与笼养虎皮鹦鹉认知相关的因素

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摘要：越来越多的证据表明，动物的认知表现在物种之间和物种内部均存在差异，然而与这种认知差异相关的因素却不一致。本研究以笼养虎皮鹦鹉（*Melopsittacus undulatus*）为研究对象，通过测量其在一般认知任务和问题解决任务中的表现，探讨性别、跗跖长度、头体积和个性特征与认知能力之间的关系。结果发现，头体积较小的个体在自我控制任务中得分更高，在联想学习任务中得分更低。雄性个体在自我控制任务中的得分更高。雄性个体在联想学习任务中的得分低于雌性。在较容易的问题解决任务中，雌性、跗跖较长的个体以及探索性得分较高的个体更倾向于解决问题。在较难的问题解决任务中，雌性比雄性更倾向于解决问题。在成功解决较难问题的虎皮鹦鹉中，雌性个体的尝试次数高于雄性。本研究结果表明，不同认知任务的个体表现与多维因素相关，并且同一因素在不同的认知任务中所起的作用也各不相同。

关键词：个性；认知；性别；头体积；跗跖长度

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Factors related to the cognitive performances in captive Budgerigars

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Abstract: [Objectives] Cognition plays an important role in many ecological processes across animals. Growing evidence has indicated individual differences in cognitive performances across multiple species, and the cases of this phenomenon have shown mixed results. However, most of these studies focused on discrete cognitive task or certain limited factors, which may lead to bias. The aims of this study are two-fold: (1) investigate the effects of personality traits (neophobia and exploration), sex, and body characteristics on four general cognitive tasks; (2) investigate whether performances in problem-solving tasks are associated with personality traits, sex, and body characteristics. **[Methods]** We conducted a series of cognitive experiments to investigate the effects of sex, tarsus length, head volume, and personality traits (exploration and neophobia) on

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general cognitive tasks and problem-solving performances of Budgerigars (*Melopsittacus undulatus*). Apparatuses with two levels of difficulty were used to measure the problem-solving performances of Budgerigars. Exploration behavior was measured in a closed apparatus (L × W × H: 120 cm × 65 cm × 65 cm), which included five artificial trees (height × diameter: 50 cm × 1.5 cm) with two branches (one at the height of 25 cm and one at the top; Fig. 1a). A transparent acrylic sheet was covered on the apparatus top for recording. Budgerigars were caught via flight cages and placed in small cages (L × W × H: 29.3 cm × 22.5 cm × 28 cm), which were covered with black cloth to keep the light out. After 10-min acclimatization, the cage door was opened, and behavior was immediately recorded for 2 min when a Budgerigar entered the apparatus. The sum of the walking, flying, and jumping behaviors of each bird in 2 min was regarded as the exploratory score. The test was conducted three times, with the intervals being more than 15 d. In the neophobia test, we recorded the time before individuals began to touch the apparatuses in inhibitory control and associative learning tasks, which were regarded as individuals' neophobia of different experimental apparatuses. The inhibitory control ability was tested by a detour reaching task. The apparatus consisted of a transparent open-ended cylinder (length × diameter: 7 cm × 7 cm) in which a food reward was placed in the center (Fig. 1b). A lead block was placed at the bottom of the apparatus, which could prevent the bird from easily moving. In each trial, an attempt was considered as successful when the individual detoured the ends of the apparatus without pecking the transparent wall three times. The test was conducted 10 times, with each lasting for 1 min. The number of successful times was seemed as the score in this task. Individuals with high scores were considered to have a better performance in inhibitory control, while a low score indicated poorer performance. The associative learning was tested by a color discrimination task. The apparatus was a rectangular block of wood (L × W × H: 15 cm × 6 cm × 3 cm) with two wells (diameter × depth: 2 cm × 1 cm; Fig. 1c). The wells were covered with dark green and light green lids. In the first trial, an individual needed to open both of the lids and find the food reward, and the reward color was set in light green. The trials were no more than 50 times per day, with the interval of 1 min. If the bird chose the wrong well, the apparatus was immediately removed and the next trial was conducted 1 min later. The individuals were regarded as pass the associative learning task when they found the correct reward well on eight of nine consecutive attempts. The total number of attempts made by the Budgerigar was counted as the score for this experiment. A low score indicates better performance in associative learning, while a high score indicates poorer performance. The reversal learning task began 24 h later when the associative learning task was finished. In this task, the food reward was in the dark green well and other experimental procedures were same as those in the associative learning task. The total number of attempts made by the Budgerigar was counted as the score for this test. Individuals with low scores are considered to have a better performance in reversal learning, while a high score indicates poorer performance. The spatial memory task was conducted with a rectangular board, which contained 8 wells with blue lids (L × W × H: 20 cm × 15 cm × 3 cm; Fig. 1d). Individuals needed to open the correct lid to get the food reward randomly placed into the well. This test encompassed four phases. In the first phase, individuals had to open the blue lids to search for the reward well. Once they found the correct well and ate the food, the board was removed. After a 5-min interval, the second phase began, with the food reward well being the same as that in the first phase. The first and second phases were training phases that allowed Budgerigars to remember the correct reward well. The third and fourth phases were test phases with a 24-h interval, and these two phases were carried out 24 h and 48 h after the second phase, respectively. Budgerigars need to use their memory from the training phases to find the correct rewarded well. If they did not find the reward well within 2 h of the testing phase, we regarded these individuals as non-solvers, and the maximum score in this phase was recorded. The total number of lids opened by Budgerigars in the third and fourth phases before they found the correct well was taken as the memory score, and the maximum score was 14. Individuals with low scores were considered to have a better performance in the spatial memory task, and high scores indicate poorer performance. The problem-solving task was carried out via two tests with different apparatuses. The apparatuses were categorized into two types, simple and complex, basing on different levels of difficulty. The simple apparatus was a petri dish with food reward (lid diameter: 70 mm; Fig. 1e), and individuals needed to open the petri dish to obtain the food reward by bill. The complex apparatus was a cuboid made of transparent acrylic sheets with an open end (L × W × H: 15 cm × 6 cm × 6 cm). Inside the complex apparatus was placed a small box with a flat stick that can be pulled out (Fig. 1f). The criterion for the success of this task was that the individuals had to use the stick to pull the box out of the apparatus and then open the lid on the box to obtain the food reward. The simple and complex apparatuses were respectively placed into the cages for 4 d (2 h from 9:00 to 11:00 and 2 h from 15:00 to 17:00 per day), and each apparatus needed to be tested for 16 h. If the individual fails to solve the problem within 16 h, the test will be deemed a failure. The number of attempts, the time before touching the apparatus, and the time to successfully opening the apparatus in problem solving tasks were recorded. In the exploration test, a linear mixed model was employed to calculate the individual repeatability of the exploration. To meet the normal distribution, exploration scores were square-root transformed and used as the response variable. The order (test sequence), sex, time, and date (days since January 1) were used as independent variables. The R package ‘rptR’ was used for data analysis. Then, the Best Linear Unbiased Prediction (BLUP) for each individual was calculated 1 000 times via the R package ‘arm’. In subsequent analyses, the mean BLUP values were used as exploration scores. In the spatial memory task, to demonstrate that Budgerigars remembered the location of the reward well, according to previous study, we considered searching more than 4.5 wells as random searching. One-sample *t*-tests were conducted on the scores of the Budgerigars in the third and fourth phases. We adopted six generalized linear mixed models (GLMMs) to analyze the effects of sex, tarsus length, exploration, and head volume on the cognitive performances in the six tests. We added neophobia as an independent variable in the inhibitory control, associative learning, and reversal learning tasks. To investigate the effects of sex and exploration on the problem-solving attempts, we adopted two GLMMs. Furthermore, we added the time before touching the apparatus as an independent variable in the problem-solving (complex apparatus) task. The ID was used as a random effect in all models, and all data analyses were conducted in R version 4.4.2. **[Results]** The repeatability of exploratory behavior was significant in exploration tests (R = 0.508, P < 0.001), and the confidence interval was [0.333, 0.651]. The average neophobia of individuals towards the inhibitory control apparatus was 373.3 ± 706.1 s, and that towards the associative-reversal learning apparatus was 141.2 ± 412.7 s. In the inhibitory control task, the average number of successful attempts was 7.42 ± 2.35. We found that a smaller head volume corresponded to a higher score in inhibitory control (Fig. 2a; Table 1), and male Budgerigars had higher scores than females (Fig. 2b; Table 1). The scores in the inhibitory control task were not significantly related to neophobia or exploration (Table 1). In the associative learning task, the average

