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单独隔离孵化对镇海林蛙蝌蚪生长发育、社交行为和运动表现的影响

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摘要:两栖类胚胎呈卵群一起孵化在反捕食、维持胚胎间的温度平衡和促进胚胎的同步发育等方面具有重要作用。在实验条件下探究孵化条件(单独隔离孵化和卵群一起孵化)对镇海林蛙(*Rana zhenhaiensis*)蝌蚪的生长发育、社交行为及其运动表现能力的影响。结果表明,孵出 2 天后,单独隔离孵化组蝌蚪的体长和发育历期均显著大于卵群一起孵化组。以体长为协变量的协方差分析表明,特定体长的单独隔离孵化组蝌蚪的体宽和体重均显著大于卵群一起孵化组的个体。在蝌蚪的活动行为中,单独隔离孵化组蝌蚪在水体上层和中层出现的频次显著小于卵群一起孵化组,而在水体底层的出现频次显著大于卵群一起孵化组。单独隔离孵化组蝌蚪个体的分布面积率、最近邻个体的距离、个体间的距离均显著大于卵群一起孵化组,但个体间的接触频次显著小于卵群一起孵化组。在运动表现方面,单独隔离孵化组胚胎的摆尾搏动频次显著小于卵群一起孵化组。单独隔离孵化组蝌蚪的运动时长和运动频次均显著小于卵群一起孵化组。本研究结果将为无尾两栖类幼期的生长发育规律提供参考数据。
关键词:两栖类; 孵化条件; 生长发育; 活动行为; 运动表现; 胚胎; 镇海林蛙

Effects of isolated-incubation embryos on the growth, development, social behavior, and locomotor performance of *Rana zhenhaiensis* tadpoles

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Abstract: Embryo-clustering incubation plays an important role in anti-predation, maintaining temperature balance between embryos, and promoting hatching synchrony for anurans. In this study, we investigated the effects of two hatching conditions (isolated-incubation and clustered-incubation) on the growth, development, social behavior, and locomotor performance of *Rana zhenhaiensis* tadpoles under laboratory conditions. Our results showed that both body length and the Gosner development stage of two-day-old hatchlings in a single-embryo treatment were significantly larger than those of the group-embryo treatment. The results of the ANCOVA (with body length as the covariate) analysis showed that both body width and body mass in the group-embryo treatment were significantly lower than those of the single-embryo treatment. For tadpole activity behavior, the occurrence frequency in the upper and middle water layers in the single-embryo treatments were significantly lower than those of the group-embryo treatment, whereas it was significantly greater in the single-embryo treatments than that of the group-embryo treatment in the lower water layers. The proportion of area occupied by tadpoles,

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the nearest neighbor distance, and the distance among individuals in the single-embryo treatment were both significantly greater than those of the group-embryo treatment, but the contact frequency between pairwise tadpoles was significantly lower than those of the group-embryo treatment. Regarding locomotor performance, we found that activity duration and activity frequency in the single-embryo treatment were significantly lower than those of the group-embryo treatment. These findings should provide valuable reference data on the growth and development of *Rana zhenhaiensis*, as well as other anuran species.

Key Words: Anura; hatchling condition; growth and development; activity behavior; locomotor performance; embryos; *Rana zhenhaiensis*

卵的集中孵化和共同筑巢行为对后代具有优势,包括反捕食作用(例如灭绝的恐龙[1]、昆虫类[2]、蜘形纲[3]、头足类[4]、鱼类[5]、以及两栖类[6]),促进胚胎对卵黄的吸收使后代个体的体型更大[7-9],改变孵化环境的湿度[7],从相邻卵的新陈代谢中获得热量[10-12],使得卵在孵化过程中位置固定不变[13],确保胚胎交流能够在同窝卵或异窝卵间进行[14-16]。爬行类和鸟类的同窝个体间会进行胚胎交流[17-19],卵震动,心率,气味,巢内CO_2浓度水平,这些都被认为是胚胎间潜在的沟通渠道[17]。胚胎间交流能够调节发育速率[8,16-18]、或者生长速率[20]促进胚胎的同步孵化。同步孵化可以降低个体被捕食风险,个体通过下沉动作躲避被捕食,从而提高个体存活几率[20-22]。

