

# 鸟类应激反应的诱发和影响因素

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**摘要:** 应激反应是动物应对环境变化或社会压力的重要机制, 表现为下丘脑-垂体-肾上腺轴 (HPA 轴) 被激活并产生糖皮质激素。鸟类的糖皮质激素主要是皮质酮。通过检测鸟类体内的皮质酮水平, 可以了解鸟类的应激状态水平, 进而了解诱发和影响鸟类应激反应的因素, 这有助于理解鸟类如何适应环境、如何权衡生活史各阶段的能量分配等。而通过长期监测动物个体的生存和应激状况, 对濒危鸟类的保育工作也具有重要参考价值。本文综述了诱发鸟类应激反应的因素, 包括天气、捕食压力、食物可获得性、人为干扰和城市化以及社会压力等。归纳出影响鸟类应激反应程度的主要因素, 包括光周期、生境、性别、年龄、社会等级和早期经历等 8 个方面。提出了应激反应在个性、认知、系统发育等领域的应用, 以及慢性应激、羽毛皮质酮检测等值得关注的內容。

**关键词:** 鸟类; 应激反应; 应激响应; 皮质酮; 个性

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## Inducement and Influencing Factors of Avian Stress Response

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**Abstract:** Stress response is an important mechanism for animals to cope with environmental or social stress. It is characterized by activation of the hypothalamic-pituitary-adrenal axis (HPA axis) and production of glucocorticoids, which is corticosterone in most bird species. The corticosterone level of a bird can be utilized to determine whether it is under stress, to identify the factors that may induce or influence such stress response, and ultimately, to reveal the mechanism of how the birds adapting to the environmental changes and balancing the energy distribution in different stages of life history. Furthermore, the long-term monitoring of corticosterone level can also provide the survival and health status of individuals, which important implications for conservation of endangered birds. This paper reviewed the factors that induce stress response in birds, including weather, predation pressure, food availability, human interference, urbanization and social stress; summarized the factors that may affect the degree of stress response of birds, including photoperiod, habitat, gender, age, social class and early experience. Moreover, this review also outlined the research

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contents with high potential for further research, including feather corticosterone determination, chronic stress as well as the application of stress response in the fields of animal personality, cognition and system development.

**Key words:** Bird; Stress response; Stress reaction; Corticosterone; Personality

应激反应 (stress response) 是动物面对外界或内部各类异常刺激时产生的适应性生理反应 (Selye 1936), 主要表现为下丘脑-垂体-肾上腺轴 (hypothalamic-pituitary-adrenal axis, HPA 轴) 被激活并产生糖皮质激素 (glucocorticoids) (Sapolsky et al. 2000)。HPA 轴被激活时, 会通过下丘脑合成并释放促肾上腺皮质激素释放激素 (corticotropin releasing hormone, CRH), CRH 进入腺垂体后与腺垂体细胞上的受体结合, 促进腺垂体分泌促肾上腺皮质激素 (adrenocorticotrophic hormone, ACTH), ACTH 进入血液, 通过循环系统最终与肾上腺皮质细胞的受体结合, 促进其分泌糖皮质激素。一般地, 动物从遇到刺激到血液中糖皮质激素水平升高的过程需要 3 ~ 5 min, 15 ~ 30 min 达到峰值, 60 ~ 90 min 回归到正常水平 (Sapolsky et al. 2000, Romero 2004, Kloet et al. 2005)。在鸟类中, 血液皮质酮 (corticosterone, 鸟类主要的糖皮质激素) 水平是判断其是否进入应激状态的重要指标 (Romero 2004, Romero et al. 2006), 此外, 粪便糖皮质激素代谢物 (fecal glucocorticoid metabolite, FCM) 可以反映出约 24 h 内个体血液中的皮质酮水平 (Sheriff et al. 2010, 2011), 羽毛样品则可以反映出鸟类个体长达数月的血浆皮质酮水平, 可用于推测个体在较长一段时间内的应激水平 (Bortolotti et al. 2008)。

糖皮质激素是动物维持正常生理活动的重要激素。靶细胞内存在 I 型和 II 型两种受体, I 型受体也被称为盐皮质激素受体 (mineralocorticoid receptor, MR), 介导允许作用 (permissive action), 可以提高血管张力, 增强心血管功能; II 型受体又称糖皮质激素受体 (glucocorticoid receptor, GR) 介导应激反

