

Predicting reproductive success in captive Puerto Rican parrots

(Amazona vittata)

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ABSTRACT

The productivity of captive breeding programs can limit efforts to restore endangered species. The ability to accurately predict which captive pairs will breed successfully improves breeding productivity by allowing managers to focus their efforts on pairs that are likely to succeed, and to re-assort pairs with a low probability of success. This could facilitate population restoration efforts that depend on captive programs. I tested whether pair duration and affiliative behaviors predict reproductive success in a captive population of the endangered Puerto Rican parrot (*Amazona vittata*). I systematically observed 18 pairs in the months prior to breeding, and tracked their reproductive success through the following breeding season. I then modeled various aspects of reproductive success as a function of *pair duration*, *allopreening*, *vocal duetting* and *allofeeding*, and used an informational approach to select the best models. The number of *eggs laid* could not be predicted with the measured variables. The best model for the number of *chicks hatched* included the independent variables *pair duration*, *allopreening frequency* and *allofeeding frequency*. The most important response variable, number of *chicks fledged*, was best predicted by *pair duration* and *allopreening frequency*. I conclude that both *pair duration* and allopreening behavior are useful for predicting reproductive success in pairs of captive Puerto Rican parrots. I recommend that managers monitor potential breeding partners for *allopreening* behaviors and manage populations to maximize average pair duration.

RESUMEN

Limitaciones en la reproducción en cautiverio puede ser factor limitante en esfuerzos de restauración de poblaciones de especies en peligro de extinción. La habilidad para poder predecir que parejas tendrán éxito reproductivo durante una temporada, ayuda a los manejadores de poblaciones en cautiverio a enfocar esfuerzos en dichas parejas y a establecer parejas nuevas con mayor probabilidad de éxito. A la larga esto facilitaría esfuerzos de reintroducción de dichas especies. En este estudio se investigará la posibilidad de predecir el éxito reproductivo en una población en cautiverio de la cotorra puertorriqueña (*Amazona vittata vittata*), especie en peligro de extinción, mediante la duración de la pareja y comportamientos afiladores. Sistemáticamente se observaron 18 parejas en los meses antes de comenzar la temporada de reproducción y se rastreó su éxito reproductivo durante la temporada de reproducción. Luego se modelaron varios aspectos del éxito reproductivo como función de la *duración de la pareja*, *mutuo acicalamiento*, *dueto vocal* y *mutua alimentación*, y se seleccionó el mejor modelo con método informático. El *total de huevos puestos* no se pudo predecir en este estudio. EL mejor modelo para *polluelos producidos* incluye las variables independientes *duración de la pareja*, *mutuo acicalamiento* y *mutua alimentación*. La variable de mayor importancia, *volantones*, se puede predecir con *duración de la pareja* y *mutuo acicalamiento*. He llegado a la conclusión de que tanto *duración de la pareja* y *mutuo acicalamiento* son variables confiables al momento de predecir el éxito reproductivo de cotorras puertorriqueñas en cautiverio. Recomiendo que los manejadores evaluar las parejas reproductoras mediante el uso de *mutuo acicalamiento* y se maneje la población para maximizar el promedio de la duración de las parejas.

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DEDICATION

God, Family, Friends and to all of those that have contribute in one way or another to rescue the only native species of parrots of Puerto Rico, *Amazona vittata vittata*.

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I will like to say thank you to all I know that in one way or another helped me along the way. Family, friends and co-workers. Special thanks to the committee members Dr. David Logue, Dr. Fernando Bird and Dr. Stefanie Whitmire for their trust and disposition to be part of the committee. Dr. Raúl E. Macchiavelli for his advice. Dr. Skip Van Bloem for his comments and suggestions. Miguel García and Ricardo Valentín for their trust by allowing me to do this study with this precious species. Jong Piel Banchs and Tomás Medina for their help during the study. Marisel López for lending me the recording equipment. Beatriz and Ricky for helping me with the observations.

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INTRODUCTION

Captive breeding programs are a “measure of last resort” to sustain species at risk of extinction. The critically endangered Puerto Rican parrot (*Amazona vittata vittata*), is being bred for release into the wild to supplement existing populations and re-colonize historical habitats (Department of Natural and Environmental Resources of Puerto Rico, DRNA, unpublished data). The reintroduction effort is limited by the reproduction rate of captive birds. Thus, a better understanding of the parrot’s breeding behavior could benefit the captive breeding program (Snyder 1996, Sutherland 1998). Behavioral studies can be use to develop novel management techniques that can increase captive productivity. By identifying specific pre-breeding behaviors that can be used to predict a pair’s reproductive success, managers can focus efforts on the best breeding pairs, evaluate potential pairs and efficiently re-assort members of pairs that are unlikely to succeed. These techniques could improve the productivity of the Puerto Rican parrot breeding effort, bolstering the reintroduction effort. The goals of this study are to determine if reproductive success can be predicted and to examine the role of pair duration and pre-breeding behaviors in captive Puerto Rican parrots. This is the first study of its kind for the large and widely distributed genus *Amazona*.

Managers of the two captive populations of Puerto Rican parrots establish new pairs by two different methods: forced pairing and free mate choice. Forced pairing best allows managers to maintain genetic diversity and avoid inbreeding, so it is a useful method when populations are very small. This method, however, can lead to elevated intrapair aggression and even fatality in Puerto Rican Parrots (DNER). Pairs of cockatiels (*Nymphicus hollandicus*) formed by free mate choice have better reproductive success than forced pairs (Yamamoto et al. 1989).

Managers at the José L. Vivaldi Lugo Aviary (the site of the present study) currently employ a form of free mate choice in which behavior is used to identify suitable breeding pairs. All single birds are placed in a flight cage where they are allowed to interact freely with each other. From November to January they are regularly monitored for affiliative and agonistic behavior. Flight synchronization, soft duetting, allopreening, allofeeding and copulation are affiliative behaviors used to identify new pairs. On the other hand territorial duetting (loud duetting), and synchronized aggression toward other members of the flock are the agonistic behaviors used to identify new pairs. Before the present study, none of these behaviors had been properly validated on this species. Prospective pairs that exhibit affiliative behavior between them and agonistic behavior towards other individuals are identified, captured and placed in a cage together. Close to the breeding season is the period when affiliative behaviors increase and managers can evaluate the compatibility of new breeding pairs and unsuccessful established pairs. By mid-January, pairs are placed in their own breeding cages. Using these methods, managers have found that reproductive success is highly variable among pairs. Greater accuracy in predicting reproductive success would have a positive effect on productivity.

Pair duration and affiliative behaviors are associated with reproductive success in some monogamous birds (Black 2001, Spoon 2007). The affiliative behaviors of interest in the present study are allopreening, vocal duetting, and allofeeding. Established and new pairs express these behaviors, therefore we have a direct way of comparison. Below, I define each of these behaviors and discuss their possible roles in pair bonding.