number of attempts to meet the criterion was 46.84 ± 31.10. Individuals with smaller head volumes had lower number of attempts (Fig. 2c; Table 1), and male Budgerigars had lower scores than females (Fig. 2d; Table 1). The attempts were not significantly related to neophobia, exploration, or tarsus length (Table 1). In the reversal learning task, the average number of attempts to meet the criterion was 60.56 ± 24.07. The attempts were not significantly related to neophobia, sex, exploration, head volume, or tarsus length (Appendix 1). In the spatial memory task, the average number of attempts to find the reward well was 4.04 ± 3.39. No significant associations were found between measured factors and spatial memory scores (Appendix 1). In the problem-solving task (simple apparatus), the problem was solved by problem solvers in 3.58 ± 3.77 h (n = 40), and the non-problem solvers did not solve the problem within 16 h (n = 12). The number of attempts was 15.58 ± 11.54 (n = 52). Among the birds, fast explorers were more likely to open the apparatus (Fig. 3a; Table 2). Females were more likely to open the apparatus than males (Table 2). Budgerigars with longer tarsus were more likely to open the apparatus (Table 2). Whether the Budgerigar could open the apparatus was not significantly related to the head volume (Table 2). Among the 40 Budgerigars that successfully solved the problem, females spent shorter time to open the apparatus (Fig. 3b; Table 2), and the time was not significantly related to exploration, tarsus length, or head volume (Table 2). The number of attempts was not significantly correlated with sex among all Budgerigars or only problem solvers (Appendix 2). In the problem-solving task (complex apparatus), the problem was solved by problem solvers in 3.49 ± 3.22 h (n = 30), and the non-problem solvers did not solve the problem within 16 h (n = 22). The number of attempts was 20.35 ± 16.54 (n = 52), and the time before touching the apparatus was 769.8 ± 1 890.4 s. Among the birds, females were more likely to solve the problem than males (Fig. 3c; Table 3). Whether the Budgerigar could open the apparatus was not significantly related to exploration, tarsus length, the time before touching the apparatus, or head volume (Table 3). Among the 30 Budgerigars that successfully solved the problem, individuals with longer tarsus spent shorter time to open the apparatus, and the time was not significantly related to sex, exploration, the time before touching the apparatus, or head volume (Table 3). Among the Budgerigars that successfully solved the problem, females had a higher number of attempts than males (estimate: 14.410, SE: 5.692, df = 26, χ^2 = 6.409, P = 0.011; Fig. 3d), while the number of attempts was not significantly correlated with exploratory behavior or the time before touching the apparatus (Appendix 3). Among all Budgerigars, the number of attempts did not significantly correlate with exploration, sex, or the time before touching the apparatus (Appendix 3). [**Conclusion**] The findings indicate that cognition is related to personality, sex, and physical conditions, which enrich the understanding of cognition and its influencing factors. In the future, more in-depth experiments should be conducted, such as additional personality tests to examine their interrelationships and connections to cognitive performance.

Key words: Personality; Cognition; Sex; Head volume; Tarsus length

认知涉及信息的提取、存储、检索和处理（Bayne et al. 2019），它在动物的许多生态过程中发挥着重要的作用（Shettleworth 2001，Cauchard et al. 2013，Shaw 2017，Medina-García and Wright 2021）。目前，越来越多的证据表明认知表现在物种之间和物种内部均存在显著差异（Ashton et al. 2018，Lambert et al. 2019，Audet et al. 2023），这些差异与个体的适合度有关（Healy 2019）。因此，研究影响个体认知表现差异的因素就显得尤为重要。

已有研究表明，个体的认知表现与个体特征和社会环境等多种因素有关（Griffin et al. 2015，Whiteside et al. 2016，Bushby et al. 2018）。其中，性别与个体在认知任务中的表现有关。例如，雌性紫辉牛鹂（*Molothrus bonariensis*）在学习灵活性方面的反应更快（Lois-Milevicich et al. 2021）。雄性和雌性尼罗罗非鱼（*Oreochromis niloticus*）由于在生殖过程中扮演着不同的角色，雌性负责在口中抚养后代，雄性则需要防御其他入侵的雄性，导致了它们认知表现的差异（Brandão et al. 2019）。

