



THE RELATIONSHIP BETWEEN FORAGING COMPLEXITY AND FORAGING PLASTICITY: IMPLICATIONS FOR THE CONSERVATION OF PEACH-FRONTED PARAKEETS

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Abstract: Reintroduction processes, whereby animals are reared in captivity and released into the wild, often fail. This failure is often attributed to the fact that released individuals not have the behavioral repertoire to cope with the wild. Compared to captive conditions, wild environments are highly complex, and therefore a released individual with greater behavioral complexity may survive better after release. Moreover, the wild presents both unpredictable features and regular changes, and thus plasticity of behavior may be crucial for survival. Considering the importance of foraging to fitness, foraging complexity and plasticity can be crucial to the success of reintroduction processes. We investigated captive individuals of *Eupsittula aurea* (Psittaciformes, Psittacidae) to evaluate if: a) food enrichment promotes foraging complexity; and b) there is a relationship between foraging complexity and plasticity. An animal that potentially has a good adjustment to wild environments would be one that has high foraging complexity and plasticity. We housed 40 parakeets under identical conditions that differed only in their diet. Twenty birds, in four replicated enclosures, were randomly allocated to the treatment diet which better replicated what would occur in the wild and consisted of multiple entire fruits, and food spatial randomization. The remaining 20 birds were placed into four control enclosures and received a diet that is currently provisioned for birds in captivity and consisted of small fruit cubes and sunflower seeds, offered on tray at a fixed location. Dietary enrichment does not affect bird foraging complexity. According to our expectations, foraging complexity influenced foraging plasticity for birds that were subject to the enriched environment. Therefore, more extensive foraging repertoires are related to a greater adjustment capacity in enriched environments, and complexity could be considered a good measure of adjustment to reintroduction success.

Keywords: environmental complexity; food enrichment; pre-release captivity; reintroduction.

INTRODUCTION

Animals reared in captivity and released into the wild as part of a conservation program often suffer from high mortality, particularly when compared

to their wild-reared conspecifics. As a result, many reintroduction processes fail, mainly due to predation and difficulty in finding and processing food (Kleiman 1989, MacMillan 1990, Sheean *et al.* 2012). Such behavioral deficiencies are therefore a

consequence of the captive rearing environment (Snyder *et al.* 1996, Rabin 2003), and low levels of survival highlight the need for attention to the behavioral aspects of the process, and improved pre-release procedures in captivity.

Captive environments are often less complex than the post release environment. A simple environment can impact an animal prior to release in two ways. Firstly, unnatural environments may not offer stimuli that a wild conspecific would experience (Newberry 1993, Villalba *et al.* 2010), and therefore are clearly detrimental for learning (Sneddon *et al.* 2000, Schrijver *et al.* 2002). Secondly, barren environment may affect welfare: not performing natural behaviors is suggestive of poor welfare, and in addition barren environments may not offer refuge to escape predation (Jordan 2005). Therefore, many of these animals present impoverished behavioral repertoires (Mathews *et al.* 2005) with a reduction in behavioral complexity (considered as diversity of behavioral categories) as a function of impoverished rearing conditions (Oliveira *et al.* 2018). Behavioral complexity reduction is often the result of stress (Dantzer 1986, Alados *et al.* 1996, Shepherdson *et al.* 2013). The post release environment is typically larger, unpredictable and more heterogeneous than the captivity environment, with an overall higher animal and plant diversity. Therefore, an animal with higher behavioral complexity may be considered to have a biological advantage (Alados *et al.* 1996, Catchpole & Slater 2008). A way to improve behavioral complexity is the addition of environmental enrichment (Stolba *et al.* 1983, Shepherdson *et al.* 2013), either by stimulating lost abilities (Griffin *et al.* 2000, Young 2003, Whiteside *et al.* 2015) and typical behavioral patterns (Whiteside *et al.* 2016), or by increasing exploratory activity (Young 2003, Whiteside *et al.* 2015, Yasumuro & Ikeda 2016) and improving welfare (Näslund *et al.* 2013). Besides being an indicator of welfare (Oliveira *et al.* 2018), behavioral complexity is also correlated to learning capacity and, therefore, behavioral plasticity (Boogert *et al.* 2008).