Allopreening occurs when one bird preens another's feathers. It has both hygienic and social functions (Radford 2006, Gill 2012). In social birds such as parrots, frequent close contact between individuals facilitates ectoparasite propagation (Radford 2006). Individuals frequently

preen to control their ectoparasite loads. Since there are body areas that individuals cannot reach by themselves (especially the head and neck), paired birds often solicit allopreening from the pair-mate. In addition, allopreening may reduce stress, facilitate pair bonding or help to manipulate the partner's behavior (Skeate 1984, Radford 2008, Gill 2012).

Vocal duetting occurs when two animals vocalize with temporal coordination. Like allopreening, duetting has long been associated with pair bonding, but it has never been conclusively linked to reproductive success (Arrowood 1988, Logue 2005, Molles & Wass 2005, Hall 2009). In the white-fronted amazon this behavior increases during the pre-breeding period as breeding season approaches, suggesting a role in the coordination of breeding (Skeate 1984). This increment in duetting may influence ovarian growth (Brockway 1965, Cheng et al. 1998) and stimulate the male to cooperate during breeding. Duetting in Puerto Rican parrots usually precedes allofeeding and copulation, which are strongly associated with egg laying, further suggesting a link between duetting and reproductive success. The efficacy of duetting as a predictor of breeding success is of particular interest to the Puerto Rican parrot recovery project because managers at the focal aviary currently use duetting as the primary criterion for selecting breeding pairs.

Mated birds sometimes offer regurgitated food to their pair-mate. In Puerto Rican parrots, this so-called "allofeeding" behavior is commonly preceded by a duet and is only practiced by established pairs. Prior to the beginning of the breeding season both mates feed each other. A well-fed female could invest more resources in egg production (Nisbet 1973), so allofeeding prior to breeding may augment egg number or quality. Allofeeding may also be used to signal commitment or mate quality (Nisbet 1973, Smith et al. 1989, Knapp & Kovach 1991, Helfenstein et al. 2003). In Puerto Rican parrots only the female incubates. Several times each day the male

brings food to the female. If the rate of feeding prior to the breeding season is an honest signal of a male's provisioning effort during incubation, allofeeding should be a good predictor of reproductive success.

Breeding pairs in the Puerto Rican parrot recovery program vary with respect to the number of years they have been together. The effect on this variation on reproductive success is not known. The duration of the pair bond and the amount of previous breeding experience predict reproductive success in some other monogamous birds (Yamamoto 1989, Black 2001). In the captive breeding program, pairs of Puerto Rican parrots are usually allowed to remain paired for many years. Only the death of a pair-mate, significant within-pair aggression or persistent mating failures provokes managers to re-assort established pair-mates.

The Puerto Rican parrot has been listed as endangered since 1968 (Snyder 1987). Efforts to breed the parrot in captivity started early in the 1970's when the number reached a low of 13 birds in the wild. As of 2012, there were captive breeding facilities and wild populations both at El Yunque National Forest and at Río Abajo Forest. Reintroductions began in 2006 to historical habitat (Rio Abajo Forest) with birds from the Río Abajo breeding facility and El Yunque National Forest captive population (DNER). Plans are under way to re-colonize another wild population at an undisclosed forest in Puerto Rico. The planned expansions of reintroduction efforts will require the captive facilities to increase production.

The goal of this project is thus to improve managers' abilities to quickly identify high-quality breeding partnerships. I selected eighteen pairs from the captive population at the Río Abajo facility. The first nine pairs were observed before the 2011 breeding season and nine more were observed before the 2012 breeding season. I evaluated the effect of *pair duration*,

allopreening frequency, allopreening average duration, *allofeeding* and *duetting* behavior of the pairs on reproductive success. Measurements of reproductive success were the number of *eggs laid*, the number of *chicks hatched*, and the number of *chicks fledged*. This study tests the hypotheses that reproductive success can be predicted by pair duration and pre-breeding behaviors.

OBJECTIVES

General:

The overall objectives of this project are to identify indicators of reproductive success and clarify the role of duetting in the Puerto Rican parrot (*Amazona vittata*). These objectives are stated as formal hypotheses (H1-H4) and their corresponding predictions below.

H1: *Allopreening frequency* and / or *average duration* is a predictor of reproductive success in the Puerto Rican Parrot.

P1a: *Allopreening frequency* and / or *average duration* predicts number of eggs laid.

P1b: *Allopreening frequency* and / or *average duration* predicts number of chicks produce.

P1c: *Allopreening frequency* and / or *average duration* predicts number of fledglings produce.

H2: *Allofeeding frequency* is a predictor of reproductive success in the Puerto Rican parrot.

P2a: *Allofeeding frequency* and / or *average duration* predicts number of eggs laid.

P2b: *Allofeeding frequency* and / or *average duration* predicts number of chicks produce.

P2c: *Allofeeding frequency* and / or *average duration* predicts number of fledglings produce.

H3: *Duetting* behavior is a predictor of reproductive success in the Puerto Rican parrot.

P3a: *Duetting* frequency predicts number of eggs laid.

P3b: *Duetting* frequency predicts number of chicks produce.

P3b: *Duetting* frequency predicts number of fledglings produce.

H4: *Pair duration* is a predictor of reproductive success in Puerto Rican parrot.

P4a: *Pair duration* predicts number of eggs laid.

P4b: *Pair duration* predicts number of chicks produce.

P4c: *Pair duration* predicts number of fledglings produce.

LITERATURE REVIEW

Captive breeding program

Captive breeding programs are used as a last resort to avoid extinction of endangered species and as a source of individuals for habitat re-colonization. The captive breeding program for the Puerto Rican parrot started in 1972, at the Patuxent Wildlife Research Center in Laurel, Maryland (Snyder et al. 1987). At the beginning, the program had difficulties breeding the species in captivity. In recent years, however, changes in husbandry techniques have allowed the captive breeding program to achieve high levels of productivity. This success has allowed managers to release birds into their historical habitat in North-Western Puerto Rico's karst region every year since 2006. Managers want to expand the reintroduction efforts, putting pressure on the captive program to produce as many birds as possible.

Incompatibility (aggression or low or no reproduction) of some pair-mates limits the success of the Puerto Rican Parrot breeding program (Snyder et al. 1987). Reproductive success in the captive breeding of monogamous birds can be achieved by allowing free mate choice (Yamamoto et al. 1989, Lupo et al. 1990). In a study with cockatiels those pairs that were forced together prior to the breeding season had lower success than pairs with longer pair duration. Free mate choice may also help to prevent the establishment of undesirable genes (reviewed by Williams & Hoffman 2009). In a study of grey partridge (*Perdix perdix*), estradiol levels were higher in individuals that formed pairs by free mate choice, and these pairs had greater reproductive success than randomly assigned forced pairs (Lupo 1990).