应, 并参与下丘脑-垂体-肾上腺轴的负反馈调节作用。由于 I 型受体的结合能力强于 II 型受体, 所以当 I 型受体饱和之后, II 型受体才会开始结合糖皮质激素。当机体处于正常状态时, 血浆糖皮质激素含量稳定, 称为本底水平糖皮质激素 (在鸟类中则为本底水平皮质酮)。而当机体进入应激状态时, 血浆糖皮质激素含量显著增加, 此时 II 型受体开始结合糖皮质激素, 进而介导一系列生物学效应, 诸如血糖升高、神经系统兴奋性增加、肌肉紧张度增加等 (Dallman et al. 1992, Sapolsky et al. 2000)。同时, 位于垂体、下丘脑等脑区的 II 型受体在与糖皮质激素结合后, 会抑制对应脑区分泌 CRH 和 ACTH, 通过负反馈作用下调血浆糖皮质激素水平 (Dallman et al. 1992, Johnson et al. 1992)。应激反应产生的糖皮质激素具有增强糖异生反应、调节免疫功能以及抑制生殖激素表达等功能 (Sapolsky et al. 2000)。在行为上则表现为增强记忆力和警觉性、增加肌肉紧张度、增加觅食行为、抑制繁殖行为和诱导迁徙行为等 (Astheimer et al. 1992, Dallman et al. 1992, Wingfield et al. 1998)。这些生理和行为方面的改变, 将机体的能量集中在短期生存相关功能上, 而抑制当前“非必须的”生理功能, 如繁殖、免疫等。急性应激 (acute stress) 反应是一种适应性行为, 可以增强动物应对突发压力事件的生存能力 (Breuner et al. 2008)。但是, 如果刺激源长期存在, 即机体处于慢性应激 (chronic stress) 时, HPA 轴的负反馈调节作用可能逐渐失效, 这时血浆中的糖皮质激素水平无法得到有效控制, 将会长期处于较高水平。而长期高水平糖皮质激素将会对机体的免疫、生殖等多方面产生负面影响 (Dallman et al. 1992, Romero 2004, Saino et al. 2005), 包括

大脑结构损伤 (Welberg et al. 2001)、预期寿命缩短 (Monaghan et al. 2012)、肌肉萎缩 (Astheimer et al. 2000)、认知障碍 (Kitaysky et al. 2003)、疾病易感性增加 (Romero et al. 2007) 等。在行为方面则可能导致繁殖和迁徙的中断 (Wingfield 2003)。

鸟类下丘脑-垂体-肾上腺轴调控的应激反应是在短期适合度和长期适合度之间的一种权衡。当鸟类遭遇强烈的外界刺激时,会上调体内皮质酮以保证短期生存 (Müller et al. 2006, Li et al. 2019)。在鸟类生活史的不同阶段,短期生存的重要程度是不同的,如处于繁殖季的个体可能会适当抑制应激反应,一定程度上牺牲短期适合度以确保繁殖的顺利进行 (O'Reilly et al. 2003)。此外,雌雄个体在繁殖中的分工有所差异,受皮质酮影响程度也不同 (Wingfield et al. 1986)。随着年龄增长,未来繁殖潜能逐渐降低,“存活”和“当前繁殖”的权重也会发生改变 (Wilcoxon et al. 2011)。这些因素均可能导致在面对压力时,不同个体之间的应激反应程度产生差异。此外,“个性”不同的个体也常常表现出应激反应方面的差异 (Cockrem 2007)。因此,研究鸟类应激反应的诱发因素和应激反应的个体差异,有助于理解鸟类如何适应环境压力、如何权衡生活史各阶段的能量分配等问题。本文从诱发鸟类应激反应的因素和影响鸟类应激反应程度的因素两个方面进行综述,对国内外鸟类应激反应研究最新进展和常用的采样方法加以总结,对今后值得关注的研究内容提出展望,旨在为鸟类应激、认知和濒危珍稀鸟类保护等领域的研究提供借鉴。

## 1 鸟类应激反应的诱发因素

### 1.1 天气

不利的天气条件,如雨雪、强风、高温、干旱等可能导致鸟类进入应激状态 (Wingfield 2013)。Rogers 等 (1993) 发现,冬季降雪会使暗眼灯草鹀 (*Junco hyemalis*) 的血浆皮质酮水平显著升高,降雪后其脂肪储备量也迅速升

高,推测应激状态高水平的皮质酮会促进脂肪积累,以抵御外界恶劣天气条件。同样,我国内蒙古地区大鸨 (*Otis tarda*) 粪便中的皮质酮代谢物含量也会在降雪过后升高 (Liu et al. 2018)。强风、阴雨天气等突发的不利因素会导致高山雨燕 (*Tachymarptis melba*) 雏鸟的血浆皮质酮含量在短期内升高 (Bize et al. 2010)。因此,鸟类可以通过上调皮质酮水平应对恶劣天气,可能是因为皮质酮有维持体温、促进觅食等功能,可以在不利气候条件下增加个体的生存率。

