SCARLET MACAW NESTING ECOLOGY AND BEHAVIOR: IMPLICATIONS FOR CONSERVATION MANAGEMENT

A Dissertation

by

GABRIELA VIGO TRAUCO

Submitted to the Office of Graduate and Professional Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

Chair of Committee,	Thomas Lacher
Committee Members,	Sharman Hoppes
	Jane Packard
	Ian Tizard
Head of Department,	Cliff Lamb

May 2020

Major Subject: Wildlife and Fisheries Sciences

ABSTRACT

Documenting parental care by wild birds is important for understanding reproductive success and promoting conservation. However, little is known about how wild parrots care for their offspring in the nest and how to use this knowledge to inform conservation actions. I documented wild Scarlet Macaw parental behavior in the lowland forests of southeastern Peru during 19 breeding seasons. I also tested using wild macaws as foster parents to increase chick survival. I found that females provide the majority of nestling care when the chicks hatch but the proportion of care given by the male gradually increases as the chicks age. I found that (1) chicks are fed on average 3.6 times per hour throughout the nesting period, (2) chicks are fed during the day and at night with major diurnal and nocturnal feeding peaks, and (3) macaw parents can store food in their crops for over 7 hours and use this to feed their chicks at night. I analyzed chick starvation due to brood reduction and found that chick starvation is the leading cause of chick mortality at my site: (1) 27% of all second hatched chicks starve, and (2) nearly all third and fourth hatched chicks starve. I found no evidence that death by starvation was caused by (1) sibling rivalry, (2) macaw food availability in the forest, or (3) hatch weight. I did find that (1) direct control of food distribution within the brood favors first hatch chicks but specifically disfavors second hatch chicks that starve to death and (2) the larger the age difference between brood members the more likely the second chick would starve. The technique of macaw foster parents was categorically successful. All relocated foster chicks were successfully accepted by their foster parents (N = 28 chicks across 3 seasons) and 89% of them fledged. Fostering increased fledging success per available nest from 17% (1999 – 2016) to 25% (2017-2019) and decreased chick death by starvation from 19% to 4%. This research has great potential benefits for in-situ and ex-situ macaw population management and conservation.

DEDICATION

To the two motors of my life: my husband Donald and my daughter Mandy Lu. Both, my strength and my inspiration. For being the light of my eyes, the smile in my face, and the motivation that keeps me moving forward.

To the parrots of my life: Pablo, Pablito, Aurora Limon, Aberlardo, Fruit Loop, Jack, Plano, Smoky and especially to La Rica, Malu, MLuis and Samantha. For introducing me to the world of animal behavior in such an extraordinary way.

ACKNOWLEDGEMENTS

I would like to thank my committee chair, Dr. Lacher, and my committee members, Dr. Hoppes, Dr. Packard, Dr. Tizard, for their guidance and support throughout the course of this research.

I extend a big thanks to Dr. Lacher for allowing me be part of the “Biodiversity Assessment and Monitoring Lab, his lab. I’ve always felt it was the right place for me.

I thank Dr. Packard and Dr. Hoppes, in particular, for teaching me that doing science as a woman is not just very hard and frustrating but it can be rewarding and even pleasant sometimes. I thank you for encouraging me to follow my instincts and to study more to understand what they meant.

I thank Dr. Tizard for kindly accepting me as part of The Schubot Center team. It was certainly my first step to achieve this degree.

I am grateful to Dr. Mariana Mateos from the Wildlife and Fisheries Department for the nomination to the Diversity and Regents Fellowship that I was awarded. It didn’t work out to be part of your lab, but I will be always grateful for the mentoring. As a Latino woman scientist, you were an extraordinary role model for me.

I would like to acknowledge the Nacional Service of Protected Areas of Peru (Servicio Nacional de Areas Protegidas SERNAMP) for providing research permits that allow the completion of this study (Resolucion Jefatural de la Reserva Nacional Tambopata, N 16-2018-SERNAMP-JEF, Resolucion Jefatural de la Reserva Nacional Tambopata, N 22-2016-SERNAMP-JEF, Resolucion 33-2015-SERNAMP- JEF, Resolucion 13-2014-SERNAMP- JEF, Resolucion 19-2013-SERNAMP- JEF, Resolucion 18-2012-SERNAMP- JEF). I also extent the

acknowledgements to the Division of Research-Office of Research Compliance from Texas A&M University for providing the required animal used permits needed to complete this investigation (AUP 2012-145 “Macaw and parrot biology in southeastern Peru”).

I extend special thanks to Dr. Janice Boyd, for the long debates about macaws, for the advice and especially for taking care of Samantha, my beloved parrot, during our long field seasons.

I thank Mark Moore from Hill Country Aviaries for all the help raising macaw chicks. For all the advice and all the chick feedings during the many nights, thank you for your encouragement and your wise words. You were right, I didn’t need a “magic flashlight”.

I thank Dr. Mabe Aguirre for her uncountable hours of dedication taking care of the macaw chicks, especially of the foster chicks. I thank you for your advice, your energy and for your knowledge. This project would not have been possible without you.

I thank Rodrigo Leon from Natura Mexicana and Rony Garcia from Wildlife Conservation Society Guatemala. Your work encouraged me in the most difficult times of this research. Your advice and friendship will be always treasured.

I thank all the organizations that provided funding to complete this research: Schubot Exotic Bird Health Center, Amigos de las Aves USA, The American Federation of Aviculture, Lafeber International Ltd, and the South Lakes Wild Animal Park. I thank Rainforest Expeditions; specially to Kurt Holle and Maximo Gonzales for all their support.

I thank all my private and crowdfunding donors. I am grateful for the trust.

I thank all the field leaders of The Macaw Society (formally known as the Tambopata Macaw Project): Adriana Bravo, Aida Figari, Daphne Matsufugi, Karina Quinteros, Jerico Solis, Carolina Caiaux, Jesus Zumaran, Aimy Caceres, Adrian Sanchez, George Olah, Darwin Solano, Gustavo Martinez, Carlos Huamani, Jorge Leon, Liz Villanueva Paipay, Dylan Whitaker, Lauren Bazley and Roshan Tailor. The huge amount of data analyzed in this study was possible because of your support.

I extend special thanks to Gustavo Martinez for leading the plant phenology aspect of this research and to Liz Villanueva Paipay and Dylan Whitaker, for leading the teams during the foster chick seasons. Very special thanks to George Olah, for all the research and life advice.

I thank the field vet leaders: Aldo Wilson, Oscar Butron, Lizzie Ortiz, Patricia Mendoza, Caterine Hermoza, Nancy Carlo, Isidora Soto and specially to Maria Belen "Mabe" Aguirre. It was a lot of macaw chicks to take care of. I thank you for your work and advice.

I extend special thanks to Dr. Sharman Hoppes for all her help, support and advice during the last 10 breeding season of this investigation. I thank Dr. Bruce Nixon for his advice and endless energy.

I thank all the "video in nest" leaders: Deisy Delgado, Lana Austin and Jorge Leon. It was an incredible amount of work that was only possible with your assistance. Thank you, Deysi, you definitely set up the bar really high for the next ones to come.

I thank Shannan Courtenay for leading the two crowdfunding campaigns and for your support in the two most exhausting field season we will ever have.

I thank all the macaw assistants, our "guacamayeros". I thank you for coming to the rainforest to work as volunteers and to help collecting data to learn how to conserve macaws.

Thanks also go to my Texas A&M University friends and colleagues: Mike Treglia, Johana Harvey, Emma Gomez, Jess Gilbert and Connie Woodman. You were all great examples of persistence and commitment.

I thank Dr. Eugienio Gonzales, director of the Soltis Center for Research and Education in Costa Rica and all the center's staff. I thank you for accommodating every detail so I could take online classes, study for prelims, and be a mom, all at the same time.

I thank my Mama Motta (mom), my Papumch (dad) for their encouragement and their nice warm hugs every time we crashed in their house after long and tiring field seasons. I am grateful to my sister Cecy and her four Cucos (sons) -Nicolas, Rodrigo, Renato and Leonardo - for the playing, the beach days, the soccer, the challenges, and the laughs.

I thank my Samantha for your company, my dearest parrot. You were certainly a source of inspiration in my most difficult moments.

I thank my dearest daughter Mandy Lu, my little one. We took you to our field site since you were inside of me and then every December. Every Christmas of your life have been in the rainforest. You knew about macaws before you knew about dogs and cats. I thank you for the compound exhaustion of been a graduate student and the mom of a young child. I am grateful for the tears and the laughs, for the long nights, but above all that, thank you for the happiness you have brought to my life.

Finally, I thank to my dearest husband, Don. I thank you for the support, for the guidance, for the warm hugs when I felt I couldn't keep going. I am grateful to you for taking care of me, for teaching me to cook, for listening to me. It is because of your support I managed to finish up this degree. It is because of you I found my "super powers". My love, WE did it!

CONTRIBUTORS AND FUNDING SOURCES

Contributors

This work was supervised by a dissertation committee consisting of Thomas Lacher (advisor) and Jane Packard from the Department of Wildlife and Fisheries and Sharman Hoppes from the Department of Small Animal Clinical Sciences, and Ian Tizard from the Department of Veterinary Pathobiology.

The data analyzed in all chapters was collected as part of work by The Macaw Society www.TheMacawSociety.org (formally known as the Tambopata Macaw Project). Data from 2000 to 2005 were taken by a team of volunteer assistants under the supervision of Dr. Donald Brightsmith from the Department of Veterinary Pathobiology. Data from 2006 to 2019 were taken also by volunteer assistants under the supervision of myself, Gabriela Vigo Trauco.

Study design of animal behavior data was designed by myself under the guidance of Dr. Jane Packard of the Wildlife and Fisheries Department and Donald Brightsmith from the Vet Pathobiology Department.

Study design of Chapter IV was designed by myself with the guidance of Dr. Donald Brightsmith and Sharman Hoppes VM. Macaw chick hand-raising procedures in the field were elaborated by myself under the guidance of Mark More co-owner of Hill Country Aviaries, Sharman Hoppes VM, and Maria Belen Aguirre VM.

The analyses in all chapters were conducted by myself, either independently or under the guidance of Donald Brightsmith or Dr. Elizabeth Hobson currently from the Department of Biological Sciences, University of Cincinnati.

Crowdfunding campaigns were organized with collaboration of Shannan Courtenay, Keith Regelmann, Janice Boyd from Amigos de las Aves, USA: The Parrot Fund and Dr. Donald Brightsmith.

All photographic material was taken by The Macaw Society team members under my supervision; however, individual photo credits are specified on figure caption.

Funding Sources

Graduate study was supported by a National Science Foundation (NSF) Graduate Research Fellowship, by a Diversity fellowship from Texas A&M University and a Regents Fellowship from the College of Agriculture and Life Science of Texas A&M University.

A travel award for expenses during the first field season was provided by a National Science Foundation (NSF) Graduate Fellowship travel grant.

This work was also made possible in part by funding given by the Schubot Exotic Bird Health Center under the direction of Dr. Ian Tizard and funds from The Brightsmith Lab.

Plant phenology work was partially funded by Dr. Janice Boyd from Amigos de las Aves USA, and The Parrot Fund (http://hatchedtoflyfree.homestead.com/).

Video inside macaw nests work was funded in part by generous donations from The American Federation of Aviculture (www.afabirds.org), Lafeber International Ltd (https://lafeberinternational.com/), the South Lakes Wild Animal Park (https://www.southlakessafarizoo.com/conservation/), and by private donors such as Lucile and Bill Smith.

Macaw foster chick work was funded in part by two crowdfunding campaigns run by Experiment.com (https://experiment.com/), including: 1) December 2017

(https://experiment.com/projects/increasing-survival-of-macaw-chicks-using-foster-macaw-parents-in-the-wild) and 2) December 2018 (https://experiment.com/projects/refining-and-improving-techniques-to-increase-survival-of-macaw-chicks-using-foster-macaw-parents-in-the-wild). Generous donors to these campaigns included: Chris Biro from Bird Recovery International, Peter Macdissi, Eduardo Nycander, Tom Bella, David Smith, Lucille H Smith, Evan, C. A. Rogers, Ashley Clayton Olive, Mario Prieto, Martha Smith Regelmann, Charlotte Bellamy, Dr. Gregory Rich, Mandy Lu, Elaine Mittell, Randall Collins, Amani Alowais, Amanda Debler, Audrey Hollaar, Patricia Rudikoff, Sheryl Robinson, Patricia Sund, Patricia LaFontaine, Evelyn Reis, Maxim Hurwicz, Katie Aston, Susan G. Friedman, PhD, Sophie Duckett, Susan Swan, Larry Sirvio, Charles Massey, Amanda Oscarsson, Barbara Bingham Deutscher, Sandi Spires, Celia Sierra Vega, Sarah Dobe-Hund, Janet Alexander, Pureum Kim, Amy Collette, James, Laurel Patrick, Brooke Durham, Mary Ault, Tom Bella, Tommy & Devin Curtis, Tracey Kidston, Carrie Whitlock, C Rogers, Barbara Heidenreich, , Leah M Henning, Patricia K. Anderson, Jamie Whittaker, Robert Mauri, Sheryl Robinson, Robert Krebs, Susan Steenstra, Debbie Goodrich, Martha Smith Regelmann, Shanna Pederson Hilger, Judith Richmond Archer, Dr. Gregory Rich, Myra Anders, Pam Longobardi, Carole Grommet, Audrey Hollaar, Steve Courtenay, James Graham, Svenning Bernstrøm, Evelyn Reis, Michelle Underhill, Nancy DeBellas, Brett A. Houk, Carolyn Taylor, Kathy Miller, Juan F. Masello, Tanja Froehlich, Kirsten Yablon, Kristian KrakkaDuune, Lynne Singerman, Simon Goodyear, Jiaying Wu, Lisa M Digioia Ross, Linda Bringle Pearl, Sue Montgomery, Nicole Sharpe, R, Frank Verstappen, Janice Koler-Matznick, Attila Pohlmann, Amanda Oscarsson, Kelly Flynn, Danielle Poirier, Melanie Catanchin, , Lori Goodsell, Marta Cálix, Elaine McIlroy, Denny Luan, Jason P Schein, Thea Boodhoo, Patrick Cross, Pureum Kim, and Eric Damon Walters.

Discounted rates for researchers lodging expenses and transportation were given by Rainforest Expeditons. SAC, thanks to Kurt Holle.

Contents of this manuscript are solely the responsibility of the author and do not necessarily represent the official views of the donors and fundraisers.

NOMENCLATURE

IUCN	International Union for Conservation of Nature
CITES	Convention on International Trade on Endangered Species

All Latin and English bird names follow the nomenclature from Handbook of the Birds of the World and Birdlife International (Birdlife International 2019a).

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

Page

CHAPTER I

INTRODUCTION

The study of the nesting ecology can be advantageous to better implement conservation actions to recover endangered species in the wild (Snyder et al. 1987c, Vaughan 2019). Psittaciformes (parrots, macaws and cockatoos) is one of the most threatened orders of birds in the world (28% of 398 species threatened, 56% declining, Olah et al. 2016). Habitat loss, degradation and fragmentation due to agriculture, logging and human settlements plus hunting and trapping are the main threats to Psittaciformes (IUCN 2019). Their beauty, intelligence and charisma as pets along with the lack of regulation and lack of law enforcement in their native countries have resulted in decades of poaching, illegal traffic, and extinction (Olah et al. 2016).

Quantification of breeding parameters has been used with many species of wild psittacines as an initial step to understand breeding dynamics, measure fledgling production and aiding conservation (Smith and Saunders 1986, Masello and Quillfeldt 2002, Renton and Brightsmith 2009, Pacifico et al. 2014). However, the difficulty of accessing parrot nest cavities plus the low frequency of nest checks in most studies, especially during the early nestling period, have provided accurate egg and hatchling counts for only a small group of parrot species [see list of species in Masello and Quillfeldt (2002)]. Breeding parameter quantification and accuracy is a key factor when used in demographic modeling to estimate risk factors and population viability, especially in endangered species (Pacifico et al. 2014). The success of conservation actions to recover declining populations is closely related to the understanding of their ecology and behavior in the wild (Snyder and Snyder 2000), as it was shown in breeding ecology studies with the Puerto Rican Amazon (*Amazona vittata*, White et al. 2006) and the Echo Parakeet (*Psittacula eques*, Jones et al. 1998).

The estimation of mortality is another important component needed in both population viability modeling and in conservation action planning (Boyd and McNab 2008). Psittacine chick mortality is usually reported in the literature; however causes of chick death are not always easy to determine especially when chicks disappear or carcass are found in advanced states of decomposition (Stoleson and Beissinger 2001). In addition, comparison among studies is not easy because authors express chick mortality causes in different ways (Enkerlin-Hoeflich 1995).

An important cause of chick mortality reported for Psittaciformes is chick starvation (Snyder et al. 1987c, Enkerlin-Hoeflich 1995). Brood reduction strategies in birds have been intensely studied in the past six decades as a way to understand hatching patterns (Clark and Wilson 1981, Stoleson and Beissinger 1995). Through the years, the initially well accepted "brood reduction hypothesis" (Lack 1954) that links mortality of last-hatched individuals with insufficient food available to raise all brood members, lost much acceptance because it was only successfully shown in a few studies (Stoleson and Beissinger 1995). Currently, brood reduction is often thought to be a non-adaptive consequence of hatching asynchronously that might be maintained for other reasons (Viñuela 2000). Brood reduction is most commonly observed in birds with asynchronous hatching where chick mortality can be caused by (1) siblicide, where smaller or younger chicks are killed by their siblings (Drummond 1987, Simmons 1988, Drummond and Havelas 1989), (2) direct filial infanticide, where parents evict specific chicks (Moreno 2012) or kill them directly (Tortosa and Redondo 1992, Heinsohn et al. 2011) or (3) indirect filial infanticide, when parents provide sub-optimal parental care and specific brood members starve to death (a.k.a chick starvation, Saunders 1982, Stoleson and Beissinger 1997b, Krebs 1998, Masello and Quillfeldt 2002).

Brood reduction has been observed in twenty species of psittacines. In the Green-rumped Parrotlet (*Forpus paserinus*) chicks (usually last and penultimate chicks) died with empty crops when nestmates had some food in the crop (Beissinger and Stoleson 1991, Beissinger and Waltman 1991). In the three sympatric Amazon parrots studied in continental Mexico, Yellow-headed Amazon (*Amazona oratrix*), Red-crowned Amazon (*Amazona viridigenales*) and Red-lored Amazon (*Amazona autumnalis*) chicks died after a slow decline in condition in a brood where other siblings survived (Enkerlin-Hoeflich 1995). In the Crimson Rosellas (*Platycercus elegans)* brood reduction it was described as chick death within the first three days without being fed or fed very little (Krebs 1998). In the Scarlet Macaw (*Ara macao*) in Peru it was called "death by malnutrition" and it was reported in second and third chicks younger than 20 days old (Nycander et al. 1995). In all of the types of chick death by starvation, caloric intake was not sufficient to maintain basic vital functions and the chick slowly perished.

To reduce chick death by starvation by chick manipulations have been suggested previously in the psittacine literature in order to increase fledgling success (Beissinger and Butcher 1992). The topic of increasing productivity in parrots with conservation purposes is not new. In the early 1990's, it was suggested that managing intensively the factors that limit population growth was the key to productivity maximization (Beissinger and Snyder 1992). In psittacines, the majority of species hatch their eggs very asynchronously over a period of 1 to 14 days (Rowley 1980, Snyder et al. 1987b, Beissinger and Waltman 1991, Marineros and Vaughan 1995, Krebs 1998, Vaughan et al. 2003b, Sanz and Rodriguez-Ferraro 2006, Vigo et al. 2011b) which results in a size based hierarchy among brood members (Smith 1975, Beissinger and Waltman 1991, Vigo Trauco 2007). Hierarchy often leads to the death of younger chicks (Rowley 1980, Beissinger and Waltman 1991, Krebs 1998, Raso et al. 2006, Vigo et al. 2011b).

In this scenario, decreasing hatching asynchrony has been proposed as a potential management tool to increase numbers of young harvestable for conservation (Beissinger and Butcher 1992). In addition, it has been suggested that last and penultimate chicks could be relocated in foster nests to increase recruitment.

The use of foster parents in avian population management is a technique with great potential to aid in the recovery of highly endangered species in the wild (Cade 1980). Foster parenting, the use of breeding pairs to raise young that were not part of their initial broods, is a well-known aviculturist technique that has been intensively used in captive breeding and reintroduction programs over the last decades (Saint Jalme 1999) and also in conservation captive breeding programs to increase recruitment (Cade 1980, Fentzloff 1984, Snyder et al. 1987a, Romer 2000). However, few studies have systematically studied how to successfully use this tool in the wild. This technique has great potential in psittacine in situ conservation efforts because there is strong evidence that parrots can be successfully used as foster parents and they are able to raise and fledge additional chicks (Rony Garcia personal communications, Sanz and Rojas-Suárez 1997).

The Scarlet Macaw (*Ara macao*), the subject of this thesis (Figure 1), is one of the most striking of tropical birds (Huber 1933). It is a large psittacine (>1kg) that inhabits both pristine and degraded tropical forest up to 1000 meters above sea level (m.a.s.l.) (Forshaw 2010). It is the third most widely distributed of all 17 species of macaws (10 200 000 km^2) with a distribution that includes 16 Central and South American countries (Birdlife International 2019b). It is listed in the Appendix I of the CITES convention (https://www.cites.org/eng/app/appendices.php) due to its popularity in the illegal wildlife trade but is still considered as a Least Concern (LC) species by the IUCN (IUCN 2019). It is locally extinct or endangered in Central American countries (Wiedenfeld 1994) and still common but rapidly declining in South America (Birdlife International 2019b). A combination of nest poaching, habitat loss due to agriculture practices and selective logging are increasing pressure on population decline throughout its range (Berkunsky et al. 2017). However in the Tambopata region of Peru, the Scarlet Macaw is still abundant (Renton and Brightsmith 2009) and is under no risk of nest poaching, which offers an incredible opportunity for natural history studies of the species in its natural environment.

The Scarlet Macaw is probably one of the best known of all South American parrots (Forshaw 2010).It has been studied in different areas of its distribution due to a combination of conservation and opportunistic reasons. In Peru, research studies involving the Scarlet Macaw in Manu and Tambopata started on the late 1980's as part of the increasing popularity of ecotourism and clay licks, cliffs where parrots eat soil (Munn 1998). The very first artificial nest used by a wild macaw was used by a Scarlet Macaw in Tambopata, Peru (Nycander et al. 1995) and that opened opportunities to study the reproduction of the species. Since that time, long-term investigations to understand clay lick use in the area, plus the abundance of the species in the area and the possibility of easy access to chicks that nest boxes offered, generated new knowledge about the species. A variety of studies done in the Tambopata area, including clay lick use (Brightsmith and Aramburu Munoz-Najar 2004, Brightsmith and Villalobos 2011); diet (Brightsmith 2006, Brightsmith et al. 2010); nesting preferences (Olah et al. 2014); chick growth (Vigo et al. 2011b); landscape use (Brightsmith et al. In prep), disease (Xenoulis et al. 2010, Olah et al. 2013) and conservation genetics (Olah et al. 2015) have been published in the last 20 years.

Figure 1. Study species: the Scarlet Macaw (*Ara macao macao*)
This photo credits: Liz Villanueva Paipay

Long-term studies of the species were also taking place at the same time in the early 1990’s, along the central Pacific coast in Costa Rica, after a preliminary population census showed Scarlet Macaw populations were rapidity declining (Arroyo et al. 2004, Vaughan 2019). In this case, the research objective was to apply breeding ecology findings (Vaughan et al. 2003b, Vaughan et al. 2008, Guittar et al. 2009) to recover populations through a combination of in-situ management and environmental education (Vaughan et al. 2003a, Vaughan et al. 2005, Vaughan et al. 2006a). Short-term studies of the ecology and breeding biology in the Usumacinta basin in Mexico and Guatemala (Iñigo-Elias 1996), in the Maya Biosphere Reserve of Guatemala and Chiquibul forest in Belize (Britt 2011), and in Guatemala area (Boyd and McNab 2008), were the baseline for intense in-situ conservation actions in order to stop nest poaching and population declines of the species. The Scarlet Macaw was also part of reintroduction efforts in Costa Rica, Peru (Brightsmith et al. 2005) and Mexico (Carabias et al. 2015). However, to date no one has published a comprehensive study that describes and analyzes the nestling ecology and behavior of the species and how to use this knowledge to implement conservation management techniques to increase its reproductive success.

This study represents the first research on nesting ecology and behavior inside the nest during the whole nestling period on a New World psittacine. Parental care observations of wild psittacines have been reported mainly from observations from outside the nest (Saunders 1982, Vaughan et al. 2008) and a few from inside the nest (Budden and Beissinger 2009, Cantor et al. 2019). Very detailed nesting observations of cockatoos (Rowley 1980, Rowley and Chapman 1991), Amazon parrots (Gnam 1991, Enkerlin-Hoeflich 1995, Renton and Salinas-Melgoza 1999)(references) and macaws (Iñigo-Elias 1996, Vaughan et al. 2008) have been published in the last 30 years. These studies go from egg incubation to the end of the nestling period but details about the first weeks of life of the broods are rare.

The novelty of my study is based on analyzing quantitative nesting behavior and parent-chick interactions in a meticulous fashion during the whole nestling period, from a large group of individuals (263 chicks from 125 broods) over a long period of time (18 breeding seasons). Other studies had used video cameras inside psittacine nests in the past but mainly as a tool to inform management actions designed to (1) reduce nest failure (White and Vilella 2004, Garcia-Anleu et al. 2017), (2) to report parental care behavior (White and Vilella 2004) and nest attendance (Cantor et al. 2019) or (3) to describe response to specific individual tagging manipulations (White and Vilella 2004). The extraordinary long term studies on the Green-rumped Parrotlet in Venezuela also used video cameras inside the nest but they were used during egg-laying time (Beissinger et al. 1998) and during short periods of the nestling period as part of specific experiments to test specific ecological theories with the goal of understanding factors that selected for early onset of incubation (Grenier and Beissinger 1999, Beissinger 2008). My research also investigates the phenomenon of chick death by starvation due to brood reduction in the Scarlet Macaw which has not been described before in the peer-reviewed literature. Moreover, it represents the first time the foster parents technique has been systematically tested with macaws in the wild.

In chapter II, I describe the nestling ecology and behavior of the Scarlet Macaw. I start describing the general breeding parameters during the 19 consecutive breeding seasons I studied (from 2000 to 2018) in southeastern Peru. I present a hatchling quality analysis in which I use weight at hatch as a surrogate for quality and I compare chicks that fledged, from single-chick broods and multiple-chick broods as well as chicks according to hatching order (first-, second-, third- and fourth hatch). I also present a description of Scarlet Macaw parental care in successful broods using data collected from video inside the nests. I describe food allocation and chick feeding schedules during the day and night. I also describe chick-feeding frequencies, for each age stage according to chick order from both, single chick broods and multiple chick broods. I add a description of the causes of chick death at the end of the chapter.

In chapter III, I present a description of Scarlet Macaw chick starvation and an analysis of possible drivers. In this chapter, I focus my work on just second chicks. As I did in the previous chapter, I use weight at hatch as a surrogate for quality and I compare second-chicks that fledged and second-chicks that starved. Then I describe the growth of chicks that starved. In my analysis of drivers of macaw chick starvation, I designed three interaction analyses: (1) chick-chick interaction, (2) parent-environment interaction and (3) parent-chick interaction. In the first analysis, I use video recordings from inside the nest to quantify aggressive behaviors among siblings. In the second analysis, I use food availability as the indicator of local environmental quality. I calculate an index of food availability and investigate its relationship with second chick starvation. In the third analysis, I investigate (1) parental care differences by analyzing interactions between parents and chicks using chick feedings as the main indicator of parental care, (2) chick quality differences using weight at hatch as an indicator of chick quality and (3) hatching synchrony differences by analyzing the age difference between first and second chicks of the same brood.

In chapter IV, I describe and test the management technique of macaw foster parents in the wild. First, I present a detailed description of the criteria to remove chicks from wild nests for relocation, chick rearing procedures in the field, and criteria to assign macaw chicks to wild macaw nests. I also present an outline of the four foster-chicks relocation experiments that I designed in order to test macaw chick fostering as a management technique in the wild. Finally, I describe the monitoring plan used to document chick acceptance in their foster nests. This plan includes a detailed description of the supplemental feeding plan done after foster chick relocation. My description and analysis of foster chick acceptance includes (1) details about first physical contact with foster parents, (2) an analysis of daily feeding ratios in which I compare how foster chicks were fed in relation to resident chicks, (3) an analysis of chick growth in which I compare foster chick growth with the growth of wild chicks from the 16 previous breeding seasons and (4) a comparison of overall recruitment between the seasons with and without foster chick manipulations.

