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Novelty and individual differences influence neophobia in orange-winged Amazon parrots (*Amazona amazonica*)

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Abstract

Environmental enrichment both improves the welfare of captive animals and increases the validity of research using these animals. Enrichment programs have been shown to prevent or reduce the development of behavioral vices, stereotypy, and fearfulness. However, the protocols used in enrichment studies can be inconsistent: under some protocols, enrichments are provided but not changed, while under others, enrichments are rotated frequently. Enrichment experiments to date have also largely ignored the influence of individual differences on fearfulness. The aim of this study was to determine whether frequent rotation of enrichment objects (''high novelty'') was more effective than simply providing enrichment objects (''low novelty'') in reducing neophobia in juvenile orange-winged Amazon parrots and to determine whether individual differences significantly affected neophobia. Thirty-four juvenile orange-winged Amazon parrots received both an 11-week high-novelty (HN) treatment and an 11-week low-novelty (LN) treatment, which were given in random order. Neophobia was assessed by measuring birds' latency to feed from a dish of highly favored food in the presence of various novel objects at approximately 10-day intervals. Our results indicate that the HN treatment significantly reduced neophobia in juvenile orange-winged Amazons. We also found that both individual variation in fearfulness and the novel object used for testing significantly affected birds' latency to feed in the presence of novel objects. Our results indicate that rotation of enrichment objects is more effective than simply providing enrichments in reducing fearful behavior in parrots. The effect of rotating enrichments was strong enough to overcome approximately four-fold differences in birds' latency to feed in the presence of different novel objects and even greater individual differences in neophobia. However, we also found that in highly fearful individuals, HN actually increased birds' latency to feed in the presence of novel objects. Our results indicate that rotation of enrichment objects is more effective than simply providing enrichments in reducing fearful behavior in parrots, but that

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both enrichment object properties and individual differences should be carefully considered in the design of future enrichment studies and protocols.

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Environmental enrichment can significantly improve both the welfare of captive animals and the validity of research conducted with those animals. Successful enrichment programs prevent the development of a variety of behavioral vices (e.g., featherpicking in parrots) in young animals or reduce the occurrence of these vices in older animals (Meehan et al., 2003). Enrichment can also reduce anxiety-related behaviors and sensitivity to environmental stressors like novelty and human handling (e.g., Meehan and Mench, 2002; Francis et al., 2002; Morley-Fletcher et al., 2003; Jones and Waddington, 1992). Furthermore, environmental enrichment plays a critical role in maintaining normal brain function and behavior in captive animals. Cage stereotypies, which are commonly associated with barren (i.e., unenriched) housing conditions, are symptoms of a more general syndrome of behavioral disinhibition that is likely mediated by altered striatal functioning (Turner and Lewis, 2004; Garner et al., 2003).

Surprisingly little attention has been paid to the issue of which properties of enrichment programs are responsible for these changes. During enrichment studies, enrichment items are commonly changed at regular intervals (e.g., Meehan and Mench, 2004; Meehan et al., 2003; van der Harst et al., 2003; Francis et al., 2002), although this practice is not universal (Frick et al., 2003; Marashi et al., 2003; van Hoek and King, 1997). A recent study attributes the decrease in neophobia seen in orange-winged Amazon parrots (*Amazona amazonica*) housed under enriched conditions to a general habituation to novelty (Meehan and Mench, 2002). However, since this study compared birds in barren housing with birds receiving enrichments that were rotated weekly (Meehan and Mench, 2002), it is impossible to determine whether the enrichments themselves were responsible for the observed decrease in neophobia, or whether this effect was due to regular exposure to novelty. However, recent evidence suggests that exposure to levels of novelty in the nursery that are much higher than those experienced by parent-reared birds that are raised in nextboxes may explain why young (<6 months of age), hand-reared orange-winged Amazon parrots exhibit significantly lower levels of neophobia than parent-reared birds of the same age (Fox and Millam, 2004), lending support to the conclusions of Meehan and Mench (2002).

