

Environmental Enrichment for Dendrobatid Frogs

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The Central Park Zoo, one of the Wildlife Conservation Society's Living Institutions in New York, recently renovated an exhibit for dart-poison frogs. Staff developed a new hollow coconut insect feeder in conjunction with this project. When the exhibit change, coconut feeder, and other enrichments were tested for effectiveness, the coconut feeder enrichment produced the greatest increase in frog activity in traditional and new exhibits. This may be due to the coconut feeder's relatively complicated nature, which randomizes the release of insects into the exhibit. The goal of this project was to help develop a best-practices approach to dendrobatid husbandry for zoological facilities to use in the future.

Environmental enrichment is a nonhuman animal husbandry technique that attempts to enhance animal welfare by providing the environmental stimuli necessary for optimal psychological and physiological well-being of the animals (Shepherdson, 1998). There are five commonly accepted ways to enrich an animal's environment: managing a dynamic habitat, encouraging social interactions between individuals, encouraging foraging behavior, introducing novel objects, and training the animal.

In addition to enhanced welfare of captive animals, the value of enrichment for zoo animals can include reduced veterinary care, facilitated animal husbandry, in-

creased reproductive behavior, and improved public education through more dynamic exhibitry (Hayes, Jennings, & Mellen, 1998). Enrichment provides an excellent opportunity to inform the public about the natural behaviors of animals and to encourage involvement in conservation activities. Enrichment items can also increase the animal's activity levels, thus making the zoo-going experience more exciting and valuable for zoo visitors.

Despite the increased popularity of environmental enrichment methods, enrichment programs for amphibians are rare (Hayes et al., 1998). Our study tested environmental enrichment methods for dendrobatid frogs. Dart-poison frogs (*Anura: Dendrobatidae*) are a neotropical group of toxic, diurnal terrestrial frogs. Our four study species were Dyeing dart-poison frogs (*Dendrobates tinctorius*), Blue dart-poison frogs (*D. azureus*), Green and Black dart-poison frogs (*D. auratus*) and Yellow-banded dart-poison frogs (*D. leucomelas*). *D. tinctorius* occur in the wild in French Guiana, Guyana, and Surinam; *D. azureus* in Surinam; *D. auratus* from southern Nicaragua to Colombia; and *D. leucomelas* in Venezuela (Anonymous, 1998).

LIFESTYLES

Dendrobatid Habitat

In the wild, dart-poison frogs are active throughout the day, foraging on the forest floor or climbing trees. *D. tinctorius* frogs in the wild were found in pools formed in tree holes and cracks. They were seen sitting 10 m up on tree trunks, with as many as five frogs inhabiting a single tree. *D. tinctorius* individuals live in pairs, and Heselhaus (1992) observed that no more than two males lived together on the same tree. In the wild, *D. auratus* remains well hidden during the dry periods and was found hidden only in moist rock crevices (Heselhaus, 1992).

Activity Patterns

D. auratus is most active in the mornings and after rain showers (Leenders, 2001). Jaeger and Hailman (1981) found that wild *D. auratus* in Panama actively foraged only in the early morning and late evening, times that had similar light levels. Heselhaus (1992) found wild *D. tinctorius* to be active throughout the day but observed that they left their tree only for short periods to look for food and rarely traveled more than 5 m from their home tree.

Foraging Behavior

Dendrobatids are opportunistic foragers who feed on small invertebrates whom they encounter. Dendrobatids rely on sight to locate their prey and often adopt a

sit-and-wait hunting style. In the wild, dart-poison frogs encounter a wide variety of prey items—including termites and ants—that give them their toxicity. Field studies have shown that ants make up 50% to 73% of the diet of wild species of *Dendrobates*, whereas ants make up only 12% to 16% of the diet of the nontoxic *Colostethus* frogs, supporting the theory that the dart-poison frogs obtain their toxins from alkaloids in the ants (Leenders, 2001). Captive dendrobatids are not toxic, however, presumably due to a routine diet of nontoxic small crickets and springtails.