Overall, this research has direct conservation implications. The increase of knowledge about nestling ecology and behavior of the Scarlet Macaw has an incredible value for conservation projects that are actively working to recovery decreasing population in areas where the species is rapidly decreasing and in danger of extinction. The understanding of the chick starvation phenomenon in the Scarlet Macaw is beneficial for the conservation of other species of macaws and parrots as well, because this phenomenon is present throughout this bird family. In addition, my experiments with wild chicks manipulation in order to test the technique of macaw fosters parents show an innovative way to increase reproductive recruitment and offers a new in-situ psittacine conservation management technique. This study provides baseline information useful for designing future manipulations with the goal to increase population recruitment not just for macaws but for other species of psittacines worldwide.

CHAPTER II

NESTING ECOLOGY AND BEHAVIOR OF THE SCARLET MACAW IN SOUTHEASTERN PERU

Introduction

Psittaciformes (parrots, macaws and cockatoos) is one of the most endangered order of birds in the world threatened in the planet (28% of 398 species, Olah et al. 2016). Habitat loss, degradation and fragmentation due to agriculture, logging and development plus hunting and trapping are the main anthropogenic threats that have caused population declines in about 56% of all parrot species (IUCN 2019). Their beauty, reputed intelligence and charisma as pets plus a general lack of regulation and law enforcement in their native countries have condemned them to decades of poaching, illegal traffic, and extinction (Olah et al. 2016).

The study of the nesting ecology can be advantageous to better implement conservation actions to recover endangered species in the wild (Snyder et al. 1987c, Vaughan 2019). As illustrated by previous breeding ecology studies with the Puerto Rican Amazon (White et al. 2006) and the Echo Parakeet (Jones et al. 1998), the success of conservation actions to recover declining populations is closely related to the understanding of their ecology and behavior in the wild (Snyder and Snyder 2000).

Quantification of breeding parameters has been used with many species of wild psittacines as an initial step to understand breeding dynamics and estimate reproductive success (Smith and Saunders 1986, Masello and Quillfeldt 2002, Renton and Brightsmith 2009). A very useful breeding parameter to report would be total chick production per active nest but it is difficult to quantify (Enkerlin-Hoeflich 1995). However, the difficulty of accessing parrot nest cavities plus the low frequency of nest checks in most studies, especially during the early nestling period, has allowed accurate eggs/hatchlings counts for only a small group of parrot species (see a list of species in Masello and Quillfeldt (2002)). Breeding parameter quantification and accuracy are key for demographic modeling to estimate risk factors and population viability, especially in endangered species, as it was shown in the Lear's Macaw (*Anodorhynchus leari*, Pacifico et al. 2014).

Parental care observations of wild psittacines have been reported mainly from observations from outside the nest (Saunders 1982, Vaughan et al. 2008) and a few from inside the nest (Budden and Beissinger 2009, Cantor et al. 2019). Very detailed nesting observations of cockatoos (Rowley 1980, Rowley and Chapman 1991), Amazon parrots (Gnam 1991, Enkerlin-Hoeflich 1995, Renton and Salinas-Melgoza 1999) and macaws (Iñigo-Elias 1996, Vaughan et al. 2008) have been published in the last 30 years. These studies go from egg incubation to the end of the nestling period but details about the first weeks of life of the broods are rare. Noteworthy, this period has probably received little study because researchers try to reduce stress on hatchlings and minimize nest abandonment (Snyder et al. 1987b).

Another important component needed in both population viability modeling and in conservation actions planning is the estimation of mortality (Boyd and McNab 2008). Psittacine chick mortality is usually reported in the literature; however causes of chick death are not always easy to determine especially when chicks disappear or carcasses are found in advanced states of decomposition (Stoleson and Beissinger 2001). In addition, comparison among studies are not easy because authors express chick fatality causes in different ways (Enkerlin-Hoeflich 1995). Important sources of chick mortality reported for psittaciformes are: (1) predation, (2) brood reduction, (3) nest failure (abandonment), (4) nest flooding, (5) parasitism, (6) social insect attacks (bee, wasp, ant, etc.), (7) human errors in manipulations and (8) poaching (Snyder et al. 1987c, Enkerlin-Hoeflich 1995). My study site in Tambopata has no nest poaching, which gives an extraordinary opportunity to quantify chick mortality by natural causes.

The Scarlet macaw is one of the most striking tropical birds (Huber 1933). It is a large psittacine (>1kg) that inhabits both pristine and degraded tropical forest up to 1000 m.a.s.l. (Forshaw 2010). As many other members of the Psittacidae family, the species shows brood reduction associated chick starvation (Nycander et al. 1995, Vaughan et al. 2003b, Vigo Trauco 2007, Boyd and McNab 2008, Vigo et al. 2011b, Britt et al. 2014, Olah et al. 2014, Vaughan 2019). In this species, starvation results in the death of about 24% of all hatched chicks and it is the most common cause of chick death (Vigo Trauco 2007).

This study represents the first research of nesting ecology and behavior inside the nest during the whole nestling period on New World psittacines. Other studies had used video cameras inside psittacine nests in the past, mainly as a tool to advise management actions to avoid nest failure (White and Vilella 2004, Garcia-Anleu et al. 2017), to report parental care behavior (White and Vilella 2004) and nest attendance (Cantor et al. 2019) or to describe response to specific individual tagging manipulations (White and Vilella 2004). The extraordinary long term studies on the Green-rumped Parrotlet in Venezuela also used video cameras inside the nest but this was during egg-laying time (Beissinger et al. 1998) and during short periods of nestling time. Both were part of specific experiments to test specific ecological theories with the goal to understand factors that selected for early onset of incubation (Grenier and Beissinger 1999, Beissinger 2008).

The main purpose of this chapter was to describe nesting ecology and behavior during the chick-rearing period in southeastern Peru with the following objectives:

Objective 1: Describe general aspects of Scarlet Macaw nesting ecology.

Objective 2: Describe Scarlet Macaw parental care in successful broods using feeding counts.

Objective 3: Report causes of Scarlet Macaw chick mortality.

Methods

Study site

Research was done in the forests surrounding the Tambopata Research Center (13°8'S, 69°36'W); located in the Tambopata National Reserve (total area = 275 000 ha) adjacent to the Bahuaja-Sonene National Park (total area = 1 091 416) in the state of Madre de Dios, southeastern Peru. The forest adjacent to the research station is defined as tropical moist forest (Holdridge Life Zone system) and is a combination of flood plain, terra firme, successional and palm swamp forest that receives around 3200 mm of rain annually (Tosi 1960, Brightsmith 2004)

Background methods

Data were collected during eighteen consecutive breeding seasons, from 2000 to 2018, as part of a broader research program about Scarlet Macaw breeding ecology, nesting behavior, clay lick use, and nestling health run by The Macaw Society (www.TheMacawSociety.org and http://vetmed.tamu.edu/macawproject) (Brightsmith 2001, Brightsmith et al. 2008, Gish 2009, Olah et al. 2014). Macaw nests were monitored from mid-October to mid-April every breeding season. Each season my team and I monitored up to 45 macaw nests (up to 16 natural and 24 artificial) using single rope climbing systems as described in (Perry 1978, Perry and Williams 1981). All nests were checked once every 2 – 3 days until the first egg was found. After an egg was found, nest monitoring ceased until 26 days later in order to reduce nest disturbance during incubation. After 26 days the nest was checked daily until the first chick hatched. For nests with chicks, the check schedule was as follows. Starting on the day I discovered the first chick; the nest was checked every day until the youngest chick of the brood was 15 days old. The nest was then checked once every 2 days until the oldest chick of the brood was 70 days old. After this age, chicks were checked every day until the last chick fledged. During each chick inspection, I weighed each chick using a digital scale. More details about chick checks can be found in Vigo et al (2011b). When chicks were found dead, the body was removed from the nest and a necropsy was performed in the field station. When chicks disappeared from nests, cause of death was considered as “unknown” unless clear evidence of predation was found. Death by starvation was declared when a chick hatched apparently healthy but did not gain weight as expected and ultimately lost weight, dying with no clinical signs of diseases. A brood was considered successful when at least one chick fledged.

In eleven breeding seasons (2007 to 2019, excluding 2015), 4 ± 2 nests per season (range 1 to 9 nests/season) were equipped with video surveillance cameras (48 different nests in total). Criteria to select a nest to assign a video camera were as follows: (1) nests that fledged or hatched at least 1 chick the last three consecutive breeding seasons, (2) nests with multi-chick broods in the three previous breeding seasons and (3) nests with good accessibility to reach chicks and to fix the camera. Video systems were installed before eggs were laid.

To monitor brood member interactions, I used the video camera system to record interactions inside the nest. Just data collected from footage is included in this study. Footages were made in two ways: non-continuous footage that targeted specific behaviors and continuous footage. The non-continuous footages were taken from 2007 to 2010, every time: (a) chicks were fed and (b) chicks were left alone in the nest. Continuous footages were taken in two different manners. From 2007 to 2010, 2-hour footages were done at three times of the day (6:30, 12:30 and 16:30 hours) without specific weekly schedule. From 2012 to 2018, 6-hour continuous footages were done at three specific times of the day (AM: 5 to 11 hours, PM: 11 to 17 hours and NIGHT: 17 to 5 hours). The 6-hour footages were made with the following overall schedule: (1) every day until the youngest chick of the brood was 15 days old or until starving chicks died, (2) every other day, alternating day and night footages. Footage collection schedules were not always followed as planned due to camera system malfunctions and extreme weather conditions. All behavioral observations were collected by two e: one from 2007 to 2010 (GV) and another from 2012 to 2018 (G. Martinez). Both observers were tested for accuracy in data collection. Continuous and non-continuous footage were used in each analysis unless otherwise indicated.

Three different types of interactions were recorded during video analysis: (1) feeding, (2) brooding and (3) preening. Only feeding behavior is included in the analysis for this chapter. Feeding refers to when an individual grasp the bill of another individual crosswise from above, bobs its head, and transfers the food by regurgitation. To quantify this behavior, I watched the video recordings from inside the nests taken with surveillance video systems during both day and night hours. Nighttime viewing was possible due to infrared lighting on the camera. I took focal group observations of known individuals from broods with one, two and three chicks. I recorded chick feedings for each particular member of the brood in an all-occurrence manner every time behavior happened. When possible, I identified which parent was feeding and which chick had been fed. For each day in each brood, I obtained (1) number of adult male feedings to the adult female and (2) number of adult male feedings to the chick(s) regardless of which chick had been fed. I summed number of feedings/day in each brood and I grouped these values by growth stages, following the chick growth stages given by Vigo et al. (2011b) but modified based on my experience from this study. Chick growth stages used were as follows: Stage I from hatching to 2 days old, Stage II-A from 3 to 18 days old, Stage II-B from 19 to 33 days old, Stage III from 34 to 65 days old, and Stage IV from 66 to fledging (86 ± 3.6 days old (Vigo Trauco 2007). I split Stage II in to Stage II-A and Stage II-B with the age chicks open their eyes as the division between the two stages. My previous, unpublished research shows that chicks open their eyes at about 17.4 ± 2.6 days old.

Due to equipment malfunction, weather unpredictability and footage quality, video data collected was not always comparable among nests. Therefore, not all data were included in the analysis. For this paper I included data that met the following requirements: 1) data where the identity of parents was known for 100% of the feedings, 2) data where the identity of chick being fed was known for over 50% of the total feedings in a single video recording, 3) broods with over 340 minutes of video data per growth stage, and 4) broods with chick hatching dates known within 2 days, and 5) broods where both chicks and parents were not given supplemental feeding.

All statistical analysis was performed using JMP pro 15 (SAS Institute Inc 2019) with $\alpha = 0.05$. Data are presented as mean and standard deviation, unless otherwise noted.

Section 1: General aspects of Scarlet Macaw breeding ecology

Breeding parameters: hatching success and fledging success

Calculations for breeding parameters were done including clutches and broods from only wild individuals; excluding reintroduced individuals that were not given supplemental food (see (Brightsmith et al. 2005) for details about reintroduced individuals).

I calculated clutch size as the mean and standard deviation of eggs in clutches where the total number of eggs laid was known because the nest was monitored before first egg was laid until quantity of the eggs was constant for five consecutive days. For these known clutches, I calculated hatching success as the total number of eggs that hatched over the total number of eggs laid.

I calculated brood size as the mean and standard deviation of chicks hatched in nests that were checked often enough to be sure individuals did not hatch and die without been noticed. The minimum nest check schedule for inclusion was (1) at least one time in first 5 days after first hatch, (2) at least one time in first 3 days after second hatch and (3) at least one time in 2 days after the third hatch. I called broods with just one chick single-chick broods and broods with more than one chick multiple-chick broods. I calculated fledging success as the number of chicks that fledged divided by the number of chicks that hatched, using only broods included in the initial brood size calculations. In three breeding seasons, the youngest members of a few broods were moved to foster nests and a few of them fledged. These chicks are not included on fledgling success calculations.

Chick weight at hatch

To analyze the relationship between hatch order and chick quality, I used chick weight at hatch as a surrogate of chick quality. Solo chicks that were weighed within 24 hours of hatch from adults that were not supplemental fed were included in this analysis. For hatch order, I classified each chick as first-hatch or first-chick, second-hatch or second-chick, third-hatch or third-chick, fourth-hatch or fourth-chicks and only-hatch or solo-chick if the chick came from a single-chick brood. In order to test if hatch weight differed in relation to hatch order, I performed an analysis of variance (ANOVA) and a comparison of means for each pair using a Tukey-Kramer HSD analysis. To analyze differences between hatch weight for chicks from single- and multiple-chick broods and between solo-chicks and first-chicks, I performed t-tests. To compared chicks from successful two-chick broods, I performed a t-test comparing weight at hatch between first chicks and second chicks from broods that fledged two chicks.

Section 2: Description of Scarlet Macaw parental care in successful broods

For this analysis, I considered a brood successful when at least one chick fledged during the breeding season.

Food allocation in the nest

I used video data to determine how food was provided to the brood and mate by both parents inside the nest. I calculated the proportion of feedings to the chicks that came from the nesting female and the proportions of chick feedings from the male. Feeding proportions were transformed using Arcsine transformation in order to fit a normal distribution before statistical analysis (McDonald 2014). To determine if male food provisioning to the nesting female varied throughout the nesting period I performed analysis of variance (ANOVA) with Arcsine transformed proportion of feedings to the female as the dependent variable, nesting stage (I, II-A, II-B, III and IV) as the independent variable and brood ID as a random effect. To evaluate specific differences in male food provisioning to the female among growth stages I performed a comparison of means for each pair using a Tukey-Kramer HSD analysis.

Brood feeding schedule

To describe daily chick feeding pattern schedules for scarlet macaw chicks, I used chick-feeding counts collected from continuous footage. For each brood for each hour of the day (0:00 to 23:00) for each day for which I had video, I used a binary score of whether or not any member of the brood was fed by the parents. Then I calculated an hourly feeding index for each brood, as the number of days feeding occurred within a given hour divided by the number of days that observations were made during that hour. I then calculated the standard deviation of this hourly feeding index (O'Gorman 1987). I then graphed the resulting proportion of times the brood was fed ± 1 standard deviation. To avoid errors in calculations due to small sample sizes in the analysis, just hours that had more than 30 minutes of video were included. In addition, broods from adults that were given supplemental food were not included. For the purposes of this analysis, I considered daytime hours as 5:00 hours to 16:59 hours and nighttime hours as 17:00 hours to 4:59 hours.

Chick feeding rates

To describe chick-feeding frequencies I calculated the total number of feedings per hour, for each age stage for first-chicks, second-chicks and solo-chicks that fledged. The feedings per hour included feedings from both male and female parents. I calculated these rates throughout the whole nesting period. I grouped chick feedings per hour per age in the five growth stages (I, II A, II B, III and IV) for broods that fledged two chicks and broods that fledged one chick. The following broods were excluded from calculations: (1) broods where chicks starved to death, (2) broods from adults that were given supplemental food, and (3) broods with chicks that switched order due to death of nest mates during the nesting period. The following observations were also excluded: (1) data from footage from non-continuous recordings, (2) data from videos where chick identity was unknown for over 50% of the feedings, (3) observations with less than 120 minutes of continuous footage per chick day of age. To analyze differences in feeding rates according to brood stage, I performed an analysis of variance ANOVA using chick brood stage as the dependent variable and chick feeding rates as the independent variable. To determine feeding differences between first and second chicks that fledged, I performed an ANOVA using chick feeding rates by age as an independent variable and brood stage as a dependent variable.

Section 3: Scarlet Macaw chick mortality

I determined cause of death by combining three sources of data: (1) nest and chick observations collected each time brood was checked, (2) chick biometric measurements and (3) chick necropsy information when performed. The main causes of death in this study were: (1) starvation, (2) predation, (3) nest conflicts, (4) sickness, (5) inexperienced parents, and (6) unknown.

Macaw chick death by starvation

To identify signs of starvation in macaw chicks, I used the physical and behavioral description of the clinical signs of macaw chick starvation from Clubb et al. (1992b), Clubb et al. (1992d), Abramson et al. (1995). Chicks that showed any of the following signs were considered candidates for starvation and were checked and weighed every day until they were found dead or had disappeared: (1) inconsistent weight gain, (2) dehydration, (3) dry or gray skin, (4) weight loss, (5) consistently empty crops, and (6) abnormal behaviors including hyperactivity, incessant screaming, or lethargy.

Macaw chick predation

Chick predation was declared when clear signs of predation events were found in the nest or surrounding nest area, such as blood, pulled feathers, body parts and tracks of predator left on nest or nest area. When bodies or body parts were found, a necropsy was performed in the field station in order to identify the predator. If identification was not possible, I assigned "unknown predator" as the cause of death.

Macaw chick death due to disputes over nests ownership or "nest fights"

Disputes over nest ownership or "nest fights" refers to altercations between a macaw pair that is already nesting in a particular nest and an intruder pair that tries to take over the nest

(Renton 2004). To identify when a nest was under dispute I used the description of macaw agonistic interactions given by Renton (2004) for Blue-and-yellow Macaws (*Ara ararauna*) in Manu, Peru. When a nest was under dispute, chicks were checked and biometric measurements were taken every day around 5pm until agonistic interactions ceased. In this chapter, just results of chick fatalities related to nest ownership disputes are reported. A description of nest fights will be presented elsewhere.

Macaw chick death by diseases

Chicks that showed inexplicable external abnormalities in its general appearance such as spots on skin, fluid in respiratory track, edemas, hematomas or hosted many external parasites (botflies, mites) for long periods of time were checked every day. Clinical signs were studied and analyzed to identify possible cause of sickness, but diagnosis was not always possible.

Results

Section 1: General aspects of Scarlet Macaw breeding ecology

From 2000 to 2017 (Table 1), my team and I monitored 192 clutches (10.6 ± 9 nests per season, 503 total eggs) and 125 broods (6.9 ± 2 nests per season, 263 chicks total). Of these cases, 89 broods fledged at least one chick (4.9 ± 2.4 nests per season, 125 fledglings). Of these totals, 179 clutches (9.9 ± 3.4 nests per season) and 109 broods (6.1 ± 2.2 nests per season) were monitored in sufficient detail for inclusion in the analyses presented here.

Table 1. Scarlet Macaw breeding report from 18 consecutive breeding seasons (2000 to 2017).
Clutches with complete egg information means that total number of eggs laid in the nest was known because the nest was checked starting before first egg was laid until the quantity of eggs was constant. Broods with complete chick information refers to broods that were checked often enough to be sure individuals did not hatch and die without being recorded. Successful broods refer to broods that fledged at least one chick.

Scarlet Macaw breeding report from Tambopata	Total
Clutches found	192
Clutches with complete egg information	179
Broods found	125
Broods with complete chick information	125
Successful broods	89
Successful broods with complete chick information	85

In general, Scarlet Macaw chicks hatched in 3-day intervals (2.9 ± 1.5 days), resulting in size differences of chicks within each brood (Figure 2)-. Second chicks hatched 3 days after first chicks (3 ± 1.6 days; n = 62 broods). Intervals were shorter for third chicks (2.6 +/ 1.3 days; n = 28 broods) and longer for fourth chicks (3.6 ± 1.6 days, n = 7 broods).

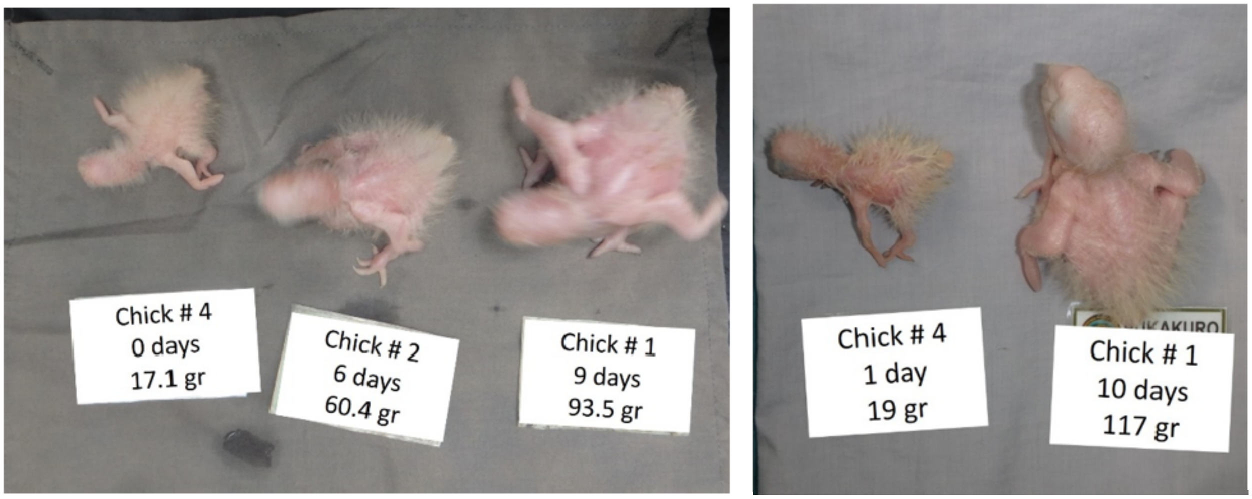

Figure 2. Typical hatching asynchrony for a brood of four chicks in a Scarlet Macaw.
Left: The brood hatched over a 9-day period. The third chick hatched three days after the second but died after two days. Right: Fourth and first member of the same brood showing size and developmental differences related to age differences. Age and mass of each individual is shown in each picture.

Age difference in relation to first chicks was 2.9 ± 1.5 days between first and second members (mode= 2 days, n= 62 broods), 5.5 ± 2.1 days between first and third members (mode=5 days, 20 broods) and 8.4 ± 1.2 days between first and fourth members of the same brood (mode= 9 days, n= 5 broods).

In this study, macaw chicks opened their eyes at 17.4 ± 2.6 (range 12 to 23 days old, N= 84 chicks with known hatching date).

Breeding parameters: hatching success and fledgling success

Scarlet macaws laid 2.7 ± 1.1 eggs per clutch (N=179 clutches, range 1 to 7 eggs, mode= 3 eggs, N = 18 seasons). They hatched 2.01 ± 0.9 chicks per brood (N=109 broods, range from 1 to 4 chicks, mode= 2, 18 consecutive breeding seasons). Overall hatching success was 55%. (N = 479 eggs). Scarlet Macaws fledged 1.4 ± 0.49 chicks per successful brood (N=85 broods fledged ≥ 1 chick, range = 1 to 2 chicks, mode=1 chick, N = 18 seasons). Fledging success was 46% (N = 263 chicks, Table 2).

Table 2. Scarlet Macaw hatching and nesting success (2000-2017).
Hatching success is the percentage of the total chicks hatched over the total eggs laid. Fledging success is the percentage of the total wild chicks that fledged over the total wild chicks that hatched.

Scarlet Macaw Breeding Parameters	**Per Nest** *Mean*	*Min*	*Max*	**N**
Eggs laid	2.68 ± 1.08	1	5	479
Chicks hatched	1.35 ± 1.22	0	4	263
Chicks fledged	1.4 ± 0.49	1	2	122
	Overall hatching success per egg			55%
	Overall fledging success per chick			46%

Chick weight at hatch

At hatching, chicks weighed 23 grams on average (23.1 ± 4.4 gr; N = 89 hatchlings; 14 seasons). Hatch weight did not differ significantly between broods with one compared to multiple chicks (t test: DF = 8.33, p-value = 0.96, N = 89 chicks, 8 solo-chicks and 81 chicks from multiple-chick broods, Table 3). However, in multiple-chick broods, weight at hatch decreased with hatching order (ANOVA: N = 81 chicks, DF = 3, F Ratio = 5.23, P-value = 0.0024). First-chicks weighed significantly more at hatch than third- and fourth-chicks (Tukey-Kramer HSD: p < 0.05 see Table 2 for additional statistical information)

Table 3. Hatching weight of Scarlet Macaw chicks.
Solo-chicks are from broods with only one chick. Chick order refers to the order of hatching of each chick in multiple-chick broods: first, second, third and fourth. Rows followed by the same letter are not significantly different (Tukey-Kramer HSD. p-value < 0.05). Data are from 14 breeding seasons.

Chick Order	**Significant Difference**		**Total Chicks**	**Average Weight (gr)**	**Standard Deviation**
Solo chick (C0)	A	B	8	23	4.6
First Chick (C1)	A		17	26.1	5.9
Second Chick (C2)	A	B	44	23.5	4
Third Chick (C3)		B	26	21.6	3.4
Fourth Chick (C4)		B	4	17.8	1.4

In multiple-chick broods where both chicks fledged, first chicks weighed slightly more at hatch than second chicks, but the difference was not quite statistically significant (N= 23 chicks: 11 first-chicks that fledged and 12 second-chicks that fledged, mean weight at hatch for first-chicks: 26.1 ± 5.3, mean weight at hatch for second-chicks: 22.9 ± 3.5 g. t-test: N= 23, t-ratio= -1.69, DF= 16.9, P-value=0.09).

Section 2: Scarlet Macaw parental care description in successful broods

From 1565 hours of video analyzed, 93% fulfilled requirements to be included in the analysis for this section.

Food allocation to the brood

Of the feedings to the chicks 71.8 ± 21.2% were from the female and 28.2 ± 21.2% from the male (N = 16 broods, 2.3 ± 1 broods per season, 7 breeding seasons, 1453 hours of video analyzed). Both female (63%) and male (37%) provided nighttime feedings (n=1658 nighttime feedings from 473 hours, 4 different pairs, 7 broods, 3 breeding seasons). Chicks were fed during the night all throughout the nesting period, from hatching up to 90 days old.

Chick feeding by the male increased significantly with brood stage, from 12% in stage 1 to 43% in stage 4 (ANOVA: F ratio=4.3, DF=4, p value= 0.0061; 1453 hours analyzed. Similarly, the proportion of feedings by the female dropped from 88% in Stage I to 57% in Stage IV (ANOVA: F ratio=4.2, DF =4, p value= 0.0067; 1453 hours analyzed. Table 4).

Nesting males fed both the nesting female and the chicks. When chicks were young, the female likely received nearly all her food from the male as she rarely left the nest and when she left it was only for a few minutes (GV and DJB unpublished data). Of the feedings done by the male inside the nest when the brood was young (Stage I), 71.6 ± 27.8% were to the female and 28.4 ± 27.8% to the chicks. However, male feedings to females significantly decreased throughout the nesting stages (ANOVA: n= 40, DF=4, F ratio=10.4, p value=<0.0001, Table 5). After the brood was 65 days old, the male did not feed the female inside the nest.

Nesting females almost never fed the nesting male. There was only one record of a female regurgitating to the male inside the nest in 1565 total hours of video analyzed.

Table 4. Scarlet Macaw parental food provisioning in the nest.
The feeding index for each parent was calculated as the percentage of total parental feedings for each stage and was transformed using the Arc Sin prior to analysis of means. Means for stages not connected by the same letter are significantly different using Tukey-Kramer HSD with p-value < 0.05. Data are from 6 breeding seasons and 14 different broods. Not all stages have data from all broods.

Growth Stage (Days)	Number of Broods	Nesting Male Feeding Index				Nesting Female Feeding Index			
		Significant Difference		Mean	Standard Deviation	Significant Difference		Mean	Standard Deviation
I (1-2)	7		B	11.7	6.7		B	88.1	7.1
II-A (3-18)	16	A	B	21.2	4.3	A	B	78.9	4.7
II-B (19-33)	7	A	B	33.1	6.7	A	B	64.4	7.1
III (34-65)	5	A		46.0	8.5	A		54.0	8.4
IV (65-84)	6	A		36.0	7.2	A		57.0	7.6

Table 5. Scarlet Macaw nesting male food allocation to mate and chicks.
The Mate Feeding Index was calculated as the percentage of feedings by the male to the female over all male feedings to chicks and to the female within each stage. Means of stages not connected by the same letter are significantly different using Tukey-Kramer HSD with p-value < 0.05. The Mate Feeding Index was transformed using Arc Sin transformation for analysis. Not all stages have data from all broods. Data are from 6 breeding seasons and 14 different broods.