恶劣天气对鸟类皮质酮水平造成的影响程度有时也取决于鸟类自身的情况。披肩榛鸡 (*Bonasa umbellus*) 体内的皮质酮水平会在下雪时升高,但当积雪超过 20 cm 时,它们通过挖雪洞的行为减少热量散失,从而使皮质酮水平迅速下降 (Shipley et al. 2019)。阿拉斯加地区铁爪鹀 (*Calcarius lapponicus*) 血浆中应激水平皮质酮在春季气温较低、积雪较多年份高于其他年份,而白冠带鹀 (*Zonotrichia leucophrys*) 却并没有出现这种年际差异 (Krause et al. 2016)。此外,鸟类的应激反应强度也受极端高温条件影响,与其耐受能力有关。在 45 °C 的高温条件下,姬地鸠 (*Geopelia cuneata*) 血浆皮质酮水平显著升高,而斑胸草雀 (*Taeniopygia guttata*) 和虎皮鹦鹉 (*Melopsittacus undulatus*) 的皮质酮水平却不受影响 (Xie et al. 2017)。因此,鸟类对不利气候条件有一定的应对能力,如果雨、雪、高温等天气在其应对能力范畴之内,它们可以将体内皮质酮维持在正常水平,以避免高水平皮质酮带来的负面影响。

### 1.2 捕食压力

被捕食会使鸟类进入急性应激状态,以增加成功逃脱的概率。关于青山雀 (*Parus caeruleus*) 的研究表明,当面对致命捕食风险时,被捕食者的血浆皮质酮水平显著升高 (Müller et al. 2006)。捕食者的存在本身也会使被捕食者长期处于慢性应激状态。Clinchy 等 (2004) 发现,在具有高被捕食压力的栖息

地中, 繁殖期野生歌带鹀 (*Melospiza melodia*) 的本底血浆皮质酮水平显著高于在被捕食压力低的栖息地中繁殖的个体。但捕食者对雏鸟造成的影响可能与成鸟不同, Ibanez-Alamo 等 (2011) 发现, 高被捕食风险巢中的乌鸫 (*Turdus merula*) 雏鸟具有更低的本底皮质酮水平, 推测雏鸟体内的皮质酮水平会影响雏鸟的乞食行为, 本底皮质酮水平低的雏鸟乞食频率也更低, 而这可以降低巢被捕食者发现的风险。总之, 上调血浆皮质酮水平是鸟类逃脱捕食的重要手段, 同时鸟类也可以根据自身需求调整下丘脑-垂体-肾上腺轴功能, 以应对长期捕食压力。

### 1.3 食物可获得性

鸟类在长期缺乏食物的情况下, 会进入慢性应激状态, 通过较高水平的皮质酮提升觅食能力。同时, 通过皮质酮对繁殖和免疫系统的抑制作用降低能量消耗, 也可能是应对食物缺乏的方式之一。丛鸦 (*Aphelocoma coerulescens*) 城郊种群因全年得到人类投喂, 食物可获得性最高, 血浆皮质酮水平较低, 而无人工投喂野生种群的食物可获得性低, 血浆皮质酮高于城郊种群 (Schoech et al. 2004)。同样, 家燕 (*Hirundo rustica*, Jennieiermann et al. 2008)、南美企鹅 (*Spheniscus magellanicus*, Walker et al. 2005) 和歌带鹀 (Clinchy et al. 2004) 的本底水平皮质酮与食物获取量均呈负相关。

鸟类在禁食态下皮质酮水平会升高, 但与恶劣天气的影响类似, 只有超出可承受范围的禁食时长才会导致持续的高水平皮质酮。阿德利企鹅 (*Pygoscelis adeliae*) 在繁殖期要经历长时间的禁食, 即求偶期不觅食, 产卵后才开始雌雄交替觅食, 绝大部分能在禁食 40 d 内保持皮质酮水平稳定。然而, 有些个体会因为配偶在觅食过程中死亡而忍受更长时间的饥饿, 它们血浆皮质酮水平会在断食 50 d 后升高 (Vleck et al. 2000), 因此, 阿德利企鹅可承受约 50 d 的禁食时间, 超出这一时限就会表现为皮质酮水平的升高, 或许是它们在减少能量消

耗, 过度饥饿状态下机体能量状态发生的显著变化。而对不需忍受长期饥饿的物种来说, 它们可承受的禁食时间就要短得多。Lynn 等 (2010) 对笼养斑胸草雀进行了禁食实验, 发现 4 h 后其血浆皮质酮水平就已经高于正常状态。