Allopreening

Allopreening occurs when one individual preens another's feathers. It is commonly observed in social birds. Allopreening has various functions and may help to increase the fitness of the actor and the groom (Radford & Plessis 2006, Lewis et al. 2007, Gill 2012). A study of green wood hoopoes (*Phoeniculus purpureus*) concluded that the function of allopreening depended on the area of the body that was preened. Allopreening to the head served a hygiene function while allopreening to the rest of the body had social implications. In this species, lower ranking group member allopreened higher ranking member more often than the reverse situation (Radford & Plessis 2006), suggesting a hierarchical status function and a possible function in forming alliances within the group. Birds also use allopreening to reduce aggression (Lewis et al. 2007). In colonial nesting common guillemots (*Uria aalge*) there is a negative relationship between allopreening rates and fighting between neighbors. Importantly, a low frequency of aggressive encounters was associated with the neighbors predicted high levels of breeding success. In monogamous buff-breasted wrens (*Cantorchilus leucotis*) allopreening was symmetrical between pair-mates. Pairs in which no allopreening was observed were more susceptible to change mates than were allopreening pairs (Gill 2012).

Lewis (2007) suggested that allopreening can be an honest signal of quality that affects mate choice. Since allopreening is an investment in the pair-mate, individuals may use allopreening to identify mates who are willing to invest heavily (Roberts 1998). Allopreening requires an individual to spend energy and time that could spend in other manners that may be more beneficial for it. Individuals who are capable of spending more time allopreening may be high quality mates (Zahavi 1975).

Allopreening has also been correlated to reproductive success in cockatiels (Spoon et al. 2006, Spoon et al. 2007). All pairs in which allopreening was directed only at the pair-mate stayed together throughout the course of that study, whereas individuals that eventually changed mates increased their allopreening rates toward the new mate and ceased allopreening with the previous mate. Those individuals that deserted their mate had reproductive success with the new partner, while the deserted individuals failed to breed in the following breeding attempt (Spoon et al. 2007). Social interaction involving touch, such as grooming in mammals, has physiological effects that reduce heart rate and stress. In some species, groomers even fall asleep during grooming (Dumbar 2010). I suggest that allopreening may have similar effect in the preened individual. This relaxing effect may promote affiliative behaviors that in turn facilitate reproductive behavior.

Allofeeding

Like allopreening, allofeeding is used to maintain pair bonds. In white-fronted amazons (*Amazona albifrons*) only paired birds engage in this behavior (Skeate 1984). Similarly, observations of Puerto Rican parrots in captivity suggest that allofeeding is limited to pair-mates (B.R.G pers. obs.). Pair-mates could use this behavior as an assessment to mate quality prior to the breeding season (Nisbet 1973, Smith 1989, Knapp & Kovach 1991, Helfenstein et al. 2003). In a study with common terns, courtship feeding by the male related positively with chick survival (Nisbet 1973). Males that offered high rates of courtship feeding also provided a wider range of food. This finding suggested that during courtship feeding, males demonstrated their capability to be good providers, a quality signal to their mates.

Allofeeding may also directly influence female condition. In pied flycatchers (*Ficedula hypoleuca*), for example, a female's nutritional state is affected by her mate's allofeeding rate (Smith 1989). When females were provided with extra food, they spent more time incubating, suggesting that female attentiveness for the nest is influenced by the amount of food provided.

Duets

A vocal duet is produced when two individuals vocalize with temporal coordination. It is phylogenetically widespread among birds, and is believed to serve various functions (Hall 2009). For example, duets may signal commitment to a partner, thereby strengthening their pair bond (Hall 2009). By initiating a duet, an individual can test whether its mate is attentive enough to respond (Smith 1994). In yellow-naped amazons (*Amazona auropalliata*), duets appear to function in coordinated territory defense. Specifically, pair-mates responded equally to male, female, and duet playback stimuli (Dahlin et al 2012). This finding suggested a territorial defense function for duets in parrots. In non-duetting ring doves (*Streptopelia risoria*) vocal stimuli induce release of luteinizing hormone which induces ovulation, coordinating breeding. Female nest *coos* stimulated areas on the female brain related to gonadotropine-releasing hormone at the same time luteinizing hormones levels in the blood increased (Cheng et al 1998). Similar effects were found for the warble vocalization in budgerigar (*Melopsittacus undulatus*). Male vocalizations induce ovarian stimulus and oviposition in females budgerigars (Brockway 1965). In males budgerigars their own vocalization stimulated testicular activity (Brockway 1967).

It has been suggested that duetting may also function in the coordination of breeding activities, although conclusive evidence is lacking (Hall 2006, Topp & Mennill 2007). In Australian magpie-larks (*Grallina cyanoleuca*) duetting activity peaks just before the beginning

of the breeding season. Most duets are initiated by the female during this period (Hall 2006). A similar pattern was found for rufous-and-white wrens (*Thryothorus rufalbus*). Female singing, duetting and male responsiveness increase during the pre-breeding season. The finding that duets often co-vary temporally with the breeding cycle raises the possibility that duetting might be related to the coordination of breeding in Puerto Rican parrots. In that species, *soft* duetting increases during the pre-breeding season (Snyder 1987). Females lead duetting in Puerto Rican parrot (Roberts and Haas 1996).

Pair duration

Pair duration has been shown to affect reproductive success in several monogamous bird species (Yamamoto et al. 1989, Bradley et al. 1990, Hall 1999, Black 2001). In barnacle geese (*Branta leucopsis*) reproductive success increases with pair duration. Cooperation is important for reproduction in this species, therefore finding a quality mate and developing coordination with the pair-mate can increase reproductive success (Black 2001). Previous experience with a mate may also be a factor for reproductive success in cockatiels. Pairs of cockatiels that were paired with a new mate before the start of the breeding season had lower reproductive activity than pairs with previous experience breeding together (Yamamoto et al. 1989). Australian magpie-lark pairs that bred together in previous seasons became reproductively active earlier than new pairs (Hall 1999). This species can make several attempts to breed in a single breeding season, so earlier breeding could produce significant fitness benefits.

Mate change can happen in many monogamous birds, including some parrots (Bradley et al. 1990, Ens 1993, Heg et al. 2003, Spoon 2007). In short-tailed shearwaters (*Puffinus*

tenuirostris), reproductive success increases as pair duration increases. Pairs with three or more years together had better reproductive success than pairs with shorter pair bonds. Pairs that failed in their previous breeding season had greater probability to divorce. (Bradley et al. 1990). Re-mating after divorce may increase reproductive success after repairing for those individuals that deserted their mate (Spoon et al. 2007). In a captive population of cockatiels (*Nymphicus hollandicus*), individuals that engaged in extra pair behavior were more likely to change their current mate. After changing mates those individuals that deserted their mate had greater reproductive success compared to those individuals that were deserted. Captive Puerto Rican parrots do not have the option of choosing a new mate if their breeding attempt fails because repairing is subject to the manager's decision. Understanding whether pair duration may increase reproductive success in Puerto Rican parrot will help managers decide when to give pairs new opportunity to re-mate.