Growth Stage (Days)	Number of Broods	Significant Difference	Mate Feeding Index (Arc Sin Transformation)		Mate Feeding Index (Percentage of Total Feedings by Male)	
			Mean	Standard Deviation	Mean	Standard Deviation
I (1-2)	7	A	1.04	0.13	71.9	0.01
II-A (3-18)	15	A B	0.65	0.09	33.6	0.06
II-B (19-33)	7	B C	0.48	0.13	20	0.08
III (34-65)	5	C	0.08	0.15	1.2	0.1
IV (65-84)	6	C	0.00	0.12	0.0	0.1

Brood feeding schedule

Analysis of 1313 hours of video from 12 broods across 76 different brood ages showed that chicks were fed throughout the day and night. The brood was fed at least once per hour ~80% of the times from 5:00 to 11:00 (Figure 3). Within this large plateau in feeding frequency there seem to be three small peaks at 5:00, 8:00 and 10:00.

Feedings decreased during the afternoon until 16:00 hours. A feeding peak was observed at 17:00 hours right before sunset. After sunset, chicks' feedings decreased until reaching the lowest feeding rate of the day at 19:00 hours. Then feedings increased until another peak at 23:00 hours; which surprisingly was nearly equivalent in magnitude to the morning feeding peaks. A final, smaller peak in feeding was observed at 3:00 AM.

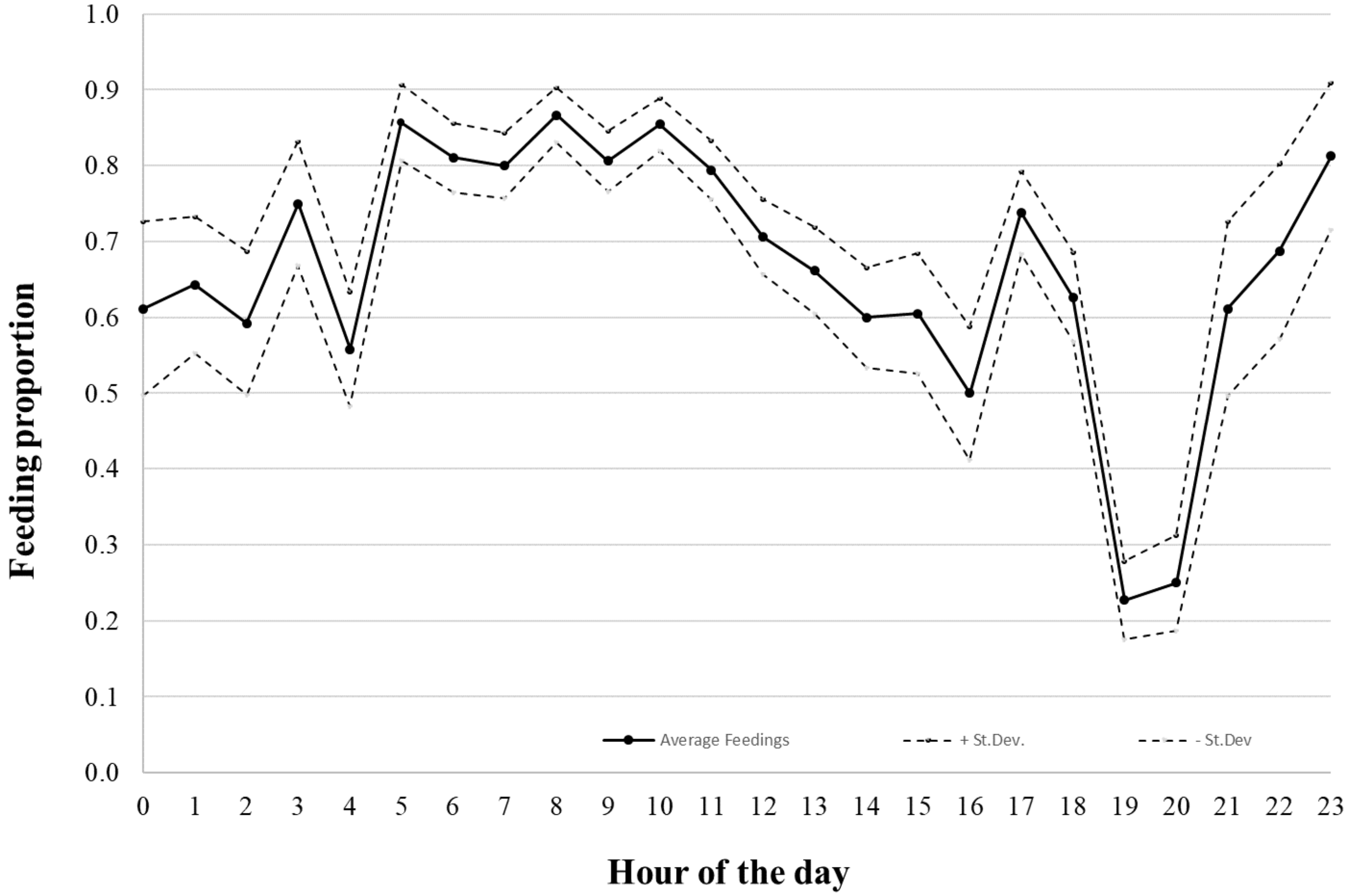

Figure 3. Feeding schedule of Scarlet Macaw broods.
The Y axis shows the proportion of the times the brood was fed at least once during the corresponding hour according to video analyses (12 broods total, over 5 seasons, sample size varies by hour of the day depending on the availability of video). The solid black line represents the proportion of times the brood was fed and the gray lines show 1 standard deviation

Chick feedings rates

Throughout the nesting period, chicks that fledged were fed approximately 4 times per hour (3.6 ± 3; N = 17, 9 broods, 8 first chicks, 8 second chicks, 1 solo chick, 6 seasons, 799 hours of video). Chick feeding rates differed significantly among development stages (ANOVA: F ratio- 2.5, DF = 4 growth stages, p value = 0.04, N = 175). At stage II-A (3 to 18 days old), chicks were fed significantly more often (1.9 ± 0.7) than at stage III (33 to 65 days old, Stage IIA feeding rate mean = 4.1 ± 0.4, Stage III feeding rate mean = 2.1 ± 0.5, Tukey-Kramer HSD with p-value < 0.05). No other differences in chick feeding rates were significantly different among brood stages (p > 0.05, Table 6).

Table 6. Feeding rates comparison across growth stages for Scarlet Macaw chicks that fledged.
The feeding rate was calculated as the total number of feedings by both parents per hour of video analyzed within each stage. Not all stages have data from all chicks. Not all chicks have data from all stages. Stage means not connected by the same letter are significantly different using Tukey-Kramer HSD with p-value < 0.05. Data are from 6 seasons and 9 broods.

Growth Stage (Days)	Number of Chicks	Feeding Rates			Statistical Difference	
		Mean	Standard Deviation	N		
I (1-2)	7	3.1	0.7	7	A	B
II-A (3-18)	14	4.1	0.4	14	A	
II-B (19-33)	8	3.4	0.6	8	A	B
III (34-65)	5	2.1	0.5	5		B
IV (65-84)	5	4.0	0.5	5	A	B

In broods where both first- and second-chicks fledged, feeding rates did not differ significantly between first- and second-chicks (C1= 3.6 ± 3 feedings/hour, C2= 3.4 ± 3.1 feedings/hour, n= 9 broods from 9 different pairs, 6 breeding seasons, ANOVA: N= 175, F ratio = 1.6, p-value= 0.2).

Section 3: Scarlet Macaw chick mortality

In Tambopata, 53% of chicks that hatched died before fledging (N= 259 chicks that hatched, 18 breeding seasons). Chick death by starvation was the leading cause of mortality (23% of 259 chicks that hatched). Starvation was only recorded for second-, third- and fourth-chicks in multiple-chick broods. Other common causes of mortality, such as predation (12% of all hatched chicks) and death due to nest ownership disputes (6% of all hatched chicks) were also recorded. Around 12% of chicks that hatched , died due to unknown reasons (Table 7).

Table 7. Cause of death for Scarlet Macaw chicks.
Chick order (first, second, third and fourth) refers to the order of hatching in each brood. Solo chicks are from broods where just one chick hatched. Each chick was considered dead when it was found dead inside or outside the nest or when it disappeared from nest before the age of 79 days (minimum recorded fledging time). Data are from 18 consecutive breeding seasons (from 2000 to 2017).

Cause of death	Solo Chicks	First Chicks	Second Chicks	Third Chicks	Fourth Chicks	Total Dead Chicks	Percent of Total Hatched	Percent of Dead Chicks
Starvation			24	30	7	61	24	45
Unknown causes	6	11	10	4		31	12	23
Predation	3	6	4	2		15	6	11
Nest ownership dispute	1	6	5			12	5	9
Disease or parasites	1	2	3	1		7	3	5
Nest malfunction	1		2			3	1	2
Inexperienced parents	2	1				3	1	2
Bee attack	1		1			2	1	1
Lightning struck nest		1	1			2	1	1
Human error (sampling)		1				1	0.4	0.7
Total chicks that died	**15**	**28**	**50**	**37**	**7**	**137**	**53**	
Total chicks that fledged	**18**	**64**	**40**	**0**	**0**	**122**	**47**	
Total chicks that hatched	**33**	**92**	**90**	**37**	**7**	**259**		

Macaw chick death by starvation

Chick death by starvation (due to brood reduction) was the most common cause of death in macaw chicks in Tambopata. Over 45% of chicks that died, starved to death (N= 137 chicks that died, Table 8). Death by starvation was not registered in broods with only one chick or for first-chicks in multiple-chick broods. Of the chicks with known causes of death (N= 107 chicks), 60% of second chicks, 91% of third-chicks and all fourth-chicks died of starvation. (Table 8).

Table 8. Comparison of starvation by hatching order of Scarlet Macaw chicks.
First, second, third and fourth chicks refers to the order of hatching within each brood. Solo chicks were in broods with just one chick. Chicks that died by unknown causes were excluded from percentages calculated within each column. Data are from 18 consecutive breeding seasons (from 2000 to 2017).

Cause of chick death	**Solo Chicks**	**First Chicks**	**Second Chicks**	**Third Chicks**	**Fourth Chicks**	**Total Chicks**
Total chicks that died	15	28	50	37	7	137
Chicks that died by starvation	0	0	24	29	7	60
Chicks that died by unknown causes	6	11	10	4	0	31
Percent of chick deaths caused by starvation	**0**	**0**	**48**	**81**	**100**	**44**

Macaw chick predation

Predation of Scarlet macaw chicks was low: it was only confirmed in 11% of 137 chick deaths. Predation represented 14% of 106 deaths with known causes. The age at predation averaged (20 ± 21 days old, range 2 to 75 days old, N = 15). In 40% of predation events, chick body or body parts were found inside the nest. In over 45% of predation events, the predator was seen in the nest vicinity before or after predation. The most commonly identified predator was Army Ants (*Eciton sp.* N = 3 nests) that preyed upon two different nests, including the same nests in two different breeding seasons. In one predation event, they took a 57-day old chick that weighed about 870 grams. Other predators identified were: Forest Falcon (*Micrastur sp.*, N = 1), Crested Owl (*Lophostrix cristata,* N = 1), Eagle sp. (probably *Spizaetus ornatus*, N=1) and Tayra

(*Eira Barbara*, N=1, Figure 4). In one case, the predator was identified as a "mammal" because of the teeth marks left on the chick's body (Table 9).

Figure 4. Predation scene of Scarlet Macaw chicks found in an artificial nest after predation attack.
First chick is at the left and second chick is at the right. Absence of head in first chicks fits what has been previously recorded on Tayra attacks. Carcasses were fresh and with no signs of decomposition. Chicks were 27 and 25 days old. These deaths are not included in mortality calculations because chicks hatched outside the 2000-2017 period.

Table 9. Predators of Scarlet Macaw chicks.
Data from 18 consecutive breeding seasons (from 2000 to 2017). Predator identification up to genus and species. Predator evidence refers to observations collected in the site, which helped identified each specific predator.

Predator	Evidence	Chick age at depredation (days)	# Chicks depredated
Army Ants (*Eciton sp.*)	Thousands of ants found arriving to nest area the day before predation event	5	2
		7	1
	Ants found inside nest and nest truck in massive quantities the day chick disappeared	57	1
Tayra (*Eira barbara*)	Predator seen depredating different species of large macaw chick few days after predation in nearby nest	16	1
Eagle (probably *Spizaetus ornatus*)	Predator seen days before in nest surrounding	30	1
Forest Falcon (*Micrastus sp.*)	Falcon depredated same nest two consecutive years and was seen on nest entrance after predation	75	1
Crested Owl (*Lophostrix cristata)*	Owl seen on vicinity day before and nested on same nest less than a month ago	10	1
Mammal	Mammal marks of teeth on chick dead body	26	1
Unknown predator	Nothing found	< 5	3
		15	1
		21	1
		25	1
Total chicks depredated			**15**

Macaw chick death due to disputes over nests ownership or "nest fights"

Disputes over nest ownership, or "nest fights" (Figure 6), were the cause of death of 12 chicks in 8 broods (Table 10). In seven of eight of the broods where there was death attributed to nest fights, all of the members of the brood died due to poor parental care provided because the nesting pair was defending the nest and not foraging, brooding, or feeding chicks normally. Age at death averaged 31 ± 23 days (N=12 chicks) and spanned nearly the entire range of chick ages (2 to 71 days). When chicks were younger than 15 days old the clinical signs were very similar to starvation (empty crop, loss of weight, shivering, etc.) which signifies that chicks were not been fed and brooded properly. In 3 of 8 broods, the nesting pair lost nest ownership and chicks were either directly killed or left to starve to death by the intruders (Figure 5). In another case, the nesting female threw her own 2-day old chick out of the nest a few hours after the fight ended.

Figure 5. Scarlet Macaw infanticide scene.
After a violent fight for the nest, intruder pair took possession of nest and intruder female executed chicks (33 and 34 days old). The researcher was observing the nest at the moment.

Figure 6. Scarlet Macaws fighting over ownership of an artificial nest.
Intruder pair is below (note two tails) and nesting male is on top of nest box. Nesting female was inside the nest at the moment of the photo. In this case, the intense fight period lasted around 4 hours. The nesting pair was able to successfully defend the nest. They did not have chicks or eggs at the time of the fight. Photo credit: Roshan Tailor.

Table 10. Scarlet macaw chick death due to nest ownership disputes.
Details from 8 broods where fights over nest ownership between Scarlet Macaw pairs resulted on chick fatalities. Data from 18 consecutive breeding seasons (from 2000 to 2017).

All brood members died due to nest dispute	Nest ownership after nest dispute	Brood ID	Hatch Order	Age at death	Additional Information
Yes	Intruder pair	Amor 2002	First Second	71 69	Nesting pair lost nest. Intruder pair stayed in nest and did not feed the chicks. Chicks died after 3 days.
		Sixto Jr. 2004	First Second	34 33	Nesting pair lost nest. Intruder pair killed chicks
		Vaginito 2010	First Second	42 38	Nesting pair lost nest. Intruder pair killed chicks
	Nesting pair	Franz 1C 2009	Only	3	Nesting female stayed in entrance defending nest from intruders and did not fed/brood chick. Nesting male was defending from outside and was seen with a third juvenile banded macaw (possible chick from previous season)
		Mandy Lu 2016	Only	2	Nesting female threw chick out of nest. It died due to impact to the ground.
		Hormiguero 2016	First Second	14 9	Nesting male was last seen few hours before fight. Additional pair defended nest with nesting female until intruders left. A second male was seen entering nest and interacting with nesting female. Second chicks died day after fight. First chick died two days after fight.
	Unk	Vaginito 2008	Only	25	
No	Nesting pair	Hugo 2013	Second	35	Since hatching, second chick did not gain weight as expected. It was underweight and weak at the moment of the fight

Macaw chick death by diseases

About 3% of 256 hatched chicks died due to disease (N = 7 chicks across 5 broods). In all of the cases, chicks showed abnormal conditions, such as hematoma marks, yellow spots on the skin, or lumps on body, but the disease-causing agent was not identified. In one brood, all three members of the brood died showing similar symptoms. In the other four broods, the remaining members of the brood successfully fledged. Four of seven chicks that died were older than 20 days old. On one occasion, infection that may have caused chick disease was linked to a deep wound that was likely received during a nest dispute. Two chicks died due to infections related to infestations of external parasites, namely bot flies (*Philornis sp*). In one of them, a botfly was inside the ear and the infection around it led to death. In the other case, the bot fly infestation was massive (26 larvae removed in one visit) and larvae inside nostrils caused significant damage to the upper respiratory pathway (Table 11).

Table 11. Clinical external signs of sickness observed in Scarlet Macaw chicks.
Nesting pair ID and Brood ID are the names assigned to differentiated different individuals/broods. Age at death correspond to the day chick was found lifeless. Sign of sickness refers to external observations of suspicious abnormalities in chick general appearance. Additional information is given in order to provide a better context of each particular brood situation. Data are from 18 consecutive seasons (2000 to 2017).

Nesting Pair ID	Brood ID	Hatch Order	Brood Size at Death	Age at Death	Other Members of Brood Died by Sickness	Clinical signs of sickness	Additional Information
Unk	PVC 2000	Third hatch	1	56	No	Bad injury on cere area and upper mandible by age 53. It was severely infected in following days. Yellow spots on face by age 55. Chick lost weight dramatically in last 4 days of life and found with no food content since age 52.	Removed from original nest at hatching, kept in nursery for 1 day and placed in foster nest as an solo chick
Unk	Franz 2002	Second hatch	2	33	No	Botfly inside ear by day 10. Scabs on abdominal area by day 13. Lump on left side abdominal area by day 16. Low weight gain but average crop size throughout its life was over half full (2.5 on a scale of 4).	Third member of brood died by starvation (age 9), 21 days before.
Unk	Invisible 2003	First hatch	1	43	No	Died with white fluid coming out of beak. Necropsy revealed lungs blocked. It did not showed signs of sickness before. Gained weight as expected and average crop was half full throughout its life	Second member of brood died by starvation (age 4), 34 days before.

Table 11. Continued.

Nesting Pair ID	Brood ID	Hatch Order	Brood Size at Death	Age at Death	Other Members of Brood Died by Sickness	Clinical signs of sickness	Additional Information
A	Tapir 2010	Second hatch	2	41	No	Botflies infestation: 26 larvae removed in one visit at 40 days old. Larvae from inside nostrils were not possible to remove. Wounds caused by bot fly larvae got maggots. Chick lethargic since age 39. Chick did not gain weight as expected throughout its life.	
B	Franz 2017	First hatch	2	13	Yes	Red hematomas starting on day 5. First on neck and back, then one big one on right side of neck (8 days) and then under left wing above femur bone (11 days). Last brood member to show signs of sickness.	
	Franz 2017	Second hatch	2	7		Red hematomas starting on day 1. First on head and right flank close to wing (day 1), then both sides of crop (day 5). First brood member to show signs of sickness.	
	Franz 2017	Third hatch	1	5		Red hematomas on cere on hatching day. Then on right flank (day 1), then left flank next to keel (day 2) and then under both wings and left flank (day 4). Second member of the brood to show signs of sickness.	Moved to foster nest on hatching day and placed as a solo chick

Other causes of macaw chick mortality

Close to 5% of macaw chick deaths registered were due to other reasons besides starvation, predation, nest conflicts and sickness. In three cases (3 broods), the chick died due to artificial nest malfunctions such as the base of the nest falling or rain water flooding the inside of the nest. Unidentified bees killed two young, featherless chicks. In two broods, chicks that were the only members in the brood died showing signs of poor parental care, such as low feeding rates and low daily gain weight. Both of them were the only member of the brood. One brood of two chicks was killed when lighting hit the wooden nest box directly and destroyed the base of it (Figure 7). One 20-day old chick died during the collection of a crop sample. A total of 23% of the 137 chick deaths were due to unknown reasons; in 8 of those cases, the body was not found.

Figure 7. Macaw artificial wooden nest hit by lightning that killed chicks.
Lightning strike separated the back of the nest from the sides and blew up the base. Chicks fell to the ground and died. The nesting pair survived. Picture shows nails used to attach nest to the tree trunk located to the left (researcher leg at the bottom right). Photo credit: George Olah.

Discussion

Section 1: General aspects of Scarlet Macaw nesting ecology

Breeding parameters: hatching success and fledgling success

Breeding parameters reported in this study were very similar to what my team registered in previous publications (Olah et al. 2014) and by others in this area almost 25 years ago (Nycander et al. 1995). Both parameters, clutch size and brood size as well as the number of fledglings per successful nest remained the same as registered in 2014. The ~ 5% differences found in hatching and fledgling success could be attributed to an increase in available artificial nests that we hung after my first analysis was published.

As reported in previous studies with *Ara macao* in Tambopata, almost 50% of the eggs laid failed to hatch, which is a large percentage of productivity loss but is similar to the other species of large macaws in the area (Nycander et al. 1995). In my case, egg failure causes are not purely related to infertility (Olah et al. 2014) and could also be attributed to embryo mortality due to a combination of external factors such breeding pair incubation inexperience and agonistic social interactions related to nest defense. It has been recorded in the Green-rumped Parrotlet in Venezuela that females in nests with high intruder pressure tend to incubate less (Grenier and Beissinger 1999) suggesting that they prioritize nest defense over egg incubation. Similar behavior was also seen with macaws in Tambopata, where my team and I have recorded agonistic interactions between nesting pairs and one or more intruder pairs that tried to take over occupied nests. my preliminary analysis of nest observation data show that a high frequency of intruder pairs correlates with reduced hatching success (Vigo and Brightsmith, unpublished data). It has also been shown by my team that the likelihood of hatching one or more eggs increased with the number of eggs in the clutch (Olah et al. 2014). A comprehensive analysis of egg incubation and causes for egg failure will be presented elsewhere.

Across its range, Scarlet Macaws fledge on average less than two fledglings per successful nest. In Lacandona, Southeastern México about 1.8 fledge per nest (Iñigo-Elias 1996), in Punta Leona, Costa Rica 1.9 (Vaughan et al. 2008) and in Tambopata, Perú 1.4 chicks per nest (Olah et al. 2014) and this study. The results from Scarlet Macaws are very similar to five other species of macaws in the Americas that also fledge a maximum of two fledglings per nest: Hyacinth macaw (*Anodorhynchus hyacinthinus*, Guedes and Harper 1995), Red-and-green macaw (*Ara chloropterus*, Munn 1992, Nycander et al. 1995, Guedes 2003, Renton and Brightsmith 2009), Blue-and-gold macaw (*Ara araruna*, Munn 1992, Renton and Brightsmith 2009), Chestnut-fronted macaw (*Ara severus*, Munn 1992) and Blue-throated Macaw (*Ara glaucugularis,* Berkunsky et al. 2016*)*. Of note is that two fledglings per nest is the maximum fledgling production recorded for all Psittaciformes over 300 g. This includes Amazon parrots (Gnam 1991, Enkerlin-Hoeflich 1995, Sanz and Rodriguez-Ferraro 2006, Dahlin et al. 2018), cockatoos (Smith and Saunders 1986, Rowley and Chapman 1991) and macaws (Munn 1992, Guedes and Harper 1995, Nycander et al. 1995, Guedes 2003, Renton and Brightsmith 2009, Berkunsky et al. 2016).

Fledging success of the Scarlet Macaw across its range fluctuates between 44% and 61% in areas with no nest poaching or where nest poaching control actions have been implemented: 45% in Peru (average of 2 previous studies and my study), 46% in Lacandona Mexico (Iñigo-Elias 1996), 52% in Guatemala (Boyd and McNab 2008) and 61% in the same area in Guatemala two years later (Britt et al. 2014). The highest value corresponds to a population that is under intense management to overcome nest poaching pressure and may not reflect natural fledging success of the species in the area. However, that locality (El Peru, Guatemala) is one of the few areas in the whole range that has reported successful triple broods; however, the frequency of this event is unknown (Rony Garcia pers. com.). The 46% fledging success I registered in Tambopata is an intermediate value compared to other macaw species that range from 91% for Red-and-green Macaw in the Pantanal of Brazil to 40% for Blue-and-yellow Macaw in Tambopata (Renton and Brightsmith 2009) and other similar body mass species of psittacines such as the Black-cockatoos (*Zanda sp*., Saunders 1982) and Red-tailed Black-cockatoo (*Calyptorhynchus bansksii*, Smith and Saunders 1986).

This study is the first detailed report of weight at hatch in the wild for the Scarlet Macaw. Despite a number of studies on breeding ecology on psittacines, (Snyder et al. 1987c, Rowley and Chapman 1991, Krebs 1998, Beissinger 2008) there is not much information about weight at hatch from wild chicks in this order of birds. A combination of the difficult nest access and fear of brood abandonment in the early stages has limited data collection around hatching (Vaughan et al. 2008). Scarlet Macaw researchers from the Lacandona area in Mexico have reported an average of 25.5 gr (n=2, range: 24-27 gr) at hatch in wild chicks (Iñigo-Elias 1996) and 17.7 gr (n=2 chicks, range: 19.2 -16.2 gr) from artificially hatched chicks (Rodrigo Leon personal communications). My average of 23.1 ± 4.4 gr. (n=89 chicks) falls right in the middle of what was reported in the Mexico population and it is higher than the 19.7 gr average (range: 15-24 gr, n=6 chicks, Abramson et al. 1995) and 21 gr to 26 g (n= 23 chicks, Clubb et al. 1992a) reported from aviculturists. Surprisingly, I had some chicks that weighed over 30 gr (n=6 hatchlings) at hatch, which is an extraordinarily large weight for a macaw hatchling; even more than the weights recorded for the two largest macaw species, the Red-and-green Macaw (max hatch weight = 23 gr) and Hyacinth Macaw (max hatch weight = 26 g. Clubb et al. 1992a).

Chick weight at hatch

In this study, I found that weight at hatch decreases with hatching order, third and fourth hatched chicks being significantly lighter than first hatched. These findings contradict assumptions of similar mass at hatch for later and earlier hatchlings on the Green-rumped Parrotlet. In that species, egg volume did not differ significantly by laying order, consequently it was assumed that hatch weight should not differ either (Beissinger and Waltman 1991). My hypothesis is that lower weight at hatch could be attributed to suboptimal incubation that results in embryonal bad-positioning that made the hatching too long, difficult and energy consuming, that resulted in a lower initial weight for the chicks that hatched later. Results from Green-rumped Parrotlets showed that last laid eggs had slightly lower (but not significantly lower) hatchability in spite of the fact they hatch in one less day than early laid eggs. This decrease in hatchability was attributed to the fact that females decreased chick brooding and started to forage to help feed older chicks, when the brood age was around 1 week old but when the last eggs were still unhatched (Grenier and Beissinger 1999). These results suggest that the last egg's incubation was not optimal. It was shown in chickens that egg rotation during incubation plays a key role in embryo development and especially in embryo positioning in the egg (Robertson 1960). Eggs that were turned in a suboptimal manner developed embryonic malposition that increased difficulty on the pip to hatch phase (malposition II) that resulted in an extra investment of energy leading to a lower weight at hatch.

Hatching is a critical developmental stage (Schubot et al. 1992) that causes up to 60% of embryonic mortality in poultry (Robertson 1960). Records from macaws pip to hatch phase length varies from 13 to 79 hours (Hyacinth Macaw, Abramson 1995) and its success depends mainly on a combination of embryo good positioning and stored energy resources. A malpositioned chick may perish at hatching but not all embryony malpositionings prevent hatching (Clubb and Phillips 1992). For instance, in chickens, 46% (n=2130 chicks) of chicks with malposition II were still able to hatch (Robertson 1960) and around 50% of psittacines that showed malposition II (n=16, 12 species of macaws, cockatoos and others) were able to hatch in captivity (Clubb and Phillips 1992). When malposition II is present, the chick is not able to breath until it has pipped the shell and it has to overwork its abdominal and neck muscles without proper oxygen supply. Extra muscle effort and movement are needed in order to break the eggshell (Robertson 1960). At the moment, to study embryo egg malpositions in psittacines is not easy, and often requires the sacrifice of the chick involved (Clubb and Phillips 1992). This would not allow researchers to take the initial "weight at hatch" to make comparisons with normal positioned chicks and test my hypothesis. However, indirect evidence from Tambopata, shows that chicks that went through a long pipping to hatching process had low weights in their first 24 hours of life (GVT personal observations).