动物个体的行为在不同时间和背景下所表现出来的一致性差异称为动物个性（Dingemanse and Réale 2005，Carere and Locurto 2011，Griffin et al. 2015），在许多动物类群中均发现动物个性的存在（Dall et al. 2012）。近些年来，越来越多的研究开始探讨动物个性与认知表现之间的关系（Šlipogor et al. 2022，Delacoux and Guenther 2023），但是关于认知与个性之间的关系仍需进一步验证（Dougherty and Guillette 2018）。例如，在虎皮鹦鹉（*Melopsittacus undulatus*）中，具有快速个性（处理压力的恐惧感低）的个体与问题解决装置的互动更多，并且问题解决的速度更快（Chen et al. 2022）。而在家八哥（*Acridotheres tristis*）中，低探索性的个体与任务的互动更多，问题解决的速度也更快（Lermite et al. 2017）。研究个性与认知之间的关系有助于理解个体的行为差异及其相关的进化和生态后果。

最新的研究发现，大脑容量与认知表现之间存在相关性（Møller 2010，Benson-Amram et al. 2016，Audet et al. 2023）。例如，Audet 等（2024）对鸣禽的研究发现，善于解决取食问题的物种在野外具有更高的技术创新率和更大的大脑。此外，一些关于大脑的研究证实大脑容量与头体积之间存在很强的正相关（Møller 2010，Jaatinen et al. 2019，Møller 2019），并且有研究表明头体积与认知能力有关（Møller 2010）。例如，在灰头鸫（*Turdus rubrocanus*）中发现头体积较大的个体更有可能学会新的技能（Lou et al. 2022）。

目前，关于影响认知表现因素的研究大多数都只集中在离散的认知任务或某些有限的因素上，这可能会导致实验结果出现偏差。因此本研究以虎皮鹦鹉为研究对象，多维度探讨影响其认知表现的因素。虎皮鹦鹉具有群居性、体型小且容易照顾的特点，被广泛应用于多种认知实验（Chen et al. 2019，解博雅等 2022，Zou et al. 2025）。本研究的问题包括两个方面：（1）研究个性特征（新异恐惧性和探索性）、性别、脑体积和身体特征与 4 项一般认知任务的关系；（2）研究问题解决任务的表现是否与个性、性别、脑体积和身体特征相关。本研究使用两种不同难度的问题解决装置来衡量虎皮鹦鹉的问题解决能力表现。

1　研究方法

1.1　研究对象及装置

1.1.1　研究对象　实验对象为 52 只笼养的成年虎皮鹦鹉，包括 27 只雄性和 25 只雌性。这些虎皮鹦鹉被饲养在飞行笼中（长 36 cm，宽 47.5 cm，高 93 cm，每笼 8 或 9 只）。室内温度保持在 25 ℃。它们每天处于 8.5 h 黑暗与 15.5 h 光照的周期。在非实验期间，为虎皮鹦鹉提供充足的食物（小米、蔬菜和红土）和水。

1.1.2　实验装置　探索性装置为一个长 120 cm、宽 65 cm、高 65 cm 的长方体木箱，装置内包含 5 棵人工树（高 50 cm，直径 1.5 cm），每棵树上有两个树枝（一个位于 25 cm 处，另一个在顶部；图 1a），长方体木箱的顶部是开放的，在其上覆盖一块透明亚克力板，便于记录。自我控制装置是一个透明的两端开口的圆柱体（长 7 cm，直径 7 cm），食物奖励放置在其中心处（图 1b），装置底部放置了一个铅块，防止装置被实验个体轻易移动。联想学习和反转学习的装置都是一个长方体木块（长 15 cm，宽 6 cm，高 3 cm），木块上面有两个直径 2 cm、深 1 cm 的圆槽，在其中放置奖励（图 1c），两

个圆槽分别用深绿色和浅绿色的盖子盖住。空间记忆装置是一块长方体木板（长 20 cm，宽 15 cm，高 3 cm），该木板上有 8 个圆槽，槽上盖有浅蓝色的盖子（图 1d）。问题解决实验包含两个装置，根据装置的不同难度分为简单装置和复杂装置。简单装置是一个带有食物奖励的培养皿（盖子直径 70 mm；图 1e），复杂装置是一个由透明亚克力板制成的一端开口长方体（长 15 cm，宽 6 cm，高 6 cm），在复杂装置内部放置一个带盖的可抽拉的塑料杯（图 1f）。

1.2 身体指标的测量

使用游标卡尺（PD-51，上海宝工工具有限公司，量程 0 ~ 150 mm，精度 0.01 mm）测量实验个体的跗跖长度和头大小，包括头长（鼻孔到枕部后端的距离）、头宽（两眼之间的间距）和头高（下颌到颅顶的距离）。