METHODS

I observed affiliative behaviors in captive pairs of Puerto Rican parrots during the pre-breeding period, and attempted to relate variation in these behaviors and in pair bond duration to variation in reproductive success. I collected behavioral and reproductive data from a total of 18 pairs over two years.

Study species

In the wild, Puerto Rican parrots appear to pair for life. Mate change has not been documented in the wild, but birds will re-mate if their partner dies (Snyder et al. 1987). In captivity, managers typically choose to “break up” pairs that exhibit high levels of within-pair aggression. Such birds will form new partnerships and can become successful breeders (DNER unpublished data).

Prior to the breeding season, pair mates exhibit a variety of affiliative behaviors including allopreening, duetting, allofeeding and copulation (Skeate 1984). Pairs allopreen throughout the year. This species has two kinds of duets, a territorial duet and a soft duet. Pairs engage in “territorial duetting” when defending their nesting sites which they defend year round (Snyder et al. 1987). “Soft duetting,” which is structurally different than territorial duetting, is commonly seen close to and during the breeding season and is usually followed by allofeeding and copulation. Soft duetting is the only form of duetting observed in the current study, so all further uses of the term “duetting” refer to soft duetting. During allofeeding either sex can donate or receive food, but one at a time. Allofeeding and copulation increase in frequency as the breeding

season approaches. Once breeding begins, between the months of December and January, the reproductively active birds become territorial and aggressive towards intruders.

Females lay two to four eggs per clutch and only the female incubates. Incubation lasts 26 days on average (Snyder et al. 1987). The male guards the territory and goes inside the nest only to feed the female and chicks. Once chicks are large enough to regulate their own body temperature, both parents search for food and feed the chicks until fledging. Parental behavior is similar in captivity and the wild (pers. obs.). Chicks fledge at about 65 days after hatching (Snyder et al. 1987).

Study Area

The study was conducted at the José L. Vivaldi Lugo Aviary, in the Río Abajo Forest in Arecibo, Puerto Rico (18.2 N, 66.4 W; 366 meters above sea level). Observation cages (120 x 120 x 120 cm, Figure. 1) were assigned randomly to each pair. Each cage had two perches and a feeding area. Pairs had at least one month to acclimate to their cages and the observer before observations began. Observations were conducted from a distance of 3 to 4 meters from each cage. Nikon Monarch 8x42 binoculars were used to identify individuals from each pair. Observers identified individuals by distinctive marks on the head and body, and by each bird's unique combination of colored leg bands.

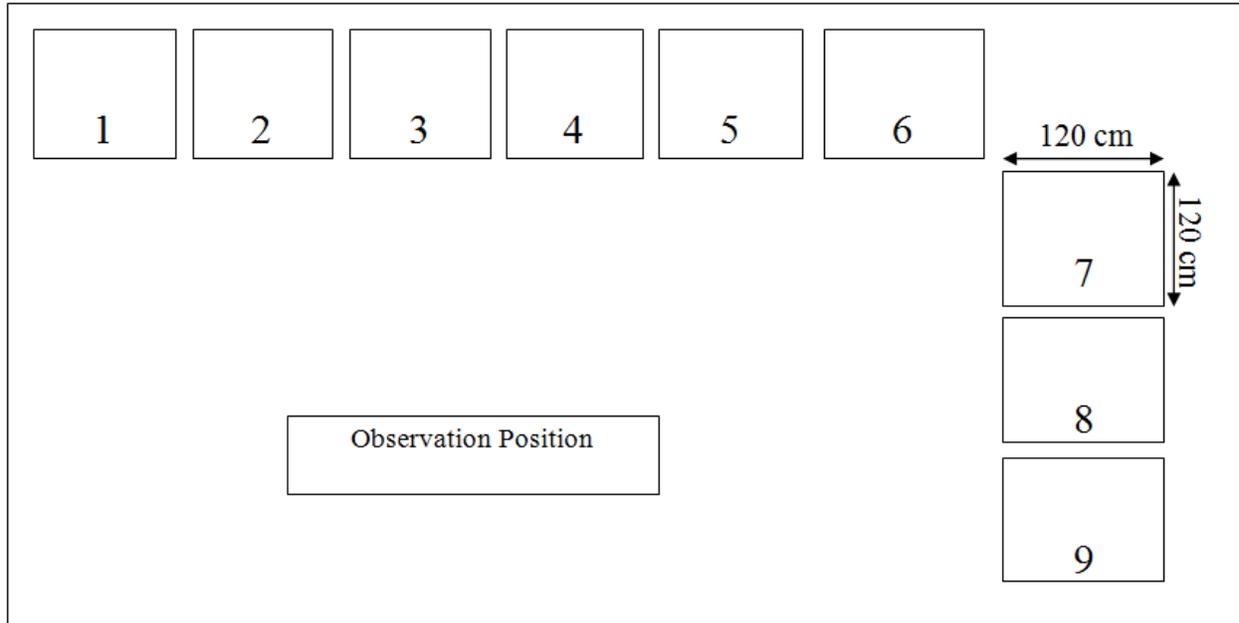


Figure 1. Arrangement of observation cages used in the study.

Pair selection for the study

Subjects for this study comprised 16 established pairs and two new pairs with no prior breeding experience. Pair mates that were known to be highly aggressive toward one another were not considered for the study. I ensured high variance in pair duration by binning all available pairs according to pair-bond duration (one year, two year, etc.), randomly selecting one pair from each bin, and adding the pair with the longest duration and a new pair with no breeding experience. Using this method, I selected nine focal pairs for the first year of the study (2010 - 2011) and nine unique pairs for the second year (2011 -2012). No individuals were used in both years.

Observations

A trained field assistant and I collected pre-breeding observations from November 25, 2010 through January 13, 2011 and from November 24, 2011 through January 17, 2012. Each pair was observed for 15 days. Observation days were chosen in response to weather and the availability of observers. By the middle of January, all breeding pairs were placed in their breeding cages by the project staff, and behavioral observations ceased. Further observations would risk disturbing the birds' reproductive activities.

The variables that were recorded were: *Allopreening Frequency* (APF), *Allopreening Average Duration* (AAD), *Allofeeding Frequency* (AF), *Duet Frequency* (DF), and *Pair Duration* (PD). These selected behaviors have been linked to pair bonding (Skeate 1984), mate compatibility (Spoon 2006), or reproductive success in other parrots (Spoon et al. 2007, Black 2001, Nisbet 1973).

