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封面图说: 泥炭藓大多生长在多水、寒冷和贫营养的生境,同时有少数的草本、矮小灌木也生长在其中,但优势植物仍然是泥炭藓属植物。泥炭藓植物植株死后逐渐堆积形成泥炭。经过若干年的生长演变,形成了大片的泥炭藓沼泽。这种沼泽地有黑黑的泥炭,绿绿的草甸和亮晶晶的斑块状水面相间相衬,远远看去就像大地铺上了锦绣地毯一样美丽壮观。

彩图提供: 陈建伟教授 国家林业局 E-mail: cites.chenjw@163.com

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黄腹山鹪莺稳定的配偶关系限制雄性欺骗者

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摘要:多数鸟类通过性特征限制在同性竞争和配偶选择中的“欺骗者”存在,与此相反,雀形目扇尾莺科部分物种表现出繁殖季节性特征消退的身体特征变化模式。在广州市南沙区通过“目字笼”对黄腹山鹪莺配偶关系稳定性的限制机制进行研究,发现虽然雌性个体到访原配个体和对照个体的次数几乎相同,但是雌性个体对原配雄性的单次选择时间明显长于对照雄性个体,总计选择时间也明显长于对照雄性个体。选择实验过程中,原配雄性的跳动次数明显高于对照个体雄性,以竖尾扑哧和鸣声恐吓等为代表的威慑行为次数也明显高于对照雄性个体。结果说明,雌性更青睐于原配个体,配对时间越长,忠诚度越高,而且原配雄性比入侵雄性个体表现出更高的活跃度和威慑行为。繁殖季节性特征消退的物种可以通过保持稳定的配偶关系以限制“欺骗者”存在。可以推测繁殖的巨大投入和雌性之间的同性竞争可能是产生这种配偶稳定性的主要原因。

关键词:限制法则;配偶关系;性特征消退;黄腹山鹪莺

Handicapping male-cheaters by stable mate relationship in yellow-bellied prinia, *Prinia flaviventris*

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Abstract: Graduated tail of birds is believed to be a significant secondary sexual trait, and takes an important role in sexual selection. By means of secondary sexual trait, most species of birds handicap the existence of male cheaters, which arise in competition among males and mate selection. However, some species of Cisticolidae, Passeriformes show a converse change, in which graduated tail of breeding plumage is shorter than that of winter plumage. It means that their sexual traits are lost in breeding season. It seems that this pattern is conflicted with Sexual Selection Theory, and may reveal a new survival strategy.

In order to explain how this peculiar pattern influences breeding strategy, we studied on yellow-bellied prinia, *Prinia flaviventris* at Nansha District, Guangzhou for about one year. Yellow-bellied prinia is monomorphic and monogamous. Both males and females have a graduated tail which is even longer than their body. It moults twice every year, including complete moult after breeding from September to December, and partial moult before breeding from March to April. Its tail is replaced in both spring moult and autumn moult, and more importantly, tail length of breeding plumage is shorter than tail length of winter plumage.

We used mate-choice cage to test whether females handicapped male-cheaters by stable mate relationship on yellow-bellied prinia. Our experiment consisted of 21 trials, and each trial lasted about 1 hour. In each trial, both experimental

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males had no significant differences of body measurements, besides the length of tail. The mate-choice cage was isolated with black cloth to minimize human disturbance, and we recorded all the experiments by Sony DCR-VX2000E video camera. In order to minimize influence of stress reaction, we ignored the beginning and ending of every experiment and only process from 16th min to 45th min (totally 1800s) of each videotape. One-way ANOVA was applied to compare different options of females to males and sexual behavior between male groups. All statistics and analysis was conducted using software SPSS 17.0.

In mate-choice cage tests, the result shows that selecting times of females to both mate group and comparison group were no significant difference, but females spent more time in front of males from mate group. As breeding time went on, this trend was becoming more obvious, that the mate relationship were more and more stable. With respect to behaviors of males, jumping times of mate group was significantly greater than those of comparison group. The times of overawing of mate group were also significantly greater than those of comparison group. Hence, we summarized that females preferred their mate males, and this preference would be more intensity with the breeding time. Mate males would do more sexual display and threaten display than extra-pair males.

According to this experiment, we considered that mate males moulted after mating, consequently, they would reduce additional investment and increase flight flexibility. Besides, both males and females moulted in breeding season, females also face the threat of cheaters. In the process, mate males will protect their consorts. Thus we summarized that the high survival cost for breeding, better aerodynamic effect of males, competition among females, and ownership effect of mate males might be principal causes of this result.