Furthermore, a number of studies of both avian and non-avian species have demonstrated that individuals demonstrate consistent and often dramatic differences in fearfulness. Such differences can arise from differences in early experience (e.g., Meaney, 2001; Fox and Millam, 2004) or may be due to other factors, such as intrinsic individual differences in "personality" or behavioral type (e.g., Benus et al., 1991; Verbeek et al., 1994; Wilson, 1998; Gosling, 1998; Capitanio, 1999; Meaney, 2001). Despite the fact that such individual differences clearly affect how individuals respond to environmental stressors such as novelty (e.g., new enrichments), the influence of individual variation in fearfulness has received little attention to date (e.g., Benus et al., 1991; Koolhaas et al., 1999; Groothius and Carere, 2005).

Therefore, the purpose of this study was to disentangle the effects of novelty (i.e., frequent rotation of enrichment objects), early experience (hand-rearing versus parent-rearing), and individual differences in fearfulness from the effects of the enrichment objects themselves. We used a group of juvenile orange-winged Amazon parrots to test the hypothesis that exposure to novelty, rather than the provision of enrichment objects, is responsible for reducing neophobia in birds housed under enriched conditions, and to examine the influence of individual differences (which may arise from differences in early experience) on birds' response to novel objects.

1. Methods

1.1. Subjects and housing

Thirty-four juvenile (6–18 months of age) orange-winged Amazon parrots were used for this study. All individuals were reared at the University of California, Davis Avian Science Research Facility during the spring of 2001 and the spring of 2002. Twelve of the birds were tame, hand-reared birds, six from the 2001 breeding season and six from the 2002 breeding season. The remaining 22 birds were parent-reared.

With the exception of three individuals that were housed singly, all birds were housed with either a sibling or an unrelated bird of similar age if no sibling was available, as in Fox and Millam (2004). Each pair of birds occupied a cage (approximately 60 cm × 90 cm × 180 cm) outfitted with two wood perches, a feeder, and a nipple drinker. Food (Roudybush low-fat maintenance diet, Roudybush, Inc., Woodland, CA) and water were available ad libitum. Approximately 100 g of fresh fruits and vegetables (carrots, broccoli, oranges, apples, grapes, chard) were provided five times per week. The photoperiod in the room was 10 h light:14 h dark.

1.2. Treatments

1.2.1. High-novelty treatment

The high-novelty (HN) treatment lasted 11 weeks. Birds assigned to the HN treatment were provided with several enrichments (destructible wooden parrot toys, foraging devices, plastic and acrylic parrot toys). Four to five times per week, two of these enrichment devices were replaced at random with different enrichments, so that each bird in the HN treatment saw a particular toy no more than once per week. Toy rotation took no more than 1–2 min per cage and was done at the same time that birds in both HN and LN conditions were given dishes of fruits and vegetables, in order to ensure that birds receiving the high-novelty treatment did not experience significantly more human contact than those receiving the low-novelty treatment.

1.2.2. Low-novelty treatment

The low-novelty (LN) treatment lasted 11 weeks. Birds assigned to the LN treatment were also provided with several enrichments of the same types provided to the birds undergoing the HN treatment. However, these enrichments were not changed during the duration of this treatment.

Half of the birds received the HN treatment for 11 weeks, followed by a 3-week break and then the LN treatment, while half of the birds received the treatments in the opposite order. Treatment order was randomly assigned.

1.3. Novel objects testing

To measure neophobia, we used a technique that had been successfully used in a previous experiment (see Fox and Millam, 2004). Briefly, birds were trained to take peanuts (a highly favored food) from a dish hung on the front of their home cage. Once birds were taking peanuts from the dish within one minute or less, we measured neophobia by hanging a novel object several inches above the peanut dish and measuring individuals' latency to take a peanut from the dish. To avoid any confounding effects of having an observer present in the room, the birds' behavior was videotaped for 30 min and latencies (in seconds) were calculated from the videotaped data. If a bird did not feed at all during the 30-min testing period, that individual's latency to feed was scored as 1500 s.