上调皮质酮水平可以增强觅食能力并减少不必要的能量消耗, 帮助鸟类应对食物匮乏的不利情况。此外, 皮质酮水平开始升高的时间可以帮助我们推测某一物种对饥饿的忍受能力, 从而更全面地了解这一物种如何从生理层面适应其行为和生活环境。

### 1.4 人为干扰和城市化

人类正在剧烈地改变着自然环境, 如何适应人类活动带来的一系列影响是许多物种面临的重要挑战 (Ditchkoff et al. 2006)。当野生鸟类被人为捕获和笼养时, 会出现强烈的应激反应 (Li et al. 2019)。游客的参观活动对野生鸟类造成的干扰弱于捕获, 但同样会诱发应激反应。受游客干扰的野生麝雉 (*Opisthocomus hoazin*) 雏鸟血浆皮质酮水平高于不受干扰的个体 (Müllner et al. 2004)。即便是长期接受人工饲养的动物, 人为干扰仍然能在一定程度上使其进入应激状态。游客的参观活动会使笼养朱鹮 (*Nipponia nippon*) 粪便中皮质酮含量升高, 且皮质酮水平与当日游客数量显著相关, 说明游客干扰会引发笼养朱鹮的急性应激 (郭彦娇 2013)。

随着城市化的发展, 人类活动对野生鸟类的影响已经逐渐从致命性的捕猎行为转变成非致命性的干扰, 研究城市鸟类的应激反应可以更好地探讨鸟类如何在生理层面适应环境变化。城市中有高强度的人为干扰、噪声等问题, 夜间光照也会对鸟类的昼夜节律产生影响, 从而扰乱鸟类的激素水平 (Ouyang et al. 2015, 刘燕等 2017)。但同时, 城市中蛇类、猛禽等自然天敌较少, 人类的投喂行为和生活垃圾也能为野生鸟类提供大量食物来源 (Ditchkoff et al. 2006, Shochat et al. 2006)。因此, 城市化对鸟类应激反应造成影响的因素可能十分复杂,

既包含上文提到的环境因素,也可能涉及鸟类为了更好地适应城市生活而对自身下丘脑-垂体-肾上腺轴功能进行的调整。北京城区的麻雀 (*Passer montanus*) 血液本底皮质酮水平显著高于生活在郊区的个体 (Zhang et al. 2011)。Beaugeard 等 (2019) 发现欧洲 11 个地区的家麻雀 (*P. domesticus*) 幼鸟羽毛皮质酮水平与城市化程度呈正相关,但幼鸟的发育和身体状况与羽毛皮质酮之间并无相关性,说明城市家麻雀在发育过程中,高水平皮质酮并不会对它们的生长发育产生负面影响,这或许是它们对城市化的一种适应。

总之,人为干扰是野生鸟类的常见压力来源,但一些物种也在调整自身的生理功能,以适应人类活动。

### 1.5 社会压力 (social stress)

鸟类在遭遇领地入侵 (territorial intrusion) 或与其他个体发生争斗时会出现应激反应。青山雀 (Landys et al. 2007)、普通鸫 (*Sitta europaea*, Landys et al. 2010)、黑喉石鹇 (*Saxicola torquata*, Canoine et al. 2005) 等多种鸟类在模拟领地入侵 (simulated territorial intrusions, STIs) 实验中都表现出了皮质酮水平升高的现象。处在应激状态时,鸟类的警觉性增加,肌肉紧张度增强,因此可以帮助鸟类更有效地进行领地防卫等行为。

诱发鸟类应激反应的社会因素不仅限于“冲突”,鸟类也可以注意到群体中其他成员的压力状态,并对此作出响应。近几年有研究发现了压力传递 (stress cross-over) 的现象,即雏鸟的应激反应可以由另一只同巢雏鸟的应激反应诱发。Noguera 等 (2017) 为一只黄腿鸥 (*Larus cachinnan*) 雏鸟植入皮质酮包埋物,发现巢内所有雏鸟都产生一系列同步的变化,包括血浆本底皮质酮水平上升、反捕食行为增强、生长缓慢和羽毛质量变差等。丛鸦也有类似现象,当巢中一只雏鸟被植入皮质酮包埋物时,巢中所有雏鸟的乞食频率都会随之升高 (Elderbrock et al. 2017)。压力传递现象可以理