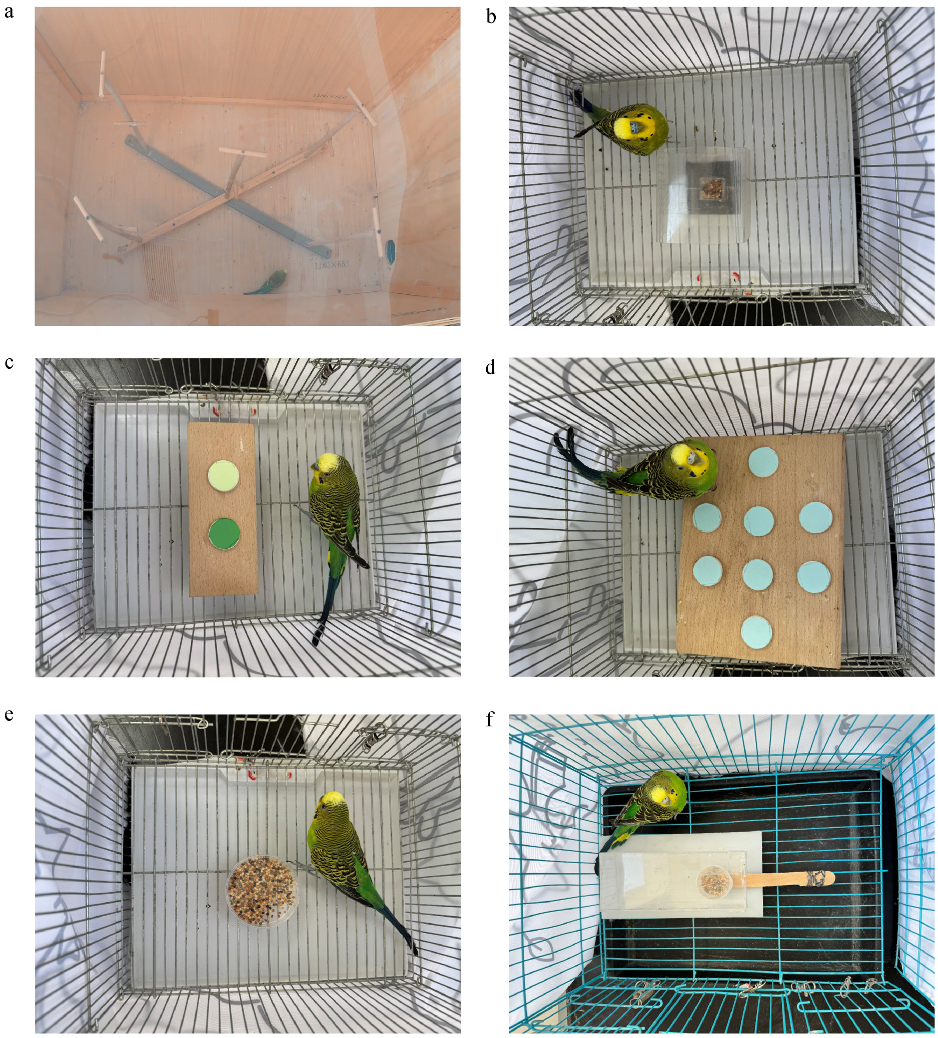

图 1 实验装置图

Fig. 1 Experimental apparatuses

a. 探索性装置；b. 自我控制装置；c. 联想-反转学习装置；d. 空间记忆装置；e. 问题解决实验（简单装置）；f. 问题解决实验（复杂装置）。

a. Exploration apparatus; b. Self-control apparatus; c. Associative-reversal learning apparatus; d. Spatial memory apparatus; e. Problem-solving apparatus (simple); f. Problem-solving apparatus (complex).

1.3 个性实验

1.3.1 探索性（exploration） 将虎皮鹦鹉从飞行笼中捉出，并放置在一个用黑色布料覆盖的小型笼（长 29.3 cm，宽 22.5 cm，高 28 cm）中。将小型笼的笼门对准探索性装置的门，经过 10 min 的适应后，打开笼门。从虎皮鹦鹉进入探索性实验装置开始（图 1a），立即记录 2 min 内虎皮鹦鹉的行走、飞行、跳跃行为的总和，并将该总和视为探索性得分，得分越高的个体判定为具有更强的探索性。每只个体均进行 3 次探索性实验，每次实验的时间间隔超过 15 d。

1.3.2 新异恐惧性（neophobia） 在自我控制任务开始前，将自我控制装置放入单个个体所在的小型笼中，记录个体从自我控制装置放入到开始接触装置之间的时间，将此时间作为个体对自我控制装置的新异恐惧反应。个体对联想学习装置的新异恐惧性测试除装置不同外，其他步骤均与上述流程相同。个体对自我控制装置或联想学习装置的新异恐惧时间越短判定为实验个体对相应装置的新异恐惧性越低。

1.4 认知实验

1.4.1 自我控制（self-control） 通过绕路取食的方式进行自我控制任务的测试。实验个体需绕到自我控制装置两端开口处才能获取食物（图 1b）。当个体绕到透明装置的两端开口处获取食物，并且在成功获取食物之前没有连续 3 次啄咬筒壁，判定该次实验成功。实验一共进行 10 次，每次实验的持续时间和间隔均为 1 min。将实验成功的次数视为个体该任务的得分。得分高的个体判定为在自我控制方面表现更好，而得分低则表现较差。

1.4.2 联想学习（associative learning） 在联想学习任务中，联想学习装置的奖励颜色是浅绿色（图 1c）。在第一次实验中，个体需要将深绿色和浅绿色两种颜色的盖子全部打开，发现只有浅绿色的盖子下的圆槽内含有食物奖励。每天的实验次数不超过 50 次，每次实验的持续时间和间隔均为 1 min。如果虎皮鹦鹉在之后的实验中打开了深绿色的盖子，立即移除装置并等待 1 min 后进行下一次实验。当个体在连续 9 次尝试中有 8 次找到浅绿色的圆槽时，视为通过联想学习任务。该实验的得分为虎皮鹦鹉所进行的总尝试次数。得分低的个体判定为联想学习方面表现更好，而得分高则判定为表现较差。

1.4.3 反转学习（reversal learning） 反转学习任务在联想学习任务完成后的 24 h 后开始。在这个实验中，食物奖励被放置在反转学习装置中带有深绿色盖子的圆槽中（图 1c），其他实验程序与联想学习任务相同。该实验的得分为虎皮鹦鹉所进行的总尝试次数。得分低的个体判定为在反转学习方面表现更好，而得分高则判定为表现较差。

1.4.4 空间记忆（spatial memory） 空间记忆装置含有 8 个带有浅蓝色盖子的圆槽，个体需要打开含有食物奖励的圆槽才能获得食物（图 1d，Ashton et al. 2018）。该实验包含 4 个阶段。在第一阶段，个体需要打开浅蓝色盖子来寻找含有奖励的圆槽。当实验个体找到正确的圆槽并吃掉食物时，就移除装置。5 min 后，开始第二阶段，含有奖励的圆槽位置与第一阶段相同。第一阶段和第二阶段是训练阶段，目的是让虎皮鹦鹉记住含有奖励圆槽的位置。第三阶段和第四阶段是测试阶段，两者之间以及第三阶段与第二阶段之间均间隔 24 h，即分别在第二阶段之后的 24 h 和 48 h 后进行。虎皮鹦鹉需要利用训练阶段的记忆来找到含有食物奖励的圆槽。在第三阶段和第四阶段中找到含有食物奖励的圆槽之前所打开的盖子数之和作为空间记忆得分。第三阶段和第四阶段的最高分都是 7 分，总的最高分是 14 分，即最高分是指在第三阶段和第四阶段中，虎皮鹦鹉找到正确的含有食物奖励的圆槽之前，可能打开盖子的最大数量。如果个体在第一阶段和第二阶段训练阶段中的任一阶段的 2 h 内未找到奖励圆槽，

记为空间记忆任务失败，没有得分，不进行后续实验。如果实验个体完成了训练阶段，但是在测试阶段（第三阶段和第四阶段）中，例如第三阶段的 2 h 内没有找到奖励圆槽，就将这些个体视为未完成第三阶段的空间记忆任务，并将它们在这一阶段的得分记录为最高分（7 分），等待 24 h 后进行第四阶段。如果它们在第四阶段的 2 h 内没有找到奖励圆槽，就将这些个体视为未完成第四阶段的空间记忆任务，并将它们在这一阶段的得分记录为最高分（7 分）。得分低的个体判定为在空间记忆任务中表现更好，而得分高则判定为表现较差。