Observations were conducted from 6:00 am until 9:15 am, a period that corresponds to the peak of intersexual interaction in parrots (Snyder 1987, pers. obs.). We observed two pairs at a time except for pair 9, which was observed alone due to the odd number of pairs in the study (Figure 1). Observers had no difficulty recording all focal behaviors from both pairs under observation because these behaviors are conspicuous and are not very frequent. Focal observations lasted for 15 minutes, with a five minute break between observation periods. Observation order for both rounds is described in Table 1.

Throughout the breeding season, we recorded the number of eggs, chicks, and fledglings produced by each pair. For eggs I counted all eggs laid by the female including fertile and infertile eggs. These are the dependant variables I used in the study. For number of eggs I consider only the first clutch to guarantee a direct comparison of eggs productivity among pairs.

I chose to ignore later clutches because managers can manipulate each of these developing stages accordingly to their necessity. If there is the need, eggs and chicks can be move from nest to nest and pairs can be recycled (eggs are removed and females laid eggs again). The movement will depend on the capacity of incubation or raising chicks of each pair. During the study all pairs were allowed to incubate two fertile eggs and no changes of chicks were done. This will guarantee an equal comparison of chicks and fledglings produced.

Data analysis

I constructed separate Poisson regression models for each dependent variable and all possible combinations of independent variables. Poisson regression is appropriate here because the response variables consist of discrete, non-negative values, representing rare events. Then I constructed a correlation between the observe values and the predicted values of each model. With the correlation we obtain the R square values that will tell us if the model is reasonable for our data results. My model selection procedure relied on Akaike's information criterion (AIC) values calculated from the log likelihoods of each model. AIC values describe a model's quality as a function of the model's ability to explain the dependent data discounted by the number of independent variables in the model. In a set of models, the model with the lowest AIC is the best. All models were compared using AIC to determine the best fitting model for each dependent variable. Models within 2.0 AIC points of the best fitting model were considered to have substantial support (Burnham and Anderson 2002, p70, Burnham and Anderson 2004). For the purpose of this study I will base my inference on the model with the lowest AIC value. Poisson regressions were calculated with Infostat Statistic Software (Di Rienzo J.A., Casanoves F., Balzarini M.G., Gonzalez L., Tablada M., Robledo C.W. InfoStat versión 2013. Grupo InfoStat,

FCA, Universidad Nacional de Córdoba, Argentina. URL <http://www.infostat.com.ar>). AIC calculations were performed with Microsoft Excel 2007.

Table 1. Focal pairs arranged by observation period and observation day. Each pair was observed twice at each period throughout the 15 days of observation.

Day	6:00 6:15	6:20 6:35	6:40 6:55	7:00 7:15	7:20 7:35	7:40 7:55	8:00 8:15	8:20 8:35	8:40 8:55	9:00 9:15
1	1, 2	3, 4	5, 6	7, 8	9	1, 2	3, 4	5, 6	7, 8	9
2	3, 4	5, 6	7, 8	9	1, 2	3, 4	5, 6	7, 8	9	1, 2
3	5, 6	7, 8	9	1, 2	3, 4	5, 6	7, 8	9	1, 2	3, 4
4	7, 8	9	1, 2	3, 4	5, 6	7, 8	9	1, 2	3, 4	5, 6
5	9	1, 2	3, 4	5, 6	7, 8	9	1, 2	3, 4	5, 6	7, 8
6	1, 2	3, 4	5, 6	7, 8	9	1, 2	3, 4	5, 6	7, 8	9
7	3, 4	5, 6	7, 8	9	1, 2	3, 4	5, 6	7, 8	9	1, 2
8	5, 6	7, 8	9	1, 2	3, 4	5, 6	7, 8	9	1, 2	3, 4
9	7, 8	9	1, 2	3, 4	5, 6	7, 8	9	1, 2	3, 4	5, 6
10	9	1, 2	3, 4	5, 6	7, 8	9	1, 2	3, 4	5, 6	7, 8
11	1, 2	3, 4	5, 6	7, 8	9	1, 2	3, 4	5, 6	7, 8	9
12	3, 4	5, 6	7, 8	9	1, 2	3, 4	5, 6	7, 8	9	1, 2
13	5, 6	7, 8	9	1, 2	3, 4	5, 6	7, 8	9	1, 2	3, 4
14	7, 8	9	1, 2	3, 4	5, 6	7, 8	9	1, 2	3, 4	5, 6
15	9	1, 2	3, 4	5, 6	7, 8	9	1, 2	3, 4	5, 6	7, 8

RESULTS

The data shows that all pairs laid two or more eggs. Of the 18 pairs eleven produce *chicks* and seven produce *fledglings*. The average of *eggs* laid by pair was 3.33. The average of *chicks* hatched by pair was 0.78 and for *fledglings* 0.61 (Table 2a). On Table 2b we can see the low frequency of events for allofeeding and for duetting. For allopreening behavior, on Table 3 the data shows that *allopreening frequency* has some correlation with eggs and chicks produce while *allopreening average duration* is correlated to chicks and fledglings. Pair duration is also correlated to chicks and fledglings. The data shows that pair duration and allopreening average duration are also correlated (Table 3). The strongest correlation is between duets and allofeeding. This is expected to happen as pairs usually allofeed after they duet.

Table 2. Summary measurements. a) Summary measurements of independent variables. b) Summary measurements of independent variables.

a.

Dependent Variables	n	Media	S.D.
Eggs	18	3.3333	0.8402
Chicks	18	0.7778	0.8782
Fledglings	18	0.6111	0.8498

b.

Independent Variables	n	Media	S.D.
Allopreening Frequency	18	17	9.5425
Allopreening Average Duration	18	43.4673	20.8662
Allofeeding Frequency	18	1	1.0847
Duets	18	2.5556	2.2809
Pair Duration	18	5.2778	3.5281

Table 3. Pearson correlations.

Variables	APF	AAD	AF	DF	PD	Eggs	Chicks	Fledglings
APF	1	0.41	0.36	0.95	0.32	0.05	0.05	0.26
AAD	0.21	1	0.1	0.06	0.01	0.88	0.01	0.01
AF	0.23	0.4	1	0.00089	0.06	0.44	0.81	0.12
DF	-0.02	0.45	0.71	1	0.72	0.78	0.82	0.23
PD	0.25	0.59	0.45	0.09	1	0.08	0.01	0.0038
Eggs	0.47	0.04	0.19	-0.07	0.42	1	0.54	0.15
Chicks	0.47	0.6	0.06	-0.06	0.62	0.15	1	0.01
Fledglings	0.28	0.62	0.38	0.3	0.65	0.36	0.61	1

APF = Allopreening frequency, AAD = Allopreening Average Duration ,

AF = Allofeeding frequency, DF = Duet frequency, PD = Pair duration

For each of the three dependant variables there were 31 possible combinations of independent variables. As for *total eggs laid* the model with the lowest AIC included only *allopreening frequency* (Appendix A; AIC = -21.26; R² = 0.2116, Deviance = 2.9301, df = 16). For the dependent variable *chicks hatched* the best model included the independent variables *allopreening frequency*, *allofeeding frequency* and *pair duration* (Appendix B; AIC = 34.56, R² =

0.56, deviance = 10.4995, df = 14). The best model for fledglings included *allopreening frequency* and *pair duration* (Appendix C; AIC = 29.864, R² = 0.46 deviance = 10.4995, df = 15). The expressions for the best model for each dependent variable are in Table 4.