解为雏鸟的一种适应性行为,当巢中一只雏鸟感受到来自捕食者或食物缺乏等方面的压力时,其他雏鸟注意到同伴的压力而在生理和行为方面作出响应。这样可以避免因自身不够敏感,对压力事件反应不够迅速而导致负面后果。这一现象在成鸟之间是否存在,成鸟是否可以通过伴侣或其他个体间接感知环境压力,是值得进一步研究的方向。

除上述因素以外,高种群密度和环境污染在其他脊椎动物类群中被证实会诱发动物的应激反应 (Wendelaar 1997, Wingfield 2013, Blondel et al. 2016), 鸟类相关研究较少 (Eeva et al. 2003, 2005), 可能由于鸟类活动能力和扩散能力较强,因此受高种群密度影响较小。但环境污染则应当引起重视,尤其是在当前城市化背景下生活在城市中的鸟类,大气、水体和噪声污染等问题是否会导致鸟类出现慢性应激反应十分值得关注。

## 2 影响鸟类应激反应的因素

### 2.1 季节变化和光周期

鸟类体内的皮质酮水平具有昼夜周期性变化的特征,如在白天较低,夜间较高 (Romero et al. 2000, Rich et al. 2001)。这一变化与光照有关,南极洲的阿德利企鹅在经历极昼现象时无显著的日节律 (Vleck et al. 2002)。

大量研究报道了鸟类的本底和应激水平皮质酮在一年中存在周期性变化。西滨鹬 (*Calidris mauri*) 是一种迁徙鸟类, O'Reilly 和 Wingfield (2003) 发现雄性西滨鹬的血浆皮质酮水平在春季迁徙期和繁殖期最低,秋季迁徙期最高,本底和应激水平皮质酮的变化模式相似。由于皮质酮具有促进糖异生、脂肪沉积和增强觅食能力的作用,高水平的皮质酮可以更好地应对迁徙过程中的高能量需求。与秋季迁徙期相比,春季迁徙后将进入繁殖期,而皮质酮对繁殖有抑制作用,这可能是西滨鹬在春季迁徙期下调皮质酮水平的主要原因。在繁殖期的不同阶段,不同物种会呈现不同的特点,

如灰脸圆尾鹱 (*Pterodroma macroptera*) 在孵卵期的应激水平皮质酮显著高于其他时期 (Adams et al. 2005); 王企鹅 (*Aptenodytes patagonicus*) 随着繁殖阶段的推进逐渐降低应激水平皮质酮, 其中, 育雏期显著低于其他时期 (Viblanc et al. 2016)。雀形目鸟类的本底水平皮质酮一般在繁殖期最高, 秋季换羽期最低 (Romero 2002)。小型雀形目鸟类一般在一个繁殖期内进行多次繁殖, 因而对能量的需求较高, 可能是它们在繁殖期上调皮质酮水平的原因。而在换羽期下调皮质酮水平则可能是因为它们要进行完全换羽, 而高水平皮质酮会对羽毛质量产生负面影响 (Romero et al. 2005)。在繁殖期内, 麻雀的本底和应激水平皮质酮与自身能量状态有关。由于得到人类的投喂, 麻雀在繁殖期各阶段都不会经历食物缺乏, 因此本底水平皮质酮在各阶段保持稳定。雄性麻雀在筑巢期需要进行领地防卫, 对能量需求较大, 应激水平皮质酮在此时高于雌性。雌性在繁殖季晚期的应激反应最强, 则可能是由于多次繁殖对机体能量消耗较大, 皮质酮对觅食能力的增强作用可以帮助维持能量平衡 (Li et al. 2015, 2017)。

总之, 在不同生活史时期中, 鸟类的行为和对能量的需求不同, 环境条件也存在差异, 这可能是导致鸟类应激反应在一年中存在周期性变化的主要原因。

## 2.2 生存环境

鸟类可以根据自身所处的环境调整下丘脑-垂体-肾上腺轴功能。生活在较为严苛和复杂的环境中, 势必要面对更多环境压力。生活在青藏高原极端环境中的白腰雪雀 (*Montifringilla taczanowskii*) 和棕颈雪雀 (*M. ruficollis*), 在越冬期表现出钝化的应激反应, 这是应对恶劣环境的特殊生理策略 (Li et al. 2020)。在繁殖期, 由于皮质酮对繁殖行为的抑制作用, 生活在复杂环境中的鸟类需要对 HPA 轴功能进行一定的抑制, 才能保证繁殖行为不会因频繁的应激反应而受到过大负面影响