蝌蚪的集群行为可能是为了减少被捕食或提高觅食效率而进化的适应行为[23-24]。蝌蚪与同种个体一起生活的经历对个体集群行为的影响依然是不清楚的,而这种观察结果在其他物种中也不尽相同[25-26]。大多数关于社交隔离的影响研究只对个体的亲缘和非亲缘个体的识别能力进行测试评估,并没有评估蝌蚪先前经历过的社交环境对后续社交行为的影响[27-28]。

野外环境中镇海林蛙(*Rana zhenhaiensis*)的卵呈团状分布,同域分布的克氏原螯虾(*Procambarus clarkia*)、食蚊鱼(*Gambusia affinis*)、蜻蜓(*Tramea chinensis*)幼虫和巴西龟(*Trachemys scripta elegans*)对蛙卵存在捕食现象[29-30],卵团经过捕食者摄食,残留的卵粒形成单独隔离孵化现象。本实验以镇海林蛙蝌蚪为实验动物,检验(1)单独隔离孵化是否会影响蝌蚪的体型大小和发育历期,(2)单独隔离孵化是否会影响蝌蚪的社交行为和运动表现。

1 材料与方法

2017 年 1 月 10 日,在校园内的临时性水体中分别采得 3 窝镇海林蛙卵团,发育历期为 10-11 期。将卵带回两栖爬行实验室后,进行卵粒分离,解除卵粒间胶质层黏连。每窝卵随机取出 120 粒,分为二组,一组作为卵群一起孵化组,另一组作为单独隔离孵化组。卵群一起孵化组的 60 粒卵置于装有曝气 24 h 自来水的塑料筐(30 cm×20 cm×12 cm)中孵化,水位高度 6.5 cm。单独隔离孵化组的 60 粒卵单独置于 60 个圆底透明塑料杯(直径 3.7 cm,高 7 cm)中饲养,水位高度 6.5 cm。温度设置 25℃,光照周期为 12L:12D,每天进行位置变换以减少温差带来的影响。

孵化过程的第 5 天,蝌蚪未孵出记录各组胚胎在 1 min 内摆尾搏动次数,每组重复 5 次。

第 9 天,蝌蚪全部孵出但未进食,对孵出的蝌蚪进行形态特征测定。用 Sony DSC-T100 数码相机拍摄后用 Image J 1.44p 软件读取蝌蚪的形态学特征,包括体长(snout-vent length)和体宽(body width);用 Sartorius 天平(±0.001 g)称体重;用 Nikon XTS30 体视显微镜鉴定发育历期[31];记录实验过程中每组蝌蚪的死亡数。蝌蚪经过形态学测量后投喂足量的牛蛙饲料(0 号,宁波天邦股份有限公司)。

第 11 天,孵出 2 天后,蝌蚪已进食,同时对环境有一定的适应时间,采用静水停饲实验法进行水层分布观测计数。水面以下 1 cm 范围内的蝌蚪为上层,水底以上 1 cm 范围内的蝌蚪为下层,其余蝌蚪为中层[32],每

组重复观测计数 3 次。

第 12 天时进行孵化条件对蝌蚪社交行为和运动表现影响的观测实验。在白色陶瓷盘(47 cm×39 cm×2.5 cm)上方架设一台 Sony DSC-T100 数码相机记录蝌蚪的行为。从 3 窝卵群一起孵化组分别随机选取 4 只蝌蚪组成 12 只一组的卵群一起孵化组,重复 4 次;从单独孵化组的 3 窝蝌蚪内分别随机选取 4 只蝌蚪组成 12 只一组的单独隔离孵化组,重复 4 次。蝌蚪放入后开始录像 25 min。在数据采集分析时去除前 5 min 的录像,然后每隔 1 min 截取 1 张图像,用 Image J 1.44p 软件读取指标,包括:蝌蚪分布范围(分布面积率,蝌蚪分布面积/容器面积),个体间距离,最近邻距离。从第 5 min 开始,每隔 5 min,统计 1 min 内蝌蚪接触次数,将两只蝌蚪距离小于 0.5 cm 时定义为一次接触[33],运动时长和运动频次。