Predators

Despite the toxins in their skin, wild dart-poison frogs do not have the luxury of being free from predators and still have to endure a daily battle for survival. Many predators are not deterred by the toxins of the dart-poison frogs, especially due to the variation in levels of toxicity among the species (Heselhaus, 1992).

Parental Care

As a group, dart-poison frogs exhibit a diversity of parental care strategies. Members of the *D. tinctorius* species group exhibit male parental care (Summers & Earn, 1999). The female deposits small (2 to 8 eggs) clutches in the leaf litter that are attended by the male; he later carries the mature (10 to 14 days) tadpoles to small pools of water in tree holes. The male may place additional tadpoles in the same pool who often are cannibalized by larger tadpoles (Summers & Earn, 1999). It also has been observed that males most often do not place more than one tadpole in a pool, but may do so when they are limited by time and availability of pools (Summers & Earn, 1999).

In species with male parental care in which only the male decides where to deposit the eggs, cannibalism among tadpoles is costly for the mother because she has no control over the placement of her tadpoles and the resulting tadpole interactions. Therefore, the female's only opportunity to reduce tadpole conflict in which other females' tadpoles may be out competing hers is to prevent her mate from mating with other females. In fact, mate guarding has been observed in the field for *D. auratus* and *D. leucomelas* (Summers & Earn, 1999).

Dart-poison frogs from the *tinctorius* group who have male parental care deposit tadpoles in pools and puddles and do not feed the tadpoles. Dart-poison frogs with female parental care, such as *D. pumilio*, deposit tadpoles in bromeliads and feed tadpoles with unfertilized eggs (Summers & Earn, 1999). Consequently, *D. pumilio* males are territorial over bromeliads, which are limited breeding resources (Donnelly, 1989).

Aggressive Behavior

In the wild, dendrobatids may defend all-purpose territories that include feeding sites, shelter, and oviposition sites (Wells, 1977). *D. auratus* males are territorial, and males will wrestle with each other to attain dominance. During the day, males call from established sites such as trunks, logs, or rocks to attract females and keep males out of their territory (Leenders, 2001). Aggressive behavior is not limited to the males; female *D. azureus* and *D. auratus* individuals have been observed wrestling to gain access to calling males (Wells, 1977). In addition, dendrobatids may exhibit a sex-role reversal in which females initiate courtship (Wells, 1977).

Habitat Change at the Zoo

Central Park Zoo, managed by the Wildlife Conservation Society in New York, has a large collection of dendrobatids, including genetically important reproductive groups of endangered species and “exhibit-only” groups of more common species. When exhibit changes were made, a large habitat was created to allow exhibition of a relatively dense population of exhibit-only dendrobatids to enhance the visitor experience and to observe the behavior of frogs in the larger group versus the frogs in “traditional” aquarium exhibit terraria.

In redesigning the exhibit, we considered the needs to address habitat changes for the frogs, activity patterns of the frogs in captivity versus in nature, foraging challenges in captivity, and behavioral interactions of species and individuals. The goal of this project was to help develop a best-practices approach to dendrobatid husbandry for zoological facilities to use in the future.

METHOD

This research was conducted from July to September 2001 at the Central Park Zoo, Wildlife Conservation Society, New York. Behavioral observations were recorded on two exhibits of captive dart-poison frogs (*Dendrobates* sp.). All frogs were captive born. The new large, “nontraditional” exhibit consisted of 23 individuals of four species (6 *D. tinctorius*, 8 *D. azureus*, 4 *D. leucomelas*, and 5 *D. auratus*), and the small, traditional exhibit contained 4 *D. tinctorius* and 4 *D. azureus* individuals. The large exhibit is a 1.07 m × 1.07 m × 1.52 m high exhibit with glass windows for viewing by the public on two adjacent sides. It is planted with various ground plants, mosses, and bromeliads, and there are tree branches and vines for climbing. There are overhead misting spouts on a randomly timed timer that spray a fine water mist over the exhibit for random amounts of time during the day. The small exhibit is a 20-gallon aquarium (0.66

m × 0.51 m × 0.64 m) tank with one glass window for public viewing. It also contains plants, mosses, a bromeliad, and one small branch for climbing. There also is a misting spout that sprays at random times throughout the day.