In addition to behavioral complexity, the translocation from captivity to natural areas, with the concomitant increase in resources/interactions unpredictability, require from the reintroduced animals the capability of ample behavioral

adjustment, *i.e.* behavioral plasticity. For example, food availability varies temporally and spatially in natural areas (Karr 1976, Renton 2001), and finding food resources in nature is considered a fundamental challenge to the adaptation of animals after release (Box 1991). In fact, lack of plasticity was considered an important causal factor for the failure of reintroduction processes (Snyder *et al.* 1994). Captive animals will need to explore new natural areas, with characteristics that differ not only from those of the captivity environment, but also from those of their original habitat (Lloyd & Powlesland 1994), highlighting the importance of behavioral plasticity (Salinas-Melgoza *et al.* 2013).

If behavioral complexity and plasticity are intertwined in the reintroduction process, a more complex repertoire could be associated with a greater capacity of individual adjustment to the natural environment. If that is the case, the measurement of complexity could help diagnostic the prospects of wildlife reintroduction projects. In this paper, we first test the hypothesis that food enrichment increases the complexity of foraging behavior. Foraging complexity can be important both because it potentially improve the animals' ability to cope with a higher diversity of food resources it will find after released, and because foraging complexity could be correlated to foraging plasticity. We also test the association between complexity and plasticity. Our model is the Peach-fronted Parakeet *Eupsittula aurea*, a much trafficked species, frequently apprehended by competent authorities. Parrots have been widely used as domestic animals (Faria & Miyaki 2006), and a recent study with Neotropical parrot populations showed that many of these populations are in decline, and capture for pet trade is one of the major factors of population decrease in this group (Berkunsky *et al.* 2017). This highlights the relevance of parakeets for conservation, making them an important model for the study of the behavioral processes that could pave the way for more successful captive animals' reintroduction to native areas.

The Peach-fronted Parakeet is a good model for being a social species, and for having a diversified diet, feeding on fruits, seeds, flowers, nuts, berries, adult insects, and insect larvae (Forshaw 1989, Paranhos *et al.* 2009), aspects that may require

large behavioral repertoires and high plasticity in the wild. We expect that captive animals with an enriched diet will show more complex foraging behaviors, and that plasticity will be higher for the individuals with higher complexity.

MATERIAL AND METHODS

Study species

Peach-fronted Parakeets live in flocks whose size depends on the availability of resources in the environment (Paranhos *et al.* 2009), and have a wide geographic distribution in Brazil, and in areas of Bolivia, Paraguay, and Argentina (Sick 1997). It inhabits secondary forests, Cerrado (savannah like areas), mangroves, and crop areas (Sick 1997), but can also occur in urban areas (van Perlo 2009). It nests in hollow trunks and termite nests (Sick 1997, Paranhos *et al.* 2008, Sigrist 2014). It is a potential pollinator of trees of the species *Mabea fistulifera* (Malpighiales, Euphorbiaceae) (Silva 2008), and predator of seeds of other trees, impacting the reproduction and demography of plants (Silva 2007). Despite feeding on seeds it can also act as a disperser (Paranhos *et al.* 2009, Oliveira *et al.* 2012). In captive environment the parakeets studied had a simple diet including treated fruit pieces such as banana, guava, passion fruit, and apple, and sunflower seeds.

Study site

The target individuals were kept during an unknown period at the Chico Mendes wild animals sorting center (CETAS), at the municipality of Salvador, state of Bahia, Brazil, and were originally retrieved from wild animals traffic by competent authorities, such as the Brazilian Institute of Environment and Renewable Natural Resources (IBAMA), the Society of Environmental Protection Police (COPPA) or the National Forest ranger, either by rescue or by spontaneous delivery. The birds underwent veterinary screening and a battery of clinical exams prior to their transfer to the releasing site at the Jequitibá Atlantic forest reserve at the municipality of Serra da Jibóia, state of Bahia, Brazil, where the study was conducted from August to October 2013. This study was conducted according to the Brazilian legislation regarding ethics in research, and it was

approved by the Ethics Committee on the use of animals in biological research (CEUA; UFBA-08/2013).