以上数据采集时间均为 14:00—15:00。数据用 STATISTICA 统计软件包(verison 6.0)分析。在作进一步统计分析前,用 Kolmogorov-Simirnov 和 Bartlet 方法分别检验数据的正态性和方差同质性。用方差分析(ANOVA)、协方差分析(ANCOVA)及后续的 Tukey′s 多重比较分析相关实验数据。非参数统计用 x^2-检验。描述性统计值用平均值±标准误表示,显著性水平设为 $\alpha=0.05$。

2　结果

单独隔离孵化组共孵出 172 尾,卵群一起孵化组共孵出 177 尾,孵化成功率组间差异不显著($x^2=2.34$, $df=1$, $P=0.126$)。

方差分析表明,孵出 2 天后,单独隔离孵化组个体体长($F_{1,347}=877.70$, $P<0.001$)和历期($F_{1,347}=10.04$, $P<0.002$)显著大于卵群一起孵化组的个体。以体长协方差分析表明,特定体长的单独隔离孵化组个体的体宽($F_{1,346}=49.51$, $P<0.001$)和体重($F_{1,346}=8.99$, $P<0.003$)均显著大于卵群一起孵化组的个体(图 1)。

方差分析表明,单独隔离孵化组胚胎摆尾搏动频次显著小于卵群一起孵化组的个体(图 2, $F_{1,28}=141.57$, $P<0.001$)。在水体的上层($F_{1,16}=148.97$, $P<0.001$)、中层($F_{1,16}=359.84$, $P<0.001$)单独隔离孵化组个体出现次数显著小于卵群一起孵化组的个体次数,在水体的底层单独隔离孵化组个体出现次数显著大于卵群一起孵化组的个体次数(图 2, $F_{1,16}=272.28$, $P<0.001$)。

方差分析表明,单独隔离孵化组个体的分布面积率($F_{1,166}=107.08$, $P<0.001$)、最近邻距离($F_{1,2014}=41.81$, $P<0.001$)、个体间距离($F_{1,15831}=114.13$, $P<0.001$)均显著大于卵群一起孵化组的个体,单独隔离孵化组个体的接触频次($F_{1,158}=75.17$, $P<0.001$)、运动时长($F_{1,1336}=119.46$, $P<0.001$)、运动频次($F_{1,38}=19.79$, $P<0.001$)均显著小于卵群一起孵化组的个体(图 3)。

3　讨论

本实验结果表明单独隔离孵化处理会使镇海林蛙蝌蚪体型变大(图 1),这与欧洲林蛙 *Rana temporaria* 蝌蚪结果一致[26],而与爬行类中的三线石龙子 *Bassiana duperreyi*[7],东澳长颈龟 *Chelodina longicollis*[8] 和蝰水蛇 *Natrix maura*[9] 结果相反,导致这样的原因可能跟物种对卵黄的吸收[9],个体的运动水平[6],种群密度及其种内竞争有关[34]。例如,更快发育和过早孵化将改变蝰水蛇胚胎对卵黄的吸收,使得幼蛇体内具有更高的脂肪含量[16]。无尾两栖类个体肌肉组织占比较大,运动过程耗能较高[6],卵群一起孵化组个体胚胎摆尾搏动更为频繁导致个体在未进食情况下更多消耗脂肪[5-36],使得个体体型相较于单独隔离孵化组个体较小。做出运动决策的可能原因是个体对能量消耗-获利的权衡,卵群一起孵化组个体发育时间较长,对卵黄的吸收更为完全,储存的能量可以用于活动代谢,而加速孵化导致个体储能不足,使个体更倾向于采取保守的保存能量策略[37]。此外,单独隔离孵化处理组的发育历期要比卵群一起孵化组大(图 1),而且发育历期的变异系数也比卵群一起孵化组大($C.V_{single}=0.0270$, $C.V_{group}=0.0259$),说明单独隔离孵化使得镇海林蛙胚胎发育加速,卵群一起孵化促进胚胎发育同步,这与 Nicieza[26] 和 Aubret[9] 的研究结果一致。当卵周围没有卵或卵较少时(单独隔离孵化),表明当前环境具有较高的被捕食风险或者说资源较少,这会促进个体加速发育,快速离开当前