Before the experiment, the daily husbandry routine for the dendrobatids included a feeding every other day of pinhead or 10-day crickets (*Gryllus domesticus*), fruit flies (*Drosophila melanogaster*), flour beetle larvae (*Tribolium* sp.), or springtails (*Collembola* sp.), depending on availability.

Enrichment Experiments

The frogs were presented daily with one of three experimental states—control, coconut, and other. The experimental enrichment schedule alternated between the three experimental states in a random order. No state was presented on any 2 consecutive days; each day was different from the previous day. On days when the observers were not present, the frogs were fed in an open petri dish placed in the front of the exhibit. Data were collected for 11 weeks, with 4 to 5 days of observation per week and approximately 5 hr of observation per day. Each enrichment state was presented at least once per week.

For the control state, the frogs were not fed. To continue the every other day feeding schedule, two control states were not performed on consecutive days. Within each exhibit, the only experimental variable was the feeding method.

The coconut enrichment state consisted of a dried hollow coconut shell, split in half, with three small holes drilled in the top and a piece of artificial vine holding the two halves together so that the insects could only escape out of the drilled holes. The coconut was filled with pinhead and 10-day old crickets, whereas sponge pieces plugged the holes; then the coconut was moved to the exhibit. The pieces of sponge were then pulled out of the holes, which allowed the small insects to escape slowly through the holes. The coconut enrichment was placed in the front of the exhibit, in plain view of the visitors.

The other enrichment state included either the placement of flower stems covered in aphids (*Aphis* sp.) in the front of the exhibit or a broadcast feed of various insect prey items (fruit flies, flour beetle larvae, springtails), which were scattered in the front of the exhibit.

Behavioral Observations

All *D. azureus* and *D. tinctorius* individuals were identified and named based on dorsal color patterns. An identification chart was produced so that each observer could accurately identify the frogs for scan sampling. Behavioral data on individual frogs were collected using point scan samples (Altmann, 1974). Observa-

tions were timed with a digital watch and recorded on data sheets. Each individual frog was observed for approximately 27 to 48 hr per enrichment state (Table 1).

Throughout the 11 weeks of the study, point scan samples were recorded on the *D. tinctorius* and *D. azureus* individuals, categorizing behaviors according to our ethogram (Table 2). For the small exhibit, we used a 1-min scan for both *D. tinctorius* and *D. azureus*. For the large exhibit, a 2-min scan was used, alternating each minute between *D. tinctorius* and *D. azureus* so that the data could be collected simultaneously on all 14 study animals in the large exhibit.

To compare the effects of the exhibits and a change in environment and social surroundings, we switched *D. tinctorius* and *D. azureus* individuals between the small and large exhibits after 7 weeks of observation. The frogs then were observed for 4 more weeks to determine if there were any activity level changes in the experimentally switched individuals. Four *D. tinctorius* individuals and four *D. azureus* individuals were moved from the large exhibit to the small exhibit, and