The birds were tested with 17 novel objects: a ball, a blue plastic cat, a black plastic box, a toy elephant, a baby rattle, a funnel, a plastic mug, a measuring cup, a stuffed animal, a shower puff, a scoop, a spatula, a small spray bottle, a large cooking spoon, a toy truck, a metal whisk, and a yellow plastic dish scrubber. Objects were presented to each bird or pair of birds in one of five different sequences, to control for any effects of presentation order. Testing began 1 week after the beginning of each 11-week treatment period, and objects were presented at approximately 10-day intervals. Each novel object was presented only once to each bird or pair of birds, but the same 34 birds were used for all novel objects tests.

1.4. Data analysis

To examine the effects of treatment (HN or LN), rearing condition, and novel object on birds' latency to feed, data were analyzed using repeated-measures ANOVA (SAS, SAS systems, Cary, NC), with latency to feed in the presence of a novel object as the dependent variable. The same birds were used for each test, so the data points for each novel objects test could therefore not be assumed to be independent. The main effects included in the model were treatment (HN or LN), rearing condition (HR or PR), and object used. The model also included three two-way interaction effects (treatment × rearing condition, treatment × object, rearing condition × object) and one three-way interaction effect (treatment × rearing condition × object).

Several videotapes were damaged during taping, causing the loss of approximately 120 observations (of 578 total observations). Data from novel objects tests using the cooking spoon were excluded from the analysis because we had latency data for only 11 birds (approximately one-third of the individuals). For all other objects, we had usable observations for at least half of the individuals, representing both treatments. The remaining missing observations were treated as missing values in the analysis.

2. Results

Using repeated-measures ANOVA, we found significant effects of treatment ($F_{1,258} = 5.75$, $p = 0.017$) and novel object used ($F_{15,331} = 6.10$, $p < 0.0001$) on birds' latency to feed in the presence of a novel object. There was a near-significant effect of rearing condition on latency to feed as well ($F_{1,30.2} = 3.35$, $p = 0.077$). The treatment × object interaction was not significant ($F_{14,312} = 1.44$, $p = 0.13$). However, there was a significant treatment × rearing condition interaction ($F_{1,330} = 5.75$, $p = 0.017$) as well as a significant interaction between object and rearing condition ($F_{15,297} = 2.67$, $p = 0.0008$). The three-way object × treatment × rearing condition interaction was also significant ($F_{11,244} = 1.99$, $p = 0.03$).

Overall, birds exhibited shorter latencies to feed in the presence of novel objects during the HN treatment than during the LN treatment. Birds fed an average of 71.6 ± 48.9 s sooner in the presence of a novel object when receiving the HN treatment. However, hand-reared birds were more strongly affected by the HN treatment: on average, HR birds fed 168.5 ± 49.6 s sooner in the presence of a novel object when receiving the HN treatment. In contrast, PR birds fed an average of 26.3 ± 69.3 s sooner under the HN treatment (see Fig. 1).

Individuals varied considerably with regard to fearfulness. Latencies to feed in the presence of a novel object, averaged across all novel object tests, ranged from 276.2 ± 144.2 to 1435 ± 47.7 s. HR birds tended to be less fearful than PR birds, although, as noted above, this effect was not statistically significant.