(Reneerkens et al. 2002, Wingfield et al. 2002)。但也有研究发现, 一些与人类共生的物种, 如麻雀 (Li et al. 2011) 和家麻雀 (Romero et al. 2006, Li et al. 2008), 即便生存在严苛的自然环境中, 仍可以从人类处获取食物和庇护所, 因此繁殖期的应激水平皮质酮与生活在良好环境中的个体并无显著差异。此外, 北极、青藏高原极端环境与北美温和环境的金翅雀属鸟类的应激水平皮质酮也无显著差异 (Li et al. 2012)。值得注意的是, 在 Li 等 (2011) 针对麻雀的研究中, 虽然两种环境中麻雀的应激水平皮质酮在繁殖期没有差异, 但却在秋季换羽期出现了显著差异。可能是由于高海拔地区气温较低, 秋冬季生存条件相对严苛, 而皮质酮增强觅食能力、促进脂肪积累等功能可以帮助当地个体更高效地储备能量, 提高冬季生存率。此现象提示鸟类能调整 HPA 轴功能, 以适应外界环境, 这一机制背后仍有其他生态学意义等待进一步探究。

## 2.3 年龄

动物个体在不同生活史阶段会表现出对压力的不同应对方式。对于雏鸟来说, 在没有自主觅食、调节体温和反捕食能力的阶段, 提高皮质酮水平不会为其带来任何益处, 反而会对生长发育造成负面影响 (Schwabl 1999)。因此 Sims 和 Holberton (2000) 提出的发育假说 (developmental hypothesis) 认为, 雏鸟在生命的早期阶段会抑制下丘脑-垂体-肾上腺轴对压力源的反应, 在雏鸟随着生长发育逐渐获得应对压力源的能力后, 应激反应才会随之出现。这一假说在多个物种的研究中都得到了证实, 包括白鹳 (*Ciconia ciconia*, Blas et al. 2006)、白冠带鹀 (Wada et al. 2007) 和南美企鹅等 (Walker et al. 2005)。

出飞后的个体随着年龄增长, 其应激策略也发生改变。丛鸦从雏鸟到 1 岁个体的血液本底水平皮质酮没有区别, 但应激水平皮质酮随年龄增长 (Rensel et al. 2010); 从 2 岁个体开始, 本底水平皮质酮依然保持稳定, 应激反应

期间产生的总皮质酮水平则随年龄下降 (Wilcoxon et al. 2011)。Lendvai 等 (2015) 对成年家麻雀进行了追踪调查, 对比同一个体在不同年龄的应激反应情况, 同样观察到了应激反应强度随年龄下降的趋势。上述两项研究的结果或可用 Williams (1966) 提出的临终投资假说 (terminal investment hypothesis) 解释, 即当一个物种的繁殖价值随年龄降低时, 其生殖努力会随年龄的增长而增加。相比于刚刚性成熟的个体, 年龄较大的个体会倾向于在“生存”和“当前繁殖”中选择后者, 因此它们适当抑制自身的应激反应, 以确保繁殖行为不会因高水平的皮质酮而受到负面影响。

总之, 个体的应激反应会随着生长发育和年龄增长改变。研究这一变化模式有助于了解雏鸟在孵化后早期阶段的生长发育情况, 以及成年个体随着年龄增长, 如何改变对“生存”和“当前繁殖”的权衡等。

## 2.4 性别

雌雄个体在生理结构、社会等级以及繁殖分工等多个方面具有明显差异, 这导致它们在面对压力时采取的应对策略往往不同。雄性西滨鹬在繁殖期间的应激水平皮质酮明显低于雌鸟, 差异在雏鸟出飞后消失 (O'Reilly et al. 2003)。这一现象可能与雌雄亲鸟在繁殖中的分工有关, 相对于雌鸟, 雄鸟更多负责领地防卫和孵卵, 而有研究表明高水平的皮质酮会降低雄鸟的领地防卫和育雏行为 (Wingfield et al. 1986), 因此雄性西滨鹬可能为了增加繁殖成功率而适应性地降低应激水平皮质酮。而斑胸滨鹬 (*Calidris melanotos*) 等雌性繁殖投入更高的物种, 则是雌鸟的应激反应弱于雄鸟 (O'Reilly et al. 2001, Bokony et al. 2009)。此外还有大量文献报道了应激反应的性别差异现象。雄性主红雀 (*Cardinalis cardinalis*) 的应激水平皮质酮普遍高于雌性个体 (Duckworth et al. 2018)。生活在高被捕食压力地区的雄性歌带鹀本底水平皮质酮显著高于低被捕食压力地区的雄性个体, 而两地雌性个体之间却没有