1.4.5 问题解决（problem-solving） 根据问题解决任务的难度，分为简单装置和复杂装置。在问题解决实验的简单装置中（带有食物奖励的带盖培养皿，图 1e），个体需要用喙打开培养皿的盖子以获取食物奖励。在问题解决实验的复杂装置中（图 1f），个体必须先从一端开口的透明长方体装置中将塑料杯拉出，然后打开杯子上的盖子以获取食物奖励。实验开始前一周，将实验个体从飞行笼放入小型笼中单独饲养。在含有简单装置的问题解决任务中，实验时间为上午 9:00 至 11:00 时和下午 15:00 至 17:00 时，每天 4 h，一共持续 4 d，共计 16 h。如果虎皮鹦鹉在 16 h 内成功打开简单装置并吃到食物奖励，就判定为虎皮鹦鹉成功完成了简单的问题解决实验，然后将简单装置撤出。如果个体在 16 h 内未能打开简单装置，则判定为未能成功完成简单的问题解决实验。记录实验个体的尝试次数和成功完成简单问题解决任务时所花费的时间。对于复杂装置，除了使用的问题解决装置不同外，其他的实验时间和实验程序与简单装置均相同。记录实验个体的尝试次数、第一次接触装置时间以及虎皮鹦鹉成功完成问题解决任务所花费的时间。

1.5 数据分析

根据 Møller（2010），鸟类头体积（ml） = （头长 × 头高 × 头宽）/1 000，头长、头高和头宽的单位均为 mm。在探索性测试中，使用线性混合模型计算个体探索行为的重复性。为了满足正态分布的要求，把探索性数据进行平方根转换，并将其作为因变量，将测试顺序、性别、时间和日期（自 1 月 1 日起的天数）作为自变量。通过 R 软件中的“rptR”包进行分析。使用 R 包中“arm”计算每只个体的最佳线性无偏预测值（best linear unbiased prediction，BLUP），计算 1 000 次。在后续分析中将 BLUP 的平均值作为探索性得分。

在空间记忆实验中，根据 Tillé 等（1996）的公式 8，$\mu_Y = r(N+1)/(A+1)$，研究虎皮鹦鹉是否记住了奖励圆槽的位置。式中，r 为成功次数，N 为总地点数，A 为含有食物的地点数，μ_Y 表示在无放回抽样情况下，动物第 r 次成功之前需要搜索地点数量的期望值，本研究中搜索超过 4.5 个圆槽被视为随机搜索。对第三和第四阶段虎皮鹦鹉的得分分别进行单样本 t 检验。

使用广义线性混合模型分析性别、个性、身体特征等因素与各认知任务得分之间的关系。在自我控制实验中，以自我控制得分为因变量，将性别、跗跖长度、探索行为、头体积和新异恐惧性（自我控制装置）作为自变量。在联想学习实验中，以联想学习得分为因变量，将性别、跗跖长度、探索行为、头体积和新异恐惧性（联想-反转装置）作为自变量。在反转学习实验中，以反转学习得分为因变量，将性别、跗跖长度、探索行为、头体积和新异恐惧性（联想-反转装置）作为自变量。在空间记忆实验中，以空间记忆得分为因变量，将性别、跗跖长度、探索行为和头体积作为自变量。在解决问题（简单装置）实验中，将能否解决问题（简单装置）作为因变量，将性别、探索性、跗跖长度和头体积作为自变量。在成功解决问题（简单装置）的虎皮鹦鹉中，将解决问题花费的时间作为因变量，性别、探索性、跗跖长度和头体积作为自变量。以解决问题（简单装置）的尝试次数为因变量，将性别和探索性作为自变量。在成功解决问题（简单装置）的虎

皮鹦鹉中，以尝试次数为因变量，将性别和探索性作为自变量，使用广义线性混合模型分析。在解决问题（复杂装置）实验中，将能否解决问题（复杂装置）作为因变量，将性别、探索性、跗跖长度、第一次接触装置时间和头体积作为自变量；以解决问题（复杂装置）的尝试次数为因变量，将性别、第一次接触装置时间和探索性作为自变量。在成功解决问题（复杂装置）的虎皮鹦鹉中，将解决问题花费的时间作为因变量，性别、探索性、跗跖长度、第一次接触装置时间和头体积作为自变量；以尝试次数为因变量，将性别、第一次接触装置时间和探索性作为自变量。在所有模型中，将个体的编号作为随机变量。所有数据分析均在 R 4.4.2 版本（R Core Team 2014）中进行。数据以平均值 ± 标准误表示。

2　结果

2.1　个性实验

实验个体的探索行为具有显著的重复性（R = 0.508，P < 0.001，置信区间为[0.333，0.651]），说明虎皮鹦鹉中存在探索性。个体对自我控制装置的新异恐惧平均时间为（373.3 ± 706.1）s（1 ~ 2 400 s）。个体对联想学习装置的新异恐惧平均时间为（141.2 ± 412.7）s（1 ~ 2 076 s）。

2.2　认知实验

2.2.1　自我控制　在自我控制任务中，共有 52 只虎皮鹦鹉参与了实验。自我控制任务成功的平均次数为（7.42 ± 2.35）次（1 ~ 10 次）。头体积越小，自我控制任务的得分越高（图 2a，表 1）。雄性虎皮鹦鹉的得分比雌性更高（图 2b，