Data collection

The target individuals (N = 40) were marked with colored and/or enumerated rings, and maintained in groups of five within enclosures of 4 x 4 x 5 m. The enclosures were located within the Atlantic forest, and contained perches, a tree, soil covered with herbaceous, and protected sites for ad libitum food and water supply.

We housed 40 parakeets under identical conditions that differed only in their diet. Twenty birds (10 males and 10 females) were randomly allocated to four replicated control enclosures and received a diet that is currently provisioned for birds in captive, and consisted of small fruit cubes and sunflower seeds, offered on a tray at a fixed location. The remaining 20 birds (6 males and 14 females) were randomly allocated to four replicated enclosures and offered a treatment diet which better reproduced what would occur in the wild, and consisted of entire fruits, with no sunflower seeds. To make the treatment diet even more similar to conditions in the wild, fruit offering sites were randomized spatially (scattered through the environment: hanging on branches, at the feeding site, and on the ground), favoring exploratory activity. The four replicated treatment groups underwent 15 days of food enrichment, consisting of a gradual replacement of the control diet for an enriched diet. When we presented birds with whole fruits they were unable to peel it, therefore we implemented the diet manipulations gradually, and thus we had to damage the peel of the fruit (and gradually decrease the amount of seeds in the diet) until they could manage with the entire fruits, grasping them with their paws, and cutting them into edible pieces with their beaks in a sequence of behaviors denominated food preparing (Table 1). We then considered that the enrichment process was successful (*i.e.*, the animals responded to the environmental enrichment and could process whole fruits adequately) once we watched individuals progress in managing entire fruits during enrichment, despite their overall deficiency to feed on whole fruits at the beginning of the enrichment process. After this initial period of 15 days, we recorded the foraging

Table 1. Foraging ethogram of *Eupsittula aurea* (Psittaciformes, Psittacidae), including the behavioral categories and description of captive environment observed behaviors.

Category	Description
Selecting	Observe, pick, select a specific food item among other food items at disposal
Transporting	Transport of food through the beak or by paw, through flight or walk, before intake
Pecking (Paranhos <i>et al.</i> 2009)	The bird pecks food, removing small portions that are swallowed directly, or are crushed and swallowed. Behaviour commonly used for pulp or pulp/seed ingestion
Rip and grinding (Paranhos <i>et al.</i> 2009)	The individual extracts the entire food item, grinding it with its beak before swallowing. Behaviour used for hard food intake, such as seeds and fruits. May be used foot to hold the food during ingestion
Rip and holding (Paranhos <i>et al.</i> 2009)	The individual picks up the food with the beak, passes it to one paw and only then begins to tear apart and eat it (Paranhos <i>et al.</i> 2009).
Stealing	The individual steals with the beak a conspecific food item, which was eating
Shake the head	The individual shakes the head to the food rest drop after or during feeding
Prepare	The individual applies pecking at food, using paw to assist handling of the food item. May or may not result in the opening of the shell of a fruit
Pecking the ground	While walking on the floor, the individual puts the head down and select food items in the environment
Drink water	With the head turned to the water tray, the bird introduces part of the beak in the water and then raises his head in standard position while the water flows into the throat
Cleaning beak	The bird passes the beak over any surface, on both sides, alternately, or only in one side

activities of each animal in video. The recordings consisted of a 12 min focal animal and focal foraging behavior sampling (Nikon camera, model L120), in which we registered only the foraging behavior of one single animal. The recordings were conducted in the morning (between 8:00 h and 13:00 h) by an observer positioned behind a visual barrier. Treatment group animals were recorded both with the enriched diet (treatment group at enriched context, ET) and, in the next day,

with the regular captivity diet (treatment group at unenriched context, UT). Control group (C) animals were recorded only with the regular captivity diet.