Section 2: Description of Scarlet Macaw parental care in successful broods

Scarlet macaws that raised successful broods exhibited distinct nesting behavior patterns during the chick rearing period. In my study, both nesting females and nesting males fed the chicks. Bi-parental care is the most common parental care strategy in bird species with an 81% occurrence (Cockburn 2006). In the Psittacidae family, it has been reported in one species of Parrotlet: the Green-rumped Parrotlet *(Forpus passerinus, Budden and Beissinger 2009),* two species of cockatoos: Black-cockatoo (Saunders 1982) and Major Mitchell's Cockatoo *(Cacatua leadbeateri,* Rowley and Chapman 1991); five species of amazon parrots: Cuban Amazon (*Amazona leucocephala bahamensis*, Gnam 1991), Puerto Rican Amazon (Snyder et al. 1987b, Wilson et al. 1995), Red-lored Amazon, Red-crowned Amazon and Yellow-headed Amazon

(Enkerlin-Hoeflich 1995) and four species of macaws: Red-fronted Macaw (*Ara rubrogenys,* Lanning 1991*)*, Lear's Macaw (Hart 1995), Great Green Macaw (*Ara ambiguus*, Bjork and Powell 1995)) including the Scarlet Macaw, my study species (Iñigo-Elias 1996, Vaughan et al. 2008).

My study is the first that quantifies parental investment inside the nest throughout the whole chick rearing period in a wild macaw. In the Puerto Rican Amazon research, bi-parental feeding of nestlings was corroborated with the use of video systems (White and Vilella 2004). It was also registered in the Green-rumped Parrotlet in Venezuela, where no difference between nesting individuals in food provisioning (similar visits and similar feeding events per visit) were found across the two days of the study (Budden and Beissinger 2009). In all the other psittacine studies I found, the nesting male entered the nest repeatedly during the chick rearing period; indirect observations, such as chick sounds while receiving regurgitation when the nesting female was outside or at the entrance of nest, led to the assumption that the male was feeding the chicks.

Nest attentiveness patterns shown in other species of psittacines are similar to the chick food allocation pattern I found in this study. When chicks hatch, the nesting female provides the majority of nest care (in my case chick feedings) and this gradually declines while the nesting male nest care increases as nestling rearing progressed (Saunders 1982, Gnam 1991, Wilson et al. 1995). This pattern was also observed in the Scarlet Macaw in Lacandona, Mexico (Iñigo-Elias 1996). Additionally, as observed in the Black-cockatoos (Saunders 1982), in the Cuban Amazon (Gnam 1991), in the Puerto Rican Amazon (Snyder et al. 1987b, Wilson et al. 1995) and in the Yellow-headed Amazon, Red-crowned Amazon and Red-lored Amazon in Mexico (Enkerlin-Hoeflich 1995). Scarlet Macaw nesting females in Tambopata are almost exclusively fed by nesting males at the beginning of the chick rearing period but the feeding by males decreased until it almost disappeared by the middle of the nesting period. These patterns reflect the physiological needs of the altricial chicks that are unable to thermoregulate (Kattan and Gómez 1992) and need the nesting female as a source of heat and food for survival (Wilson et al. 1995). They also suggest that there is a trade-off between staying in the nest with the chicks and providing enough food for the growing brood. At the beginning of the chick rearing period, when nesting females devotedly stay with the young, nesting males' food provisioning may be sufficient for feeding her and the chicks that need just around 40 ml of food per day per chick (aviculturist daily requirement for the species according to Clubb et al. (1992b). However, when chicks get bigger this may no longer be the case. If we consider that it will take an adult Scarlet Macaw with maximum crop capacity of 140 ml (Voren and Jordan 1992d) at least two full crops to reach the 260 ml that aviculturist reported as a daily portion for a healthy 50 day old macaw chick (Clubb et al. 1992b), without adding the amount of food required to produce energy needed to fly, forage and deliver food to the nest, it is quite clear that just one nesting individual is not enough to feed just one chick at that age. It is likely that as thermoregulatory abilities of chicks develop, females have to join males on foraging expeditions in order to guarantee a successful brood.

Feeding schedule patterns showed that the whole morning (from 05:00 to 11:00 hours) is an important feeding time as well as the late afternoon, right before dusk. In other macaw species, feeding schedules were not recorded directly but they can be inferred from the daily frequency of recorded feedings. In the Red-fronted Macaw, adults entered nests 2 to 6 times per day (Lanning 1991) and in the Lear's Macaw 4 times per day (Hart 1995). Similar nest visitation frequency was observed in the Cuban Amazon in the Bahamas, where nesting males came back to the nest around 4 times per day mainly in the morning and late afternoon (Gnam 1991). Interestingly, in the case of the Yellow-headed Amazon, Red-crowned Amazon and Red-lored Amazon in Mexico, nesting pairs fed chicks only in the early morning and late evening (Enkerlin-Hoeflich 1995).

One novel discovery of my work is that chicks are fed during the night. My results showed that the midnight feeding peak was similar in magnitude to the morning peaks and that chicks are given additional feedings around 3 am. This observation, combined with the fact that the adult macaws do not forage after dark (after about 6 PM), clearly shows that macaw parents are storing food in their crops for over 7 hours and using this to feed their chicks at night. Our findings are supported from observations of Puerto Rican Amazons where chicks had food first thing in the morning evidence from chick crop observations done right after nesting pairs left after overnight at the nest, suggested that Puerto Rican Amazon chicks were also fed through the night (Snyder et al. 1987b). No other psittacine research has directly observed nocturnal chick feedings. However, studies of a variety of other psittacines such as the Major Mitchell's Cockatoo, Black-cockatoos, Cuban Amazon, Yellow-headed Amazon, Red-crowned Amazon, Red-lored Amazon and Scarlet Macaw, show that one or more adults roost in the nest, providing the opportunity for nocturnal chick feedings (Saunders 1982, Gnam 1991, Rowley and Chapman 1991, Enkerlin-Hoeflich 1995, Iñigo-Elias 1996).

My studies are in agreement with findings in Scarlet Macaws from Costa Rica (Vaughan et al. 2008) and in the Puerto Rican Amazons (Wilson et al. 1995) where brood age influences parental time in the nest. In my study, parental time in the nest decreases when brood age increases. Chick feeding frequency from younger broods (up to 18 days old) was higher than from older broods (from 30 to 65 day old), which is similar to previous findings.

Feeding counts is not a variable that has been quantified often in wild psittacines research. Even when video systems where used, footage was mainly use to quantify nest general attendance (Cantor et al. 2019), report of specific behaviors (White and Vilella 2004) and report predation events (Garcia-Anleu et al. 2017). However, there is some information about chick feeding rates from work done in captivity. My findings are quite different from captivity recommendations. Scarlet Macaw chicks in Tambopata are fed around the clock all day and night at a rate of 3.6 ± times per hour all throughout the nesting period. Even in the growth stages where I found significant differences (4.1/ hr. in Stage II A: 3 to 18 days old vs. 2.1/hr. in Stage III: 33 to 65 days old) chicks are being fed at a very high rate. According to hand feeding recommendations for psittacine chicks, it is recommended to increase the volume of food not the frequency of feedings as the chick's growth and development progresses (Voren and Jordan 1992d). In captivity, the recommendation is to feed psittacine hatchings every two hours, then move to every three to four hours at around age 5 days and then slowly decrease feedings until the chick is fed at 8 hour intervals (Voren and Jordan 1992d).

Differences I observed in wild chick feeding frequencies may be attributed to differences in the chick diet provided. In the wild, the chick diet is a chunky mix of seed, clay and liquid (Brightsmith et al. 2010, Cornejo et al. 2011, Cornejo 2012), which might be more difficult to digest than puree like formula given in captivity (Voren and Jordan 1992d). It is well known in captive breeding that slow movement in the crop can cause the crop to lose elasticity and become less effective (Voren and Jordan 1992e). Moreover, content can become sour (sour crop) that allows fungal *(Candida albicans)* growth that can severely compromise digestion and cause crop stasis and death (Voren and Jordan 1992e). It is very likely that wild macaws avoid all these chick digestion problems by giving them little portions of very chunky food very frequently instead of large less frequent portions.

Section 3: Scarlet Macaw chick mortality

Starvation (associated with brood reduction) is the main cause of chick mortality in the Tambopata area (45%), followed by chick predation (11%), chick death due to nest fights (9%) and diseases (5%). These results are not in agreement with observations from Amazon parrots in Mexico (Enkerlin-Hoeflich 1995, Renton and Salinas-Melgoza 2004), Bahamas (Gnam 1991), Argentina (Berkunsky et al. 2016), and in the Scarlet Macaw in Guatemala and El Salvador (Boyd and McNab 2008), where the main cause of mortality is chick predation. For cockatoos in Australia, starvation is an important cause of chick mortality (Smith and Saunders 1986, Smith 1991).

Documenting psittacine chick mortality is challenging due to low accessibility to nest cavities (Masello and Quillfeldt 2002) and rapid decay rates that make it very difficult to access fresh carcasses, obtain good necropsies, and determine cause of chick death (Stoleson and Beissinger 1997a). This reality is reflected in the 23% of "unknown causes of chick mortality" that I registered in this 18-year study. Other long-term studies reported large percentages of unknown reasons for nest failure as well. For example, studies on large psittacines in Costa Rica and Peru reported that 48% and 82% of nest failure causes were unknown (Renton and Brightsmith 2009, Dahlin et al. 2018).

In the following sections, I will explore the main causes of chick mortality in Tambopata.

Macaw chick death by starvation

Chick starvation has been reported in twenty species of psittacines ranging from small parrotlets to medium sized Amazon parrots and cockatoos to large macaws (See details of species in Appendix 6). In the majority of the species, with the exception of the Green-rumped Parrotlet (Beissinger and Waltman 1991), the Black-billed Amazon (Koenig 2001) and Black-cockatoos (Saunders 1982, Smith and Saunders 1986), starvation is reported as a cause of nestling mortality (Sanz and Rojas-Suárez 1997, Robinet and Salas 1999) but details about occurrence and impact of malnutrition on general chick survival are not clearly documented.

In the Scarlet Macaw in Tambopata, chick starvation was the major cause of nestling mortality (45% of chick fatalities). A similar scenario was reported in the Crimson Rosella with 42% chicks starving within days of hatching and 17% later in the nestling period (Krebs 1998). I did not find cases of chick starvation in older chicks. A more extreme scenario was observed with the Black-cockatoos where over 95% of chick fatalities were due to chick starvation (Saunders 1982). Reports from previous studies with Scarlet Macaws in the Tambopata area also document chicks with signs of malnutrition that died in their first weeks of life (Nycander et al. 1995). It was also reported in Costa Rica (Vaughan 2019) but was not reported in Mexico, Guatemala, El Salvador or Belize; perhaps because of low frequency of nest monitoring in those studies (Boyd and McNab 2008).

Similar to my findings on Scarlet Macaws in Tambopata, chick starvation was found to be related to hatching order in other psittacines, tending to be higher for the last and penultimate member of the brood (Saunders 1982, Smith and Saunders 1986, Waltman and Beissinger 1992, Koenig 2001, Masello and Quillfeldt 2002). In my study, mortality of third and fourth chicks tended to be almost complete , which is similar to observations on the Black-Cockatoo where over 90% of second chicks starved to death (Saunders 1982).

In the Scarlet Macaw in Tambopata, chick starvation is the main method of brood reduction; likewise in the Green-rumped Parrotlet (Beissinger 2008), the White-tailed Black-

Cockatoo (Rowley and Chapman 1991) and the Crimson Rosella (Krebs 1998). It was not an important chick mortality factor for the three Amazon parrot species (Yellow-headed Amazon, Red-crowed Amazon and Red-lored Amazon) studied in Mexico (Enkerlin-Hoeflich 1995) which could be attributed to difficulties of data collection during the first weeks of the nestling period when this phenomenon is more prevalent.

Chick starvation description and analysis of causation will be presented elsewhere.

Macaw chick predation

One of the most common reasons for nest failure in Neotropical birds is predation (Ricklefs 1969). However, Scarlet Macaw chick predation in Tambopata is very low. Just 6% of the chicks that hatched were depredated, which represents 11% of total chick deaths in 18 years of intense monitoring. This finding is very different from what most other psittacine studies report. For Yellow-shouldered Amazon (*Amazona barbadenis*) in Venezuela, chick predation was the second most common cause of chick loss, after poaching (Sanz and Rodríquez-Ferraro 2006). In the three Amazon parrot species studied in mainland Mexico, predation was the leading cause of chick loss (Enkerlin-Hoeflich 1995).I In the Turquoise-fronted Amazon (*Amazona aestiva*) in Argentina, predation caused 50% of nest failures (Berkunsky et al. 2016). For the Scarlet Macaw in Guatemala, chick predation is considered a main cause of known nest failure (Britt et al. 2014, Garcia-Anleu et al. 2017) and in Belize it is the second leading one after poaching (Britt et al. 2014).

One possible explanation for low chick predation in Tambopata could be the characteristics of nests used. For instance, in two species of cliff nesters, the Burrowing Parrot (*Cyanoliseus patagonus*, Masello and Quillfeldt 2002)) and Lear's Macaw (Hart 1995),predation was not seen. This possibly because of difficult access for predatory mammals and reptiles to the nests (Masello and Quillfeldt 2002). On the opposite extreme, predation of Crimson Rosellas chicks in Australia was as high as 66% when nest boxes had large entrances. When this design defect was corrected, predation decreased to zero (Krebs 1998). It is also likely that psittacine tree cavity nesting species have adapted to use cavities that are more difficult to predate. Studies on nest characteristics and preferences show Amazon parrot species that have high chick predation by snakes, preferred deeper cavities with narrower entrances (De la parra Martinez et al. 2015). Large bodied macaws, which suffer less chick predation, used relatively shallow nests with a larger entrance diameter. Such is the case of the Scarlet Macaw (Olah et al. 2014) and Hyacinth Macaw (Pinho and B. 2003). Additionally, large macaws preferred to nest in larger trees at a greater height from the ground (Brightsmith 2005, Renton and Brightsmith 2009, De la parra Martinez et al. 2015). In the case of the Scarlet Macaw, in trees with less canopy connectivity (Renton and Brightsmith 2009, Britt 2011) that are close to each other at high density (Olah et al. 2014). This latest preference might be key in relation to predation because it improves predator detection (Eberhard 2002). I have observed nesting Scarlet Macaw pairs that nest close by respond in unison when predators (e.g. hawk eagles, humans, etc.) are seen in the vicinity of the nest area. They called and flew in circles above the nesting area. Nesting pairs from nearby nests also joined the behavior. Even if one of the nesting pairs was not in the nest at the moment, is very unlikely that the predator would be able to notice and take the chicks.

An important aspect of chick predation reported for all the studies I have reviewed to date, is that chick predation usually happens when chicks are alone in the nest. For instance, in the case of the three Amazon parrots researched in Mexico; food was delivered to chicks twice per day in a very predictable schedule. The rest of the time, chicks were by themselves (Enkerlin-Hoeflich 1995). In the three confirmed cases of Scarlet Macaw predation by Forest

Falcons (*Micrastur* sp) in Guatemala, chicks were also alone (Garcia-Anleu et al. 2017). According to previous findings of our team, nesting success increased with proportion of time the adults were present during nest inspections which translates to successful nests having adult macaws around more of the time (Olah et al. 2014). Parental presence at the nest may be key for reducing nest predation because most predators small enough to enter in to the nest can likely be repelled by the adult macaws with their formidable beaks. My team and I witnessed a Common Opossum (*Didelphis marsupialis*) that was about 3 m from the nest entrance, being attacked by a nesting pair of Scarlet Macaws and eventually being knocked to the ground. This species is a confirmed nest predator of Scarlet Macaw in Costa Rica (Vaughan et al. 2003b).

My study contains an unprecedented report of predation of a big healthy macaw chick (~57 days old) by Army Ants. It was reported in the Red-tailed Black-cockatoo that 6-7 weeks old chicks were found covered by ants (n=4 chicks) but it was unclear if the attack was the cause of death or if the chicks were already dying (Smith and Saunders 1986). Some of the other predators identified in my area, such as the Tayra (Figure 4) and the Forest Falcon have been previously reported as macaw chick predators (Nycander et al. 1995, Garcia-Anleu et al. 2017). Also, I have reports of Kinkajou (*Potos flavus*) sleeping inside non-active macaw nests, inspecting active nests at night (Figure 8) and predating macaw eggs, but no evidence of chick predation.

Figure 8. Kinkajou inspecting an active Scarlet Macaw nest at night.
The nesting male is on the top and the nesting female is guarding the nest entrance. A sequence of pictures was taken by a camera trap at 01:42 am. The photos show the nesting male flying at the kinkajou before the latter disappeared from view. Two eggs that had been incubated at the time of the picture, were found broken open about 5 days later.

Macaw chick death due to disputes over nest ownership "nest fights"

Agonistic interactions around nests (a.k.a. nest fights) have been recorded in many species of psittacines, including parrotlets (Grenier and Beissinger 1999), Amazon parrots (Snyder et al. 1987c, Enkerlin-Hoeflich 1995), rosellas (Krebs 1998), cockatoos (Saunders 1982) and macaws (Munn 1992, Guedes and Harper 1995, Renton 2004), including the Scarlet Macaw (Nycander et al. 1995, Iñigo-Elias 1996, Vaughan et al. 2003b). In all of the cases, including this study, the behavior displayed was similar. The resident individual(s) chased intruder individual(s) and launched attacks either while walking on tree branches or flying towards the intruder (Saunders 1982, Enkerlin-Hoeflich 1995, Grenier and Beissinger 1999). If the agonistic interaction escalated, more aggressive behaviors such as wing displays or barking-like guttural sounds were observed (Enkerlin-Hoeflich 1998). In extreme cases, when interaction escalated even more, direct contact fights with bill and feet contact were observed, especially in macaws (Munn 1992, Nycander et al. 1995, Iñigo-Elias 1996, Renton 2004). In some instances, intruders and residents hit each other in flight, locked feet, and fell through the air (breaking off before hitting the ground). These nest fights often resulted in physical injuries, including deep claw scratches, bite marks and open wounds on the face (Figure 9). On one occasion, fight lesions caused a very experienced nesting female to lose her left eye (Figure 10).

Chick mortality due to nest fights reported in this study show that nest fights influence reproductive success in the Scarlet Macaw. As seen in other psittacine studies, nest fights decreased the use of suitable cavities, as in the Crimson Rosella in Australia, where old pairs assaulted new pairs preventing them from nesting and destroying their eggs (Krebs 1998). Nest fights also reduced hatching success, as shown in the Green-rumped Parrotlet in Venezuela, where females incubated less and left the nest more often to defend the nest (Grenier and Beissinger 1999). These fights also decreased fledgling success, as seen in the extreme cases of infanticide on the Blue-and-yellow Macaw in Manu, Peru (Renton 2004) and in the Green-rumped Parrotlet (Bonebrake and Beissinger 2010). Chick fatalities as a result of nest fights have not been reported from other Scarlet Macaw studies. However, there are reports of intense nest fights from Mexico (Iñigo-Elias 1996), Costa Rica (Vaughan et al. 2003b), and Perú (Munn 1992, Nycander et al. 1995), which show that Scarlet Macaw nest defense interactions are not specific to the Tambopata area.

Figure 9. View from nest tree and nest box during a "nest fight" documented in the pre-laying period.
The nest box is located in the bottom central area of picture. Both nesting individuals are inside the nest. The nesting male is on the entrance of the nest box. The pair on top of the nest box is the intruder pair. Five additional Scarlet Macaw pairs were observed in the nest tree during the fight, all showing signs of distress, such as opening wings and barking sounds but not directly participating in the nest fight. The nesting pair was able to maintain nest ownership. The dispute lasted about 6 hours. Photo credit: Lauren Bazley.

Figure 10. Close up of injury on female adult Scarlet Macaw obtained during a nest fight. This banded female was seen trying to take over an occupied natural nest with her mate. They did not succeed. The female's eye was badly injured during a fight probably by bites. The nest fight occurred nine years before the picture was taken. The eye is completely blind but this female was still alive and flying in the wild as of on January 2019.

This study is the first to document infanticide in the Scarlet Macaw. Infanticide by nest intruders was reported in the Blue-and-gold macaw in one occasion (Renton 2004). Here, I am reporting seven cases of direct infanticide; six of them performed by intruder pairs and one done by resident nesting females. Little is known about infanticide in macaws, its frequency and its relation to macaw agonistic interactions around the nest. However, it could be similar to the Green-rumped Parrotlet where infanticide is higher in high quality nest sites that experience stronger intraspecific competition (Bonebrake and Beissinger 2010). Individual case descriptions of infanticide in the Scarlet Macaw in Tambopata will be documented elsewhere.

Frequency of nest fights in the Scarlet Macaw have not been documented. In Mexico, disputes were observed before eggs were laid and at the beginning of the incubation period (Iñigo-Elias 1996), which is similar to my nest fight observations from Tambopata (GVT not published) and to Red-and-green Macaw nest fights reports from Manu, Peru ((Munn 1992). However, my team and I have also observed nest fights later on the nestling period (Vigo not published, Renton and Brightsmith 2009). In the Blue-and-yellow nest fights were more frequently at the end of the nestling period (Renton 2004). According to my preliminary analysis of nest fight observations, nest fights are more common during the first two weeks of the nestling period but chick fatalities are more common during the second half of the nestling period (Vigo and Brightsmith unpublished data). A comprehensive analysis of Scarlet Macaw agonistic interactions and nest fights will be presented elsewhere.

Macaw chick death by diseases

Psittacines are susceptible to a variety of diseases and many of them can be problematic to manage because they can exist in carrier state for months without detection and they are incurable by current methods (Derrickson and Snyder 1992). Therefore, the ability to detect diseases in chicks is very limited. Unless obvious signs of abnormalities appear, death by disease in psittacine chicks will most likely be categorized as unknown.

I have three cases of chick mortality, all members of one brood, where the disease may have been contagious. In this case, all brood members died showing similar abnormalities. Even the individual I relocated to another nest on the day it hatched, as part of a fostering experiment, got the disease and died. The most dramatic case of possible disease transmission in psittacine chicks from the literature is the one reported in the Galah (*Eolophus roseicapilla*) in Australia, where 62% of chick deaths (n= 104 chicks, on 19 of 23 nests) were attributed to an unknown aggressive disease where chicks had only 38% survival after infection (Smith and Saunders 1986). This unknown disease was also reported to be contagious to Long-billed Corellas (*Cacauta tenuirostris*) after they usurped a nest from a Galah pair (Smith and Saunders 1986).

In Tambopata, botfly larvae in macaw chicks are a common problem so it is not a surprise it caused chick fatalities. In general, botfly infestation is poorly reported in the psittacine literature. In Tambopata, botfly larvae have a prevalence of 29 % and an average intensity of 5 per infected chick (Olah et al. 2013) which is higher than the 3 per chick found on Lilac-crowned Amazons in Mexico (Renton 2002). In my study, larvae were located in the head 24% of the times (7% nares, 7% face and 10% ears). In these locations there is a high likelihood of infection, especially if larvae are located deep in open nasal or aural cavities. However, confirmed death due to botfly infestation was rare (3 cases) and massive botfly infestations like the one found in this study (26 botfly larvae at once and over 60 total) are likely very rare. Similar botfly larvae infestations, but less intense, have been reported for Hyacinth macaw (31 larvae/chick), Scarlet Macaw (>15 larvae/chick), and Turquoise-fronted Amazon (> 25 larvae/chick, Olah et al. 2013). Botfly larvae were not found in three Amazon parrot species in Mexico (Enkerlin-Hoeflich 1995) or in the Turquoise-fronted Amazon in Argentina (Berkunsky et al. 2016). However, botflies were reported in the Lilac-crowed Amazon in Mexico (Renton 2002). They were also reported in the Scarlet Macaw in Guatemala and El Salvador as a factor that reduces chick survival but the incidence was not reported (Boyd and McNab 2008).

There are a few reports of chick mortality in psittacines that can be attributed to sickness acquired due to bad nest cavity conditions. There is one report of one chick of Yellow-shouldered Amazon from a nest cavity with wet substrate, which showed furuncles around the cloacae that may have caused a fatal infection (Sanz and Rodriguez-Ferraro 2006). In my study, one chick that died with white fluid coming out of the beak, was housed in a nest that had a history of flooding and the substrate was very wet all the time. Wet and cold for longer periods of time could have contributed to the illness.

Conclusions

In this study I documented wild Scarlet Macaw parental behavior in the lowland forests of southeastern Peru during 19 breeding seasons. In spite of the fact that the species laid on average 2.7 +/- 1 eggs (1 to 5 per nest) and 1.35 +/- 1 chicks hatched (1 to 4 per nest), only 1.4 +/- 0.5 chicks fledged per nest (1 to 2 chicks per nest). Chick starvation was the leading cause of chick death, resulting in 45% of all chick mortality. In the area, all fourth hatched chicks starved, nearly all third chicks starved, over 20% of second chicks starved, and basically no first chicks starved. Chick mortality due to predation was very low, only 6% of chicks that hatched.

The species displays a bi-parental care strategy. I found that females provided the majority of nestling care when the chicks hatched but the proportion of care given by the male gradually but significantly increased as the chicks aged. I found that (1) chicks were fed on average 3.6 times per hour throughout the nestling period, (2) chicks were fed during the day and at night with major diurnal and nocturnal feeding peaks, and (3) macaw parents can store food in their crops for over 7 hours and use this to feed their chicks at night. In addition, I found that nesting males frequently fed their mates, but that the nesting females did not feed the males.

Due to its high-level of extinction risk as an order (Olah et al. 2016), studies of breeding ecology on Psittaciformes have increased in the past decades. From parakeets to macaws, (Beissinger 2008, Vaughan 2019) from pure ecology (Snyder et al. 1987c, Rowley and Chapman 1991) to complex genetics studies (Olah et al. 2015, Stojanovic et al. 2018); scientists, conservationist and government agencies worldwide have been trying to untangle psittacine natural history with the hopes to find a way to recover declining wild populations (Juniper 2003, Boyd and McNab 2008). My study of nestling ecology and behavior on the Scarlet Macaw in Tambopata aims to provide important insights from the chick-rearing period in the wild that could be applied to in in-situ and ex-situ conservation actions with the goal to recover endangered populations of macaws in the Americas.

CHAPTER III

STARVATION IN WILD SCARLET MACAW CHICKS

Introduction

Starvation is a severe deficit in caloric intake, under the level needed to maintain basic body functions and survival (Beers and Robert Berkow 2004). In psittacines, it has been reported in both Neotropical and Australian species across all body sizes in the order; from ~20 gr parrotlets to ~ 1200 g. macaws (seeVigo In prep CH 2for summary). However, it has been described in little detail in the wild.

There are three types of chick starvation reported in the wild. The most frequently mentioned in the literature is the one related to brood reduction however, at least two more types of chick starvation have been reported in wild psittacines. “Chick starvation to fledge”, or the death of a full-term nestling while the siblings survived, occurs during the time parents are restricting food in order to encourage chicks to fledge. In this case, chick death is attributed to insufficient energy reserves (Koenig 2001). It has been reported in the Black-billed Amazon (*Amazona agilis*, Koenig 2001), Yellow-headed Amazon, (Enkerlin-Hoeflich 1995), Crimson Rosella (Krebs 1998), Black-cockatoo (Saunders 1982) and was also reported by my team in the Scarlet Macaw in Tambopata on one occasion. “Chick starvation due to nest defense”, or death of chicks as a result of poor parental care (insufficient feeding and brooding) while defending the nest from intruder pair(s), occurs when nesting pairs under attack prioritize nest defense over chick rearing. This is apparently not reported in the literature, but I reported it in the Scarlet Macaw in Tambopata (Vigo In prep CH 2). The most commonly reported type of starvation is “Chick starvation associated with.” It has been observed in twenty species of psittacines. In the

Green-rumped Parrotlet, it was directly associated with chicks that died with empty crops, usually last and penultimate chicks, when nestmates still had food in the crop (Beissinger and Stoleson 1991, Beissinger and Waltman 1991). In a study of three sympatric Amazon parrots in northeastern Mexico, Yellow-headed Amazon, Red-crowned Amazon and Red-lored Amazon chicks died after a slow decline in condition in a brood where other siblings survived (Enkerlin-Hoeflich 1995). In Crimson Rosellas, it was described as chick death within the first three days where chicks were not fed or were fed very little (Krebs 1998). In the Scarlet Macaw in Peru this was called "death by malnutrition" and has been reported in second and third chicks younger than 20 days old (Nycander et al. 1995). In all of the types of chick death by starvation, caloric intake is not sufficient to maintain basic vital functions and the chick slowly perishes.