The parent-reared birds exhibited much greater variability in fearfulness (i.e., average latency to feed in the presence of novel objects across all novel object tests) than did the hand-reared birds. Ten of the twelve hand-reared birds had average latencies to feed of 750 s or less across all novel object tests, and only one bird had an average latency to feed > 1000s. Only 12 of 22 parent-reared birds had average latencies of 750 s or less across all tests, and 6 birds had average

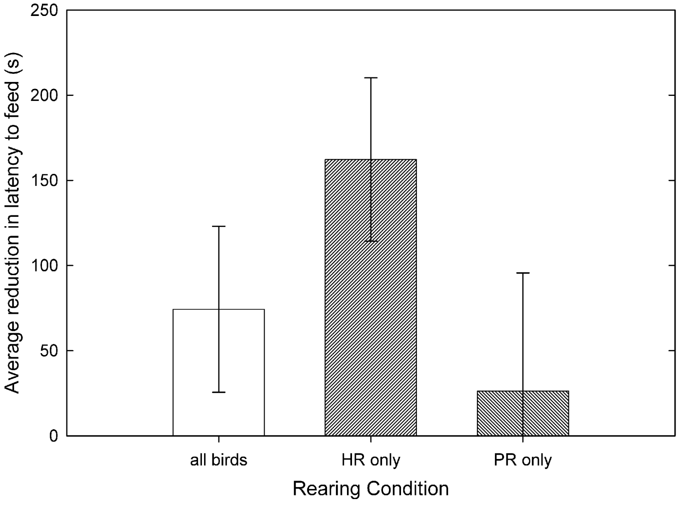

Fig. 1. Average reduction in latency (in seconds, mean ± S.E.) to feed from a dish of favored food in the presence of novel objects when birds are housed under high-novelty (HN) conditions. On average, housing under HN conditions significantly reduced individuals' latency to feed in the presence of a novel object ("all birds," repeated-measures ANOVA, $F_{1,258} = 5.75$, $p = 0.017$). However, hand-reared (HR only) birds exhibited a significantly greater reduction in feeding latency than did parent-reared birds (PR only) during HN treatment (repeated-measures ANOVA, treatment × rearing condition interaction effect, $F_{1,330} = 7.06$, $p = 0.008$).

latencies to feed >1000s. Additionally, individual responses to HN treatment were quite variable among parent-reared birds, as indicated by the large standard error (see Fig. 1).

Regression analyses revealed that individual differences in neophobia profoundly affected how individual PR birds responded to high-novelty treatment (see Fig. 2a and b). For PR birds with average latencies to feed <750 s across all tests, there was a significant negative relationship between average latency to feed in the presence of a novel object across both all tests and the difference in latency to feed under HN versus LN treatment ($r^2 = 0.46$, $p = 0.01$). Thus, moderately fearful birds experienced a greater decrease in neophobia as a result of high-novelty treatment than did less fearful birds. In contrast, for PR birds with average feeding latencies above 750 s across all tests, there was a significant positive relationship between average latency to feed in the presence of novel objects across all tests and the difference in latency to feed under HN versus LN treatment ($r^2 = 0.62$, $p = 0.004$). Thus, HN treatment was less effective in reducing fearfulness in the most fearful birds, and in some cases, latency to feed in the presence of a novel object was actually greater during HN treatment than during LN treatment. For those parent-reared birds with average overall feeding latencies >1000s, the average latency to feed during HN treatment was 139.9 ± 59.3 s *greater* than during LN treatment. Similarly, for the one hand-reared bird with an average overall feeding latency >1000 s, the difference in average latency to feed between HN and LN treatments was −15.2 s (in contrast to the average of −168.5 s for all hand-reared birds).

Birds also responded quite differently to the novel objects used for testing. Latencies to feed ranged from a minimum of 297.0 ± 98.8 s in the presence of the funnel to a maximum of 1134.4 ± 127.8 s in the presence of the black plastic box. The significant treatment × rearing condition × object interaction indicates that, in addition to the type of novel object presented, both rearing condition and treatment also influence birds' latency to feed in the presence of particular objects.