Table 4. Best model for each dependent variable.

Log (<i>Total Eggs Laid</i>) = 0.9922 + APF 0.121
Log (<i>Chicks Hatched</i>) = -1.9132 + 0.0509 APF + -0.4386 AF + 0.2201 PD
Log (<i>Fledglings</i>) = -2.64 + 0.0468 APF + 0.2295 PD

APF = Allopreening frequency, AF = Allofeeding frequency, PD = Pair duration

Table 5. Best models measurements.

Dependent variable	Independent variable	P value	AIC	R ²	Deviance	Df
Eggs laid	APF	0.3737	-	0.2116	2.9301	16
Chicks hatched	APF	0.0694	34.56	0.5625	9.9684	14
	AF	0.1779				
	PD	0.0156				
Fledglings	APF	0.1368	29.864	0.4624	10.4995	15
	PD	0.0041				

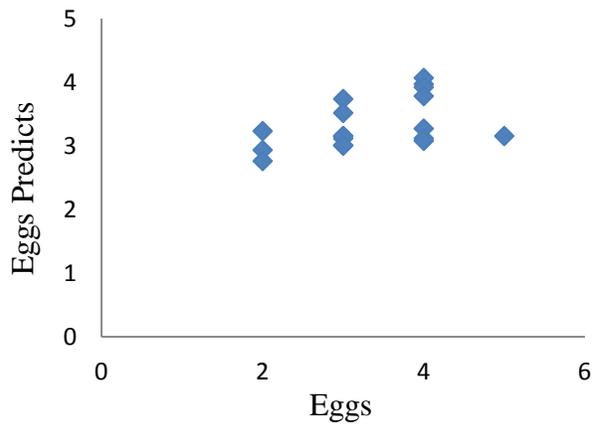
APF = Allopreening frequency, AF = Allofeeding frequency, PD = Pair duration

I did not detect a statistically significance influence of the independent variable (Table 5) and no reasonable predictability (Figure 2a) in the best model *for total eggs laid*, so I did not interpret them further. For the model *chicks hatched* only pair duration had a statistically significant influence (Table 5). For each additional year a mated pair stays together, the pair has a 24.6% more *chicks* hatch. This model has reasonable predictability for *chicks* produce Figure

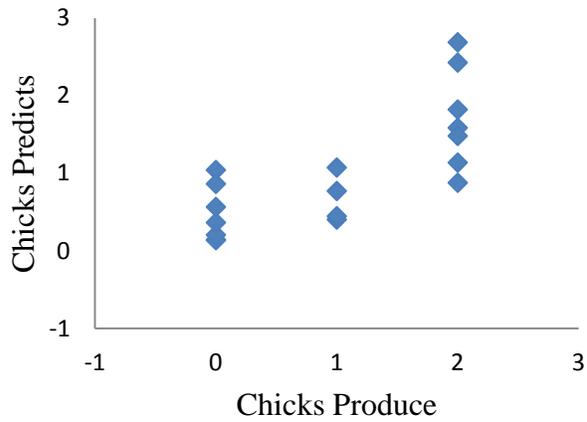
2b). For the best model for *fledglings* only *pair duration* has a significant effect (Table 5). For each additional year a mated pair stays together, the pair increases the number of *fledglings* by 24.6%.

This model has a reasonable predictability of *fledglings* produce (Figure 2c).

a)



b)



c)

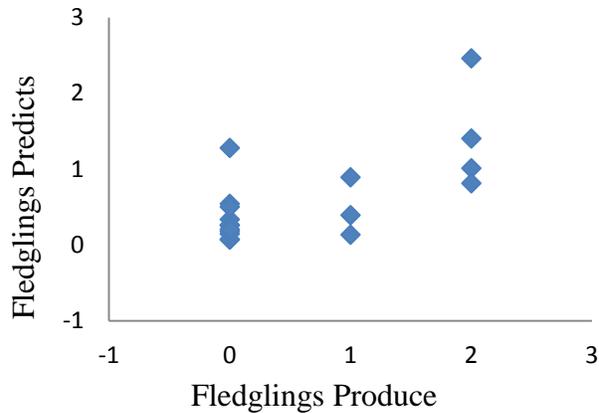


Figure 2. Correlation graphs of predicts of the models with lowest AIC vs observe value. a)

When we correlate the predicted value with the observe value we obtain a value for $R^2 = 0.21$ for the best model of *eggs* produce. Thus we can say that the model is not reasonable to predict *eggs* produce. b) When we correlate the predicted value with the observe value we obtain a value for $R^2 = 0.5625$ for the best model of *chicks* produce. Thus we can say that the model is reasonable to predict *chicks* produce. c) When we correlate the predicted value with the observe value we obtain a value for $R^2 = 0.4624$ for the best model of *fledglings* produce. Thus we can say that the model is reasonable to predict *fledglings* produce.

For *chicks* hatched the simplest models with a Δ_i lower than two is *pair duration* with the third lowest AIC value and *allopreening average duration* in the seventh lowest AIC value. The model with the second lowest AIC value was *allopreening frequency* and *pair duration*. For *fledglings* produce the simplest model with Δ_i lower than two is *pair duration* with the second lowest AIC value.

DISCUSSION

I set out to develop a low-cost method to predict reproductive success in captive pairs of Puerto Rican parrots. My results indicate that *pair duration* and *allopreening frequency* are the independent variables that can be use as predictors of reproductive success in captive Puerto Rican parrot. *Pair duration* is present in the model for *chicks* and *fledglings* produce. On the other hand *allopreening frequency* is present in all the models with the lowest AIC values for the dependent variables. My findings suggest a relation between these two variables and reproductive success. Other studies have demonstrated the importance of *pair duration* and *allopreening* for predicting reproductive success in monogamous birds (Yamamoto et al. 1989, Bradley et al. 1990, Hall 1999, Black 2001, Spoon et al. 2006, Spoon et al. 2007). Given this information we have a better understanding of the natural history of the Puerto Rican parrot and have better decision making to improve reproductive success in the captive breeding program of this endangered parrot.