Brood reduction strategies in birds have been intensely studied in the past six decades as a way to understand hatching patterns (Clark and Wilson 1981, Stoleson and Beissinger 1995). Through the years, the initially well accepted "Brood reduction hypothesis" (Lack 1954) that links mortality of last-hatched individuals with insufficient food availability to raise all brood members, has lost much acceptance because it was only supported by a few field studies (Stoleson and Beissinger 1995). Currently, brood reduction is often thought to be a non-adaptive consequence of hatching asynchrony that might be maintained for other reasons (Viñuela 2000). Brood reduction is most commonly observed in birds with asynchronous hatching where chick mortality can be caused by (1) siblicide, where smaller or younger brood members are killed by other brood members (Drummond 1987, Simmons 1988, Drummond and Havelas 1989), (2) direct filial infanticide, where parents evict specific chicks (Moreno 2012) or kill them (Tortosa and Redondo 1992, Heinsohn et al. 2011) or (3) indirect filial infanticide, when parents provide sub-optimal parental care (a.k.a chick starvation, Saunders 1982, Stoleson and Beissinger 1997b, Krebs 1998, Masello and Quillfeldt 2002).

Siblicide

Sibling rivalry within broods has been recorded in a wide range of bird species, including sea birds such as boobies, gulls and pelicans (Drummond 1987, Drummond and Havelas 1989), some Ciconiformes like the egrets and herons (Mock 1987) and several species of birds of prey (Simmons 1988). High levels of sibling rivalry can lead to death of subordinate members of broods, through physical harm, eviction from the nest or forced starvation (Morandini and Ferrer 2015). In parrots in general, sibling competition within broods is low (Krebs 2002). It occurs mainly during feeding times during attempts to obtain food; either by begging (vocalizing and moving wings) and by scramble competition between brood members in order to obtain positions closer to a feeding parent (Krebs 2002).

Filial infanticide

Avian filial infanticide is probably under reported in the literature due to a combination of difficulty of direct observations, observer bias, and the lack of long-term studies (Moreno 2012). *Active filial infanticide*, when a parent executes its own live offspring, has been reported in sixteen species of birds, including sparrows, coots, falcons, eagles, roadrunners, woodpeckers, spoonbills, storks (see a list of species in Moreno 2012) and one species of parrot, the Eclectus parrot (*Eclectus rotatus*, Heinsohn et al. 2011). In the majority of the species, parents evict the younger nestling from nest but in the case of the White Stork (*Ciconia Ciconia*, Tortosa and Redondo 1992), the Peregrine Falco (*Falco peregrinus tundrius*, Alastair et al. 2013) and the Eclectus parrot (Heinsohn et al. 2011), observations of attacks and beak marks on chick carcass suggest parents were directly responsible for chick death. *Passive filial infanticide*, or suboptimal nourishment of specific nestlings that results in death by starvation, has been reported as a cause of mortality in many species of parrots (see in Vigo In prep CH 2for a list of species). However, it has been rarely recognized as infanticide, probably because it has been meticulously studied on very few occasions (Beissinger 2008). It is commonly called "chick starvation" and it is collectively accepted as a brood reduction mechanism (Braun and Hunt 1983).

In the current study I investigated the phenomenon of chick death by starvation associated with in the Scarlet Macaw in Southeastern Peru. The Scarlet Macaw is a large bird (> 1kg body weight) that is widely distributed in Central and South America (Forshaw 1989). They are secondary cavity nesters that engage in reproduction related activities, such as nest defense, incubation and rearing chicks, for more than six months per year (Renton and Brightsmith 2009). Across its range, brood reduction has been documented repeatedly in the species (Nycander et al. 1995, Vigo Trauco 2007, Boyd and McNab 2008, Britt et al. 2014, Olah et al. 2014, Vaughan 2019). In southeastern Peru, starvation is the leading cause of chick death, resulting in 45% of all chick mortality. Here all fourth hatched chicks starve, nearly all third chicks starve, about 20% of second chicks starve, and basically no first chicks starve (Vigo In prep CH 2). The species is extremely altricial; chicks are blind and not able to thermoregulate for almost 20% of the nestling period (Clubb et al. 1992b, Voren and Jordan 1992b, Vigo et al. 2011b). They display bi-parental care strategy, where both female and male feed the chicks during the ~ 90 days nestling period (Vigo In prep CH 2).

This study explores the reasons behind chick starvation related to brood reduction in the Scarlet Macaw in the Tambopata region of southeastern Peru. To do this I examine the interactions between siblings, between the environment and parents and between parents and offspring.

Sibling interactions

There are few studies on parrots that investigate interactions between brood members (Stamps et al. 1985, Krebs et al. 1999) but it is thought that sibling competition in parrots is low (Krebs 2002). In macaws, direct sibling aggression that may result in brood reduction is highly unlikely due to the fact that nestlings are blind for almost 20% of the chick rearing, precisely during the time when most brood reduction takes place (Vigo In prep CH 2). In addition, sibling competition in parrot nestlings focalizes during feeding time as part of attempts to obtain food (Krebs 2002). In general, parents move around the nest during feeding visits, and seek out particular nestlings, ignoring actively begging nestlings and refuse to feed nestlings grabbing at their bill (Stamps et al. 1985, Krebs et al. 1999). Relationship between begging and food allocation in parrots is complex and is not strongly linked to nestling hunger (Stamps et al. 1985, Krebs and Margrath 2000, Krebs 2001, Budden and Beissinger 2009). Scramble competition with the goal to be closer to a feeding parent was observed in captive Budgies (Stamps et al. 1985), wild Crimson Rosellas (Krebs and Margrath 2000), wild Green-rumped Parrotlets (Budden and Beissinger 2009), and White-tailed Black Cockatoos (Saunders 1982) but direct aggression was not recorded. However, aggressive interactions against second chicks (the ones that starved) were recorded in the White-tailed Black Cockatoo (Saunders 1982). I formally address the theory of sibling rivalry as a cause of chick starvation.

Parent-environment interactions

In birds with asynchronous hatching, like parrots, variation in food supply predictability has been proposed as a driver of optimal clutch size. In bird species in which food supply varies unpredictably, the optimal clutch size should reflect the average maximum number of young that can be raised under favorable conditions (Lack 1947). Moreover, food scarcity was proposed as the main mechanisms for “brood adjustment” where youngest nestlings are either outcompeted by larger brood members or actively neglected and starved to death (Lack 1954, Ricklefs 1965, Clark and Wilson 1981). The “Brood reduction Hypothesis” also call the “Resource tracking hypothesis” proposes that brood size adjustments reflect parental ability to supply food and that nestlings that have received low parental investment or that will required high future investment will be eliminated (Stoleson and Beissinger 1995). This hypothesis holds for a number of bird species including birds of prey (Marc 1983), sea birds (Drummond 1987, Drummond and Havelas 1989), penguins (Browne et al. 2011) and a number of passerines (Harper et al. 1992). In psittacines, there is still a debate about its applicability, however the majority of evidence from parrot research goes against food limitation as the driver of brood reduction by chick starvation (Enkerlin-Hoeflich 1995, Stoleson and Beissinger 1997b, Krebs 1998, Krebs 1999, Koenig 2001). In this study, I test the theory that food availability influences chick starvation in the Scarlet Macaw.

Parent-offspring interactions

In parrots, chick feeding strategies differ a great deal from other birds, mainly because parents allocate food directly to specific chicks and mostly ignore chick begging (Stamps et al. 1985, Krebs 2002, Budden and Beissinger 2009). Food allocation quantification has been used as a way to understand parental care strategies in a variety of bird species, such as raptors (Simmons 1988), herons (Mock 1987), boobies (Drummond 1987, Drummond and Havelas 1989), kittiwakes (Braun and Hunt 1983) , some passerines (Ricklefs 1965, Morandini and Ferrer 2015) and parrots (Stamps et al. 1985, Krebs and Margrath 2000, Budden and Beissinger 2009). Direct food allocation represents one extreme of the food allocation pattern. At the other extreme is low selectiveness in food allocation by the parents in which nestlings form a strictly enforced dominance hierarchy that determines access to food (Krebs 2002). In psittacines, two patterns of direct food allocation have been described. In the first pattern, feeding preferences favor the last-hatched individuals, especially by the female. Such is the case of Budgies, where females fed all chicks equally but fed last-hatched chicks first (Stamps et al. 1985) and the case of the Crimson Rosella, where hungry last-hatched chicks was fed more by both parents (Krebs and Margrath 2000). In the second pattern, feeding preferences disfavor last-hatched, as observed on the Green-rumped Parrotlet, where both female and male parents fed youngest chicks less (Budden and Beissinger 2009). In this investigation I tested the theory that direct food allocation disfavored the younger chicks in Scarlet Macaw broods that showed chick death by starvation.

Direct food allocation is based on physical cues such as chick gender (Heinsohn et al. 2011), condition (Stamps et al. 1985), size (Cotton et al. 1999) and age (Braun and Hunt 1983). In this context, a physical cue that has been little investigated in parrots is the size of the chicks at hatch. Hatchling weight is related to egg volume (Braun and Hunt 1983, Beissinger and Waltman 1991) and it may reflect incubation differences (Grenier and Beissinger 1999) that can result in hatchling weaknesses (Clubb and Phillips 1992). This is especially true if sub-optimal incubation resulted in embryo malposition (Robertson 1960) that interfered with the pipping/hatching process (Clubb and Phillips 1992, Abramson et al. 1995, Vigo In prep CH 2). A light weight hatchling may trigger differences in food allocation as was observed in Budgies, where lighter chicks were fed more frequently than larger chicks of the same age (Stamps et al. 1985). In experiments with chickens, long incubation delays reduced hatchling weight (Ruiz and Lunam 2010). Therefore, due to the fact that in macaw incubation starts when the first egg is laid (GVT unpublished data), with little or no incubation delay, weight at hatch should be similar regardless of hatch order. However, in the Scarlet Macaw, weight at hatch significantly decreases with hatch order; third and fourth hatched chicks were lighter at hatch than first chicks and it is precisely the third and fourth that always died by starvation (Vigo In prep CH 2). In this study I evaluate the relationship between weight at hatch and death by starvation of Scarlet Macaw chicks.

In psittacine species where parents selectively under feed last-hatched chicks (Beissinger and Stoleson 1991, Krebs and Margrath 2000, Koenig 2001), it has been hypothesized that size disparities trigger unequal food allocation that results in chick starvation (Masello and Quillfeldt 2002, Beissinger 2008, Bonebrake and Beissinger 2010). However, brood manipulations done in wild Scarlet Macaw chicks showed that macaw parents fledged brood members that are up to 9 days apart with weight differences over 250 g (and ~78% (Vigo In prep CH 4). These results suggest that the size difference factor it is not the absolute cue that triggers parental differential feeding, at least in the Scarlet Macaw. Brood size differences are linked with age differences in brood members. Siblings that hatch closer together in time will be more similar in size than siblings that hatched with a greater time difference (Stoleson and Beissinger 1997b); in other words, broods that hatch more synchronously result in chicks that are more similar in age and more importantly result in chicks with similar parental care requirements. It is well known by aviculturist that psittacine chicks < 5 days old need to be monitored more carefully and housed separately from older chicks, in part because temperature fluctuations can be fatal at this stage of development (Clubb et al. 1992b, Voren and Jordan 1992e). Therefore, broods with large age differences contain members with a variety of rearing requirements based purely on age specific developmental needs. In this study, I tested the age difference between brood members' relationship with chick starvation in the Scarlet Macaw.

In this study, my objective was to determine the drivers of macaw chick death by starvation associated with by determining why nearly 25% of second hatched macaw chicks die by starvation and nearly half do not die of starvation. To do that, I tested the following hypotheses:

H1: Chick-chick interaction hypothesis:

Chick death by starvation results from aggressive interactions within broods: Second hatched chicks that are target of aggression from their older nest mates have a higher chance of death by starvation.

H2: Parent-environment interaction hypothesis:

Second chicks raised during periods of high food availability have a higher chance of survival compared to second chicks raised during periods of low food availability.

H3: Parent-chick interaction hypothesis:

H3.1 Chick death by starvation is driven by direct food allocation to specific chicks and specific targeted parental neglect (Filial infanticide): Second chicks that receive less feedings have a higher chance of starvation than second chicks that received more feedings

H 3.2 Chick death by starvation is driven by body condition at hatch (hatch weight): Second chicks that weigh less at hatching are more likely to starve than second chicks that weigh more at hatching

H 3.3 Chick death by starvation is driven by brood age differences: Second chicks that are born later with respect to their older siblings have a higher chance of starvation

Methods

Study site

Research was conducted in the forests surrounding the Tambopata Research Center (13°8’S, 69°36’W), in the Tambopata National Reserve (275 000 ha) adjacent to the Bahuaja-Sonene National Park (1 091 416) in the state of Madre de Dios, southeastern Peru. The forest adjacent to the research station is tropical moist forest (Holdridge Life Zone system) and is a combination of flood plain, terra firme, successional, and palm swamp forest that receives around 3200 mm of rain annually (Tosi 1960, Brightsmith 2004)

Background methodology

Data were collected during eighteen consecutive breeding seasons, from 2000 to 2018, as part of research done by The Macaw Society www.TheMacawSociety and http://vetmed.tamu.edu/macawproject (Brightsmith 2001, Brightsmith et al. 2008, Gish 2009, Olah et al. 2014). Macaw nests were monitored from mid-October to mid-April every breeding season. Each season I monitored up to 46 macaw nests (around 16 natural and 24 artificial per year) using single rope climbing systems as described in (Perry 1978, Perry and Williams 1981). In eleven breeding seasons (2007 to 2019, excluding 2011 & 2015), I installed video cameras in 4 ± 2 nests per season (range 1 to 9 nest with camera/season). Video systems were installed before eggs were laid. Criteria to select nests for video camera placement were as follow: (1) nests that hatched or fledged at least 1 chick the last three consecutive breeding seasons, (2) nests with multi-chick broods in the three previous breeding seasons, and (3) nests with good accessibility to reach chicks and access the camera.

All nests were checked once every 2 to 3 days until the first egg was found. After an egg was found, nest monitoring ceased until 26 days later and continued once the first chick hatched.

Once chicks hatched, the nest check schedule was as follows. From the day I discovered the first chick, the nest was checked every day until the youngest chick of the brood was 15 days old. The nest was then checked every 2 days until the oldest chick of the brood was 70 days old. After this age, nests were checked every day until the last chick fledged. In each visit, the weight of each chick was taken using a digital scale. More details about chick checks are available in Vigo et al. (2011b). When chicks were found dead, the body was removed from the nest and a necropsy was performed in the field station. When chicks disappeared from nests, cause of death was considered as "unknown" unless clear evidence of predation was found. Death by starvation was declared when a chick hatched apparently healthy but did not gain weigh as expected and ultimately lost weight, dying with no clinical signs of disease.

To monitor brood member interactions, I used the video camera system to record interactions inside the nest. Recordings were made in two ways. Non-continuous recordings were taken from 2007 to 2010, every time (a) chicks were fed and (b) chicks were left alone in the nest. Continuous recordings were taken in two different manners. From 2007 to 2010, two-hour recordings were done at three times of the day (6:30, 12:30 and 16:30 hours) without a specific weekly schedule. From 2012 to 2018, 6-hour continuous recordings were done at three specific times of the day (AM: 5:00 to 11:00, PM: 11:00 to 17:00 and NIGHT: 17:00 to 05:00). The 6-hr recordings were made with the following overall schedule: (1) every day until younger chick of the brood was 15 days old or until starving chicks died and (2) every other day, alternating day and night recordings. Recording schedule was not always followed due to camera systems malfunctioning or extreme weather conditions. Experienced observers took behavioral observations: one from 2007 to 2010 (GV) and another from 2012 to 2018 (Gustavo Martinez).

Both observers were tested for accuracy in data collection. Both continuous and non-continuous types of recordings were used in each analysis unless otherwise indicated.

For these analyses, I included and compared second chicks that starved to death and second chicks that did not starve and went on to fledge successfully (n=81 chicks, 18 breeding seasons, average chicks per season = 4, range 2 to 9 chicks/season). Not all of the second chicks from the 18-year period were included in each analysis, because (1) hatching date was not known with the same precision in all broods, (2) not all chicks were weighed on their hatching date, (3) not all broods under study had a video system in their nest, (4) observers were not always able to distinguish between the two chicks during video data collection, and (5) plant phenology information was collected in just eight of eighteen breeding seasons. For those reasons, 54 second chicks (67% of initial sample) were included in at least one of the analysis performed (17 chicks that starved and 37 chicks that did not starve). Indeed, just 5 second chicks (3 chicks that starved and 2 chicks that did not starve) had data for all variables and were part of all of the analysis. This very small sample size made it impossible to test all factors simultaneously in a multi-variate analysis. For this reason, each analysis is conducted with a different subset of the available chicks.

All statistical analysis was performed using JMP pro 13 with an $\alpha = 0.05$. Data are presented as (mean ± standard deviation, N) unless stated otherwise.

Section 1: Description of macaw chick starvation

Weight at hatch

I used the chick body weight collected during the first 24 hours after hatching as a surrogate measure of chick quality. To test differences between chicks that starved (disregarding hatching order) and chicks that fledge, I performed a t-test. Besides, I used just chicks from double broods where weight at hatch was recorded for both brood members. I grouped chicks in three "chick outcome" groups: (1) first chicks that fledged, (2) second chicks that fledged and (3) second chicks that starved. I performed an analysis of variance ANOVA using weight at hatch as the dependent variable and "chick outcome" groups as the independent variable. To explore chick quality differences at hatch between members from successful double broods and members from double broods with starvation, I used chicks from broods with weight at hatch from both members. I grouped chicks in four "detailed chick outcome" groups: (1) First chicks that fledged from successful double broods, (2) Second chicks that fledged from successful double broods and (3) First chicks that fledged from double broods with starvation and (4) Second chicks that starved. I performed an analysis of variance ANOVA using weight at hatch as the dependent variable and chick outcome groups as the independent variable. An outlier second chick (Hugo II 2013) that starved at a much greater age than all other second chicks that starved was removed from calculations. This chick was always found with an empty crop during its first week of life but the crop of its sibling was also small. Its gain weight was extremely low and inconsistent, with a few days gaining a few grams followed by a big weight loss day (>10% of its body mass). Big differences in crop size started at day 10 of age; when first chick had almost full to full crops vs completely empty crops. Hugo II 2013 died at 36 days of age, with 192 gr, which is the average weight of a 12-day old chick.

Growth description of chicks that starved

Chicks that starved were grouped in three groups according their hatching order: second chicks that starved, third chicks that starved and fourth chicks that starved. To increase accuracy in calculations, chicks were included only if (1) the chick was weighed within 24 hours of hatching, (2) the body was found within 24 hours of death, (3) the chick was not given supplemental feedings, (4) the parents were not supplemental fed and (5) the chick order did not change through the life of the chick. An outlier second chick, Hugo II 2013, that starved at 36 days was removed from calculations.

Section 2: Drivers behind macaw chick starvation in Tambopata

I will address in turn the hypotheses that death by starvation is due to: (1) chick-chick interference, (2) parent-environment interactions and (3) parent-chick interactions. In this analysis, comparisons between chicks that starved and chicks that fledged were performed using just second chicks.

Chick – chick interaction analysis

To monitor interactions between chicks, I used the continuous and non-continuous video recordings from inside the nests taken as previously explained during 8 breeding seasons (2007 to 2010 and 2012 to 2014). To determine evidence of aggressive competition between chicks, I recorded two behaviors: (1) Chicks pushing another chick's body with its own body and (2) Chicks pushing an adults' beak while the adult is feeding another chick. Chick pushing is a characteristic behavior from aggressive sibling competition that in some non-psittacine species results in siblicide (Braun and Hunt 1983). Chicks pushing an adults' beak while the adult is feeding another chick is a behavior registered in parrots during feeding and it can be used as an indicator of dominance attempts in scramble competition (Stamps et al. 1985)

For both behaviors, I recorded all occurrences of each particular behavior in a continuous manner each time it happened. Chicks that pushed either another chick or an adult beak, was considered the initiator and chick that was pushed was considered the receiver.

Chick pushing

Chick pushing was recorded when any brood member was in contact with another chick and exerted body force against the other chick. The push did not have to produce a reaction from the one being pushed to be counted. Each individual "push" was counted as a unit and tallied. For each first chick and each second chick, I calculated (1) the frequency of pushes per minute and (2) the frequency of being pushed by another chick per minute. With these two rates, I performed three t-tests assuming unequal variances in order to investigate: (1) if pushing by first and second chicks differed significantly, (2) if second chicks were pushed more or less than first chicks and (3) if second chicks that died by starvation were pushed more or less than second chicks that did not starve to death. To investigate the relationship between frequency of second chicks being pushed and death by starvation of the second chick I performed a Logistic Regression with starvation status (starved vs. not starved) as the dependent variable and frequency of pushes to the second chick as the independent variable

Adult beak pushing

Adult beak pushing was scored when a chick contacted and exerted force on the adult's beak while another member of the brood was being fed. Each individual "push" was counted as a unit. A continuous sequence observation was used in order to record the outcome of the interaction. Three possible outcomes were recorded: (1) Lose = when initiator chick does not make the adult stop feeding the other chick, (2) Win = when initiator chick makes adult stop feeding the other chick and adult switches to feed the initiator chicks, (3) Win neutral = when initiator chick makes adult stop feeding the other chick but adult does not start feeding initiator chick. To investigate the relationship between death by starvation and second chicks pushing adults' beak during feedings, I performed a logistical regression analysis with starvation status as the dependent variable and pushing adult beak counts as the independent variable.

Parent – environment interaction analysis

In this study, I used food availability as the sole indicator of local environmental quality. I estimated potential food availability in the forests around the research center through the plant phenology of tree species consumed by Scarlet Macaws. Plant phenology information was collected monthly from November to February during 8 breeding seasons (2009 to 2018 excluding 2015) in a radius of 5 km around the research center. Phenology data were collected once a month by a single well-trained observer from 20 plots, five in each of four different habitats: successional forest, terra firme forest, palm swamp and floodplain forest. Each plot has about 70 trees over 10 cm diameter for a total of about 1300 trees. Presence/absence of four plant reproductive parts were recoded: unripe, and ripe fruits (Brightsmith et al. 2018). Because more than 80% of Scarlet Macaw recorded food items are ripe and unripe fruits (Brightsmith et al. 2006, Vaughan et al. 2006b, Lee et al. 2014) I recorded the presence and absence of unripe and ripe fruits for each tree species (Brightsmith et al. 2018).

I calculated an index of daily food availability using the monthly phenology data (percent of trees with ripe or unripe fruit) only for plant species known to be eaten by Scarlet Macaws. The list of plant species eaten by Scarlet Macaw was compiled from the literature and from direct observations done at my site (Gilardi 1996, Brightsmith et al. 2006, Vaughan et al. 2006b, Lee et al. 2014) and Brightsmith et al. Unpublished data). I fit lines between consecutive monthly phenology values and used the equations of those lines to calculate daily values of the estimated percent of trees with ripe or unripe fruit. I used the estimated percent of trees in the forest with ripe or unripe fruit as my index of daily food availability. I calculated the average index of daily food availability for each chick (total 17 second chicks: 8 chicks that starved and 9 chicks that fledged; 6 breeding seasons) during the following periods: (1) the seven days before and seven days after hatching (14 days total) and (2) the first 15 days of the life of the brood. Just chicks with hatching day known ± 1.5 days and with wild parents that were not supplementary fed were included.

In order to investigate the relationship between second chick death by starvation (starved chicks vs. not starved chicks) and the food availability in the forest I performed a logistic regression analysis using starvation status (starved vs. not starved) as the dependent variable and the average index of daily food availability for each chick as the independent variable. This analysis was repeated for both time periods (hatching ± 7 days and the first 15 days of the brood).

Parent- chick interaction analysis

Parental care analysis

To analyze interactions between parents and chicks I used chick feedings as the main indicator of parental care. Chick feeding was recorded when the adult grasped the bill of the chick crosswise from above and bobbed its head, transferring food by regurgitation. To quantify this behavior, I watched continuous video recordings from inside the nests taken during both day and night hours. I took focal group observations of known individuals from broods with two chicks. I recorded all feedings to each particular chick in a continuous manner each time it happened regardless of which parent was feeding and I calculated the number of feedings per hour for each chick in each brood.

Chick feeding rate comparison: double broods with starvation and double without starvation

To explore differences in feedings to first and second members of the same brood between successful double broods and double broods with starvation, I calculated the difference/hour between feedings to the first and feedings to the second member of the brood, irrespective of which adult was feeding. I calculated this difference during the "starvation period" (0 to 36 days of age for the second first chick of the brood) in all double broods without starvation and in double broods where second chicks starved to death. To determine general differences in chick feedings between first chicks and second chicks I performed a t-test. To determine the relationship between feeding rate differences and starvation of the second member of the brood, I grouped second chicks by survival status as follows: (1) Second chicks that starved and (2) Second chicks that fledged. I performed a nominal logistic regression using the difference of feedings/hour from second chicks as independent variable and "Second chick survival status in double broods" as dependent variable.

Chick feeding ratios

I calculated the relative proportion of second chick feedings to first chick feedings in each brood (the "C2/C1 feeding ratio"). When identity of chicks in a brood was not known for over 50% of feedings in a single video recording section, feeding counts from that entire video were discarded. In the case of broods with second chicks that starved, calculations were done for the period when both chicks were alive. In the case of brood with second chicks that fledged, calculations were included for: (1) the first 15 days of life of the brood and (2) for the starvation risk period (the first 36 days of life of the second chick of the brood). "Starvation risk period" is defined by the oldest age recorded for second chick death by starvation. Just individuals with at least 340 minutes of total observations were included in this analysis (average recording length =

4,142 min, range: 345 min to 12,517). Just chicks with hatching day known ± 2 days and with wild parents that were not supplemental fed were included.

To evaluate feeding differences between second chicks that starved and second chicks that did not starve I performed a t-test comparing C2/C1 feeding ratios. To analyze the relationship between second chick death by starvation (starved vs. not starved) and the relative proportion of feedings to the second chick over the first chick, I performed a logistic regression analysis with starvation status (starved vs. not starved) as the dependent variable and the C2/C1 feeding ratio as the independent variable.

Chick quality analysis

To investigate the relationship between chick death by starvation and body condition, I used weight at hatch as my indicator of chick quality. I included only second chicks with hatch date known by ± 1 day and with weight information collected when individuals were younger than 2 days old. I compared the hatching weights of second chicks that starved to death and second chicks that did not starve using a t-test. I also analyzed the relationship between hatching weight and chick death by starvation by performing a logistical regression analysis with starvation status (starved vs. not starved) as dependent variable and weight at hatch as the independent variable.

Hatching synchrony analysis

To investigate the relationship between chick death by starvation and brood hatching synchrony, I analyzed the age difference between first and second chicks of the same brood. To do this, I use broods with combined hatching date certainty of ± 2 days. I estimated hatching date certainty calculating the middle date between last date each particular egg was seen and first date its corresponding chick was found. Combined hatching date certainty is the addition of hatching date certainty from both chicks of the brood. Hatching date certainty of first chicks varied due to the fact that exact egg laid dates were not known in all of the cases because not all nests were checked every day before first egg was found. However, second chicks hatching date varied less because nests were normally being checked every day in order to monitor the first chick. A total of 29% of second chicks (n=81 chicks) were found within 24 hours of hatching. To analyze the relationship between first and second chicks' age difference and death by starvation, I performed a logistic regression with starvation status (starved vs. not starved) as dependent variable and the age difference between first and second and chicks from the same brood as the independent variable.

Results

Chick death by starvation (associated with) was the most common cause of death in macaw chicks in Tambopata. Over 45% of chicks that died starved to death (N= 137 chicks that died, Table 8). Death by starvation was not registered in broods with only one chick or for first hatched chicks in multiple chick broods. Of the chicks with known causes of death (N= 107 chicks), 60% of second chicks, 91% of third chicks and all fourth chicks died of starvation.

Section 1: Description of macaw chick starvation

Weight at hatch in chicks that starved

Overall, chick weight at hatch for chicks that starved was 22.4 ± 3.7 g (N= 47 chicks that starved: 20 second chicks, 22 third chicks and 2 fourth chicks from 12 breeding seasons). Weight at hatch was related to starvation status (starved vs. fledged, nominal logistic regression: n= 72 chicks, X^2=5.4, DF=1, p value= 0.02): chicks that starved (disregarding hatching order) hatched with a significantly lower weight than chicks that fledged (t test: n= 25 chicks that fledged and 47 chicks that starved, t ratio = -2.22, p value= 0.03). However, weight at hatch of second chicks that starved (24.34 ± 2.1 g) was not significantly different from weight at hatch from first chicks that fledged (27.3 ± 5.4 g) or second chicks that fledged (25.2 ± 2.8 g, ANOVA: n= 16 chicks from 8 double broods: 8 first chicks that fledged, 3 second chicks that fledged and 5 second chicks that starved, DF=2, F ratio=0.8, p-value=0.5). In addition, weight at hatch for second chicks that starved did not differ significantly from the first chicks in their own brood (ANOVA: n=16 chicks, 3 pair of chicks from double successful broods and five pairs of chicks from double broods with starvation, DF=3, F ratio=0.9, p value=0.5).