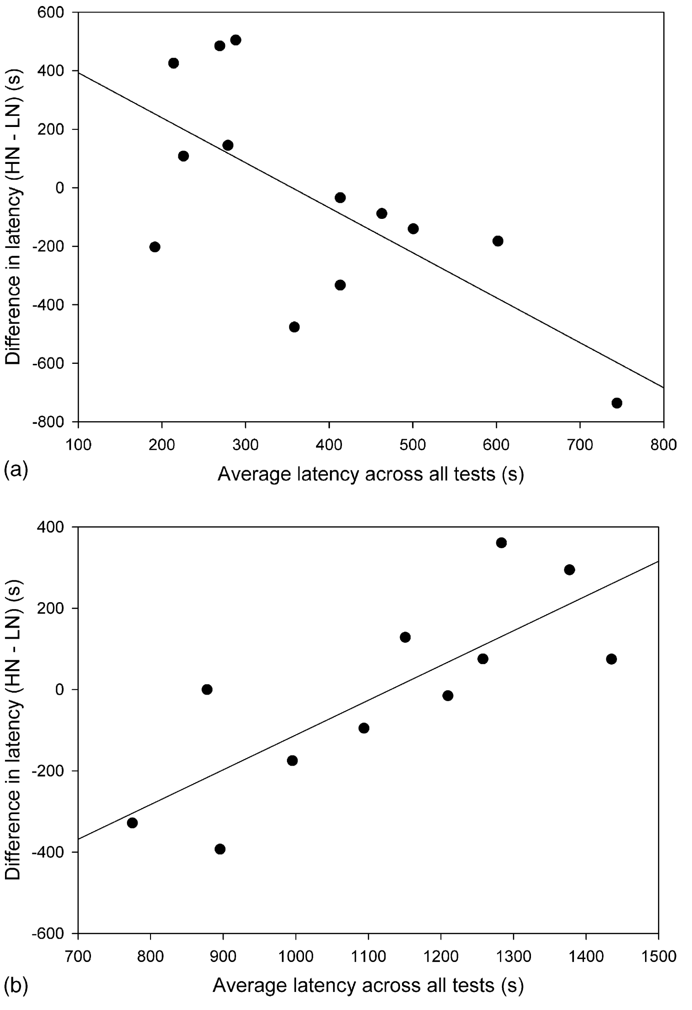

Fig. 2. (a) For PR birds with average latencies to feed in the presence of a novel object of <750 s (across all novel object tests), there is a significant negative correlation between an individual's overall average latency to feed and the change in feeding latency between HN and LN treatment ($r^2 = 0.46$, $p = 0.01$), indicating that HN treatment causes a greater decrease in fearfulness in moderately neophobic birds. (b) For PR birds with average latencies to feed in the presence of a novel object of >750 s (across all novel object tests), there is a significant positive correlation between an individual's overall average latency to feed and the change in feeding latency between HN and LN treatment ($r^2 = 0.62$, $p = 0.004$). In the most fearful individuals, HN treatment can actually increase fearfulness.

3. Discussion

The main goal of this study was to determine whether low neophobia in orange-winged Amazon parrots housed under enriched conditions was due to the enrichments themselves or to "habituation to novelty" due to frequent rotation of enrichment objects. While simply providing environmental enrichment has been shown to have beneficial effects (e.g., Frick et al., 2003; Marashi et al., 2003; van Hoek and King, 1997), it is clear from the results of this study that frequent rotation of enrichments is more effective than enrichments alone in reducing neophobia in orange-winged Amazon parrots. Additionally, frequent rotation of novel objects was apparently more effective in reducing fearfulness in hand-reared birds than in parent-reared birds.