差异 (Clinchy et al. 2011)。此外大嘴乌鸦 (*Corvus macrorhynchos*, Ode et al. 2015)、蓝脸鲣鸟 (*Sula granti*, Grace et al. 2018) 和斑胸草雀 (Emmerson et al. 2018) 均存在应激反应的性别差异。总之, 性别是影响应激反应的一个重要因素, 在进行相关研究时应尽可能将性别因素考虑在内, 这样不仅能使研究结果更加完整和全面, 还能结合雌雄个体在其他方面的差异, 进一步探讨鸟类如何通过调节应激激素来适应环境。

## 2.5 社会等级

动物的社会群体中常常会有等级形成, 高等级个体在繁殖、觅食等多个方面享有优先权, 在应激策略上也可能与低等级个体有所差异 (Sapolsky 2005)。Schwabl 等 (1988) 发现等级较高的白喉带鹀 (*Zonotrichia albicollis*) 血浆本底水平皮质酮和应激水平皮质酮均低于低等级个体。但关于北美白眉山雀 (*Parus gambeli*, Pravosudov et al. 2003)、绿头鸭 (*Anas platyrhynchos*, Poisbleau et al. 2005) 和针尾鸭 (*A. acuta*, Poisbleau et al. 2005) 3 个物种的研究发现, 本底水平皮质酮不受社会等级影响, 且高等级个体的应激水平皮质酮更高。此外, Ode 等 (2015) 的研究发现, 不同性别的大嘴乌鸦在社会等级与粪便中皮质酮代谢物之间的关系上表现出了相反的结果, 等级较高的雄性皮质酮含量更高, 而雌性则等级越高皮质酮含量越低。上述研究表明, 社会等级对鸟类皮质酮水平具有重要影响, 但在不同类群中, 其影响模式存在差异。传统观点认为, 低等级个体会由于缺少食物或争斗失败等因素承受更多压力, 因此体内皮质酮水平更高。但也有学者认为, 高等级个体需要更高水平的皮质酮用于对低等级个体进行“监管”, 或进行更多争斗以维持自己的等级, 而高水平皮质酮对健康造成的不利影响会被高等级个体拥有的其他优势所抵消 (Creel et al. 2013)。

## 2.6 早期经历 (early-life experiences)

动物个体在早期发育过程中的经历被认为

可以对下丘脑-垂体-肾上腺轴的功能产生“编程效应 (early-life programming)”，造成的影响可持续到成年以后 (Seckl 2004)。Lynn 和 Kern (2017, 2018) 模拟了东蓝鸫 (*Sialia sialis*) 雌鸟离巢时雏鸟体温降低的情况，发现这一操作会让雏鸟的血浆皮质酮水平显著升高，并且多次重复操作会导致雏鸟后期 (实验停止后至少 7 d) 的应激水平皮质酮低于对照组。成年但没有进行繁殖的蓝脸鳾鸟会接近并“虐待”无人看守的雏鸟，被虐待次数较多的个体在 6~8 年后仍表现出与其他个体不同的皮质酮水平 (Grace et al. 2018)。以上研究表明，雏鸟期的应激经历会对其 HPA 轴的功能产生重要且持久的影响。

下丘脑-垂体-肾上腺轴功能的塑造不只发生在雏鸟时期，Emmerson 和 Spencer (2018) 对笼养的亚成体斑胸草雀进行了种群大小的控制实验，发现亚成体阶段生活在较大种群 (5 只/笼) 中的雌鸟，成年后的应激水平皮质酮显著高于小种群组 (2 只/笼) 的雌鸟。说明在亚成体阶段与同种个体的社交经历同样会影响成年后的 HPA 轴功能。但不同的社交活动 (争斗或互助等) 所造成的影响可能存在差异，因此尚有待对不同类型的社交活动进行分别探讨。

### 2.7 遗传

应激反应的个体差异也可能与遗传因素有关。Partecke 等 (2006) 在城市和森林两个区域捕捉了乌鸫的雏鸟，并在相同环境中进行人工育雏，出飞后对其应激反应强度进行评价。两组乌鸫的本底水平皮质酮没有差异，但来自城市种群的乌鸫具有更低的应激水平皮质酮，暗示城市鸟类在应激反应方面的改变可能已具有遗传性。值得注意的是，这项研究中的雏鸟并非人工孵化，被捕获前曾在城市或森林环境中短暂生活，因此出飞后应激反应的差异也可能是被捕获前受不同环境驯化的结果。Jenkins 等 (2014) 首次对家燕皮质酮水平的遗传力进行了研究，野生家燕种群的本底水平皮质酮遗传力为 0.152，应激水平皮质酮遗传力为 0.343。