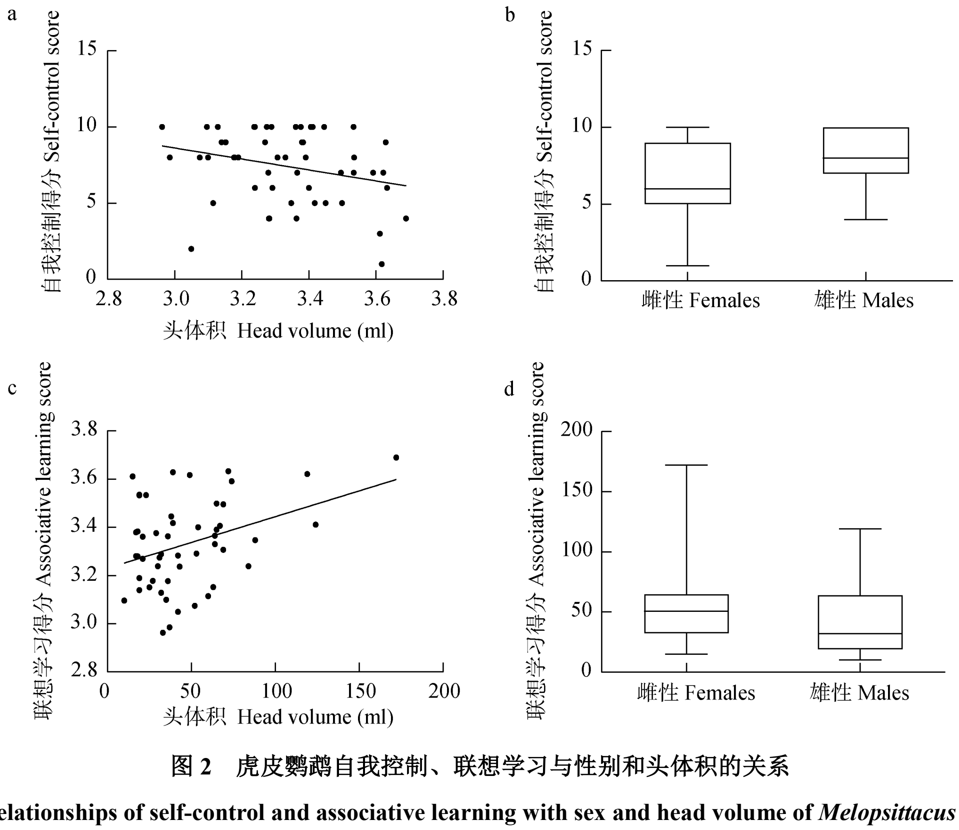

图 2　虎皮鹦鹉自我控制、联想学习与性别和头体积的关系

Fig. 2　Relationships of self-control and associative learning with sex and head volume of *Melopsittacus undulatus*

a. 自我控制得分和头体积之间的关系；b. 自我控制得分和性别之间的关系；c. 联想学习得分和头体积之间的关系；d. 联想学习得分和性别之间的关系。

a. Relationship between self-control score and head volume; b. Relationship between self-control score and sex; c. Relationship between associative learning score and head volume; d. Relationship between associative learning score and sex.

表 1　虎皮鹦鹉两种认知任务与性别、探索性、新异恐惧性、跗跖长度和头体积之间的关系

Table 1　Relationships of the two cognitive tasks with sex, exploration, neophobia, tarsus length, and head volume of *Melopsittacus undulatus*

	自变量 Independent variable	估计值 Estimate	标准误 SE	自由度 *df*	卡方值 χ^2	*P* 值 *P*-value
自我控制 Self-control (*n* = 52)	性别 Sex	–2.293	0.590	46	15.088	< 0.001
	探索性 Exploration	–0.398	0.340	46	1.366	0.243
	新异恐惧性（自我控制）Neophobia (self-control)	< 0.001	< 0.001	46	0.729	0.393
	跗跖长度 Tarsus length	–0.961	0.509	46	3.568	0.059
	头体积 Head volume	–4.031	1.622	46	6.179	0.011
联想学习 Associative learning (*n* = 51)	性别 Sex	17.340	8.489	45	4.173	0.041
	探索性 Exploration	2.168	4.789	45	0.205	0.651
	新异恐惧性（联想-反转）Neophobia (Associative-reversal)	–0.011	0.010	45	1.096	0.295
	跗跖长度 Tarsus length	–4.344	7.152	45	0.369	0.544
	头体积 Head volume	76.272	23.239	45	10.772	0.001

$P < 0.05$ 被认为是显著的。$P < 0.05$ are considered significant.

表 1）。自我控制任务的得分与跗跖长度、新异恐惧或探索行为之间均无显著相关性（表 1）。

2.2.2　联想学习　在联想学习任务中，共有 51 只虎皮鹦鹉参与了实验。达到标准所需的平均尝试次数为（46.84 ± 31.10）次（10 ~ 172 次）。头体积较小的个体得分较低（图 2c，表 1）。雄性虎皮鹦鹉的得分低于雌性（图 2d，表 1）。尝试次数与新异恐惧、探索行为或跗跖长度之间均无显著相关性（表 1）。

2.2.3　反转学习　在反转学习任务中，共有 50 只虎皮鹦鹉参与了实验。达到标准所需的平均尝试次数为（60.56 ± 24.07）次（18 ~ 125 次）。尝试次数与新异恐惧、性别、探索行为、头体积或跗跖长度之间均无显著相关性（附录 1）。

2.2.4　空间记忆　在空间记忆任务中，共有 47 只虎皮鹦鹉参与了实验。找到奖励圆槽的平均尝试次数为（4.04 ± 3.39）次（0 ~ 14 次）。在空间记忆测试的第三阶段（24 h 后），虎皮鹦鹉搜索的圆槽数量显著少于随机搜索的水平（2.021 ± 0.286，n = 47，单样本 t 检验：t = –8.664，P < 0.001，df = 46）。在空间记忆测试的第四阶段（48 h 后），虎皮鹦鹉搜索的圆槽数量显著少于随机搜索的水平（2.021 ± 0.283，n = 47，单样本 t 检验：t = –8.763，P < 0.001，df = 46）。这表明，虎皮鹦鹉记住了食物的位置。尝试次数与性别、探索行为、头体积或跗跖长度之间均无显著相关性（附录 1）。

2.2.5　问题解决　在问题解决（简单装置）实验中，52 只虎皮鹦鹉中有 40 只成功解决了问题，平均用时（3.58 ± 3.77）h（0.01 ~ 15.98 h）。12 只个体在 16 h 内未能解决问题。所有个体的平均尝试次数为（15.58 ± 11.54）次（1 ~ 69 次）。在 52 只个体中，快速探索者更有可能打开装置（图 3a，表 2），雌性比雄性更有可能打开装置（图 3b，表 2），跗跖较长的个体更有可能打开装置（表 2）。虎皮鹦鹉能否打开装置与头体积之间无显著相关性（表 2）。在 40 只成功解决问题的虎皮鹦鹉中，雌性打开装置所用的时间更短（表 2），打开装置所花费的时间与探索行为、跗跖长度或头体积之间均无显著相关性（表 2）。不管是在所有的虎皮鹦鹉中还是成功解决问题的虎皮鹦鹉中，尝试次数与探索性和性别均无显著差异（附录 2）。

在问题解决（复杂装置）中，52 只虎皮鹦鹉中有 30 只解决了问题，平均用时（3.49 ± 3.22）h（0.04 ~ 9.69 h），22 只个体在 16 h 内未