TABLE 1
Total Observation Time per Individual

Species	Individual	Total Time Observed ^a			
		Control	Coconut	Other	
<i>D. azureus</i>	A	27:05:00	35:43:00	41:51:00	
	B	29:44:00	37:04:00	41:19:00	
	C	29:44:00	37:04:00	41:19:00	
	D	29:44:00	37:04:00	41:19:00	
	E	27:05:00	35:43:00	41:51:00	
	F	27:05:00	35:43:00	41:51:00	
	G	29:44:00	37:04:00	41:19:00	
	H	19:50:00	23:38:00	27:40:00	
	I	29:14:00	27:26:00	36:35:00	
	J	29:14:00	27:26:00	36:35:00	
	K	29:14:00	27:26:00	36:35:00	
	L	29:14:00	27:26:00	36:35:00	
	<i>D. tinctorius</i>	A	32:01:00	46:50:00	37:29:00
		B	34:38:00	48:11:00	37:02:00
C		32:01:00	46:50:00	37:29:00	
D		34:38:00	48:11:00	37:02:00	
E		32:01:00	46:50:00	37:29:00	
F		32:01:00	46:50:00	37:29:00	
G		29:12:00	32:11:00	36:40:00	
H		29:12:00	32:11:00	36:40:00	
I		29:12:00	32:11:00	36:40:00	
J		29:12:00	32:11:00	36:40:00	

^aTime is in hours:minutes:seconds.

TABLE 2
Ethogram

<i>Behavior</i>	<i>Included Behaviors</i>
Moving	Moving, vertical climbing, jumping
Hunting	Hunting, walking towards prey
Agonistic	Wrestling, chasing, being chased
Resting	Sitting still
Breeding	In plant, laying eggs, rubbing body on leaf, courtship behavior
Out of sight	Not visible to observer

four *D. tinctorius* individuals and four *D. azureus* individuals were moved from the small exhibit to the large exhibit, thus keeping the total number of frogs and frogs per species in each exhibit constant.

Our null hypothesis was that there would be no change in activity between exhibits or between experimental states. We predicted that in both the large and small exhibits, there would be a significantly higher level of activity for the enrichment states compared with the control state. We could not predict if the coconut or other enrichment states would have a higher activity level, so we tested them against each other. We predicted that there would be a difference in activity levels for the control state in both exhibits, but we did not predict which would have higher activity levels.

For the experimental exhibit switch, we expected activity levels to increase from the original exhibit to the new experimental exhibit for all experimental/enrichment states (including the control state). We also expected activity levels to increase for individuals moved from the small exhibit to the large exhibit. We did not predict whether activity levels would increase or decrease for individuals moved from the large exhibit to the small exhibit. The Wilcoxon matched-pairs signed rank test was used to test these predictions (Siegel, 1956).

RESULTS

Activity Levels

To determine the change in activity levels across enrichments, the behaviors were grouped into active, inactive, and out of sight (Table 3). Data collected before an enrichment item was presented on an enrichment day were not included in the data analysis. For both *D. azureus* and *D. tinctorius* in both exhibits, the coconut enrichment state increased activity levels from the control state but failed to produce a statistically significant change (Figure 1; Table 4). The other enrichment state had a varied effect on the frogs, either increasing activity from the control state or remaining near control state activity levels.

TABLE 3
Revised Ethogram—Active Versus Inactive

<i>State</i>	<i>Included Behaviors</i>
Active	Moving, hunting, agonistic behavior, breeding
Inactive	Resting
Out of sight	Out of sight