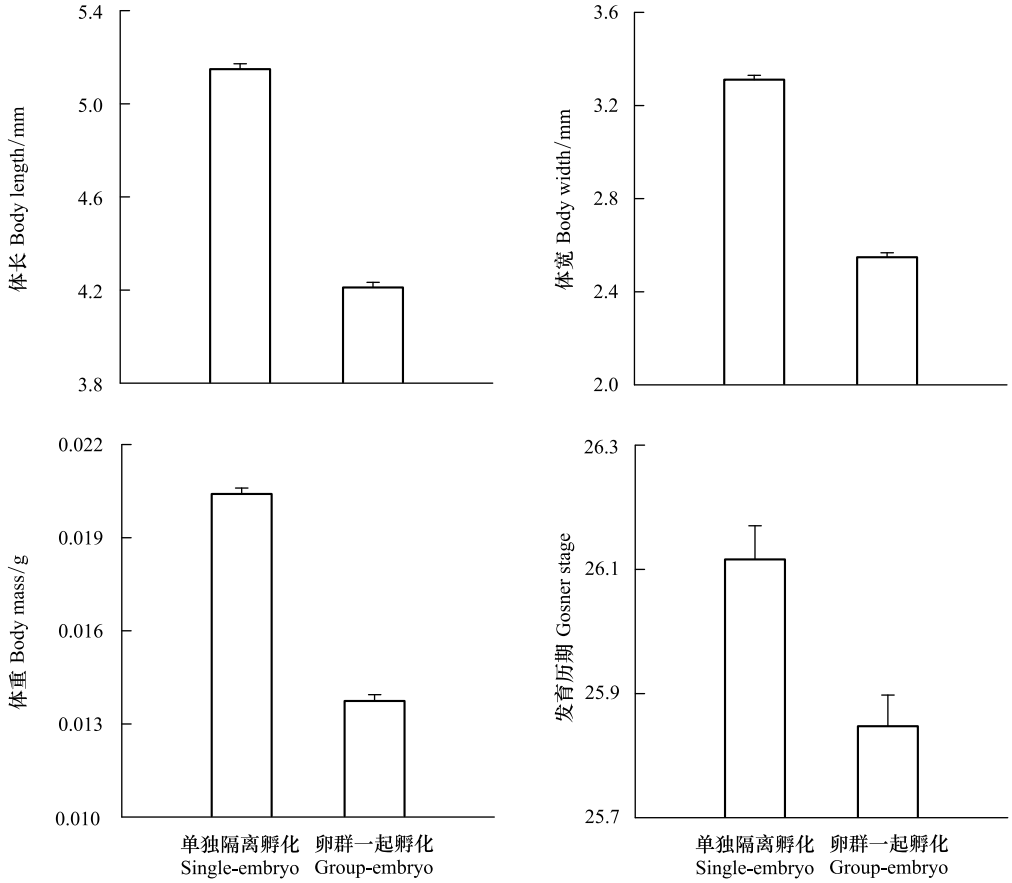

图 1 卵群一起孵化和单独隔离孵化下镇海林蛙蝌蚪发育历期和形态特征的描述性统计值(平均值±标准误)

Fig.1 Descriptive statistics of Gosner developmental stage and morphological traits of *R. zhenhaiensis* larvae incubated under single-embryo and group-embryo treatment: Body length, Body width, Body mass and Gosner development stage (mean±SE)

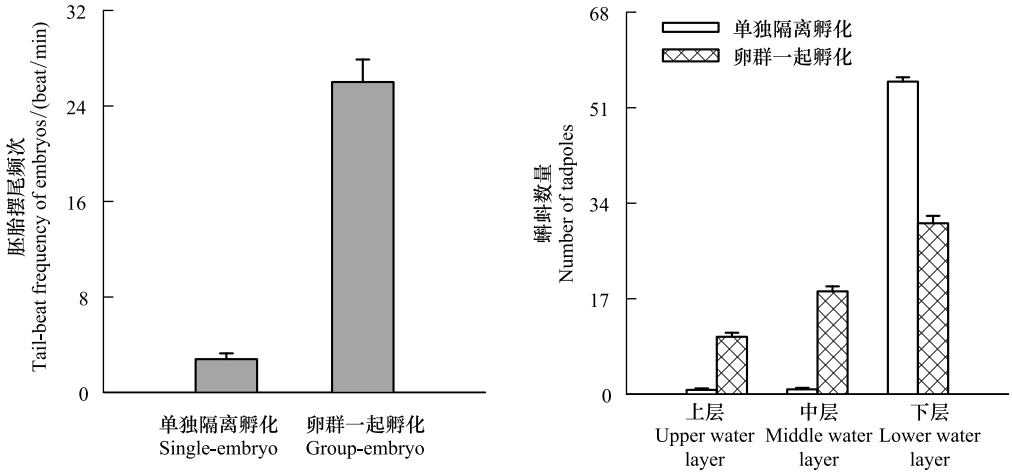

图 2 卵群一起孵化和单独隔离孵化对镇海林蛙胚胎摆尾频次和蝌蚪活动水层分布比较(平均值±标准误)