For *eggs* produce the results demonstrate that there are no variables capable of predicting reproductive success in the way it was measured for the present study. The model with the lowest AIC value had only *allopreening frequency* which had no effect ($p = 0.3737$). One possible explanation is that eggs simply cannot be predicted because females lay a determine number of eggs per clutch. It is more of a physiological factor that cannot be determine by the methods use for this study. On the other hand *chicks* and *fledglings* can be predicted because the success of a pair to produce a *chick* or a *fledgling* relies on the capability of the pair to accomplish this (Black 1996). The independent variables for this study have been previously linked to reproductive success (Yamamoto et al. 1989, Bradley et al. 1990, Hall 1999, Black

2001, Spoon et al. 2006, Spoon et al. 2007). Another explanation for this is the nature of the data. This study consists of evaluating rare events. Low samples size can lead to false negative. A possible solution is run the study for a longer period of time an increase the number of pairs use, if possible given the nature of the restrictions to study this species.

Allopreening frequency was correlated with *eggs* and *chicks* produce but *allopreening average duration* has a stronger correlation with *chicks* and *fledglings* produce (Table 3). *Allopreening average duration* is the seventh model with the lowest AIC value for *chicks* and it is within 2 units of the model with the lowest AIC value (Appendix B). Nevertheless *Allopreening frequency* was included in the best models for predicting *chicks* and *fledglings* production. In cavity nesting parrots, like the Puerto Rican parrot, females spend large amounts of time inside the cavity during the breeding season (Snyder et al. 1987). During this time, the female depends on her mate for food and protection. Allopreening may be used by the parrot as a mate quality signal before the breeding season. It may allow the female to gauge the male's commitment, and encourage the male to cooperate with the female. In buff-breasted wrens, allopreening behavior helps reduce aggression within members of a group (Gill 2012). Curtis & Wang (2003) suggest a mechanism that may link allopreening to reduced aggression and higher reproductive success. They found that allopreening reduces stress and promotes the release of hormones that induce pair-bonding. This, in turn, may promote more consistent incubation behavior, increasing the probability of hatching *eggs* and raising *chicks* to *fledging*.

The importance of allopreening behavior for captive breeding relies in the potential as an evaluating tool for established or new reproductive pairs. Puerto Rican parrots are territorial and highly aggressive up to the point that they can badly hurt each other (Snyder 1987). Once a pair is established allopreening behavior can be use to strengthen the pair bond and reduce stress

(Nisbet 1973, Spoon 2007, Gill 2012), reducing the possibilities of within pair aggression and increasing their chances of reproductive success. Within pair aggression is the main reason for re-sorting established pairs in the captive population of the Puerto Rican parrot.

The best predictor for reproductive success for this study was *pair duration*. Clearly experience plays an important role for reproductive success in captive Puerto Rican parrots, as previous studies of wild and captive monogamous birds have demonstrated (Black 1995, Black 2001, Gill 2012, Yamamoto et al. 1989). Natural bonded pairs in the captive program at the Jose Luis Vivaldi Lugo facilities stay together unless agonistic behavior is documented. This type of management gives pair-mates time to acclimate to their partners and coordinate breeding effort. My results seem to validate this approach, as I found that *pair duration* is a predictor of *chicks* and *fledglings* produced. For every year a pair stays together, the pair-mates can increase the productivity for *chicks* and *fledglings* in approximate 25%. Thus it is important that pair mates are given the chance of completing a successful first reproductive attempt. In the wild, other monogamous species can change mate if they fail a reproductive attempt (Bradley et al. 1990, Ens 1993, Heg et al. 2003, Spoon 2007). Forcing pairs to stay together after continuous fail reproductive attempt could lead to pair-mate aggression. Thus it is possible that the causal relationship goes in the other direction, and only successful pairs refrain from aggression, allowing them to remain together for many years. A longitudinal study would be required to test this alternative explanation.

The model that includes only *pair duration* was the second best model for *fledglings* produce and the third best model for *chicks* hatched. In both situations the models have substantial support. In fact *pair duration* is correlated to *chicks* and *fledglings* produce (Table 3), indicating a positive relation of pair duration with *chicks* and *fledglings* produce. This suggests

that longer the pair stays together as breeding partners, the better their chances of increase reproductive success. Now previous studies have suggested that pair duration is affected by reproductive success (Hall 1999, Black 2001), as those pairs that fail to reproduce eventually change mate. Therefore we cannot state that pair duration causes the increment of chicks and fledgling but it is closely related to these results.

Interestingly, *duetting frequency* did not predict reproductive success in this study. This was unexpected because studies on other species of parrots have demonstrated that acoustic signals alone are important for stimulating ovulation in females and testes stimulation in males (Bockway 1965, Brockway 1967). In Puerto Rican parrots, duetting rate increases as breeding season approaches (Personal observation). This suggests a possible breeding coordination function of duet for breeding pairs. Further, it may be the case the structure of duets, rather than the frequency with which they are given, is related to breeding success. In budgerigars, only certain type of song is responsible for ovarian and testes stimulation (Bockway 1965, Brockway 1967). I therefore suggest studying the effects of duet synchronization on breeding coordination and reproductive success.

It is important to denote that the rareness of some of these behaviors may reflect Type II error. For example allofeeding and duets are very rare behaviors. Allofeeding has been related to reproductive success in other studies. A longer observation period may produce different results. The rareness of the behaviors evaluated on the present study is not the only factor in not finding concise results for some of the variables. Cage arrangement during the breeding season may have influence the results. The breeding cages at the José L. Vivaldi Lugo aviary are separated by physical barriers that do not allow direct visual contact between cages but does not isolate breeding pairs from vocalizations. As it has already been discussed vocalizations have influence

on gonads stimulations. Pair bonding vocalizations may influence positively reproductive success (Brockway 1965 and 1967, Cheng et al. 1998), on the other hand territorial vocalizations may intimidate individuals, having the reverse effect. Another factor could be the frequency of human presence in the breeding areas. Parrots are prey upon animals that are easily intimidated by larger animals, like humans. Pairs with longer *pair duration* may be less affected than pairs with shorter *pair duration* by the presence of the personal near the breeding areas, having a possible effect of *pair duration* on the results. One factor that I did not take into consideration for the present study was age of the individuals. The way the breeding pairs are manipulated at the captive program may give the impression that age could be a factor, since once a pair is form they are not separated unless a special event happens. As a consequence if these factors were measured we may have seen that pair duration correlates with age of the birds.

The present study was done with captive reared animals. As a result I emphasize that the results of this study must be taken cautiously when applying to a wild population. In captivity the animals do not undergoes the pressure of finding food, competition for cavities or predation. These factors may affect behaviors like allofeeding frequency because they do not have to travel long distances to find food. Allopeening behavior may be affected too as animals will be expose to predation and a larger load of ectoparasites. This means that the time spend in the mentioned behaviors may differ from captive birds to wild birds. On the other hand these findings may apply to other captive breeding program of related species. These findings have potential economic impact for recovery programs and for commercial breeders. More effective techniques may reduce the cost of operation and specifically for recovery programs it may shorten the effort by reaching the goal of delisting a species sooner.