We concluded that stable mate relation in species whose sexual traits were lost in breeding season could handicap the existence of male-cheaters. We conjectured that breeding investment and competition between females might be the main reasons for stale mate relationship.

Key Words: handicap laws; mate relationship; regression of sexual traits; *Prinia flaviventris*

以延长的尾羽为主要代表的鸟类第二性特征被认为在其配偶选择和同性竞争中起到重要的作用^[1], 拥有更长尾羽的雄性个体能够获得包括领域^[2-3]、雌性青睐^[4-9]和父权比例^[10-11]等方面的优势。夸张的性特征通常伴随着巨大的生存代价, 限制了“欺骗者”的存在^[12-14]。这使得性特征能够作为雄性适应性的忠实信号^[15-16]。

雀形目扇尾莺科的部分雌雄单态性物种却表现出繁殖季节性特征消退的奇特身体变化特征^[17-18]。换羽后雄性个体尾羽长度短于拖延换羽的“欺骗者”, 较早的交配会使其在同性竞争中处于劣势而失去领域和配偶, 从而无法限制“欺骗者”的存在。另外, 这类物种的雌雄个体在换羽后通常会同时面临长尾羽的竞争个体, 此时若保持稳定的配偶关系则有助于繁殖的继续进行, 从而达到最大的繁殖利益。因此提出以下假说: 繁殖季节性特征消失的物种必须存在有效的机制以限制“欺骗者”, 其会通过保持稳定的配偶关系以限制“欺骗者”的存在。并藉此推测: 繁殖行为的巨大投入和雌性之间的同性竞争可能是产生这种稳定性的主要原因。

为此, 使用“目字笼”对黄腹山鹪莺 (*Prinia flaviventris*) 配偶的稳定性进行研究, 验证黄腹山鹪莺是否保持稳定的配偶关系, 并藉此为这类物种进化机制的探讨和理论发展提供重要的研究基础。同时也为黄腹山鹪莺等扇尾莺科鸟类的野外保护对策以及人工养殖、繁育提供科学依据。

1 方法

1.1 实验物种

黄腹山鹪莺属于雀形目 (Passeriformes) 扇尾莺科 (Cisticolidae), 为雌雄单态性鸟类, 在华南地区广泛分布。尾呈楔形, 长度超过身体量度的一半^[19-20]。黄腹山鹪莺的繁殖期从每年的3月份到9月份, 其繁殖前后各有一次换羽, 包括9—12月的秋季完全换羽和3—4月的春季不完全换羽^[18]。尾羽在两次换羽中都会更

换,并且繁殖羽的尾羽短于冬羽尾羽^[17-18]。楔形尾羽因为空气动力学效果较差而被认为是鸟类的性特征^[21],因此,黄腹山鹧鸪尾羽的这种变化特征意味着其性特征在繁殖季的消失。

1.2 实验个体的捕捉和饲养

通过架设单向雾网捕捉黄腹山鹧鸪。随着繁殖季节的到来,携带 Olympus(8×42)倍双筒望远镜对研究区域进行地毯式普查,观察其的筑巢情况。一旦发现其有巢情,立即对巢址进行标记,并在筑巢植株周围三面布雾网,定点捕捉配对个体。捕捉时间应选在发现巢情的当天傍晚或次日清晨,此时能见度较低,能有效提高同时捕捉到配对个体的成功率。同时应当注意,定点捕捉过程中,应尽量避免捕捉已产卵、育雏的个体,以保证其野外繁殖成功率不受影响,尽可能降低本研究对研究地域自然生态的影响。

对所有的捕捉个体,一律进行室内笼养,准备用于实验。此时要通过罩笼衣的方法使其逐渐适应笼养环境,避免因个体的应激反应对实验的影响。

1.3 实验设计和数据收集

共有 53 只黄腹山鹧鸪成体个体参与实验,包括 21 只雌性个体和 32 只雄性个体。除雾网捕捉的 49 只野生个体,其中包括 21 对配对个体;另外 4 只为原先笼养个体。经过对比设计,共计进行 21 组实验。实验选用的所有雄性个体除尾羽长度存在明显差异外,其它身体量度基本上没有显著差异,其中身长=体长-尾长(表 1)。

对所有捕捉到的成体个体进行身体量度的测量。使用 HEC-300 电子秤(100/0.01g)称量体重,使用 UPMachine CS108 数显卡尺(200/0.01mm)测量身体度量值。