Growth description of chicks that starved

Chicks that starved usually showed very small or empty crops throughout their lives, averaging 0.8 ± 0.8 on a scale from zero to four (Table 12). Their daily weight was under the average daily weight of chicks that fledged (from 30 to 60% under), even when they reached their maximum weight. Nearly all died at a very young age (from 1 to 20 days old). One outlier chick died at 36 days old, after losing around 20% of the maximum weight reached. (for a graphical example see Figure 11 and 12).

Age at death significantly differed by brood order. Fourth chicks and third chicks died significantly sooner than second chicks (N= 16 chicks that starved: 8 second chicks, 14 third chicks and 3 fourth chicks. Pairwise Student's t test: T ratio ≤ -2.4, DF=23, $p \leq 0.03$).

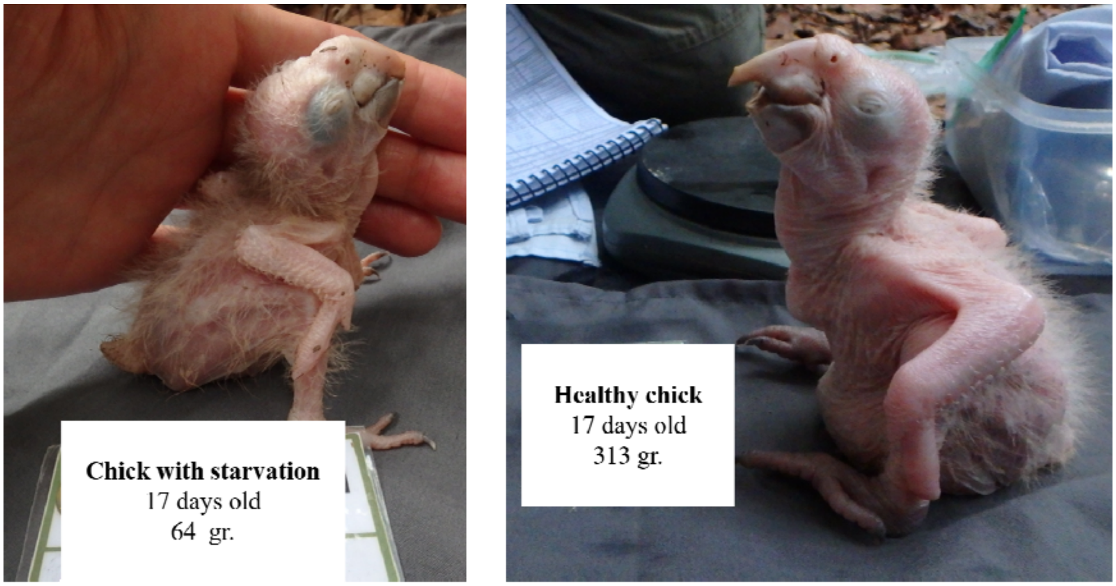

Figure 11. Photographic comparison between Scarlet Macaw chicks.
Second chick with starvation (left) and healthy second chick (right) at the same age. Ages and weights are showed in each picture.

Figure 12. Severe case of chick starvation in Scarlet Macaw.
The second chick (bottom) hatched four days after first chick (top). Signs of starvation (eg. stunted growth, reddish skin coloration and bulky eyes) are clearly seen in second chick. The first chick weighed 465 g at 22 days consistent with the expected weight for its age (465 g). The second chick weighed 96 g at 18 days, much less than the expected weight for its age (327 g).
The second chick (bottom) died at 25 days.

Table 12. General growth information by hatch order of Scarlet Macaw chicks that died of starvation. Hatch order refers to the order of hatch of each member of the brood (second to fourth). Weight is presented in grams. Age is given in days. Crop size refers to the size of the crop on a scale of 0 to 4 (0 =empty, 4=full) quantified in the field by an experience observer. Max weight is the highest weight registered throughout the life of each chick. Weight at death and age at death refer to the last values collected before the chick was found dead. A single chick that starved at age 36 was an outlier in all measurements and was removed from the data presented here (see text). Data from 18 consecutive breeding seasons from 2000 to 2018.

Growth Information	**Hatch Order**					
	Second Chick (n=8)		**Third Chick (n=13)**		**Fourth Chick (n=4)**	
	Mean ± St. Dev	**Range**	**Mean ± St. Dev**	**Range**	**Mean ± St. Dev**	**Range**
Weight at hatch	**21.7 ± 4.7**	15.6 - 29.7	**20.8 ± 2.6**	18 - 27	**18.9 ± 1.4**	17.2 - 20.5
Max. weight	**47.9 ± 23.6**	19.5 - 81	**28.3 ± 13.7**	18 - 68	**18.9 ± 1.4**	17.2 - 20.5
Age at max. weight	**7 ± 6**	0 - 18	**2 ± 2**	0 - 6	**1 ±1**	0 - 1
Weight at death	**37.1 ± 19.1**	17 - 65	**21.9 ± 9.1**	15 - 49	**16.9 ± 2.9**	13.6 - 20.5
Age at death	**10 ± 6**	1 - 17.	**6 ± 4**	2 - 14.	**3 ± 1**	2 - 4.
Crop size throughout its life	**0.8 ± 0.8**	0 - 2.1	**0.8 ± 0.8**	0 - 2.1	**0.7 ± 0.9**	0 - 1.8

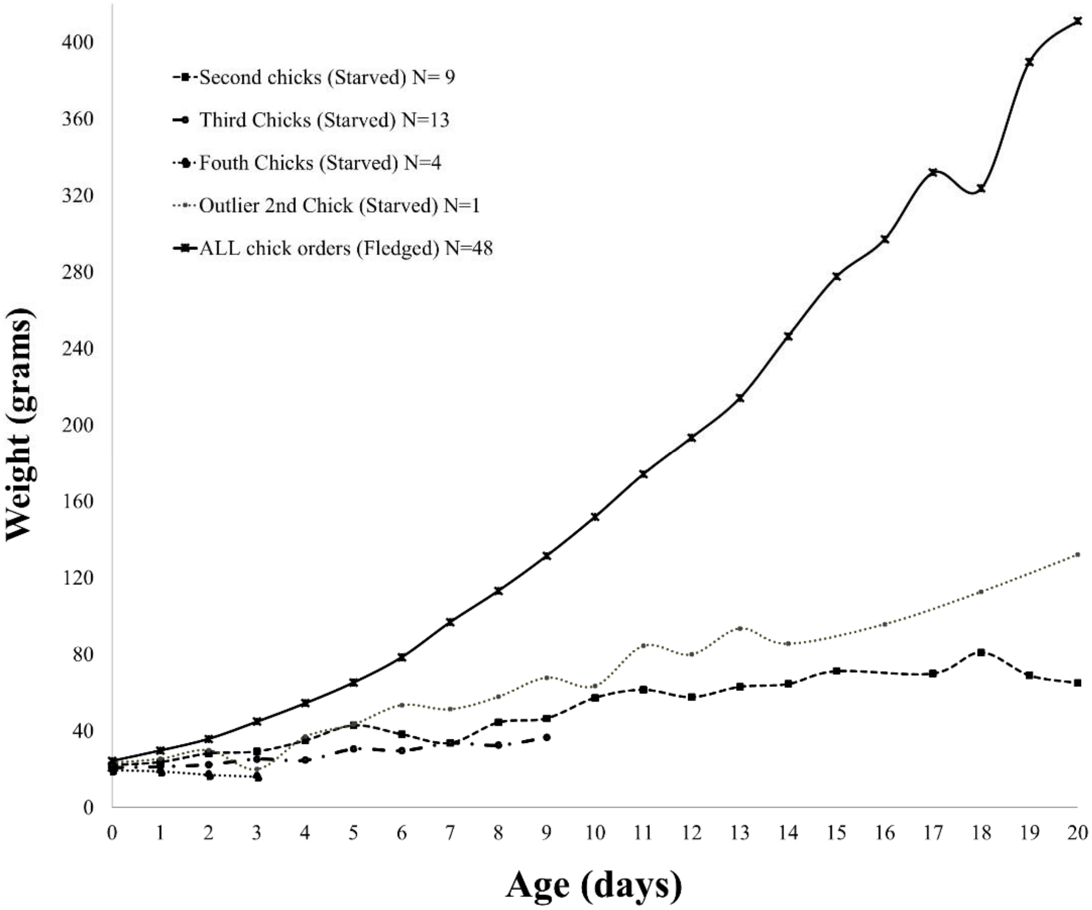

Figure 13. Weight gain in Scarlet Macaw chicks that died of starvation.

Dark dotted lines correspond to the average weight per day for chicks that starved, grouped by hatching order. The darkest line corresponds to the average weight of all chicks that fledge lumped for all hatching orders. The light dotted line corresponds to a second chick that starved at 35 days and was an outlier in all measurements. Weight is presented in grams and age in days. Lines for second, third and fourth chicks end on the day of maximum age of death by starvation for each group. Lines for fledged chicks and the single outlier are truncated at 20 days for graphing purposes. Data from 2000 to 2018.

Section 2: Drivers behind macaw chick starvation in Tambopata

In the following sections, I address in turn the hypotheses that death by starvation is due to: (1) chick-chick interference, (2) parent-environment interactions and (3) parent-chick interaction.

Chick- chick interaction

Chick pushing

I observed 47 times in which a chick was directly pushing with its body another chick's body. This was found during 56,022 minutes (~934 hours) of video analyzed from 51 chicks from 8 double broods, 11 triple broods and 1 quadruple brood over 7 breeding seasons. Of these, 12 broods had chicks that starved and 8 did not starve (age range observed= 0 to 79 days old). Pushing behavior was observed when chick ages ranged from three to 69 days old. This gives a rate of 1 push per 19.9 hours of observation. During these same videos, I recorded a total of 10,859 chick feeding events. The pushing to feeding ratio was about 1:231.

The frequency with which a second chick was pushed by a first chick was not significantly related to the death by starvation of that second chick (Mean pushes chicks starved = 0.0013 pushes/min, N= 7 chicks. Mean pushes chicks did not starve = 0.0007 pushes/min, N=13 chicks. Logistic Regression: N=20, $X1^2$ =0.31, DF=1, p-value= 0.58).

Chick pushing adults' beak while adult is feeding another chick

In 2426 chick-feeding events in 10,414 minutes of video analyzed, I observed just 5 times where a chick pushed the adult's beak while the adult was feeding another chick in the brood (n= 38 chicks, 4 breeding seasons 14 broods: 3 double broods, 11 triple broods; 4 broods with second chicks that died by starvation; age range observed = 0 to 36 days old). The behavior was observed when chick ages ranged from eight to 17 days old; when all brood members observed still had their eyes closed (average chicks opened its eyes at 17.4 ± 2.6). In all the cases, the chick that was pushed when it was been fed was the smallest sized of the brood. Of the 5 times, the pushing chick redirected the parent to feed it 2 times. Just first chicks successfully stopped adult feeding and redirected it towards themselves.

Pushing adults' beak during feedings was not significantly related to death by starvation of the second chick (Logistic Regression: n=14 second chicks: 5 chicks starved and 9 chicks did not starve, $\chi^2 = 0.21$, DF= 1, p-value = 0.65) or the third chick (Logistic regression: n=14: 13 chicks starved and 1 did not starve, χ^2=0.53, DF=1, p-value=0.70)

Parent – environment interaction

My index of Scarlet macaw food availability in the forest during the period from seven days before to seven days after hatching was not significantly associated with death by starvation of second chicks (Average % of trees with macaw food: for starved chicks= 35 +/- 0.02 %, for not starved chicks= 34.9 +/- 0.02, Logistic regression: N=14 second chicks: 5 starved and 9 did not starve, 6 breeding seasons, 4 +/- 0.9 chicks/season, X12= 0.01; DF=1; p-value=0.9). In addition, my index of Scarlet Macaw food availability in the forest during the first 15 days of life was not significantly associated with death by starvation of the second chick (Average % of trees with macaw food: for starved chicks= 35.4 +/- 0.01 %, for not starved chicks= 35.9 +/- 0.03, Logistic regression: N= 17 second chicks: 8 starved and 9 did not starve, 6 breeding seasons, 4.9 +/- 0.7 chicks/season, X12=0.28, DF=1, p-value=0.59). Similarly, food availability in the forest during the starvation period (the first 36 days of life), was not significantly associated with death by starvation of second chicks (Average % of trees with macaw food: for starved chicks= 35.4 +/- 0.01 %, for not starved chicks= 36.3 +/- 0.03; Logistic regression: N= 16 second chicks: 8 starved and 8 did not starved, 6 breeding seasons, 4.6 +/- 0.8 chicks/season, χ^2= 0.7, DF=1, p-value= 0.39).

Parent- chick interaction

Parental care

Chick feeding rates comparison: double broods with starvation and double broods without starvation

Overall feedings to first chicks averaged 5.4 ± 3 times/hour. This is significantly greater than feedings to second chicks (2.9 ± 1.7 per hr. N= 14 broods from 5 breeding seasons including 5 successful double broods and 9 double broods with second chick starvation, t-test: t=2.5, DF= 11.7, p value= 0.03).

In broods where both chicks fledged, the feedings to the second chicks averaged 1 ± 1.2 (N = 6) feeding/hour less than first chicks. In broods where the second chick starved, feedings to the second chick averaged 4 ± 2.8 (N =9) feedings/hour less than first chicks. The difference in feedings between the first and second chicks was significantly greater when the second chick starved than when the second chick fledged (Nominal logistic regression: N= 15 double broods, 9 double broods with second chick starvation and 6 successful double broods, R square= 0.3, X^2= 6.1, p-value=0.014).

Chick feeding ratios

Second chicks that died of starvation were fed significantly less than second chicks that did not die by starvation when compared to the first chicks in their broods (data from first 15 days of life for the second chick, C2:C1 feeding ratio for second chicks that starved: 0.46 ± 0.16, N = 9. C2:C1 feeding ratio of second chicks that did not starve = 0.77 ± 0.28, N = 5, t-test: -2.68, DF=5.45, p value= 0.04). A similar pattern was observed during the full chick starvation period (36 first days of life of the second chick, C2:C1 feeding ratio for second chicks that starved: 0.43 ± 0.23, N = 9, C2:C1 feeding ratio of second chick that did not starve = 0.84 ± 0.24, N = 5, t-test: -3.49, DF=8.1, p value= 0.008). Death by starvation was significantly negatively related to the

C2:C1 feeding ratio for both the 0 to 15 and 0 to 36-day periods (N= 14 chicks: 9 second chicks that starved and 5 that did not starve, Logistic Regression ($_{0\ \text{to}\ 15\ \text{days}}$): χ^2 = 7.6, DF = 1, P = 0.0058, Logistic Regression ($_{0\ \text{to}\ 36\ \text{days}}$): χ^2 = 8.31, DF = 1, P = 0.0039).

Chick weight analysis

Hatch weight did not differ significantly between second chicks that died by starvation and second chicks that did not starve (mean starved: 22.2 ± 5 g, N= 14 chicks, mean did not starve: 24.5 +/- 3.5 g, N = 21 chicks, t-test: t = -1.44, DF=21.5, p = 0.164). Moreover, death by starvation was not significantly related to weight at hatch (Logistic Regression: N= 35 chicks, 14 starved and 21 did not starve, X12= 2.43, DF =1, p=0.12).

Brood members age difference analysis

Second chicks that died by starvation hatched significantly later than second chicks that did not die by starvation (starved= 4.1 ± 2.2 days later, N=13; did not starve = 2.7 ± 1.1 days later, N = 33, t test: t= 2.14, DF= 14.4, p-value=0.04). The probability of death by starvation of second chick was significantly positively related to age difference between first and second chick (Logistic Regression: n= 46 second chicks, 13 starved and 33 did not starved; $X1^2$ = 6.96, DF=1, p-value= 0.008).

Discussion

Section 1: Description of macaw chick starvation

Chick weight at hatch has not been commonly used for comparisons in psittacines research. It was reported in a few parrot species in the wild, like in the Black-billed Amazon (Koenig 2001) and the Green-rumped Parrotlet (Stoleson and Beissinger 1997b) but mainly as part of chick growth analysis and not as a topic of its own.

In this study, chicks that starved (all hatching orders combined) hatched with a significantly lower weight than chicks that fledged and hatch weight decreased with hatch order (third and fourth hatched chicks significantly lighter than first hatched). It was expected than chicks that starved in general weighed less than the ones that fledge. It has been hypothesized that lower weight at hatch could be attributed to suboptimal incubation (egg rotation) that resulted in embryonal malpositioning that made hatching too long, difficult and energy/mass consuming, that resulted in a lower initial weight on latter hatched chicks (Vigo In prep CH 2) that are precisely the ones that starved.

What is interesting is that at hatching, second chicks that starved did not weigh differently than second chicks that fledge, or first chicks that fledge or older sibling from its own brood. These results suggest that second chicks that starved were incubated similarly to the ones that did not starve and consequently hatch with a similar body mass that could be an indicator that they were similar "quality" compared to the ones that did not starve and fledged. The fact that ~25% of second chicks starved to death is not likely to be related to initial chick body condition.

Growth description of chicks that starved

In chicks that starved to death in Tambopata, I registered (1) empty crop (Beissinger and Stoleson 1991), (2) slow decline in body condition (Enkerlin-Hoeflich 1995) and (3) malnutrition (Nycander et al. 1995), which are the three main characteristics related to chick death by starvation observed in psittacines in the wild. Psittacine "chick malnutrition" has been well documented in captivity because if not identified and treated on time, is a cause of reduced growth, stunting syndrome and chick death (Voren and Jordan 1992e).

All signs of malnutrition that I observed in chicks that starved to death in my study in Tambopata were already described by psittacine captive breeders. Malnutrition signs such as boney and thin appearance, dull (not bright) eyes, lower than expected weight for its age, eyelid opening very high instead of in the middle of the eye and poor growth rate, have been use for the last two decades to identify starvation problems and prevent chick death in captive breeding (Clubb et al. 1992d, Voren and Jordan 1992e, Abramson et al. 1995). The low weight gain and slow decline in body condition I observed in Scarlet Macaw chicks that starved, is called "stunted growth" in captivity. It has been described in great detail in captive macaw chicks (Clubb et al. 1992d, Voren and Jordan 1992e, Abramson et al. 1995). The two main stunting growth signs reported in captive breeding that I identified in chicks that died by starvation were (1) low or no weight gain and (2) disproportionally large head for the rest of the body. These are signs of early and intermediate stages of stunted growth respectively (Speer 1995). Signs of advance stunting, such as (1) weight loss, (2) grayish purple skin that is extremely tight on the body and (3) hyperactivity and loud when awake, were observed in Tambopata when chicks starved over a period of five days or longer.

My results of fourth and third and chicks dying sooner than second chicks may be related to the number of feedings each chick type received. My preliminary results on chick feeding patterns on chicks that starved showed that second chicks were fed a little, third chicks even less, and fourth chicks were rarely fed (Vigo unpublished data). In captivity, macaw hatchlings need to be fed as soon as they start to appear restless and vocalize a little (Abramson et al. 1995), which is around 4 hours after hatching (Mark Moore personal communications). After that, they need to be fed preferably every 2 hours or at least 9 times/day, otherwise they will dehydrate, lose weight and die (Clubb et al. 1992b). In Tambopata, fourth chicks starved to death quicker because they were rarely fed by their parents.

Section 2: Drivers behind macaw chick starvation in Tambopata

Chick-chick interaction analysis: siblicide

My results clearly show that sibling rivalry was not a cause of starvation of the second chick in Scarlet Macaw nests in Tambopata. The frequency of chick pushing observed was extremely low (0.05 pushes/hour) and it was not significantly related to second chick starvation. In additon, chicks pushed adults' beaks while feeding another chick just five times in over 10 000 minutes of video analyzed. My preliminary observations show that chicks displayed a subtle scramble competition "to try to get closer" to feeding parents but, due to the fact that chick's eyes were close when this action happened, it was not guaranteed that the chick was moving towards the parent. In the Scarlet Macaw in Tambopata, parents are apparently not distributing food based on the outcome of chick interactions

Parent-environment interaction analysis

I found that food availability in the adjacent forest was not significantly associated with death by starvation of the second chick; not during the first 20 days of life of the broods (older chick that starved to death), not during the first 15 days of life of the broods (average age of starvation of second chicks) and not during the 7-day period pre and post hatching. These results agreed with previous findings on the Green-rumped Parrotlet where brood manipulation and supplemental feeding experiments in the field showed that size differences among brood members influenced survival of last and penultimate chicks more than supplemental food provided (Stoleson and Beissinger 1997b). In that study, large broods (n= 8 chicks) where members were similar in size (hatched more synchronously), were able to raise all young whereas brood reduction happened when brood members' sizes were more dissimilar (hatched asynchronously). However, when last-hatched chick were supplemental fed three times during their first 17 days of life (~ 60% of its nestling period), its probability of fledging increased (from 20% to 60%) but it was still below that the early hatched chicks (> 90% probability fledging). Supplemental feeding did not increase survival of penultimate chicks (Stoleson and Beissinger 1997b). In the case of Scarlet macaw chicks in Tambopata, death by starvation of second chicks was not higher when there was less food available and it was not lower when there was more food available in the forest.

The majority of studies of wild psittacines have found evidence that refutes the idea that food limitation is the driver of chick starvation associated with. In the Red-crowned Amazon in Mexico, chick starvation related to brood reduction did not occur through food stress and starvation did not happen during the peaks in food demand (Enkerlin-Hoeflich 1995). In the Black-billed Amazon in Jamaica, starvation of the last (fourth) chick appeared to be a result of unequal distribution of food among siblings as a result of size differences associated with asynchronous hatching (Koenig 2001). In the Puerto Rican Amazon one chick died due to “inadequate nourishment” while two larger siblings were kept at high growth rates (Snyder et al. 1987b). Finally, in the Crimson Rosella in Australia, chick starvation was not higher in the driest year when there was presumably less food (Krebs 1999)

However, a few studies have found evidence that food limitation might be indirectly related to starvation of the second chick (brood reduction). In Australia, Black-cockatoos from a population where 5% of second chicks survived may have had more available food than in a location where no second chicks survived (Saunders 1982). Interestingly, populations that fledged second chicks foraged closer to their nests and in areas one fourth the size of populations where no second chicks survived (Saunders 1982). This suggests that there was a relationship with food but not necessarily with food availability but perhaps with parental ability to provision food adequately. Indeed, it was observed in the same species of cockatoo that hot weather reduced foraging time because parents, that usually forage all day long, foraged just in the early morning and late afternoon and not during heat of the day (Saunders 1982).

The lack of relationship between food availability and death by starvation of the second chick in my study could be attributed to: (1) a conflict with the scale of the area I quantified food availability, (2) an issue with chick diet specificity, or (3) a true lack of relationship between food and starvation. The area in which I quantified food availability could be too small. Scarlet macaw males have been recorded to travel >150 km from their nest sites in the non-breeding season but they seem to spend most of their time within 5 km of their nests when chicks are ≥ 40 days old (Brightsmith et al. In prep). At the moment, there is no information about macaw movements during the chick starvation period. A food availability quantification in an area bigger than 2.5 radius km would be needed to test this hypothesis.

Chick diet specificity could be important because hatchlings and very young macaw chicks may need a particular type of diet that could be different from the ones adult macaws eat the rest of the year. The list of plant species consumed by Scarlet Macaw used for my analysis comes from observation of foraging observations year around, not just from the breeding season or the time when chicks were very young. This hypothesis will be hard to test. Wild macaw chicks diets in the wild have been studied (Cornejo 2012) but only for chicks older than 20 days, which is over the average age of starvation of second chicks. To obtain crop samples from <20 days old chicks would be extremely difficult because diameter of tubes and sampling utensils is not wide enough for the size of seeds hatchlings are fed (Vigo personal observation). To trap parents to obtain crop samples when chicks are that small could put in danger the survival of the whole brood because of possible changes in nesting behavior that may interfered with chick brooding and feeding.

Parent-chick interaction analysis

<u>Parental care</u>

I found that Scarlet Macaw shows direct control of food distribution within the brood. Parents actively allocated more food to first chicks and less to second chicks, even in broods where second chicks did not starve to death. In addition, difference in feeding of first chicks when second chicks starved was significantly larger than when second chick fledged. Direct control of food distribution within the brood was also reported in captive Budgerigars (Stamps et al. 1985), wild Crimson Rosellas (Krebs et al. 1999) and wild Green-rumped Parrotlets (Budden and Beissinger 2009). In all of the cases, including my study, parents fed responding little to nestling behavior, especially when chicks were very young, blind and with low locomotion control (< 10 days old).

In contrast to my findings, in Budgies (Stamps et al. 1985) and Crimson Rosellas (Krebs and Margrath 2000) last-chicks were selectively fed more; especially by the female. Females budgies fed all chicks equally regardless of hatching order but undersized nestlings were fed as though they were younger and last-hatched were preferably fed first (Stamps et al. 1985). In the Crimson Rosellas, brood manipulation experiments showed that hungry last-hatched chicks were fed more by both male and female but when the whole brood was hungry, parents were not able to compensate and chicks lost mass over the day. In this case, males switched to feed all brood members and female switched to feed first chick (Krebs and Margrath 2000). Apparently, when adverse conditions started compromising chick survival, females fed the chicks that had already received a bigger energy investment with the hope of fledging at least one chick. It is possible that the Scarlet Macaw in Tambopata has a similar chick feeding strategy and that is why they preferer to feed more first-hatched chicks. However, it is difficult to infer similarities from feeding behavior registered in the Crimson Rosella because the experiment was done five days after the end of the starvation period of the species (3 days old) and my feeding observations with Scarlet Macaw chicks were done during the starvation period. It is possible feeding strategies and patterns change after brood reduction is completed.

Interestingly, the two patterns of direct food allocation registered in psittacines are not rigid. The one where preferences favor last-hatched young vary in relation to brood size (small vs. large broods, Krebs and Margrath 2000) and the one that disfavor last-hatch (Budden and Beissinger 2009) vary in relation to chick hunger (individual vs. whole brood hunger). These suggest that psittacine parental food allocation patterns might not be the same throughout the nestling stage. Indeed, the fact that growth parameters between first and second Scarlet Macaw chicks that fledged are not significantly different (Vigo et all 2010) points to a change in direct control of food allocation that favors second chicks and allows it to catch up and grow similarly to the first sibling.

Similar to my findings, in the Green-rumped Parrotlet, last-hatched chicks in the broods were fed less. However, in that species, parental and maternal food allocation strategies differ in relation to brood size. Last-hatched chicks from large broods (n=8 chicks) were fed less by females than in small broods (n=4 chicks). Besides, in small broods, females fed all chicks evenly but in large broods, females fed smaller chicks more frequently but not the last-hatched one. Males fed small offspring less often in both, small or large brood sizes (Budden and Beissinger 2009). In Tambopata, circumstantial evidence from parent-chick interactions showed differences in parental/maternal chick food allocation strategies; such as males feeding starving chicks that females are not feeding anymore (Vigo personal observations). It is possible that Scarlet Macaw chick food allocation strategies are similar to the Green-rumped Parrotlet but this hypothesis needs to be tested.

Chick feeding ratios

The difference in feeding ratios between second chicks that fledged and second chicks that starved clearly shows that Scarlet Macaw parents were not only directly allocating more food to one specific chick but also directly limiting food to another one. I have observed parent-chick interactions from different nests in which the female keeps trying to feed first-hatched chicks when their crops are completely full while the second-hatched chick is in the other side of the nest, begging, with an empty crop.

My findings of adults directly limiting food allocation to second chicks that starved are similar to observations on chick crop contents done in the Green-rumped Parrotlet that showed that food was not distributed evenly within brood. In that case, crop contents revisions three times per day showed that intermediate chicks in control nests (chick order 5) were fed at least once per day but penultimate chick had 8% probabilities of not being fed for an entire day and 25% of last-hatched chicks were not fed for an entire day. Therefore, food distribution among chicks in large brood was extremely unequal (Stoleson and Beissinger 1997b). Other species of parrots such as the Black-billed Amazon (Koenig 2001) and the Crimson Rosella (Krebs and Margrath 2000) have also recorded empty crops in last-hatched chicks that later died of starvation. Similarly to the Green-rumped Parrotlet (Bonebrake and Beissinger 2010), starvation of the second chick in Tambopata resulted from unequal food distribution rather than food scarcity

Chick quality

I did not find a significant relationship between weight at hatch and death by starvation of second chicks. In addition, all second chicks analyzed (starved and not starved), hatched with statistically similar weights. These findings support my previous results in this topic that showed that, when comparing whole double broods with and without starvation, second chicks that starved hatch weight was not different from first or second chick that fledged. I was unable to find literature relating chick weight at hatch and chick starvation. However, experiments done with wild Green-rumped Parrotlet suggested that mass at hatching for later hatched was similar to earlier hatched because egg volume, which was the variable measured, did not significantly differ by laying order. (Beissinger and Waltman 1991). Indeed, strong correlations were found between egg weight and hatch weight in Japanese Qual (Marks 1974). In experiments with chickens, chick weight at hatch was related to two factors. (1) Storage periods, where long incubation delays reduced hatchling weight and (2) Hen age, where hatchling weight significantly increased with hen age (Ruiz and

Lunam 2010). My results show that chick initial body condition by itself cannot explain starvation of the second chick. In Tambopata, some of the heaviest and some of the lightest second hatchlings died by starvation.