The study resulted in a total 720 min of foraging behavior recordings. The data were decoded considering a foraging ethogram (Table 1), based on the literature (Paranhos *et al.* 2009) and on preliminary observations of foraging behavior at CETAS facility and in the study site.

Statistical analyses

We checked the data for normality and homoscedasticity (Kolmogorov-Smirnov and Shapiro-Wilk tests) and performed data transformations (log) if necessary.

Estimating foraging complexity and plasticity

Complexity can be measured either as the difficulty to describe or to create a system, or else as its degree of organization (Lloyd 2001). Considering that we are merely trying to describe the complexity or changes in the complexity of a behavioral system, we adopted a descriptive measurement of complexity to evaluate whether enrichment increases individual foraging complexity. Thus, complexity was quantified considering the richness and abundance of behaviors, through the Uncertainty Index of Information Theory in the context of ethological data (Lehner 1996). This information based measure reflects the idea that complex behavioral systems have more degrees of freedom for its expression, and thus produce more varied and less repetitive performances, in opposition to stereotyped behavioral systems such as, for example, that of caged animals under potentially stressful conditions. We thus considered behavioral complexity as:

$$U_x = - \sum P_x \log_2 P_x$$

where U_x is the mean uncertainty in the prediction of the next behavior, and P_x is the probability of each behavioral category (x) in the food repertoire. The higher the U_x , the higher is the complexity of the behavioral repertoire (Lehner 1996).

To test if repertoire complexity predicts the ability to adjust to the context, we estimated the behavioral plasticity of the individuals. Behavioral plasticity was measured as the change in behavior following changes in context (see review in Japyassú & Malange 2014). Since we were interested in the individual's general adjustment ability, and not in the ability to adjust one particular behavior, we considered adjustments in any behavior present in the individual foraging repertoire. For this we measured changes not only in one, but in the whole repertoire of behaviors, estimating overall individual plasticity through the

sum of the changes (in function of enrichment) in each of the foraging repertoire behaviors, according to the formula:

$$P = \sum_{i=1}^q |ET_i - UT_i|$$

where q is the number of behavioral categories, ET_i is the frequency of behavior i under ET, and UT_i is the frequency of behavior i under UT. Plasticity scores were further standardized by dividing each individual score by the maximum score within the population.

Enrichment effects on foraging complexity

To evaluate if food enrichment increases foraging complexity, we compared the complexity values of control vs. UT groups. We performed a linear mixed model (LMM) analysis comparing C vs. UT. We considered the (log) complexity as outcome, the treatment (C and UT) and sex as fixed effects, and aviary grouping as a random factor (intercepts and context slopes). We obtained p-values through a likelihood ratio test comparing the full model to the "null" LMM (excluding the treatment from the fixed effects).

Effects of complexity on plasticity

We also performed LMM analysis of the relationship between (log) plasticity and (log) complexity. We included plasticity as outcome, complexity, treatment (UT and ET), the interaction between complexity and treatment, and sex as fixed effects (without interaction terms, see below), and aviary grouping (intercepts and slopes) and individual identity as random effects. We obtained p-values through a likelihood ratio test comparing the full model to the "null" LMM, excluding first the interaction term from the fixed effects, to evaluate if there was difference in the way complexity influences plasticity between the treatments, and further excluding treatment from the fixed effects, to evaluate the relationship between complexity and plasticity.

The analyses were performed in R environment (R Core Team 2017), with a significance level of $\alpha = 0.05$. LMM were built by using the "lme4" package (Bates *et al.* 2015), and we used "ggplot2" package (Wickham 2009) to construct LMM graphic.

RESULTS

Food enrichment did not influence behavioral complexity when the C and UT groups were compared (model 1 vs. model 2: $\chi^2 = 0.556$, $p = 0.455$; Table 2).