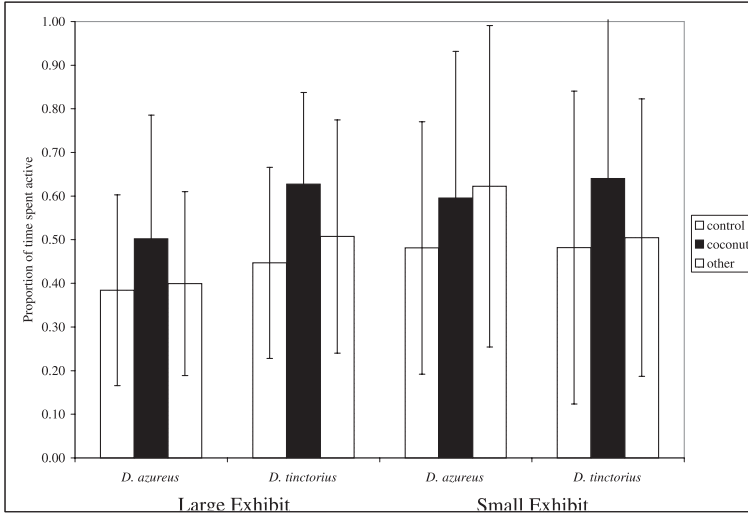


FIGURE 1 Proportion of time spent active for each enrichment state with 95% confidence intervals. Values for each species are the mean activity levels of all the individuals, including individuals included in the experimental exhibit switch.

TABLE 4
Proportion of Time Spent Active for Each Enrichment State

<i>Enrichment State</i>	<i>Large Exhibit</i>				<i>Small Exhibit</i>			
	<i>D. azureus</i>		<i>D. tinctorius</i>		<i>D. azureus</i>		<i>D. tinctorius</i>	
	<i>Proportion Active</i>	<i>N</i>	<i>Proportion Active</i>	<i>N</i>	<i>Proportion Active</i>	<i>N</i>	<i>Proportion Active</i>	<i>N</i>
Control	0.38	12	0.45	10	0.48	8	0.48	8
Coconut	0.50	12	0.63	10	0.60	7	0.64	8
Other	0.40	12	0.51	10	0.62	8	0.50	8

Note. Values for each species are the mean activity levels of all the individuals, including individuals included in the experimental exhibit switch.

Wilcoxon Matched-Pairs Signed Rank Test

Although the effects of the enrichments on activity levels were not statistically significant when tested across species and exhibits, some enrichment states produced significant results when tested within a species (Table 5). For *D. azureus*, proportion of time spent active was significantly greater for the coconut enrichment versus the control state in the large exhibit ($N = 11, T = 9, p < .025$), the other enrichment versus the control state in the small exhibit ($N = 7, T = 1.5, p < .025$), and the other enrichment versus the control state in the large exhibit ($N = 12, T = 9.5, p < .025$). For *D. tinctorius*, proportion of time spent active was significantly greater for the coconut enrichment versus the control state in the large exhibit ($N = 10, T = 1, p < .005$), the coconut enrichment versus the control state in the small exhibit ($N = 8, T = 1, p < .01$), the coconut enrichment versus the other enrichment in the large exhibit ($N = 10, T = 4, p < .02$), and the coconut enrichment versus the other enrichment in the small exhibit ($N = 8, T = 2, p = .02$).

TABLE 5
Statistically Significant Wilcoxon Matched-Pairs Signed Rank Tests for Dart-Poison Frogs Under Different Enrichment Strategies and Switched Between Small and Large Exhibits

<i>Species</i>	<i>Wilcoxon Matched-Pairs Signed Rank Test</i>	<i>One- or Two-Tailed?</i>	<i>H1: > Proportion Active^a</i>	<i>N</i>	<i>T</i>	<i>p Value</i>
<i>D. azureus</i>	Large: coconut vs. control	One	Coconut	11	9	< .025
	Small: Other vs. control	One	Other	7	1.5	< .025
	Large: Coconut vs. other	Two	—	12	9.5	< .025
	Other: Large vs. small ^b	Two	—	8	3	< .05
	Coconut: Original vs. experimental ^b	One	Experimental	7	2	.025
<i>D. tinctorius</i>	Large: Coconut vs. control	One	Coconut	10	1	< .005
	Small: Coconut vs. control	One	Coconut	8	1	< .01
	Large: Coconut vs. other	Two	—	10	4	< .02
	Small: Coconut vs. other	Two	—	8	2	.02
	Coconut: Original vs. experimental ^b	One	Experimental	8	0	.005

^aH1: > proportion active indicates that state was predicted to have a higher proportion active for a one-tailed test. ^bNote that these tests were performed only on individuals that were experimentally switched between exhibits.