在室内条件下,通过将雌雄个体放置在“目字笼”的方法检测黄腹山鹧鸪配偶关系的稳定性,每次实验持续时间约为 1 h。为避免应激反应对试验结果准确性的影响,只对试验录像的第 16—45min(共计 1800s)进行统计分析,同时“目字笼”除正面外,其他方向均用笼布挂罩。观察不同繁殖时期尾羽长度的差异对配偶关系稳定性的影响。

实验对象在目字笼中的放置位置如图 1。随机地将不同尾羽长度的雄性分别置于左右两侧笼中,其中每组试验中的尾羽较短的雄性为原配个体,尾羽较长的雄性为对照个体。所选择的试验雄性个体除尾羽长度外,其它身体量度参数应没有显著差异。在实验过程中,为保证每组“目字笼”实验的独立性,每只原配雄性只参与一组实验。

在试验过程中,使用 Sony DCR-VX2000E 摄像机作为行为观察的辅助记录手段。采用 ONE-WAY ANOVA 对采集到的数据进行差异性检验,所有分析在 SPSS 17.0 软件中完成。

3 结果

3.1 雌性选择

雌性个体到访原配个体和对照个体的次数几乎相同(One-way ANOVA, $P > 0.05$),但是雌性个体对原配雄性的单次选择时间明显长于对照个体(One-way ANOVA, $P < 0.05$),总计选择时间也明显长于对照个体(One-way ANOVA, $P < 0.05$)(表 2)。这说明雌性个体倾向于选择原配个体,黄腹山鹧鸪交配后保持稳定的配偶关系。

表 1 黄腹山鹧鸪实验雄性身体量度的对比(M±SD)

Table 1 Comparisons of body measurements between mate males and comparison males

	原配雄性(n=21) Mate males	对照雄性(n=11) Comparison males
体重 Wight/g	6.36±0.67 a	6.39±1.01 a
身长 Trunk/mm	59.98±5.24 a	60.02±5.41 a
翼长 Wing/mm	45.07±2.57 a	45.99±1.14 a
嘴峰长 Beak/mm	9.88±0.51 a	9.79±0.49 a
跗蹠长 Tarso/mm	21.81±1.33 a	21.54±1.29 a
趾长 Toe/mm	10.88±1.17 a	10.93±1.01 a
爪长 Claw/mm	5.19±0.63 a	5.35±0.50 a
尾长 Tail/mm	70.55±5.58 A	74.86±5.13 B

同一列中,不同上标字母表示显著差异,大写字母差异水平为 $P < 0.05$;小写字母差异水平为 $P > 0.05$



图 1 试验用目字笼

Fig. 1 Schematic diagram of the mate-choice cage

表 2 黄腹山鹧鸪雌性个体对不同雄性个体的选择 (M±SD)

Table 2 Different options for females to mate males and comparison males

	选择次数 Select times	单次选择时间 Time for each trial/s	选择时间 Total select time/s
原配雄性 (n=21) Mate males	12.49±10.42 a	101.41±151.51 A	1255.62±405.44 A
对照雄性 (n=21) Comparison males	12.21±10.17 a	44.47±54.16 B	545.86±406.99 B

实验表明:随着繁殖时间的增加,雌性个体的这种选择性更为明显,即更倾向于选择原配的雄性个体,雌雄个体间的配偶关系也更加稳定(图 2)。

3.2 雄性个体的行为表现

实验过程中,原配个体跳动的次数明显高于对照个体 (One-way ANOVA, $P < 0.05$),竖尾和鸣声恐吓的次数也明显高于对照个体 (One-way ANOVA, both $P < 0.05$) (表 3)。这说明原配雄性个体比对照个体更为活跃,更有进攻性。

4 讨论

实验结果显示,雌性个体更倾向于选择原配的雄性个体,并且随着繁殖时间的延长,这种选择性更加明显。相对于对照个体,原配雄性更为活跃,更加有进攻性。

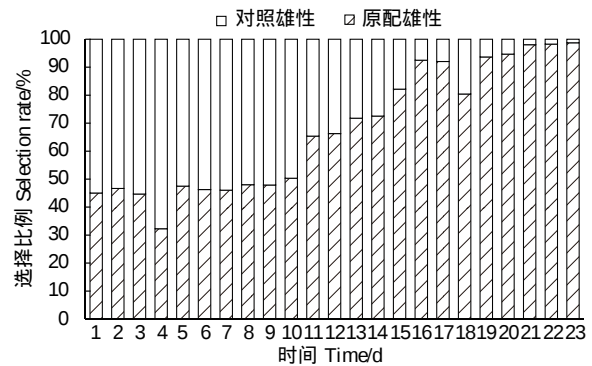


图 2 不同繁殖期黄腹山鹧鸪雌性个体对不同雄性个体的选择时间对比

Fig.2 Different choosing time for females to mate males and comparison males during different reproductive periods

