差,导致动物交配延迟和潜在的种群减少^[102]。海洋船舶噪音减少了欧洲绿蟹(*Carcinus maenas*)的体色变化,从而影响其伪装^[103]。夜间的

人造光也会影响两栖动物的行为和基于颜色的交流,光污染可以改变它们的昼夜节律,降低在黎明或黄昏活跃的物种基于颜色的信号有效性,从而扰乱交配信号和猎物检测^[104-105]。

1.5 其他因素

捕食是驱动动物体色变化的主要进化力量,人为捕捉对猎物物种施加选择压力,体色变化成为一种重要的生存机制。1834—1933年,加拿大东部的赤狐(*Vulpes vulpes*)银色变异频率减少,纯合子银狐(RR)的皮毛价值大约是赤狐(rr)皮毛的4倍,因此银狐更有可能被猎人捕捉,银色频率从1840年的约16%下降到1930年的5%^[106]。银狐的被捕猎概率高于赤狐,导致银色种群数量下降^[107]。

人类通过驯化、选择性繁殖和基因编辑等手段改变了野生动物的遗传信息。这些改变可能直接影响动物的体色表达,甚至创造出具有全新体色特征的新品种。例如,在龟类动物中,养殖场为了获得颜色艳丽或繁殖率高的龟类,对它们进行人为杂交,使其体色发生变化。这些龟类在放生活动中会被释放到野外环境中,造成野生动物的基因污染^[108],从而改变野生龟类的体色。

2 存在的问题

综上,人为活动对动物体色适应的影响获得了大量的研究证据,栖息地破坏、全球气候变暖、城市化和环境污染等人为活动因素破坏了动物基于体色的伪装、通讯和体温调节等功能。动物改变体色以增强在人为活动干扰下的反捕食和体温调节能力,但这种适应速度无法跟上环境变化的速度,种群面临强大的生存压力。因此,全面理解人为活动对动物体色适应的影响,对于野生动物保护工作至关重要。然而,当前的研究仍存在问题,阻碍了全面理解人为活动对动物体色适应的影响,也不利于对野生动物制定有针对性的保护计划。

2.1 不同干扰类型缺乏综合考虑

不同的人为干扰类型之间存在着相关关系,城市化往往会带来环境的污染,也会造成栖息地的破坏,因此需要综合去考虑这些因素对动物体色的影响。例如,鸟类在城市环境中暗色的个体增加,但尚不清楚是由城市化的灰调背景引起还是污染引起。因此,综合考虑这些干扰的影响非常重要,但目前相关研究缺乏,不利于全面理解野生动物在人类世的

非自然选择压力下的体色适应。

2.2 人为干扰造成的生态系统被破坏的影响研究不足

人为活动破坏了生态系统的平衡,导致食物链和生态位关系发生变化,可能影响野生动物的生存策略和体色进化适应。捕食者的减少可能引发猎物种群数量的增加和体色特征的变化,外来物种的入侵则可能改变本地物种的体色适应策略。相反,猎物的减少引发捕食者外源性色素的摄取减少,从而影响体色的形成^[51]。因此,研究人为活动干扰下食物链的动态变化对动物体色适应的影响至关重要,但目前研究较少。

2.3 对于动物体色变化的适宜区间有待研究

动物体色具有可塑性,能够帮助它们适应环境的变化,但这种能力的阈限并不清楚。人为活动造成的环境变化速度是过去自然环境演变速度所无法比拟的,动物的体色适应可能无法跟上环境快速变化的速度,人为影响会带来严重的生态后果。因此,研究动物体色适应人为活动的阈限,对于评估动物在未来面临的人为干扰压力至关重要。然而,关于动物体色变化的适应区间研究不足,不足以支持开展有针对性的动物保护计划。

2.4 人为活动导致体色变化的机理研究不足

人为活动造成的动物体色变化的研究往往关注的是体色可塑性的结果,但这种体色的变化可能会造成基因的变化^[90],在动物种群中形成稳定的生活史特征,通过基因复制而将变化后的体色遗传给后代,进而引起快速的生态适应策略。人为活动造成的生态干扰压力远远超过了自然选择压力,可能会加快动物体色的快速进化。开展人为活动导致动物体色变化的机理研究,可以评估体色适应性进化对策,但目前相关研究仍不足。

3 结语

动物体色因易测量和变异大等特点,长期以来都是理解动物进化和适应的重要内容。人为活动导致环境的快速变化,降低了野生动物的适应能力。自然栖息地被人工或破碎的环境所取代,动物体色的产生、感知和功能等受到影响,致使捕食增加和繁殖成功率降低。全球气候变暖,导致许多动物面临更强的捕食和体温调节压力。城市化改变了自然生态系统的结构,栖息地背景从绿色变为高度城市化

地区的灰色,影响了动物的反捕食和体温调节功能。环境污染会改变水体环境、噪音环境和光照环境等,影响动物体色的形成和信号的传输。为了应对环境的变化,动物通过主动改变体色以增强反捕食和体温调节适应能力,但同时也会失去其他选择优势,而且环境变化的速度超过很多动物的体色适应速度,种群面临强大的生存压力。全面理解人为活动对动物体色适应的影响,对于日益受到人类改变的世界中的野生动物保护工作和生物多样性管理至关重要。未来的研究应该综合考虑不同干扰类型的影响、人为活动造成的生态系统破坏、动物体色变化的适宜区间和体色变化的机理等,为理解人为活动对动物体色变化的影响提供更多的研究证据。人为活动对动物体色变化的研究需要进一步完善相关理论和方法,多学科交叉融合,也需要在人为环境中检验野生动物体色变化的生态意义,为人为活动日益增强背景下的野生动物保护提供理论依据。

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