Experimental Exhibit Switch—Original Versus Experimental Exhibit

Activity levels increased for each enrichment state when individuals were moved from their original exhibit to the experimental exhibit—regardless of which the exhibit to which they were switched (Figure 2; Table 6). These increases in activity were not statistically significant for the species as a whole but produced some significant trends when we looked at the activity of the individuals within a species. As predicted, the proportion of time spent active was significantly greater for the coconut enrichment in the experimental exhibit when

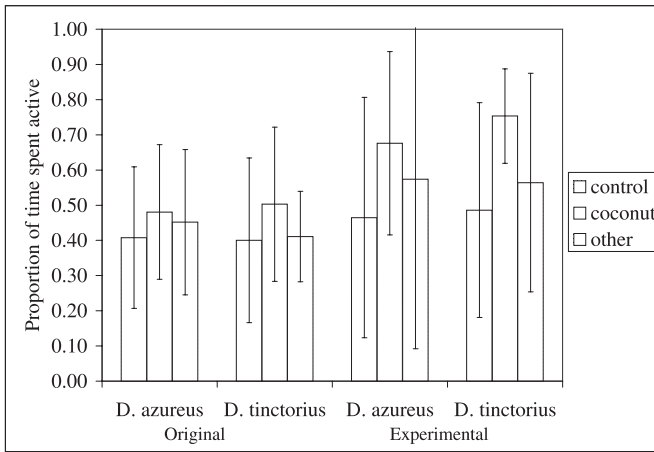


FIGURE 2 Experimental exhibit switch: Original versus experimental exhibit—proportion of time spent active in original versus exhibit for each enrichment state with 95% confidence intervals.

TABLE 6
Experimental Exhibit Switch: Original Versus Experimental Exhibit—Proportion of Time Spent Active for Original Versus Experimental Exhibit for Each Enrichment State

Enrichment State	Original Exhibit				Experimental Exhibit			
	<i>D. azureus</i>		<i>D. tinctorius</i>		<i>D. azureus</i>		<i>D. tinctorius</i>	
	Proportion Active	N	Proportion Active	N	Proportion Active	N	Proportion Active	N
Control	0.41	8	0.40	8	0.46	8	0.49	8
Coconut	0.48	8	0.50	8	0.68	7	0.75	8
Other	0.45	8	0.41	8	0.57	8	0.56	8

compared with the coconut enrichment in the original exhibit for both *D. azureus* ($N = 7$, $T = 2$, $p = .025$) and *D. tinctorius* ($N = 8$, $T = 0$, $p = .005$). We also predicted that activity levels would be higher in the experimental exhibit compared with the original exhibit for the control and other enrichment states, but they failed to show a statistically significant trend within each species.

DISCUSSION

Activity Levels

For *D. azureus* and *D. tinctorius* individuals in both exhibits, the coconut enrichment state increased activity levels from the control state. The *D. azureus* individuals in the small exhibit experienced higher activity levels with the Other enrichment than with the Coconut enrichment. The *D. azureus* individuals in the large exhibit and the *D. tinctorius* individuals in the small and large exhibits remained at activity levels near control state levels for the other enrichment state. These increases in activity between enrichment states for each species showed interesting trends but probably were not statistically significant because of large confidence intervals resulting from the large amount of individual variation within each species. Although across species the changes in activity levels were not significant, some enrichment states produced statistically significant results within each species.

Within both species in the large exhibit, the coconut enrichment state resulted in a significantly greater proportion of time spent active than in the other and control states. Within the *D. tinctorius* individuals in the small exhibit, the coconut state again significantly increased activity levels over the other and control states. Within the *D. azureus* individuals in the small exhibit, the other enrichment state significantly increased activity levels when compared with the control state.