Although hand-reared and parent-reared birds differed in their responses to high-novelty treatment, it is not clear that this difference was in fact due to a difference in early experience. On average, hand-reared birds did tend to have shorter overall latencies to feed than parent-reared birds, consistent with the observation that hand-reared whooping cranes spend more time foraging and less time on vigilance behaviors than parent-reared individuals (Kreger et al., 2005; Kreger et al., 2004). Hand-reared birds' stronger response to high-novelty treatment is also consistent with studies that have shown that maternally separated rats exhibit strong responses to post-weaning enrichment (which reverses many of the behavioral deficits associated with maternal separation) (Hellemans et al., 2004; Francis et al., 2002). Thus, one conclusion that could be drawn from these data is that hand-rearing, which involves protracted maternal separation, reduces fearfulness and increases sensitivity to environmental enrichment in orange-winged Amazon parrots. However, based on our findings of differential responsiveness to novelty in parent-reared birds based on overall levels of fearfulness, it seems more likely that the apparent differences between parent-reared and hand-reared birds in responsiveness to high-novelty treatment in fact reflect greater individual variation in fearfulness among parent-reared birds. It remains unclear whether the tendency for hand-reared birds to be less fearful overall than parent-reared birds is in fact related to rearing condition (see Fox and Millam, 2004), or is simply reflective of a smaller sample size (12 HR versus 22 PR birds).

High-novelty treatment appears to be particularly effective in reducing fearfulness in moderately fearful birds, and actually can increase fearfulness in birds exhibiting high levels of neophobia (see Fig. 2a and b). This is unsurprising, given evidence that more fearful animals respond differently to social and non-social stressors than less fearful animals (e.g., Benus et al., 1991; Koolhaas et al., 1999; Groothius and Carere, 2005). For example, broiler chicks which exhibit longer latencies to traverse a T-maze (indicative of higher fearfulness and lower exploratory tendency) exhibit a stronger corticosterone response to partial immersion in water (Marin and Jones, 1999). Similarly, great tits from a line selected for long latencies to explore novel objects show an enhanced corticosterone response to confrontation with an aggressive, resident male bird than do birds from a line selected for short exploration latencies (Carere et al., 2003). Furthermore, work by Moncek et al. (2004) has shown that frequent rotation of enrichments can act as an environmental stressor. Rats receiving a treatment in which enrichment objects were changed three times a week (similar to our HN treatment) had larger adrenals, increased corticosterone release in response to buspirone challenge, and higher resting plasma corticosterone levels relative to controls—all of which indicate chronic stress (Moncek et al., 2004). We therefore hypothesize that individual variation in fearfulness in orange-winged Amazon parrots reflects differences in stress reactivity. This variation in stress reactivity accounts for the opposite effects of HN treatment in birds with high levels versus low levels of neophobia.

With regard to the design of enrichment programs, it is also clear that careful attention must be paid to the choice of enrichment objects in order to minimize stress. Although the objects used for testing were all equally unfamiliar to the birds and of similar sizes, there was a highly significant effect of object on birds' latency to feed, indicating that the parrots perceived some objects very differently from others. However, it remains unclear what properties determined the degree to which the birds avoided particular objects. The non-significant treatment $\times$ novel object interaction suggests that housing conditions and enrichment object properties act separately to influence birds' responses to unfamiliar enrichments.

4. Conclusion

Understanding how both the various properties of enrichment protocols (e.g., level of novelty, objects used) and individual differences in behavioral type influence behavior can facilitate the design of enrichment programs for captive animals. The results of this experiment suggest that overall, rotation of enrichment objects is more successful than enrichment alone in reducing fearful behavior, at least in orange-winged Amazons. However, our results also suggest that it would be prudent to consider individual behavioral traits when designing enrichment protocols, since HN treatment actually *increased* fearfulness in the most fearful individuals. Furthermore, in order to minimize stress in animals housed under enriched conditions, the types of enrichments used must also be considered, since some objects may be perceived as significantly more frightening than others.

These results also indicate that greater care is needed when designing experiments to test the efficacy of enrichment protocols. The highly significant effect of novel object properties on birds' latency to feed in the presence of these novel objects suggest that experimenters should carefully consider both the enrichments and testing objects used in future enrichment studies. In order to avoid obscuring treatment effects, it would also be wise to test for differences in fearfulness and/or exploratory tendency in experimental animals prior to assigning them to treatment groups and to carefully control for these differences through counterbalancing or other techniques. Relatively simple techniques for quantifying fearfulness and exploratory tendency in birds can be found in Verbeek et al. (1994) and Fox and Millam (2004).

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