Brood member age difference

Age differences between first and last hatched wild psittacine chicks, can span from 7 to 16 days and result in huge size disparities among brood members (Stoleson and Beissinger 1997b). My analysis indicates that the larger the age difference between brood members the more likely the second chick would starve to death. When second chicks hatched up to two days after the first chick hatched, it had just a 6% chance of starvation but when it hatched over 5 days later, its chances of starving increased to over 80%. Similar findings come from brood manipulation experiments done in the Green-rumped Parrotlet. In those experiments, probability of survival to fledging was a function of the size and degree of synchrony of the brood, and of hatch order within the brood (Stoleson and Beissinger 1997b). The research showed that last-hatch and penultimate hatched chicks in large synchronized broods (smaller age difference among brood members) had low probability of starvation but a few of these youngest chicks fledged from experimentally asynchronized broods with large age differences among brood members.

My results agree with the suggestion from the literature that large chick size differences related to hatching asynchrony is likely the cause of chick starvation associated with (Stoleson and Beissinger 1997b, Koenig 2001, Budden and Beissinger 2009). In the Scarlet Macaw, a 5 day old chick weighs 62.6 +/- 10.8 gr, which is almost 3 times the weight of a hatchling (Vigo Trauco 2007). Therefore, a brood with members with such a large size difference will surely be disadvantageous for the younger one; especially in a species that direct allocates food to the first hatch (this chapter).

However, my results from Scarlet Macaw brood manipulations showed that big size differences (over 250 gr difference) did not affect survival of small brood members when chicks were older than 20 days old because both brood members were in the same developmental stages (see description of developmental stages Vigo In prep CH 4)). A 20 days old and a 30 days old chick (Stage II-B chicks) are in the same growth stage, with similar parental care needs. But a hatchling (Stage I chick) and a 5-day old chick (Stage II-A chick) display different mass growth patterns (Vigo et al. 2011b) and because of that, their parental care requirements are different. Indeed, in very young psittacines, feeding and brooding requirements are extremely age specific (Voren and Jordan 1992b). A newly hatched chick and a 3-day old chick do not have the same feeding and brooding necessities. Recommended brooding temperatures in captivity for newly hatched macaw chicks and 5-9 days old chicks differ by over 6 degrees C. Indeed, it is well known by aviculturist that < 5 days old chicks need to be monitored separately because temperature is critical during this stage of development to such an extreme that temperature fluctuations can be fatal to the chicks (Clubb et al. 1992b, Voren and Jordan 1992e). All these evidences suggest that the differences in developmental stage are indeed the reason why second chicks that hatched more spread apart from their older sibling starved to dead more often. My findings suggest that Scarlet Macaw nesting pairs are able to adjust individual parental care for chicks with up to 4 days age difference between first and second hatch and reach almost 75% of fledgling success for the second chick. In the case of large age differences (over 5 days) if breeder (or parents in the wild) fail to provide specific feeding and brooding care to the younger chick, its condition will deteriorates quickly and most likely die (Voren and Jordan 1992b).

Conclusions

In this study, I analyzed chick starvation associated with and found that chick starvation is the leading cause of chick mortality at my site, 27% of all second hatched chicks starve, and nearly all third and fourth hatched chicks starve. I found no evidence that death by starvation was caused by (1) sibling rivalry, (2) macaw food availability in the forest, or (3) hatch weight. I did find that (1) direct control of food distribution within the brood favors first hatch chicks but specifically disfavors second hatch chicks that starve to death and (2) the larger the age difference between brood members the more likely the second chick would starve. In this study, my findings showed that macaw chick starvation associated with is related to the inability of parents to direct allocate food based on chick developmental stage when brood member age difference is large. I conclude that differences in chick rearing requirements related to large age differences between chicks resultant from hatching asynchrony are the main driver for death by starvation of second chicks in Tambopata.

Wild psittacine populations are declining all over their ranges, and the Scarlet Macaw is not an exception (Olah et al. 2016). It is important to understand their incubation patterns and reproductive strategies, not only to increase our knowledge of the species but also to promote their conservation in the wild in an effective manner (Beissinger and Snyder 1992). This is especially true when 50% of chick production per breeding season is lost associated with, like in the Scarlet Macaw in Tambopata (Vigo In prep CH 2). From a conservation perspective, it is pointless to let a heathy new hatchling macaw chick starved to death. My research findings on chick death by starvation give a starting point for conservation practitioners, the age difference among brood members, that can be used as a predictor in chick manipulations in order to increase chick survival and population recruitment in the wild.

CHAPTER IV

INCREASING SURVIVAL OF WILD MACAW CHICKS USING FOSTER PARENTS

Introduction

The use of foster parents in avian population management is a technique with great potential to aid in the recovery of highly endangered species in the wild (Cade 1980). Foster parenting, the use of breeding pairs to raise young that were not part of their initial broods, is a well-known aviculturist technique that has been intensively used in captive breeding and reintroduction programs over the last decades (Saint Jalme 1999) and also in conservation captive breeding programs to increase reproduction (Cade 1980, Fentzloff 1984, Snyder et al. 1987a, Romer 2000). However, few studies have systematically studied how to successfully use this tool in the wild.

The topic of increasing productivity in parrots with conservation purposes is not new. Back in the early 90's, it was suggested that managing intensively the factors that limit population growth in a particular species was the key to productivity maximization (Beissinger and Snyder 1992). One of the techniques proposed at the time was to increase fledging success (Beissinger and Butcher 1992). In psittacines, the majority of species hatch their eggs asynchronously over a period of 1 to 14 days (Rowley 1980, Snyder et al. 1987b, Beissinger and Waltman 1991, Marineros and Vaughan 1995, Krebs 1998, Vaughan et al. 2003b, Sanz and Rodriguez-Ferraro 2006, Vigo et al. 2011b) which results in a size based hierarchy among brood members (Smith 1975, Beissinger and Waltman 1991, Vigo Trauco 2007) which often leads to the death of younger chicks (Rowley 1980, Beissinger and Waltman 1991, Krebs 1998, Raso et al. 2006, Vigo et al. 2011b). In this scenario, decreasing hatching asynchrony has been proposed as a potential management tool to increase numbers of young for harvesting with conservation purposes (Beissinger and Butcher 1992) . Last and penultimate chicks could be relocated in foster nests to increase overall reproductive output.

This technique has great potential for in-situ conservation efforts because there is strong evidence that psittacines can be successfully used as foster parents and they are able to raise and fledge additional chicks (Rony Garcia, personal communications, Sanz and Rojas-Suárez 1997).

Chick fostering has been successfully used in commercial aviculture to raise finches (*Lonchura estriata, Lonchura cucullata, Lonchura cantas*, etc) and with captive psittacines of the genera *Cylopsitta, Alisterus, Amazona, Pionus* and *Cacatua* (Rowley 1980, Stoodley 1986, Snyder et al. 1987a, Dingle 1998, Romer 2000), mainly as an emergency tool when chicks were rejected by parents or fell out of the nest (Stoodley 1986, Yantz 1986, Dingle 1998). It has also been used in captive breeding programs for psittacines (Snyder et al. 1987a, Romer 2000). In the wild, it had proven to be useful for recovering the Puerto Rican Amazon (Snyder et al. 1987a) and increasing population recruitment in the Yellow-shouldered Amazon in Venezuela (Sanz and Rojas-Suárez 1997). It has also been used as a tool to study parent/offspring interactions in Crimson Rosellas (Krebs et al. 1999) and Galahs (Rowley 1980) in Australia.

The Scarlet Macaw (*Ara macao*), one of the most iconic members of the Psittacidae family and an important flagship species of the tropical forest, is widely distributed in the Americas from Southeastern Mexico to Peru and Bolivia (Forshaw 1989).However, most populations in Central America are currently declining due to a combination of habitat loss and poaching for the local pet trade (Rowley and Chapman 1991, Wiedenfeld 1994, Iñigo-Elias 1996, Krebs 1999, Portillo Reyes 2005, Vigo et al. 2011b). As with many other members of the Psittacidae family, the species shows brood reduction by chick starvation (Vaughan et al. 2003b, Vigo et al. 2011b). This starvation results in the death of 22% of all hatched chicks and is the most common cause of chick death (Vigo Trauco 2007). In Tambopata, Peru, an area with no nest poaching, clutches have on average three eggs, resulting in broods of about two chicks but just a mean of 1.4 chicks fledge per nest per season (Vigo In prep CH 2). Overall, 27% of second chicks and all third and fourth chicks die by starvation, which results in a substantial loss of hatchlings. In areas where Scarlet Macaw populations are declining, valuable chicks that could help increase population numbers starve to death. Increasing survival of those starving chicks could provide significant numbers of young that can directly increase wild populations. Those chicks are the core of my experiments on foster parents in Tambopata.

There is little information published on Scarlet Macaws as foster parents. In the late 90s in Carara National Park in Costa Rica one chick rescued from poachers was placed in a wild nest that had just one chick and both chicks fledged (Vaughan et al. 2003b). There are also reports from captivity where a Scarlet Macaw pair was used as a surrogate to raise chicks of the Blue-headed Macaw (*Primolious couloni*, Bentin and Leyva 2018). In a conservation project in Guatemala, Scarlet Macaw chicks as old as 30 days were placed in macaw nests that already had one chick. The additional chicks were successfully adopted and fledged even though age differences between brood members was >15 days (Rony Garcia personal communications).

The use of Scarlet Macaws as foster parents in the wild offers a good system not only to test the technique in-situ, but also to test the main drivers of chick death by starvation. The main driver behind death by starvation appears to be brood members' age difference: first chicks apparently do not die of starvation and the chance of younger chicks starving is directly proportional to age difference in relation to the first chick of the brood (Vigo In prep CH 3). In the case of second chicks, if age difference was 3 to 4 days the probability of death was 24% but if this difference was 5 days or more, the probability of death by starvation jumped to 80% (Vigo In prep CH 3). If age difference among brood members is merely the ultimate reason why the younger member of the brood starved to death, age differences in foster broods would need to be less than 5 days to ensure that none of the brood members will perish.

The main objective of this paper was to develop and test new techniques to increase survival of Scarlet Macaw chicks in the wild by reducing chick starvation using foster parents. In addition, I wanted to test if the age difference among brood members was the sole driver of chick death by starvation. To do this, I tested the following main hypothesis:

H1: Wild Scarlet Macaws accept chicks that are not their offspring and raise them until fledgling.

H2: Using foster parents increases the survival of chicks at risk of starvation and increases the overall population reproductive success

H3: Age difference among brood members is not the only ultimate driver of chick death by starvation.

Methods

Study site

This research was done in the forests surrounding the Tambopata Research Center (13º8'S, 69º36'W); located in the Tambopata National Reserve (275,000 ha) adjacent to the Bahuaja-Sonene National Park (1,091,416) in the state of Madre de Dios, southeastern Peru. The forest adjacent to the research station is defined as tropical moist forest (Holdridge life zones system) and is a combination of flood plain, terra firme, successional, and palm swamp forests that receives around 3200 mm of rain annually (Tosi 1960, Brightsmith 2004)

Background methodology

I conducted my research during three consecutive breeding seasons, as part of a program of investigation on Scarlet Macaw breeding ecology, nesting behavior and health run by The Macaw Society, www.TheMacawSociety.org and http://vetmed.tamu.edu/macawproject (Brightsmith 2001, Brightsmith et al. 2008, Gish 2009, Olah et al. 2014). Macaw nests were monitored from mid-

October to mid-April every breeding season. Each season I monitored about 40 macaw nests (16 natural, 24 artificial) using single rope climbing systems as described in (Perry 1978, Perry and Williams 1981). Eight nests per season were equipped with video surveillance cameras. All nests were checked once every 2 – 3 days until the first egg was found. After an egg was found, nest monitoring ceased until 26 days later and continued daily until all viable eggs had hatched. In order to reduce disturbance at the nest and maximize hatching success, I did not weigh, measure or manipulate broods until the second chick hatched in each brood.

Chick relocation procedures

Criteria to remove chicks for relocation

Macaw chicks were removed from their original nests according to the following criteria. First chicks were removed if second chicks hatched >3 days after the first chick (n= 7 chicks), if they showed signs of life-threatening botfly related infections (n= 1 chick) or when adding a foster chick as the younger brood member (n=3 chicks). Second chicks were removed if they showed signs of starvation (n=5 chicks), signs of life-threatening botfly related infections (n=2 chicks) or if the chick was needed for relocation to another nest where the clutch or brood was depredated but parents kept visiting the nest (n=1 chick). All third chicks (n=11 chicks) and all forth chicks (n=2 chicks) were removed regardless of age differences with brood mates because of their nearly 100% chance of starvation if left with the parents.

Timing to remove chicks from original nests

Where the second chick hatched >3 days after the first, the first chicks were removed as soon as the younger sibling hatched. First and second chicks with signs of botfly related infection were removed when infection was clearly getting worse, but was still localized in one area. Second chicks with signs of starvation were removed when they were still active and begging (usually within 3 days of not gaining weight as expected, before they started to lose weight). Third and fourth chicks were removed immediately after hatching. In total, I removed eleven first chicks, eight second chicks and eleven third chicks and two fourth chicks from their nests for use in this experiment.

Criteria to remove chicks for relocation

Macaw chicks were removed from their original nests according to the following criteria. First chicks were removed if second chicks hatched >3 days after the first chick (n= 7 chicks), if they showed signs of life-threatening botfly related infections (n= 1 chick) or when adding a foster chick as the younger brood member (n=3 chicks). Second chicks were removed if they showed signs of starvation (n=5 chicks), signs of life-threatening botfly related infections (n=2 chicks) or if the chick was needed for relocation to another nest where the clutch or brood was depredated but parents kept visiting the nest (n=1 chick). All third chicks (n=11 chicks) and all forth chicks (n=2 chicks) were removed regardless of age differences with brood mates because of their nearly 100% chance of starvation if left with the parents.

Timing to remove chicks from original nests

Where the second chick hatched >3 days after the first, the first chicks were removed as soon as the younger sibling hatched. First and second chicks with signs of botfly related infection were removed when infection was clearly getting worse, but was still localized in one area. Second chicks with signs of starvation were removed when they were still active and begging (usually within 3 days of not gaining weight as expected, before they started to lose weight). Third and fourth chicks were removed immediately after hatching. In total, I removed eleven first chicks, eight second chicks and eleven third chicks and two fourth chicks from their nests for use in this experiment.

Removed chicks' initial conditions

The majority of the chicks (67%) arrived healthy to my nursery. Eleven first chicks and nine third chicks weighed as expected for their ages according to data in Vigo et al (2011a). Two third chicks arrived underweight (17.9 gr/ each one), one with early signs of dehydration and the other one with apparent good condition. Three second chicks were brought in as soon as they did not gain weight as expected but were still in the range for their ages. One of the second chicks arrived underweight for its age, showing signs of starvation (empty crop, grayish color, dry skin and prominent ocular area). Another second chick that showed a congenital foot malformation was brought as soon as it did not gain weight as expected for its age, at 2 days of age. The three chicks showing signs of botfly related infection did not have botflies when arrived to the nursery because they were removed in the field. Both fourth chicks arrived underweight. One arrived right after hatching with 17.1 gr and the other one, that was left in its original nest with a sibling 9 days older, was removed at age 5 when started to showed early signs of starvation.

Macaw chick rearing in the nursery

Chicks were kept in a box with three solid wood sides, a solid wood base, and a wire mesh front and top. I used a Brinsea EcoGlow Brooder for chicks as a source of heat. Heat and humidity in the box were monitored with an off the shelf digital thermometer-hygrometer. Chicks were maintained at temperature and humidity conditions following the recommendations in Voren and Jordan (1992d). In general, chicks were syringe fed Zupreem Embrace baby bird hand feeding formula prepared following the age specific manufacture recommendations (https://www.zupreem.com/products/birds/embrace-plus/). Chicks that came in sick, weak or underweight were given custom diets used commonly in commercial aviculture (for more details see Appendix 1). All chicks that arrived showing signs of botfly related infection (N = 4) were treated with oral antibiotics and/or local antibiotic cream.

Criteria to assign macaw chicks to wild macaw nests

Individual chicks were assigned to foster nests with only one chick that was in the same "developmental stage" but not necessarily the same age. To define the macaw chick developmental stages, I used the four mass growth stages presented in (Vigo et al. 2011b) with the following modification: I divided Stage 2 in two sub-stages around the age of eye opening, about18 days. Therefore, my five developmental stages for macaw chicks were: Stage 1, 0 to 2 days old (hatchling), Stage 2A, 3 to 18 days old (naked to light pinfeathers & eyes closed), Stage 2B, 19 to 33 days (light pinfeathers to heavy pinfeathers, eyes open), Stage 3, 34 to 65 days (heavy pinfeathers to mostly feathered), and Stage 4, 66 days to fledging (mostly feathered to fully feathered).

Criteria to select foster parents

Previous studies using foster parrots in wild psittacines have recommended a number of characteristics for foster parents that may influence in acceptance of foster chicks (Snyder et al. 1987a, Sanz and Rojas-Suárez 1997). I have modified these recommendations using my previous knowledge of the species in the area in order to create criteria to select nesting pairs to host foster chicks. The majority of nesting pairs used as foster parents were selected using the following criteria: (1) Pairs nesting in artificial nests; (2) Known pairs (banded individuals) older than 8 years old; (3) Pairs with at least one chick that fledged in a previous season; (4) Pairs with no records of chick death by unknown reasons; (5) Pairs with no records of chick death due to poor parental care in solo chicks, such as hypothermia or low daily feeding rates; and (6) Pairs with no records suggesting they have little breeding experience, such as slow growth/poor body condition in chicks. Due to a lack of suitable nesting pairs, one foster chick was place with an unknown nesting pair.

Foster chick relocation experiments and timing

Macaw chicks were placed back with wild macaw nests as part of four complementary experiments.

Experiment 1: Acceptance (n= 11 chicks)

The goal of this experiment was to test whether or not wild macaws would accept chicks that are not their own and raise them until fledgling. For this, I chose nests where there was a single resident chick. Into this nest I placed a foster chick that was within 2 days of age of the resident chick (≤2 days older or younger). When the resident chick was younger than the foster chick, I placed the foster chick in the nest within 48 hours of the resident chick opening its eyes (~18 days old). When the foster chick was younger, it was placed in nest as soon as it had fully opened its eyes (approximately 17 days old).

Experiment 2: Age difference (n=10 chicks)

The goal of this experiment was to test that absolute age difference does not drive death by starvation. For this, I chose nests where there was a single resident chick and I placed a single foster chick that was ≥3 days older than the resident chick. Foster chicks were placed in wild nests within 48 hours of the resident chick opening its eyes at 18 days on average. In all but 2 cases, the foster chick was the biological sibling of the resident chick.

Experiment 3: Empty Nest Acceptance (n=5 chicks)

In order to test whether or not wild macaws accept chicks and raise them to fledging, even when they do not have eggs or chicks at the time of relocation and when adoptive chicks are large and old, I did the following. At a macaw nest where the chicks had been depredated, within 36 hours of predation, I placed a foster chick in the nest that was in the same developmental stage as the depredated resident chicks. At a nest where the natural eggs failed to hatch but the pair was still incubating an artificial egg (as part of a distinct study on incubation) I placed a < 3-day old foster chick in the nest at about the time of expected hatching.

In experiment 1 and experiment 2, the "opening eyes" represented the key moment to place the foster chick in its foster nest. By having both chicks with open eyes, all chicks were able to see the parents and effectively beg for food in a similar fashion. On average, chicks were placed back in nests at 22 +/- 9 days old (min =14, max= 46 days old, n= 28 chicks).

Experiment 4: Experimental triple brood (n=2 chicks)

In order to test if an additional chick would be accepted in a double brood, I added a third chick in a nest with two chicks, as the younger member of the brood. The third chick was removed from the nest at hatching, and placed in the nest when 18 days old. The day the third chick was placed, the first chick was removed from the nest to give the third chick a chance to become accustomed to life with the parents. The first chick was then placed back in the next 5 days later. All three brood members in this experiment were full siblings hatched over a period of 5 days. Details about this experiment are presented elsewhere.

Foster chick relocation schedule

In all but three cases, foster chicks were placed in nests between 8:00 and 9:30 AM with a crop half-full of food. At the time of the relocation, the resident chick was pulled from the nest weighed and measured and then both chicks, the resident and foster were placed back into the nest at the same time. In the three relocations following chick/egg predation, foster chicks were placed in the nest between 11am and 2pm. No chicks were relocated on rainy days.

Observations of foster parents/foster chick interactions

In 13 of 15 foster nests, an experienced observer arrived at the foster nests at about 5:00 AM on relocation day and took observations of parent/chick interactions using the nest video system until 5 pm. Observers took focal group observations of known individuals to record all contact and feeding behaviors between the parent and the chicks. The recorded behaviors were (1) feeding, (2) preening and (3) brooding. Feeding refers to when adults grasp the bill of the chick crosswise from above and bob during regurgitation. Preening refers to when an adult gently touches the chicks' body with its beak in a continuous manner. Brooding refers when an adult position its body in direct contact with chick's body. I considered the time nesting individuals (nesting females or nesting males) enter the nest and are visible on the video camera as the moment of awareness of foster chick presence in the nest.

Monitoring of foster chick in receiver nest

I intensively monitored each foster nest for 10 days after each foster chick relocation. The monitoring process included (1) checking for foster crop content twice per day (5am and 5pm); (2) providing supplemental food to the foster chick any time I checked the nest and found its crop was more than half-empty (aka fed from 0 to 2 times per day), (3) monitoring weight gain by weighing both chicks at 5:00 am daily; (4) monitoring interactions between the foster chick, resident chick and foster parents using video security cameras with an observer in the field when cameras were available (13 foster nests with video cameras); (5) counting feedings per day of both foster and resident chicks as seen through the video surveillance cameras both live in the field and later from video recordings when cameras were available (See appendix 4, for details of hours analyzed). To count feedings, I performed a focal group observation of known individuals. I recorded all feedings of each particular chick in a continuous manner each time they happened.

Supplemental feeding plan after relocation of foster chick

Our objective with the supplemental feeding was to allow foster parents, foster siblings and foster chicks to learn how to interact with each other without compromising the foster chick's nutrition and overall health. I assumed that it would take time for foster parents to adjust to new brood size requirements and for foster chicks that were syringe fed prior to introduction, to learn how to consume chunky food regurgitated by the adult macaws. Our supplemental feeding plan had three stages. (1) Intensive supplemental feeding period. (from the day that the foster chick was placed in the foster nest to 10 days after relocation). The foster chick was checked and fed twice per day until the crop was ¾ full. I decreased the supplemental feedings slowly, until a half-full crop around day 5 after relocation, in order to stimulate chick begging from the foster parents. In extreme cases (n=2 chicks), foster chicks were just fed once (in the afternoon) in order to promote hunger and begging by the foster chicks. (2) Moderate supplemental feeding period (from day 10 after foster chick relocations until the foster chick was 40 days old). I checked the foster chick every day and provided supplemental food when the foster chick gain weight was less than 50% of the expected weight for its age on two consecutive days. (3) Passive supplemental feeding period (from 40 days old until foster chick fledged). I checked the foster chick every other day and provided supplemental food if its keel was perceivable but there was moderate breast muscle development still found around it (body condition score = 2, Gregory and Robins 1998). In my first seasons, resident chicks were not supplemental fed. In my second and third seasons, 75% of resident chicks lost weight during the 10-day adaptation period (n= 12 resident chicks). To address this, resident chicks were given supplemental food when the daily weight gain was 50% less than expected for its age. In all resident chick supplemental feeding cases, the crop was left only half full.

Foster chick acceptance criteria

I established three levels of foster parent acceptance of foster chicks. (1) Initial level: foster parents preen foster chick repeatedly and/or start attempting to feed foster chick. Attempts to feed refers to when the foster parent grabs the foster chick beak in an attempt to start regurgitation and then releases the beak. (2) Intermediate level: foster parents consistently feed foster chick (as seen by video camera) and/or foster chick shows a half-full crop on daily checkups, (3) Advanced level:

foster parents feed both foster chick and resident chick similarly. When the foster chick was the solo chick in the nest, I established just one level of foster parent acceptance, as when the foster parents start feeding the foster chick. Foster chick relocation was considered successful when the foster chick was being fed by foster parents.

Foster chick acceptance analysis

Acceptance of foster chicks by their new parents was quantitatively measured in the following ways.

Chick feeding ratios

In order to show how foster parents were accepting foster chicks I calculated a ratio of feedings per day (foster/resident chick) for each day in each nest during the first 10 days after relocation. I analyzed feeding ratios collected in two different ways: from direct field observations (1 season) and from video recordings (2 seasons). A total of 418 hours was observed in the field by multiple observers and 573 hours of video were scored by a single observer (Table 1). Feeding ratios from video observations include 227 hours of night observations.

Foster chick growth

In order to evaluate foster chick quality and acceptance I calculated the logistic growth curves of the 23 foster chicks that fledged and compared them with the growth curves of the 81 wild macaws that fledged in my study area during the previous 19 breeding seasons (Vigo et al. 2011b). For this analysis, I only included chicks with weight measurements taken on 25 or more days and measurements taken during the first week of life (Vigo et al. 2011b). The wild chicks used in this analysis were individuals that fledged from nests with no foster chicks, with parents that were not supplemental fed, had no major health issues, and were not supplemental fed themselves. To calculate the logistic growth curves, I used the chick weight collected using a digital scale. I used a logistic model with the equation $W = A / (1 + e\,(^{-B * (T-C)}))$, where W = weight in grams, T = age of the chick in days, A = the asymptotic size (body mass), B = growth rate constant, C = age in days for which the growth rate is maximal, and e = the natural constant (Vigo et al. 2011b) . I also compared growth parameters of foster chicks and wild chicks grouped base on brood size/hatch order. Wild chick groups were as follows: single chicks (N=17), first chicks (N=38) and, second chicks (N=26). Curves were fitted using Data Fit 9.1.32 (Oakdale Engineering, 2014, Oakdale, Pennsylvania, USA). To determine if growth differed between wild chicks and foster chicks, I compared the three growth parameters using a Wilcoxon-Mann Whitney non-parametric test. Statistical comparisons were done using JMP Pro 15, with a confidence interval of 0.95 and a p-value of 0.05.

Foster chicks influence on breeding success

Previous studies on breeding ecology of psittacines have used breeding parameters to compare among and within seasons (Sanz and Rodriguez-Ferraro 2006)**.** In my case, in order to measure the impact of my chick relocations I compared the overall breeding success for my monitored nests during the 3 seasons working with foster chicks and the previous 16 seasons with no foster chicks. Macaw nests were monitored from mid-October to mid-April every breeding season. I used five breeding success parameters: (1) Chicks that fledge per available nest (# chicks that fledge / # available nests), (2) Chicks that fledge per nest with eggs (# chicks that fledge / # nests with at least one egg, (3) Chicks that fledge per nest with at least one chick (# chicks that fledge / # nests with at least one chick, (4) Percentage of younger chicks that died by starvation (# of chick starved / # second chicks, third chicks and fourth chicks hatched), (5) Percentage of chicks that fledge (# hatched chicks/ # fledged chicks). Macaw nests included for this part of the study included natural and artificial cavities. Nests where total clutch size and total number hatched were not known exactly were removed from the analysis. Nests where adults or chicks received supplemental food were not included. To determine if breeding success differed between seasons with foster chicks and seasons without foster chicks I compared both groups using a Wilcoxon-Mann Whitney non-parametric test. Statistical comparisons were done using JMP Pro 15, with a confidence interval of 0.95. All results are presented as (mean ± standard deviation) unless otherwise reported.

Results

Twenty-eight wild macaw chicks were placed in nests with wild macaw foster parents. All of them were successfully accepted and 89 % of them (N=25 chicks) fledged from their foster nests.

In total, I had 22 foster broods (4 single foster broods,17 double foster broods and 1 triple brood). In five double foster broods, both chicks were foster chicks. Overall, I had 15% (4 of n=27 chicks) of foster chicks placed as solo chicks and 75% of them fledged. All 36% of foster chicks (10 of n=28 of chicks) placed as first chicks fledged and all but two of the 46 % (13 of n=28 chicks) placed as second chicks fledged. The one foster chick placed as a third chick, in an experimental triple brood, successfully fledged.