Experimental Exhibit Switch

To compare the effects of the exhibits and a change in environment and social surroundings, 16 *D. azureus* and *D. tinctorius* individuals were switched between the large and small exhibits. As predicted, activity levels increased from the original exhibit to the new exhibit regardless of the exhibit to which the frogs were moved. One might expect that individuals moved from the large exhibit to the small exhibit might exhibit a suppressed activity level due to space constraints and lack of social interactions. Although this may affect the frogs' behavior, they also are exposed to many new stimuli that could increase activity levels. The small exhibit provides the switched individuals with opportunities

for new spatial learning due to the novel physical environment. It also provides them with an altered social composition due to the new dominance hierarchy created by separating a small part of the group.

Control State

The control state provided the baseline behavioral data with which we could analyze the effects of the enrichment states. We assumed that there was no residual effect of the enrichments and treated each control day equally, regardless of the enrichment state that came before it.

Coconut Enrichment State

As predicted, the coconut enrichment state produced the greatest increase in activity. This may be due to the coconut feeder's complicated nature, which randomizes the release of insects into the exhibit. Similar to ants leaving a nest in the wild, the frogs have to wait until the prey "decides" to exit the feeder, unlike open-dish feeders in which the prey are vulnerable at all times. Because the prey are released at random times, each emerging insect reinforces the frogs' waiting behavior. Like gamblers "working" a one-armed bandit slot machine and other variable interval reinforcement schedules, the frogs cannot "predict" when an insect will emerge for consumption. We observed that they continued to wait until the interval between insect emergences had been sufficiently long to allow them to lose interest. Some individuals took much longer to lose interest and would hunt around the coconut as long as it was in the exhibit. Note that the rate of insect emergence can increase or decrease the size of the holes in the coconut.

Other Enrichment State

The other enrichment state increased activity levels when compared with the Control state but was a less "effective" enrichment than the coconut feeder, given our goal of increased activity levels. The broadcast feed was extremely effective at initially increasing activity. Because the prey had no protection, however, they were consumed very quickly, and activity levels returned to control levels. The aphid enrichment and petri dish feeding method had the same drawback of an initial burst of activity as the prey quickly were consumed.

Coconut Enrichment Versus Other Enrichment

The coconut enrichment provided a sustained increase in activity and foraging behavior because of the random distribution of prey, whereas the other enrichment provided an initial burst of activity as the unprotected prey are consumed.

Both enrichments provide the daily diet allotment, but the coconut enrichment provides enrichment over a greater period.

The main differences in the two exhibits are the size and number of frogs in each exhibit. The large exhibit has a complex physical layout with many hiding places and is able to support many individuals. The large exhibit also includes a large amount of vertical space and stratification, which provides more spatial area for use and allows different species to coexist peacefully. Smaller species such as *D. leucomelas* spent more time climbing the branches and the walls, whereas larger species such as *D. tinctorius* spent more time on the ground and in the lower vegetation.

An additional difference between the two exhibits concerns the reliability of observed activity levels. For data analysis, the behaviors were grouped into active, resting, and out of sight. In the small exhibit because there were few places for the frogs to hide completely from the observer, most of the activity of the frogs was recorded accurately. In the large exhibit, however, approximately half the ground area of the exhibit was hidden from view by the observer. Therefore, it was not always possible to find the individuals, resulting in a relatively higher out of sight proportion than in the small exhibit. Because it is not possible to determine how much time the frogs were active while out of sight, the active proportion for the large exhibit may be less accurate than for the small exhibit.

The large exhibit provided increased interspecific and intraspecific contact by housing a larger number of individuals in the same exhibit. The increased social contact resulted in some breeding behavior and agonistic behavior such as wrestling and chasing but no visible dominance hierarchy. There was no visible competition for food; when a foraging enrichment item was presented, the frogs simply climbed on top of one another to access the prey. This multispecies setup, however, is not recommended for breeding populations because all eggs laid by *D. auratus* and *D. tinctorius* were consumed by *D. leucomelas*.