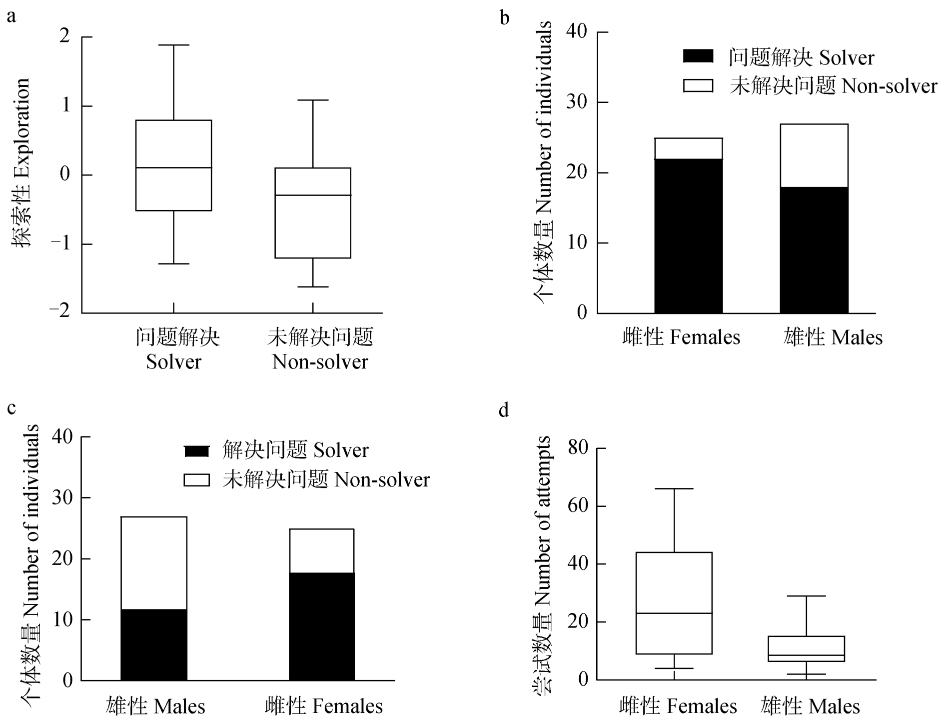

图 3　虎皮鹦鹉问题解决与性别、跗跖长度和探索性的关系

Fig. 3　Relationships of problem-solving performance with sex, tarsus length, and exploration of *Melopsittacus undulatus*

a. 问题解决的表现（简单装置）与探索性之间的关系；b. 问题解决的表现（简单装置）与性别之间的关系；c. 问题解决的表现（复杂装置）与性别之间的关系；d. 问题解决的表现（复杂装置）尝试次数与性别之间的关系。

a. Relationship between problem-solving performance (simple apparatus) and exploration; b. Relationship between problem-solving performance (simple apparatus) and sex; c. Relationship between problem-solving performance (complex apparatus) and sex; d. Relationship between the number of attempts in problem-solving performance (complex apparatus) and sex.

表 2　虎皮鹦鹉问题解决（简单装置）与性别、探索性、跗跖长度和头体积之间的关系

Table 2　Relationships of the problem-solving task (simple apparatus) with sex, exploration, tarsus length and head volume of *Melopsittacus undulatus*

	自变量 Independent variable	估计值 Estimate	标准误 SE	自由度 *df*	卡方值 χ^2	*P* 值 *P*-value
能否解决问题 Whether the problem can be solved (*n* = 52)	性别 Sex	0.288	0.113	47	6.543	0.011
	探索性 Exploration	0.151	0.065	47	5.396	0.020
	跗跖长度 Tarsus length	0.246	0.097	47	6.474	0.011
	头体积 Head volume	−0.152	0.304	47	0.249	0.618
成功解决问题 Successfully solving the problem (*n* = 40)	性别 Sex	−3.277	1.255	35	6.816	0.009
	探索性 Exploration	−0.304	0.709	35	0.184	0.668
	跗跖长度 Tarsus length	−0.551	1.035	35	0.283	0.595
	头体积 Head volume	2.140	3.117	35	0.472	0.492

$P < 0.05$ 被认为是显著的。$P < 0.05$ are considered significant.

能解决问题。所有个体的平均尝试次数为（20.35 ± 16.54）次（0 ~ 66 次）。第一次接触装置的平均时间为（769.8 ± 1 890.4）s（1 ~ 7 200 s）。在 52 只虎皮鹦鹉中，雌性比雄性更有可能解决问题（图 3c，表 3），虎皮鹦鹉能否打开装置与探索行为、跗跖长度、第一次接触装置时间或头体积之间均无显著相关性（表 3）。在 30 只成功解决问题的虎皮鹦鹉中，跗跖较长的个体打开装置所用的时间更短（表 3），打开装置所用时间与性别、探索行为、第一次接触装置时间或头体积之间均无显著相关性（表 3）。在成功解决问题的虎皮鹦鹉中，雌性的尝试次数高于雄性（估计值为 14.410，标准误为 5.692，$df = 26$，$\chi^2 = 6.409$，$P = 0.011$；图 3d），而尝试次数与探索性或第一次接触装置时间均无显著相关性（附录 3）。在所有的虎皮鹦鹉中，尝试次数与探索性、性别、第一次接触装置时间均无显著相关性（附录 3）。

3 讨论

本研究发现，虎皮鹦鹉的认知能力与它们的身体特征、性别和个性有关。此外，问题解决实验的表现与个体的个性以及实验装置的难度有关。

头体积较小的虎皮鹦鹉在自我控制和联想学习任务中的表现更好，这一发现与其他对头体积的认知研究的结果并不一致（Kabadayi et al. 2016，Lou et al. 2022）。一个可能的原因是这些任务是由大脑的特定区域控制的（Güntürkün 2005，Rössler and Auersperg 2023）。例如，较大的上纹状体腹侧（hyperstriatum ventral，HV）与更高的觅食创新率相关（Timmermans et al. 2000）。除了与大脑大小有关，认知能力也与神经元数量和神经元之间的连接有关（Olkowicz et al. 2016，Sol et al. 2022）。头体积是否与某些认知任务（如自我控制和联想学习任务）相关的脑神经发育有关，未来还需进一步验证。

在自我控制任务中，雄性虎皮鹦鹉的表现优于雌性，而在问题解决实验中，雌性的表现则优于雄性。一个可能的解释是两性在社会分工上存在差异。在虎皮鹦鹉求偶期间，雄性虎皮鹦鹉需要向雌性喂食（Brockway 1974）。此外，当雌性孵卵时，雄性会在数天内为雌性提供食物（Kubiak 2020）。因此，雄性需要控制

表 3　虎皮鹦鹉问题解决（复杂装置）与性别、探索性、跗跖长度、头体积和第一次接触装置时间之间的关系

Table 3　Relationships of the problem-solving task (complex apparatus) with sex, exploration, tarsus length, head volume, and time before touching the apparatus of *Melopsittacus undulatus*