表 3 黄腹山鹧鸪不同雄性个体间的行为比较 (M±SD)

Table 3 Comparisons of behaviors between male males and comparison males

	跳动次数 Jump times	威慑次数 Overawe times		
		竖尾 Tail shake	扑翅 Wing beat	鸣声恐吓 Song threat
原配组 (n=21) Mate males	70.83±16.97 A	8.87±1.14 A	6.01±2.37 a	7.07±2.73 A
对照组 (n=21) Comparison males	62.68±16.94 B	7.96±0.89 B	5.74±2.58 a	4.66±3.33 B

结果说明,黄腹山鹧鸪交配后会保持稳定的配偶关系,“欺骗者”难以通过拖延换羽来赢得繁殖机会。导致这种变化的原因包括以下:

(1) 能量效应 雌雄个体交配后,雌性个体已经进行了巨大的繁殖投入,中途更换配偶会造成前期繁殖投入的全部损失。根据 Bateman 原则,繁殖个体通常会选择最优的繁殖策略来保证繁殖收益最大化,而中途更换配偶会增加额外的繁殖投入,显然不是最优的繁殖策略^[22-23]。为保证繁殖收益最大化,雌性个体雌性更青睐于原配个体,且配对时间越长,这种青睐性越明显,雌性对配偶的忠诚度越高。

另外,繁殖前期长尾羽雄性表现出比短尾羽个体拥有更大能力以应对繁殖过程的巨大能耗;随着繁殖行为的进行,配偶雄性及时换羽以减少不必要的能量消耗,以保证繁殖的最终成功。但此时“欺骗者”为保持原尾羽已耗费许多能量,同时还要为争夺配偶、领域而大量消耗能量,自身已不足以支持整个繁殖过程。

如果雌性选择欺骗者个体,其繁殖收益的不确定性增加,无法达到繁殖收益的最大化,所以雌性个体应该更倾向于保持稳定的配偶关系,以达到最大的繁殖收益。

(2) 飞行效应 黄腹山鹧鸪为楔形尾羽,尾羽长度越长其空气动力学效果越差^[21],短尾羽的原配个体拥有更好的空气动力学效果,飞行的灵活性得以增加,因而捕食效率更高,并可以更有效地躲避捕食者,从而达到更高的繁殖成功率。而“欺骗者”的长尾羽空气动力学效果差,相对于已经换羽完成的原配个体,更容易被捕食,从而增加繁殖的不确定性,无法保证繁殖成功率。

(3) 雌性间的同性竞争 黄腹山鹪莺是雌雄单态性的物种,雌性和雄性个体一样会表现出繁殖季节性特征消退的特状^[19-20]。这说明不仅雌性选择雄性,雄性个体也会选择雌性个体^[24]。雌雄个体交配后,雌性也会进行春季换羽,因此雌性个体也会面临雌性欺骗者的竞争。如果无法保持稳定的配偶关系,雌性个体可能也会被雌性欺骗者夺走配偶。因此保持稳定的配偶关系不仅仅对雄性有利,对雌性也同样有利的。

实验过程中,原配雄性比对照个体更为活跃,表现出更多的威慑行为,这可能与拥有者效应有关。原配个体是雌性个体的拥有者,对照个体的出现会威胁其配偶地位,如若原配个体失去配偶会造成繁殖投入的巨大损失。因此原配个体会全力保护配偶,以保证自己的繁殖投入。而对照个体并没有先期的繁殖投入,即使没有获得雌性个体的青睐也不会有繁殖投入的损失。因此原配个体会比对照个体更加活跃,做出更多的威慑行为。

以黄腹山鹪莺为代表的繁殖季节性特征消退的物种,会在交配后保持稳定的配偶关系,并且交配时间越长,配偶稳定度越高,并藉此机制以限制“欺骗者”的存在。繁殖的巨大投入、飞行效应和雌性之间的同性竞争是产生这种稳定性机制的主要原因。

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