Foraging enrichments often are the most effective type of enrichment. Prey diversity and presentation were increased during the experimental enrichment period. Hayes et al. (1998) stated that prey who are difficult to catch can be enriching, and both the coconut feeder and the aphid enrichment made the prey items more difficult to obtain. The aphid enrichment increased difficulty in foraging because the aphids did not move and dart-poison frogs normally hunt by searching for movement. Even though the aphids did not move, the frogs discovered them almost immediately the first time the aphid enrichment was presented to them. Perhaps the aphids fit the frogs' instinctive prey search image, which would explain how they would know to hunt the aphids.

The coconut enrichment item was presented to the frogs between 10 a.m. and 2 p.m., and this randomized presentation schedule was meant to imitate the random availability of prey in nature and encourage opportunistic foraging. However, because the coconut enrichment randomizes the frequency of insect emergences, opportunistic foraging would be encouraged even if the enrichment was presented at

the same time every day. More important than variation in feeding time might be variation in feeding location, preventing individuals from aggregating at the learned feeding site. The individuals in the large exhibit spent a large amount of time resting and foraging at the feeding site in the front of the exhibit, even when no foraging item was present, indicating that they associated feeding with that one site. Changing the feeding location and the uncertainty it introduces for the frogs can be an enrichment in itself; one drawback is that certain feeding locations may minimize visibility for the public.

Imitating tropical rain showers, misting occurred at random times and for random lengths throughout all experimental states in both exhibits. Dart-poison frogs are most active after a rain shower in the wild (Leenders, 2001) and in captivity. Dendrobatids need sufficient humidity to obtain water from the environment. They spend a lot of time hiding in moist crevices between rocks and plants to avoid desiccation, and the frogs' activity was directly proportional to the amount of moisture in the exhibit. Misting increased activity and visibility of frogs to observers in each state and can be used as a habitat enrichment item. Similar to a foraging enrichment that has unpredictable food availability, a randomly timed water mister provides unpredictable water availability.

The enrichments succeeded in increasing activity levels in the frogs' diurnal time budgets and in enhancing the frogs' physical and mental activities. The large exhibit provided a large amount of physical surroundings to explore, which increases the frogs' physical well-being, as behaviors such as climbing are encouraged. Dendrobatids have good spatial memory; the males return to specific pools of water to deposit tadpoles. The frogs may adjust to a large amount of stimuli provided by new physical surroundings. In addition, the frogs must learn the feeding site, which encourages mental activity and presumably an increase in well-being. More diverse prey availability also should enhance the frogs' mental wellness as they encounter items that fit their instinctive prey search images. Increased social interactions due to the larger number of individuals in one exhibit contributed to physical well-being, as certain individuals engaged in harmless agonistic behaviors such as short bouts of wrestling. The species we housed together are from different areas of Latin America, and it is highly unlikely that they would encounter the same mix of species in nature. When planning multispecies exhibits, it is important to obtain adequate information about the behavior of each species to prevent potential harmful conflicts between species.

Although "lower" taxa are commonly forgotten when designing environmental enrichment programs, enrichment can be very beneficial for amphibians. Enrichment can encourage innate foraging behaviors and enhance animal activity and visibility for the public. In redesigning the Central Park Zoo's dart-poison frog exhibit, we considered the needs to address habitat changes for the frogs, activity patterns of the frogs in captivity versus in nature, foraging challenges in captivity, and behavioral interactions of species and individuals. The goal of this project was to

help develop a best-practices approach to amphibian husbandry for zoological facilities to use in the future. However, this study focused on a small species group of charismatic frogs, and the results may not apply to all amphibians. In addition, we focused on only a single frog life stage by testing nonbreeding adults in the enrichment scenarios we designed. Additional research with other innovative enrichment devices that are consistent with each species' natural history needs should be tested to increase the welfare of the wide variety of other amphibians living in zoos and aquariums.

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