Fig.2 Comparisons of the tail-beat frequency of embryos and the occurrence frequency of *R. zhenhaiensis* tadpoles between single-embryo and group-embryo treatment (mean±SE)

环境[9]。而较大窝卵数(卵群一起孵化)表明当前环境相对安全或者说资源充裕,个体没有必要加速发育从当前环境逃离,而且逃离这里也是有风险的[38],所以蝌蚪选择同步发育共同分担风险。以往的研究也表明了

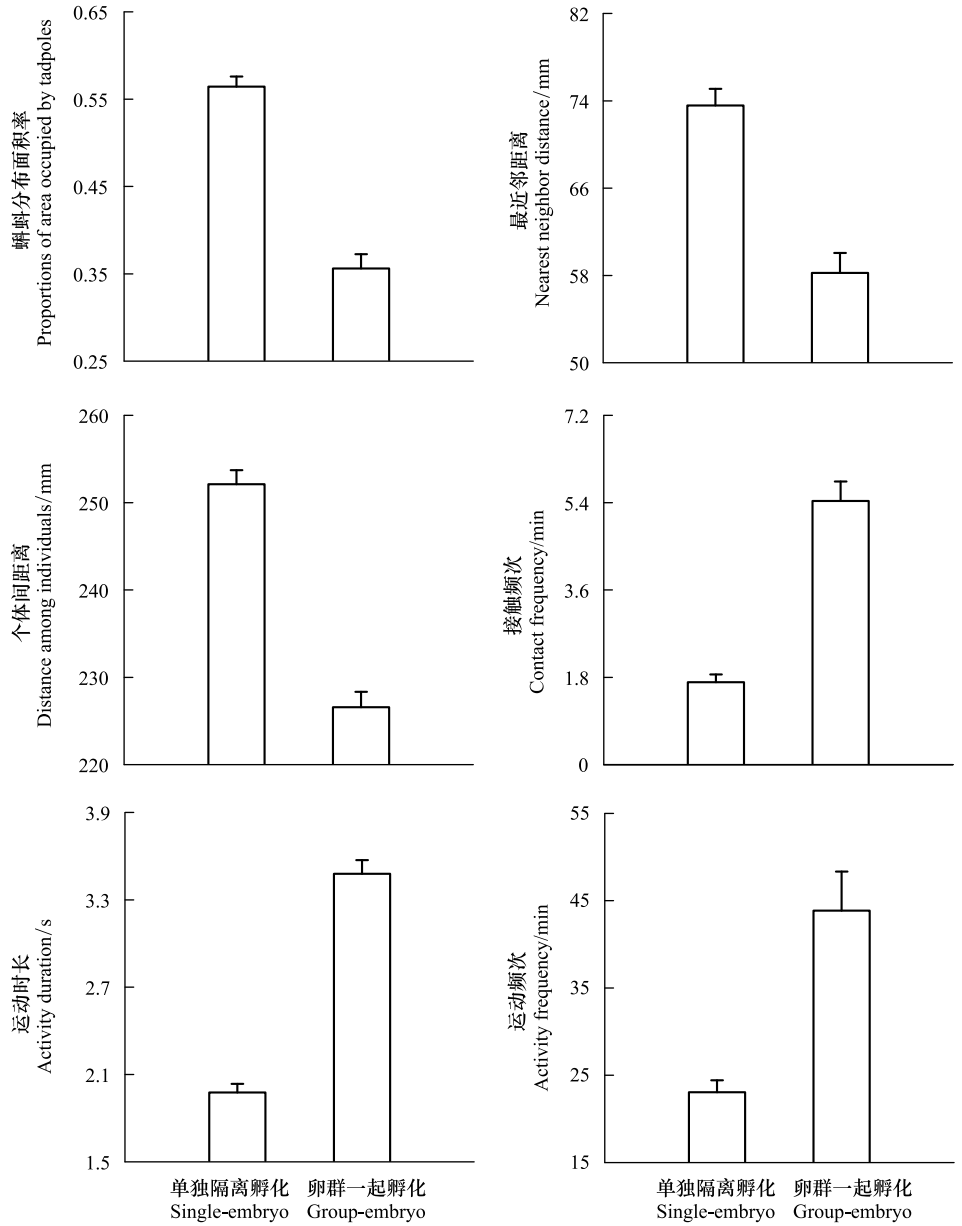

图 3　卵群一起孵化和单独隔离孵化对蝌蚪的活动行为和运动表现的影响：分布面积率、最近邻距离、个体间距离、接触频次、运动时长和运动频次(平均值±标准误)

Fig.3　Effects of hatchling condition on the activity behavior and locomotor performance of *R. zhenhaiensis* tadpoles: the proportions of area occupied by tadpoles, nearest neighbor distance, distance among individuals, contact frequency, activity duration and activity frequency (mean±SE)

发育同步可以提高后代个体的存活几率[20-22]。这种情况也存在于其他动物,例如,海龟产卵的浅层地下巢穴存在自上而下的温度梯度(相差 6℃[39]),底部卵(孵化温度较低)会通过加速发育或过早孵化促进个体同步孵化,虽然过早孵化会降低孵化个体的运动表现[16-18],但从长远角度看集群同步孵化带来的好处可以弥补这一缺陷[21]。

在本实验中单独隔离孵化处理使得蝌蚪集群行为减弱,个体间的接触频次显著降低,蝌蚪的分布面积比率、最近邻距离和个体间距离显著大于卵群一起孵化组(图 3)。动物常会通过空间集群行为作为反捕食策略[40-41],例如通过个体间的协调运动威慑捕食者,或提高个体的警觉效率,或减弱由于稀释效应而导致的个体被捕食者检测到的可能性,从而降低捕食风险[42];蝌蚪的集群行为可能是试验动物对特定食物的偏好而不