Plasticity and foraging complexity after enrichment

Repertoire complexity influences repertoire plasticity, but the relationship differs between the UT and ET contexts (model 1 vs. model 2: $\chi^2 = 114.48$, $p < 0.001$; model 1 vs. model 3: $\chi^2 = 106.64$, $p < 0.001$; Table 3 and Figures 1 and 2)

DISCUSSION

Enrichment and foraging complexity

Food enrichment did not lead to an increase in foraging complexity. Thus more complex environments, with higher heterogeneity of elements and spatial unpredictability do not necessarily require a more complex behavioral repertoire, and the

exploration of this enriched environment could eventually be accomplished through a few behavioral changes. Some studies suggest that environmental complexity can change behavioral expression (Leggio *et al.* 2005), but this outcome is mainly the result of distinct goals of these studies. For example, while some studies focus on welfare, comparing behavioral complexity under highly disparate environments (Oliveira *et al.* 2018), or including substantial changes in environment, such as increasing social group size and including new objects (Leggio *et al.* 2005), we perform relatively minor environmental modifications, changing mostly the format and spatial position of the same diet components.

Changes in stress levels can also help explain the disconnection between behavioral complexity and enrichment. Stress is connected to low behavioral complexity (Dantzer 1986, Alados *et al.* 1996, Shepherdson *et al.* 2013), and enrichment reduces stress (Shepherdson *et al.* 2013), thus leading potentially to an increased behavioral complexity. However, it is possible that in the pre-release environment the animals were all under

Table 2. Linear mixed models outcomes for 40 individuals of *Eupsittula aurea* (Psittaciformes, Psittacidae) from control group (C) and unenriched treatment (UT) contexts. Model 1 is the full model, and model 2 is the null model dropping the treatment (C and UT) from the fixed effects.

Coefficients	Response			
	Model 1		Model 2	
	Estimate	Standard error	Estimate	Standard error
Fixed effects				
(Intercept)	0.3	0.12	0.4	0.07
Sex	0.1	0.1	0.1	0.1
Treatment	0.1	0.13	-	-
Random effects				
Number of groups	8	-	8	-
Correlation	-1	-	-1	-
Observations	40	-	40	-

low stress, irrespective of food treatment (with or without enrichment). The pre-release enclosures both for the control and treatment groups were large, with a tree and herbaceous cover, and situated in the understory of a large forest fragment, a much enriched environment in comparison with the previous enclosure. If that is the case, food enrichment may have not been much effective in reducing even more the already

low pre-release enclosure stress levels, thus rendering treatment and control groups similar in relation to stress levels.

Plasticity and foraging complexity

As predicted, complexity positively influenced plasticity in the ET context (Figure 1). Thus, more extensive behavioral repertoires are associated to a greater adjustment capacity, and a possible

Table 3. Linear mixed models outcomes for 20 individuals of *Eupsittula aurea* (Psittaciformes, Psittacidae) from unenriched treatment and enriched treatment contexts. Model 1 is the full model, model 2 is the null model dropping the interaction between complexity and treatment estimate, and model 3 is the null model dropping treatment further the interaction estimate.

Coefficients	Response					
	Model 1		Model 2		Model 3	
	Estimate	Standard error	Estimate	Standard error	Estimate	Standard error
Fixed effects						
(Intercept)	-6.76	8.973 ⁻²	-6.58	1.284 ⁻¹	-7	9.849 ⁻²
Sex	-4.17	1.638 ⁻¹	-4.77	1.434 ⁻¹	-4	1.545 ⁻¹
Complexity	3.603 ⁻¹²	1.382 ⁻⁶	-13.7	1.849 ⁻⁵	-11	1.492 ⁻⁵
Treatment	4.935 ⁻¹²	8.55 ⁻⁷	1.321 ⁻⁸	5.780 ⁻⁶	-	-
Treatment * Complexity	-12.1	1.769 ⁻⁶	-	-	-	-
Random effects						
Number of groups	4	-	4	-	4	-
Correlation	-1	-	0.45	-	0.7	-
Observations	40	-	40	-	40	-

mechanism for this association is that the individual simply has at their disposal a larger range of possible behaviors to adjust to new contexts. This result agrees with the association between complexity and learning, that is: learning leads to repertoire complexity (Boogert *et al.* 2008). Learning, considered as behavioral changes throughout lifetime experience, is one essential component connecting environmental information to proper behavioral response, a connection required for adaptive behavioral plasticity (Mery & Burns 2010).