I recommend new cage designs that facilitate the expression of these behaviors and allow ease of observation that may improve the recruitment of productive pairs. Evaluate new and current pairs that have had recent reproductive failure. The addition of cameras that can help monitor breeding cages and the inside of the nest, can improve decision making when resorting failed pairs. This will help avoid re-mate problematic individual and allowed better individuals to re-mate. For future studies I suggest investigating the role of the male during the breeding period. In a wild population of Puerto Rican parrots at Río Abajo, managers have observed that no more than one chick at a time has been raised to fledging in nests where the male do not assist in feeding (DNER). Attending to the male's role could help managers distinguish high productivity nest from low productivity. It could also reduce the unnecessary loss of chicks, if managers remove chicks from nests with inattentive fathers and place them in foster care. Another possible avenue for optimizing the Puerto Rican parrot breeding project involves research into endocrine patterns during the breeding season. Hormone levels have never been monitored in this species during the breeding season. There may be a relationship between hormone levels and reproductive success in the captive populations. It is well known that high levels of stress may affect reproductive success in birds. Identifying pairs that have high stress hormones levels would allow managers to implement strategies to reduce stress in those pairs. I also recommend studying the possible effect of age on reproductive success and the effect of age at pair formation on pair duration.

In conclusion, I found that *pair duration* and *allopreening* behavior, are useful predictors of reproductive success in Puerto Rican parrots. I recommend that managers use these criteria to evaluate potential breeding pairs prior to the breeding season. It is thus of importance to allowed new pairs to successfully complete the first reproductive attempt. Failure to breed may lead pairs

to loss interest in their current mate (Spoon et al. 2007), resulting in possible agonistic behavior within pair mates. Allopreening is a good tool to measure the interest of an individual on its mate, because when an individual is losing interest on its current mate will progressively cease allopreening (Spoon et al. 2007). Improving reproductive success in endangered species program has a crucial impact on conservation effort by shortening the duration that captive breeding is required and by reducing the costs of producing animals in captivity. This study is an example of how focused animal behavior research can aid species conservation efforts.

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APPENDIX

Appendix A. AIC results for models used to predict *eggs*.

AIC Results Total Eggs Laid		
Variable	AIC	Δ_i
APF	-21.2562	0
PD	-21.1146	0.1416
AF	-20.61	0.6462
DF	-20.4954	0.7608
AAD	-20.482	0.7742
APF,PD	-19.6396	1.6166
AAD,PD	-19.3918	1.8644
APF,AF	-19.287	1.9692
APF,DF	-19.2706	1.9856
APF ,AAD	-19.2672	1.989
DF,PD	-19.1698	2.0864
AF,PD	-19.1148	2.1414
AF,DF	-18.9536	2.3026
AAD,AF	-18.6158	2.6404
AAD,DF	-18.5178	2.7384
APF,AAD,PD	-18.0014	3.2548
APF,DF,PD	-17.688	3.5682
APF,AF,PD	-17.651	3.6052
APF,AF,DF	-17.4414	3.8148
AAD,AF,PD	-17.4016	3.8546
AAD,DF,PD	-17.392	3.8642
APF,AAD,AF	-17.3202	3.936
APF,AAD,DF	-17.2738	3.9824
AF,DF,PD	-17.2584	3.9978
AAD,AF,DF	-16.9604	4.2958
APF,AAD,DF,PD	-16.0048	5.2514
APF,AAD,AF,PD	-16.0022	5.254
APF,AF,DF,PD	-15.6998	5.5564
APF,AAD,AF,DF	-15.4462	5.81
AAD,AF,DF,PD	-15.4124	5.8438
APF,AAD,AF,DF,PD	-14.0228	7.2334

APF = Allopreening frequency, AAD = Allopreening Average Duration ,

AF = Allofeeding frequency, DF = Duet frequency, PD = Pair duration.

Appendix B. AIC results for models used to predict *chicks*.

AIC Results Chicks		
Variable	AIC	Δ_i
APF,AF,PD	34.56	0
APF,PD	34.7	0.14
PD	34.78	0.22
APF ,AAD	35.64	1.08
AAD,DF	35.64	1.08
APF,DF,PD	35.756	1.196
AAD	35.7848	1.2248
AF,PD	35.82	1.26
APF,AAD,DF	35.984	1.424
DF,PD	36.08	1.52
APF,AF,DF,PD	36.268	1.708
APF,AAD,AF,PD	36.318	1.758
APF,AAD,AF	36.41	1.85
AAD,PD	36.5	1.94
APF,AAD,PD	36.55	1.99
AAD,DF,PD	36.9404	2.3804
APF	37.0756	2.5156
AAD,AF	37.08	2.52
APF,AAD,DF,PD	37.114	2.554
AAD,AF,PD	37.274	2.714
AAD,AF,DF	37.582	3.022
AF,DF,PD	37.81	3.25
APF,AAD,AF,DF	37.95	3.39
APF,AAD,AF,DF,PD	38.234	3.674
AAD,AF,DF,PD	38.916	4.356
APF,DF	39.04	4.48
APF,AF	39.06	4.5
AF	39.9508	5.3908
DF	39.954	5.394
APF,AF,DF	41.046	6.486
AF,DF	41.64	7.08

APF = Allopreening frequency, AAD = Allopreening Average Duration ,

AF = Allofeeding frequency, DF = Duet frequency, PD = Pair duration

Appendix C. AIC results for models used to predict *fledglings*.

AIC Results Fledglings		
Independent Variable	AIC	Δ_i
APF,PD	29.864	0
PD	30.0816	0.2176
APF,AF,PD	30.6332	0.7692
AF,PD	31.8222	1.9582
DF,PD	31.83	1.966
APF,AAD,PD	31.8528	1.9888
AAD,PD	32.0638	2.1998
APF,AF,DF,PD	32.3806	2.5166
APF,AAD,AF,PD	32.6198	2.7558
APF,AAD	33.0286	3.1646
AAD	33.167	3.303
APF,AAD,DF,PD	33.3128	3.4488
AAD,DF,PD	33.6506	3.7866
AAD,AF,PD	33.767	3.903
AF,DF,PD	33.8028	3.9388
APF,AAD,AF,DF,PD	33.9152	4.0512
AAD,DF	34.1854	4.3214
APF,AAD,DF	34.3672	4.5032
APF,AAD,AF	34.7652	4.9012
AAD,AF	35.1228	5.2588
AAD,AF,DF,PD	35.6506	5.7866
APF, DF, PD	35.6836	5.8196
AAD,AF,DF	35.6836	5.8196
APF,AAD,AF,DF	36.3188	6.4548
APF	36.5522	6.6882
APF,AF	38.1644	8.3004
APF,DF	38.3	8.436
AF	38.567	8.703
DF	39.2932	9.4292
APF,AF,DF	40.1644	10.3004
AF,DF	40.403	10.539

APF = Allopreening frequency, AAD = Allopreening Average Duration ,
 AF = Allofeeding frequency, DF = Duet frequency, PD = Pair duration