是对同种个体信息的偏好造成的(锄足蟾 *Scaphiopus multiplicatus*[43]);在自然环境中观察到的蝌蚪的聚集行为也有可能是由于产卵数量大或环境刺激(如温度,底物的偏好或食物团块)的结果而不是社交行为调节的结果(欧洲林蛙 *R. temporaria*[44])。本行为观察实验过程中并未给予蝌蚪食物,并在恒定温度条件完成,所以有理由认为先前的孵化条件会影响个体后续的集群行为模式。

卵群一起孵化时个体间可以通过卵震动、心率变化和化学信号彼此进行交流,在胚胎间建立"社交枢纽,Social bonds"[9,14-17]。单独隔离孵化处理阻断了胚胎间的"社交枢纽",不仅改变了个体的集群行为模式,还改变了个体的运动表现(图 3)。单独隔离孵化组个体对周围环境的警觉性较高,更倾向于待在水底,活动水平较低(图 2)。这与黄条背蟾蜍 *Bufo calamita* 蝌蚪在有捕食者存在的情况下会减弱活动水平并且改变空间分布的结果一致[45]。而卵群一起孵化组个体对外界环境探索的范围更加宽泛,活动水平也高于单独隔离孵化组。这种行为在卡斯卡迪蛙 *Rana cascadae*[46] 和欧洲林蛙 *R. temporaria*[26] 蝌蚪中也有发现。在绝大多数的无尾两栖类中,当个体感知到当前环境具有较高的捕食风险时通常会选择减少运动[26,47-48]。这种行为策略可以降低捕食者的检测速率,因为蝌蚪的天敌通常是视觉导向(如蜻蜓 *Diastatops obscura* 幼虫)或通过水体振动(如狼蛛 *Schizocosa ocreata*)来感知猎物,尤其是生活在临时性水体内的个体[49]。

总之,单独隔离孵化使得孵化个体发育较快,体型较大,社会性和活动水平较低,依靠扩大活动范围和个体间距离逃离高被捕食风险区。而卵群一起孵化使得个体发育同步,社会性更高,通过数量优势提高警惕或进行集体防御[42],从而稀释个体被捕食风险并增加个体存活机率[20-22]。

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