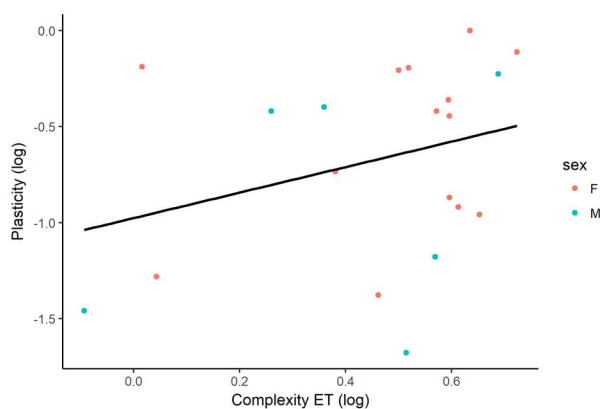


Figure 1. Plasticity is affected by complexity in challenging foraging contexts. Plasticity increases with foraging repertoire complexity under the more challenging, enriched foraging (ET) context.

In the UT context, however, the relationship between complexity and plasticity was not

significant (Figure 2). Poor environments do not require complex behavior, and under impoverished contexts it is possible that all solutions converge to the same few optimal solutions, with no room for the expression of any underlying between individual differences in repertoire complexity.

Overall, our results show that one should consider complexity as an indicator of plasticity in enriched, pre-release environments (*e.g.* large enclosures that are not behaviorally restrictive). Considering that highly plastic individuals with complex behavioral repertoires should perform better in the wild (Catchpole & Slater 2008, Salinas-Melgoza *et al.* 2013), our results imply that under enriched environmental conditions complexity should be considered a reliable predictor of reintroduction success. Enriched and more unpredictable environments allow individuals with a more complex behavioral repertoire to better explore the enriched environment and change their behavior in response to contextual changes. Individuals with more complex behavioral repertoires seem to use resources more efficiently, matching behavior to environmental complexity. Behavioral complexity and plasticity should then be taken into account in reintroduction processes.

The evaluation of the complexity of other behavioral systems, such as courtship or defensive strategies, under enriched environments can shed

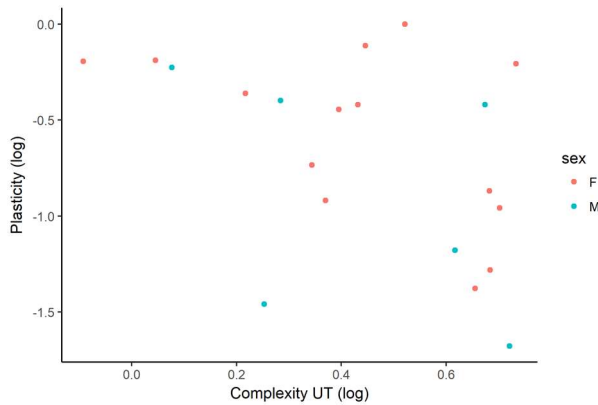


Figure 2. Plasticity is not affected by repertoire complexity under the less challenging, unenriched foraging (UT) context.

light on interesting avenues for new conservation approaches, increasing the possibility of successful reintroductions. Moreover, to fully understand the impact that behavioral plasticity and complexity have on reintroduction processes it is essential to investigate how they influence the animal after release. Notwithstanding the difficulty of measuring repeatedly animals in the wild, these studies could shed light on the dynamics of behaviors after release, thus helping to devise more reasonable conservation strategies.

In this study, we found that the evaluation of behavioral complexity helps to predict enhanced plasticity with a non-invasive measurement approach. Thus, it could help the assessment of the prospects of particular reintroduction projects, because groups of individuals with higher behavioral complexity would potentially have higher success after release. Therefore, the measurement of complexity could be considered a fundamental diagnostic tool for the success of wildlife reintroduction processes. Also, the search for mechanisms that increase behavior complexity is an interesting focus for future studies and may guide pre-release strategies.

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