说明本底水平皮质酮和应激水平皮质酮均受遗传因素影响，且应激水平皮质酮受遗传因素的影响更大。两项研究均表明，遗传因素在鸟类应激反应的个体差异中起到一定作用，尤其对应激水平皮质酮有更大影响。

### 2.8 个性

动物个性 (animal personality) 是指在不同情境下影响动物的行为倾向，在不同个体间具有较大差异，同一个体则在一生中保持稳定 (Gosling 2001, Sih et al. 2004)，是行为生态学领域近年的研究热点 (Coates et al. 2019, Smit et al. 2019, Wilson et al. 2019)。“探索性 (exploration)” 是研究较多的一种动物个性，根据动物个体在陌生环境中的活动情况，可以将个体分为“快速 (好奇)” 和“慢速 (木讷)” 两种个性 (Verbeek et al. 1994, Réale et al. 2007, Sih et al. 2008)。很多研究发现，上述两种个性的鸟类个体在皮质酮水平上存在差异，如快速探索组的大山雀 (*Parus major*) 本底和应激水平皮质酮都显著低于慢速组 (Carere et al. 2003, Stöwe et al. 2010, Baugh et al. 2012)。因此，不同个性的个体可能在下丘脑-垂体-肾上腺轴功能上存在一定差异，也可能正是这一差异导致了个体间不同的行为模式，从而表现为个性的不同。

鸟类个体的应激反应也可能与预期繁殖成效 (Bokony et al. 2009)、脂肪储存量 (Wingfield et al. 1994)、不同生活史对策 (Carere et al. 2003) 等因素有关。

## 3 展望

应激反应是动物个体应对不利生存环境的重要机制，一直受到国内外学者们的关注 (Sapolsky et al. 2000, Romero 2004, 2006, Creel et al. 2013)。在应激反应中介导多项生物学效应的应激激素也一直是重点研究对象。

本底和应激水平皮质酮作为重要的生理指标，除了可以在研究鸟类的繁殖、迁徙等行为时对鸟类的繁殖策略、能量分配问题进行探讨，



目前也被用于评估个体健康状况 (Strasser et al. 2011)、预测寿命与存活率 (Koren et al. 2012, Monaghan et al. 2012)、评价栖息地质量 (Crino et al. 2018) 等, 未来或可应用于动物个性、认知和系统发育等领域。目前关于动物个性的研究中, 多用行为学实验判定个性, 而通过应激激素相关指标对动物个体进行个性的划分, 将为动物个性研究提供新的视角和可检测的量化研究方向 (Cockrem 2007, Koolhaas et al. 2010)。由于个体下丘脑-垂体-肾上腺轴的功能受早期多种外界因素影响, 探究这些因素对鸟类学习能力和个性的塑造作用, 或许能为近期备受关注的“鸟类认知”领域研究提供一些参考 (Griffin et al. 2015, Medina-García et al. 2017, Chen et al. 2019)。此外, 有研究发现, 应激反应相关指标在亲缘关系较近的物种之间差异很小, 哪怕它们处于完全不同的栖息地中 (Li et al. 2012, 2020), 因此比较物种间应激反应的差异或可为系统发育领域的相关研究提供理论支持。

在濒危动物保护研究中, 慢性应激现象值得关注。慢性应激状态会降低动物的身体质量, 还可能导致繁殖失败 (Ouyang et al. 2012)。因此对于保护动物来说, 监测应激激素水平, 及时掌握个体和群体的生存状态 (栖息地质量、环境影响等) 和健康状况, 对制定针对性的保护管理措施十分重要。此外, 随着全球变暖现象日益加重, 极端天气逐渐增多, 越来越多的国内外学者开始关注野生动物在这一趋势下的生存状况, 及其对气候变化的响应 (Zhang et al. 2017, Gao et al. 2018, Riddell et al. 2019, Walker et al. 2019)。对保护动物的应激水平进行长期监测, 有助于分析气候变化是否对这些物种造成不利影响, 并及时制定应对方案。

在检测样品方面, 粪便和羽毛样本对个体损伤较少, 适合应用于濒危鸟类。但由于两种样品所反映的皮质酮水平存在一定的滞后性, 有必要对不同鸟类物种在血液、粪便和羽毛中应激激素水平的时滞关系开展针对性研究。此

外, 皮质酮在羽毛样本中的稳定性、羽毛的尺寸和颜色对皮质酮含量的影响等都是该领域中值得关注的问题 (Romero et al. 2016)。虽然这项技术出现的时间尚短, 相关实验方法仍在改进 (Alba et al. 2019), 但其在探究如天气、栖息地质量、城市化等在较长时间段内发生变化的环境因素对鸟类应激反应的影响方面具有很大潜力。

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