	自变量 Independent variable	估计值 Estimate	标准误 SE	自由度 *df*	卡方值 χ^2	*P* 值 *P*-value
能否解决问题 Whether the problem can be solved (*n* = 52)	性别 Sex	0.325	0.141	46	5.332	0.021
	探索性 Exploration	0.023	0.085	46	0.072	0.788
	跗跖长度 Tarsus length	0.122	0.121	46	1.013	0.314
	头体积 Head volume	−0.037	0.400	46	0.008	0.927
	第一次接触装置时间 Time before touching the apparatus	−0.001	< 0.001	46	2.158	0.142
成功解决问题 Successfully solving the problem (*n* = 30)	性别 Sex	0.943	1.256	24	0.564	0.453
	探索性 Exploration	−0.530	0.748	24	0.502	0.479
	跗跖长度 Tarsus length	−2.427	1.207	24	4.043	0.044
	头体积 Head volume	−2.941	3.432	24	0.735	0.391
	第一次接触装置时间 Time before touching the apparatus	−0.001	< 0.001	24	0.168	0.682

$P < 0.05$ 被认为是显著的。$P < 0.05$ are considered significant.

自己的进食动机，从而确保孵卵的雌性有充足的食物资源。对于雌性而言，问题解决的能力使个体能够快速适应环境变化，增加繁殖成功率并降低风险（Cauchard et al. 2013）。雌性虎皮鹦鹉在问题解决过程中尝试次数多于雄性。在孵卵期间，雌性虎皮鹦鹉孵卵，而雄性为它们提供食物。在雏鸟育雏期间，雌性需要转变角色，它们也要为雏鸟提供食物（Kubiak 2020）。所以，问题解决的能力可能有助于雌性在繁殖过程中快速适应不同的情境。由于自我控制任务开始前需进行绕行训练，本次实验的结果可能不完全反映自我控制能力，后续需要通过进行绕行训练做进一步研究。

在本研究中发现快速探索的个体在问题解决任务中表现更好。对此有两种可能的解释：第一，不同个性特征之间的相互作用。在这种情况下，快速探索者可能通过本研究中未包含的其他潜在机制完成任务。第二，快速探索者具有更强的创新性（Sol et al. 2011）。问题解决任务与创新行为有关（Griffin and Guez 2014），而快速探索者能够快速获取信息（Verbeek et al. 1994，Guillette et al. 2009，Griffin et al. 2015），这有助于增加创新行为中的信息收集。但是，在本研究中未发现探索行为与问题解决的尝试次数之间存在相关性。此外，在更复杂的问题解决任务中，发现虎皮鹦鹉的表现与探索行为无显著相关性。一般来说，难度更高的任务可能需要更多时间来完成（Chang et al. 2018）。在本研究中，以 16 h 作为阈值可能不足以让个体完成任务。随着任务难度的增加，个体可能需要更多信息来解决问题。未来的研究需要关注在复杂环境中探索行为、信息获取与决策过程之间的关系，并理解不同个性特征之间的相互作用及其与问题解决能力的关系。

本研究结果表明，认知能力与个性、性别和身体特征有关，这为进一步理解认知及其影响因素提供了更深入的见解。在未来，应开展更深入的实验，例如进行更多的个性测试，以检验它们之间的相互关系以及与认知表现的联系。

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附录 1　虎皮鹦鹉两项认知任务与性别、探索性、新异恐惧性、跗跖长度和头体积之间的关系

Appendix 1　Relationships of the two cognitive tasks with sex, exploration, neophobia, tarsus length, and head volume of *Melopsittacus undulatus*

	自变量 Independent variable	估计值 Estimate	标准误 SE	自由度 *df*	卡方值 χ^2	*P* 值 *P*-value
反转学习 Reversal learning (*n* = 50)	性别 Sex	13.855	7.297	44	3.605	0.058
	探索性 Exploration	−1.014	4.104	44	0.061	0.805
	新异恐惧性（联想-反转） Neophobia (associative-reversal)	−0.002	0.009	44	0.036	0.850
	跗跖长度 Tarsus length	1.177	6.130	44	0.037	0.848
	头体积 Head volume	4.286	20.104	44	0.046	0.831
空间记忆 Spatial memory (*n* = 47)	性别 Sex	−0.039	1.081	42	0.001	0.971
	探索性 Exploration	0.448	0.602	42	0.554	0.457
	跗跖长度 Tarsus length	−0.663	0.899	42	0.544	0.461
	头体积 Head volume	−3.918	2.945	42	1.770	0.183

附录 2　虎皮鹦鹉问题解决任务（简单装置）尝试次数与性别和探索性之间的关系

Appendix 2　Relationships of the number of attempts in problem-solving task (simple apparatus) with sex and exploration of *Melopsittacus undulatus*

	自变量 Independent variable	估计值 Estimate	标准误 SE	自由度 *df*	卡方值 χ^2	*P* 值 *P*-value
尝试次数 Number of attempts (*n* = 52)	性别 Sex	−1.264	3.262	49	0.150	0.698
	探索性 Exploration	0.170	1.910	49	0.008	0.929
成功解决问题的尝试次数 Number of attempts to successfully solve the problem (*n* = 40)	性别 Sex	−2.454	2.481	37	0.978	0.323
	探索性 Exploration	2.821	1.460	37	3.735	0.053

附录 3　虎皮鹦鹉问题解决任务（复杂装置）尝试次数与性别、第一次接触装置时间和探索性之间的关系

Appendix 3　Relationships of the number of attempts in problem-solving task (complex apparatus) with sex, exploration, and time before touching the apparatus of *Melopsittacus undulatus*

	自变量 Independent variable	估计值 Estimate	标准误 SE	自由度 *df*	卡方值 χ^2	*P* 值 *P*-value
成功解决问题的尝试次数 Number of attempts to successfully solve the problem (*n* = 30)	性别 Sex	14.410	5.692	26	6.409	0.011
	探索性 Exploration	2.723	3.224	26	0.713	0.398
	第一次接触装置时间 Time before touching the apparatus	−0.003	0.002	26	2.150	0.143
尝试次数 Number of attempts (*n* = 52)	性别 Sex	7.336	4.548	48	2.601	0.107
	探索性 Exploration	2.714	2.734	48	0.986	0.321
	第一次接触装置时间 Time before touching the apparatus	−0.001	0.001	48	0.280	0.597

$P < 0.05$ 被认为是显著的。$P < 0.05$ are considered significant.