Of the 28 foster chicks, 29% (8 of n= 28 chicks) were members of multiple broods with age differences >5 days (4 foster chicks as first chicks, 3 foster chicks as second chicks and 1 foster chick as a third chick). In all of these eight foster broods, all chicks successfully fledged.

In all foster broods (n=14 broods: 12 with video cameras and 2 without video cameras) in the first two seasons of this experiment, I placed the foster chick when the nesting female was within sight of the nest area (min=0 m, max= 10 m). In two cases, the nesting female stayed inside the nest covered with a towel when we placed the foster chick. In all but two cases, the nesting male was not present. In the majority of the cases, nesting pairs were present during the precise moment when foster chicks were placed in their nest (100% females, 80% males, n= 10 nesting pairs). The behavior of foster parents when returning to the nest and/or noticing the foster chick followed the same pattern. In all foster broods with video cameras (N=12 broods with video cameras), the first foster parent to have physical contact with the foster chick was the nesting female (Figure 14). First contact behavior was mostly preening (61% of the time, N=14 chicks with video cameras) but some foster parents went straight to feed the foster chick (39% of the time, N=14 chicks with video cameras). On average, first contact was made 4.2 minutes after the foster mother arrived to the nest (N=14 chicks with video available, range = 0.8 - 14 min) and first feeding was given on average after 13 minutes (N= 13 of 14 chicks with video available, range = 0.8 - 76 min).

The three chicks that did not fledge died of predation, lightning and possible disease (See appendix for details).

I aborted one chick relocation experiment 3.5 hours after a chick was placed in the nest because sweat bees (Halictidae) from a nearby beehive started entering the nest cavity and attacking the foster chick. I removed the foster chick and declared the nest cavity unsuitable for fostering chicks.

Figure 14. Nesting female returning to her nest right after foster chick was placed.
Chicks are in the base of the nest with the foster chick to the right and the resident chick to the left.

Foster chick acceptance categories

Initial level of chick acceptance: first physical contact

In all nests with cameras (N=15), the first physical contact between an adult and foster chick happened in the first 15 minutes after the nesting female arrived at the nest. In the two cases when females took the longest to touch the foster chick (14 minutes) it was because she was paying attention to the climber getting ready to repel down from the tree. In one case I had video of the nesting female when I removed an artificial egg and left a three-day old chick. When the female entered the nest and saw the foster chick (and not the artificial egg she left), she puffed up her head and nape feathers while carefully observing the chick on the bottom on the nest, eyes wide open. Right after that, she perched on the entrance of the nest. The female performed this behavior twice during 2 minutes and then she started feeding the chick. The following day the observed behavior of the pair fell into typical patterns for a pair with a recently-hatched chick.

Intermediate level of chick acceptance: foster chick first' half-full crop

All foster chicks that were members of multiple broods needed on average 4.6 +/- 3.3 days to consistently have half-full crops when checked (N=23 chicks, min= 2 days, max=15 days).

Foster chick acceptance analysis

Foster chick-feeding ratios

Daily feeding ratios from observations done in the field by multiple observers and from recorded observations done by one single observer showed similar patterns. Foster chicks were initially fed less than resident chicks (daily feeding ratio of 0.37 +/- 0.25 on relocation day, N= 8 chick pairs), but feeding ratio increased progressively until feedings were similar for both chicks 10 days after relocation (daily feeding ratio = 0.8 ± 0.4, N=8 chick pairs, Figure 15).

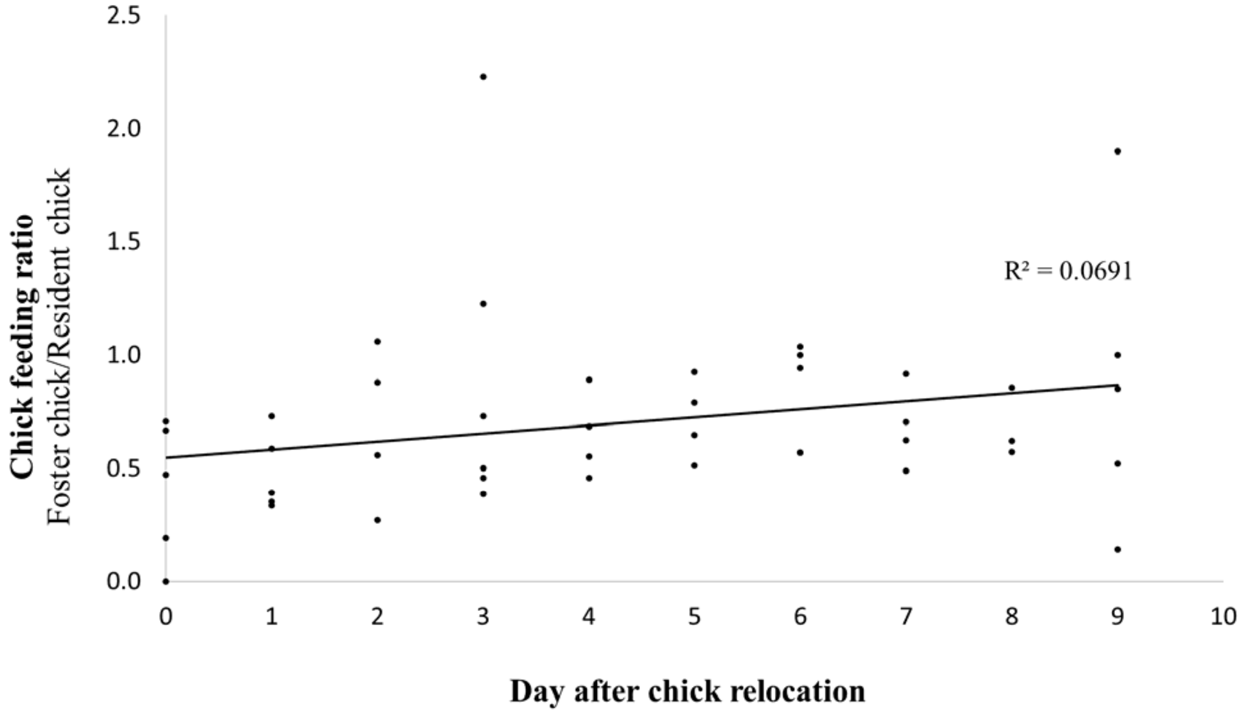

Figure 15. Acceptance of Scarlet Macaw foster chicks during the first 10 days after placement in foster nests.
Acceptance of foster chicks in their new nests was measured by counting feedings per day of both foster and resident chicks and calculating daily feeding ratios. Each point on the graph corresponds to the feeding ratio in one foster nest on one day. The solid line represents the positive linear trend observed and shows that foster chicks feedings increased during the first 10 days in foster nest. Day zero in X axis equal to the day of relocation. These data are from the recorded observations (see Table 1 and Methods for additional descriptions of these data).

Foster chick growth

Foster chicks reached similar maximum weights compared to wild chicks (asymptotic size from logistic equation: all wild chicks combined: 1014.2 +/- 79.7 g, N=81, foster chicks 1020.3 +/- 81.1 g, N=23, Wilcoxon Rank Sum: X^2= 0.14, df=1, p=0.7) and both grew at a similar rate (growth rate from logistic equation: all wild chicks combined 0.116 +/- 0.016, N=81, foster chicks 0.120 +/- 0.014, N = 23, Wilcoxon Rank Sum: X^2=0.47 df=1, p=0.5). However, foster chicks reached maximum growth rate at a younger age (Age at maximum growth rate from logistic equation: all wild chicks combined 26.3 +/- 3 days, N=81, foster chicks: 23.9 +/- 1.7 days, Wilcoxon Rank Sum: X2= 13.6, N=23, df=1, p=0.0022, Table 13).

Foster chicks grew significantly faster than second chicks (growth rate from logistic equation: foster chicks 0.111 +/- 0.015, n=23 chicks, second chicks, 0.121 +/- 0.014, n=26 chicks. Wilcoxon each pair nonparametric comparison: Z= -1.96, p= 0.05). Foster chick growth was not significantly different than solo chicks or first chicks (Wilcoxon each pair nonparametric comparison: Z > 0.84 *, p > 0.06, Table 14). Foster chicks reached maximum growth rate at a significantly younger age than both first and second chicks: 1.5 days younger than first chicks (first chicks: 25.7 +/- 2.4 days old, n=38 chicks; foster chicks: 23.9 +/- 1.7 days old, n=23 chicks. Wilcoxon each pair nonparametric comparison: Z=-2.61, p=0.009) and 3.5 days younger than second chicks (second chicks: 28.2 +/- 3.2 days old, n=26 chicks, foster chicks 23.9 +/- 1.7 days old, n=23 chicks. Wilcoxon each pair nonparametric comparison: Z=5.18, p=<0.001, Table 14)

Table 13. Growth parameters for wild and foster Scarlet Macaw chicks.
All parameters were calculated using the logistic growth model (Ricklefs 1968, Vigo et al. 2011b). The only growth parameter that differed significantly between chick type is indicated by an asterisk, based on a Wilcoxon Rank Sum Test (DF = 1, (p < 0.05).

Chick Type	**Number of Individuals**	**Asymptotic Size A (mean)**	**Growth Rate B (mean)**	**Age of Maximum Growth Rate* C (mean)**
Foster Chicks	23	1020.3 ± 81.1	0.120 ± 0.014	23.9 ± 1.7
Wild Chicks	81	1014.2 ± 79.7	0.116 ± 0.016	26.3 ± 3

Table 14. Effect of hatch order on growth parameters for Scarlet Macaw chicks.
All parameters were calculated using the logistic growth model (Ricklefs 1968). "Solo chicks" are chicks in one-chick broods. "First chicks" are older chicks in two chicks' broods and "second chicks" are younger chicks in two chicks broods. Within a column, values followed by a different superscript letter differed significantly using a Wilcoxon Rank Sum Test (DF = 1, p < 0.05).

Chick Type	**Number of Individuals**	**Maximum Growth** **A** **(mean)**	**Growth Rate** **B** **(mean)**	**Age at Maximum Growth** **C** **(mean)**
Foster chicks	23	1020 ± 81.1^{A}	0.121 ± 0.014^{B}	23.9 ± 1.7^{D}
Solo chick	17	1028 ± 83.2^{A}	0.126 ± 0.013^{B}	24.7 ± 2.3^{D}
First chick	38	1022 ± 75.4^{A}	0.115 ± 0.014^{B}	25.7 ± 2.4^{E}
Second chick	26	993 ± 77.7^{A}	0.111 ± 0.015^{C}	28.2 ± 3.2^{F}

Foster chicks influence on breeding success

During my three seasons with chick relocations, more chicks fledged and fewer younger chicks died by starvation. The mean number of chicks that fledged per available nest was significantly greater in seasons with foster chicks (0.43 ± 0.05 chicks, N = 3 seasons) than in seasons without foster chicks (0.23 ± 0.86 chicks, N = 16 seasons. Wilcoxon Rank Sum: DF=1, X^2= 7.2, p=0.007). The number of chicks that fledge per nest with eggs was also significantly greater in seasons with foster chicks (1.13 +/- 0.15 chicks, N=3 seasons) than in seasons with no foster chicks (0.56 +/- 0.21 chicks, N= 16 seasons. Wilcoxon Rank Sum: DF=1, X^2= 7.1, p=0.008). The number of chicks that fledged per nest were chicks hatched was also significantly greater in seasons with foster chicks (1.5 +/- 0.3 chicks, N= 3 seasons) compared to seasons without foster chicks (0.86 +/- 0.24 chicks, N= 16 seasons. Wilcoxon Rank Sum: DF=1, X^2= 6.1, p= 0.01). In addition, the percentage of young members of broods that died by starvation was significantly reduced when compared seasons with foster chicks (0.06 +/- 0.03, N= 3 seasons) and seasons without foster chicks (0.35 +/- 0.22 chicks, N= 16 seasons, Wilcoxon Rank Sum: DF=1, X^2= 5.5, p= 0.02, Table 15).

Table 15. Effect of foster nests on seasonal breeding success of Scarlet Macaw. Seasons with no foster chicks (2000 to 2016) were compared to seasons with chick fostering experiments (2017 to2019). In the fostering experiments, I placed, swapped or added, foster chicks to specific nests (see text). The breeding season was mid-October to mid-April. Available nests refer to cavities (N = 40) that were not occupied by other species by the beginning of the breeding season I calculated χ^2 and p-values using Wilcoxon Rank Sum Tests (DF = 1).

Breeding Success Parameters	Seasons with foster nests (n = 3)	Seasons without foster nests (n = 16)	χ^2	p-value
Chicks that fledged per available cavity	0.43 ± 0.05	0.23 ± 0.86	7.2	0.036
Chicks that fledged per nest with eggs	1.13 ± 0.15	0.56 ± 0.21	7.1	0.007
Chicks that fledged per nest where at least one chick hatched	1.5 ± 0.3	0.86 ± 0.24	7.1	0.01
Percentage of younger chicks that starved	0.06 ± 0.03	0.35 ± 0.22	5.5	0.02
Percentage of chicks that fledged	0.7 ± 0.05	0.46 ± 0.14	5.5	0.02

Discussion

The management technique of using wild Scarlet macaws as foster parents was categorically successful for four reasons: (1) all foster chicks were accepted by new parents with no chick rejection, (2) foster chicks were fed at rates similar to resident chicks, (3) foster chicks' growth was similar to wild chicks' growth, (4) almost 90% foster chicks fledged. Moreover, the use of foster parents dramatically reduced chick mortality due to starvation and increased overall reproductive success in the area.

Scarlet Macaws as foster parents in the wild

There are just a few studies of foster parents in wild psittacines and most of them are quite complete. Their objectives vary from a management tool to increase population recruitment (Snyder et al. 1987a, Sanz and Rojas-Suárez 1997), to a scientific technique to understand nesting behavior, such a parent/chick recognition (Rowley 1980), hunger response (Krebs 2001) and food allocation (Krebs et al. 1999). None of them addressed the potential conflict of increasing brood size in species that show brood reduction strategies in the early stages of the nesting period. Moreover, the circumstantial evidence that wild Scarlet Macaws in Guatemala are able to foster and fledge additional chicks (Rony Garcia, program leader for WCS personal communications) and from research from Costa Rica (Vaughan et al. 2003b) did not provide sufficient detail on how a species allowed their own chicks to starve at the beginning of the nesting period, and later accepted an additional unrelated chick later in the same nesting event.

I designed my experiments avoiding placing foster chicks during what I called "the starvation risk period". According to my investigations on brood reduction by chick starvation of Scarlet Macaws (Vigo In prep CH 3), I observed that fourth chicks are always left to starve in the first week of life, third chicks in their first two weeks and in second chicks, no death by starvation was recorded in chicks older than 25 days. In fact, 88 % of second chicks that starved were younger than 20 days old. For that reason, I consider "the starvation risk period" in Scarlet Macaw is from zero to 20 days old (Vigo and Brightsmith, in prep). I did not place additional chicks in foster nests when the youngest member of the foster brood was on average younger than 22 days old. A similar strategy was used in relocating Yellow-shouldered Amazon foster chicks, where Solo chicks older than two weeks were used as foster chicks because mortality rates are higher in the first weeks of life (Sanz and Rojas-Suárez 1997). In foster chicks of Puerto Rican Amazons (Snyder et al. 1987a) and the Galah (Rowley 1980) individuals as young as one week old were accepted in whole brood swaps. These two studies warn about using older foster chicks due to the evidence that adults do not recognize small chicks as individuals but they do recognize older chicks. No warnings are made about placing young foster chicks during starvation risk periods.

A difference between my foster parent experiments and previous studies with wild psittacine foster parents is the presence/absence of the nesting pair when foster chicks were placed in foster nests. In the two Amazon parrot studies in Puerto Rico and Venezuela and in the Galah study in Australia, (Rowley 1980)foster chicks were placed in nests when foster parents were absent in order to minimize disturbance and possibly nest abandonment. Many authors state that they thought the parents did not detect the placement of the foster chick, but in my study that was clearly not the case. In my case, the majority of nesting pairs were present during the precise moment when foster chicks were placed in their nest. In a few cases, the female nesting individual was even inside the nest, so the argument that foster parents did not detect an additional chick is not valid in my case. In this study, I did not consider the nesting pair presence/absence in the nest as an important aspect because in my study site in Tambopata, Scarlet Macaw pairs are very accustomed to humans checking their nest and manipulating their chicks. My research project has been intensively monitoring macaw nests in this area for the last 20 years and there are no records of nest poaching in the area for over 30 years The majority of my nesting pairs no longer display the disturbance behaviors typical for macaws/parrots during nest checks (Snyder et al. 1987b). Disturbance behaviors such as alarm calls when a climbing team arrives, flying in circles around a nest giving alarm calls, alarm calls while perched, and fleeing from the nest area are rarely observed in my study area; especially when it is an old breeding pair re nesting in the same nest (Vigo and Brightsmith unpublished data).

Foster chick acceptance and rejection

Overall acceptance of foster chicks by foster parents in my investigation was excellent but expected. There are some published records from aviculture practices and from wild psittacines research showing that different genera of the family Psittacidae are able to foster additional chicks successfully. This has been observed in the wild, in the genera *Cacatua, Amazona*, *Platycercus* and

Ara (Rowley 1980, Sanz and Rojas-Suárez 1997 ,Rony Garcia, personal communications, Krebs 2001) and in captivity, in the genera *Cylopsitta, Alisterus, Amazona, Pionus* and *Cacatua* (Rowley 1980, Stoodley 1986, Snyder et al. 1987a, Dingle 1998, Romer 2000). In all the experiments done in the wild, including my, when foster chicks were accepted, fostering manipulations has caused no major disruption of adult nesting behavior (Snyder et al. 1987a). Both nesting females and nesting males continue with nesting related activities with no major changes. In the case of the Galah, the main disruption of adult nesting behavior happened when whole broods were swapped for unrelated broods. Some pairs hesitated over several hours to first enter their nest, but once one entered the nest (generally the female), the other nesting adult followed. This hesitation is explained by the fact that older Galah chicks (few weeks from fledgling) reply to their own parent's calls when they arrive at the nest and foster chicks did not respond to foster parent's calls when they arrived (Rowley 1980). In my case, I did not detect entrance of nest hesitation as in the Galahs. Usually Scarlet Macaw nesting females in Tambopata are eager to come back and check on their chicks as soon as they are returned to the nest after having been manipulated.

High acceptance of foster chicks after chick predation or egg hatching failure was surprising but also expected; mainly because it has been reported in studies with foster chicks in Amazon parrots in the wild. In Yellow-shouldered parrots, three of four foster chicks placed after full predation events were accepted (Sanz and Rojas-Suárez 1997). In wild Puerto Rican Amazons two foster chicks placed after eggs failed to hatch were accepted, even though the foster chicks were another species: Hispaniolan Amazons (*Amazona ventralis*, Snyder et al. 1987a). In my study in Tambopata, in the cases of foster chick acceptance after the resident brood was depredated, after chicks were kill by lightning, and after egg hatching failure, nesting pair behavior was very similar to that reported by the previous studies with Amazon parrots (Snyder et al. 1987a, Iñigo-Elias 1996, Sanz and Rojas-Suárez 1997).There is some initial hesitation, especially the very first time the foster chick was seen, but once it was fed, the nesting pair behavior fell into the normal attendance pattern according to the foster chick’s age.

In all three studies, including my, the timing in which the foster chick was placed after the empty nest was a key aspect (Snyder et al. 1987a, Sanz and Rojas-Suárez 1997). In the case of replacing unviable eggs with a foster chick, the swap needs to be done as close to the estimated hatching date as possible. The hatching period is a very sensitive period for the nesting pair. It offers a very small window to replace eggs for foster chicks. Nesting individuals, especially nesting females, tend to decline in attentiveness a few days after the end of the normal incubation period if the eggs fail to hatch (Snyder et al. 1987b). Even though the nesting pair keeps visiting the nest after egg failure, visits are more related to a desire to defend the nest cavity and maintain ownership (Vigo personal observations, Renton 2004, Renton and Brightsmith 2009).

An unexpected result in my study was that all foster chicks were accepted. In three of four foster parent experiments from the literature, a few foster chicks were rejected in each. In the Puerto Rican Amazon case (Snyder et al. 1987a), two older chicks that were swapped for one foster chick were rejected, even when the foster chick was an offspring of the foster parents. In the Galah study (Rowley 1980) 5% of foster chicks (n=10 chicks, 3 broods) were rejected; perhaps because all of them were placed very closed to fledgling time. In these two cases chick rejection was attributed to the old age of the chicks due to the evidence than in all rejection cases, foster parents seemed to “recognize” their own chicks either by vocalizations or by unique physical cues (Rowley 1980). In the Yellow-shouldered Amazon (Sanz and Rojas-Suárez 1997), 9.3% (n=5 chicks) were rejected. Here, rejection was attributed to a low feeding response of foster chicks and different developmental stages between foster chicks and wild offspring. Only the Crimson Rosella study did not mentioned chick rejection at all (Krebs et al. 1999)

A tentative explanation for the zero foster chick rejection found in my study is that I measured rejection in a different way than in the three previous studies (Rowley 1980, Snyder et al. 1987a, Sanz and Rojas-Suárez 1997) .I considered that a foster chick was rejected when daily-feeding ratios (foster/resident chick) were not similar and when the tendency of feeding-ratios was not positive after 10 days of foster chick relocation. In the Puerto Rican Amazon, the indicator of acceptance was also feedings but based on crop size observations after a few days and not direct observations of feeding (Snyder et al. 1987a). In addition, rejection happened when whole broods were swapped but not when chicks were added to a brood. I did not swap entire broods, so these rejections are not comparable to my case. In the Yellow-shouldered Parrot, the foster chick acceptance indicator was also feedings based on crop size and observations of the absence of injuries at the end of day of relocation. Here, when foster chicks did not have large crops until the next morning after relocations, they were removed and placed in another nest. Interestingly, in my study, the only cases in which foster chicks showed large crops in the day after relocation were when the foster chick was the Solo chick in the nest. All my foster chicks that were members of multiple broods needed on average 5 days to show half-full crops. They were fed by foster parents, clearly observed it in videos, but did not have large crops. Under my acceptance/rejection criteria those chicks were not considered rejected.

Zero foster chick rejection in my study might be due to the fact that I matched ages/developmental stages between foster chicks and resident chicks. Developmental stages in my experiment were defined based on my extensive knowledge on the nesting biology of the species (Vigo et al. 2011b). Therefore, my foster chicks looked very similar to the resident chicks in nearly all cases. The importance of matching similar ages between foster chicks and resident chicks in chick additions, chick swaps and whole brood swaps was mentioned in all the previous studies (Rony Garcia, personal communications, Rowley 1980, Snyder et al. 1987a, Sanz and Rojas-Suárez

1997). All investigations that worked with psittacine foster parent address the fact that foster chick acceptance and especially rejection were related to age differences among chicks involved (Rowley 1980, Snyder et al. 1987a, Rony Garcia personal communications, Sanz and Rojas-Suárez 1997). In the Yellow-shouldered Parrot and in the Galah, foster chicks and foster broods that differed in age from the resident chicks and broods were rejected. In the Puerto Rican Amazon and in the Crimson Rosella studies the authors considered that pairing chicks that "look similar" to be very important.

Foster chick acceptance analysis: chick-feeding rates

No previous studies of wild Psittacidae as foster parents have analyzed acceptance of foster chicks using chick feedings as an indicator of acceptance. In this study, I used chick-feeding counts because it showed a direct impact of foster parent parental care strategies on survival in foster chick. The used of feedings per day ratios in my study showed that foster chick acceptance was a slow process that needed more than one day of post-relocation monitoring before concluding failure. In the Crimson Rosella study in Australia, feedings (food transfers) were used as a tool to: (1) quantify hunger response when broods or individual chicks were placed back in the original nest (Krebs et al. 1999), and (2) to understand food allocation among the brood (Krebs 2001). However, in both experiments, resident broods and chicks were placed back in their original nest three hours later, so there was no way to analyze daily feeding rates. In the Galah (Rowley 1980) and Puerto Rican Amazon studies (Snyder et al. 1987a) feedings were used in a descriptive manner, not in an analytical manner.

Other studies have addressed the first response of foster chicks to foster parents. In my study of Scarlet Macaw foster parents, my results were unexpected because the foster chick reaction I observed could be considered a "distress" response. The majority of foster chicks (n=23) were syringe fed from a few days old to 20 days of age. Because of that, they showed low or even nonexistent feeding response when approached by an adult macaw. When foster parents, usually nesting females, grabbed a foster chick beak in an attempt to regurgitate, the foster chick usually shook its head and pulled it away. Similar reactions were observed with the Puerto Rican Amazon in which some hand-raised chicks gave fright responses and distress vocalizations when they were placed into the wild nests and first encountered adult parrots attempting to brood and feed them (Snyder et al. 1987a). The first response to foster parents in Galah Cockatoo chicks was not a distress response, instead, the chicks gave little or no response, especially for chicks in the second half of their nesting period. At that age, Galah chicks start to respond to parent calls when they arrive at the nest and foster chicks did not reply to foster parent call when they first arrived to the nest. However, after a few hours of not being fed, the tendency for rejection in the nestling was overruled by hunger. Once the nestling was hungry, begging and vocalizations attracted foster parents that proceeded to enter the nest and feed them (Rowley 1980).

In my case, the pulling away behavior and distress response of Scarlet Macaw foster chicks decreased slowly as they learned how to receive food from the adult macaws during the first 10 days post relocation. During this transition period, foster chicks in my study were given supplemental food once or twice per day, so even though they were not responding well at feeding time with foster parents, they were not losing weight or showing signs of nutritional deficiency. I concluded that supplemental feeding after foster chicks were placed in foster nests facilitated foster chicks' learning the feeding response behaviors.

Foster chick acceptance analysis: chick growth rates

An interesting finding was that foster chicks in my study were not only accepted by foster parents, but also were treated as a wild chick raised by wild parents during the whole nesting period. These results fit perfectly with the compensatory growth principle that states that given adequate conditions, slow development as a result of low nutrition is followed by accelerate growth. Growth rates becomes similar to nestlings that did not experience stress at all (Schew and Ricklefs

1998). My hand-raising procedures in the nursery and my supplemental food plan during the first 10 days after relocation provided enough nutrition to foster chicks, so they were able to compensate for the low nutritional intake received from foster parents during the first days in foster nests, and this allowed them to catch-up and attain maximum growth rates and maximum weights similar to the wild chicks.

The fact that foster chicks reached the maximum growth rate almost two days earlier than resident chicks is likely a direct consequence of my hand-feeding procedures. Captive raised Scarlet Macaw chicks grow differently than their wild equivalents. Indeed purely captive-raised chicks reached the maximum growth rate even sooner than foster chicks in this study (Vigo Trauco 2007). These differences in growth might be related to differences in the consistency of macaw chicks' diets. In the wild, the diet of macaw chicks contains full seeds and even tree bark (Brightsmith et al. 2010) so it may take more time and energy to digest than the puree like formula that is used in captivity (Cornejo et al. 2013). In order to get my chicks extra fat in preparation for the adaptation process in their new foster nest, we provided a high fat diet (formula with nuts and peanut butter added (Brightsmith et al. 2006, Cornejo 2012)), large portions, and high feeding frequency.

Using foster chicks to test starvation drivers

The main driver behind brood reduction is the age difference among brood members (Vigo In prep CH 3). This age difference effect predicts that the bigger the age difference among brood members the higher the risk of starvation of younger brood members. In my foster parent experiments, I have tested that this effect does not apply when brood members were older than 20 days. I had 25% of foster chicks (7 chicks) that were over 5 days younger/older than the foster sibling. In all seven foster broods, both chick members successfully fledged. These results support my predictions that younger chicks from multiple broods are more prone to die by starvation when they are younger than 20 days old and that a chick starvation risk period actually exists. One reason why age difference might not be causing death by starvation in multiple broods with chicks older than 20 days old is that the younger the chicks, the more age specific the parental care requirements (aka: brooding and feeding). A just hatched chick and a 3-day old chick may not have the same feeding or brooding requirements. It is well known by aviculturists that there is a strong need to monitor chicks <5 days old separately because temperature is critical during this stage of development. Moreover, extreme temperature fluctuations during first stages of life can be harmful or even fatal to the chicks (Voren and Jordan 1992c). Recommendations for brooding temperatures in captivity indicate that newly hatched chicks need to be keep 2 C warmer than 5-9 days old chicks. In the wild, a nesting female needs to adjust brooding requirements according to her different aged chicks. The recommended feeding frequency also varies from every hour for hatchlings to every 3 to 4 hours for 5 to 9-day old chicks (Clubb et al. 1992c, Voren and Jordan 1992c, a). When the pinfeathers of chicks start to show, around 18 days old, chicks are less affected by temperature and when they are heavy pin feathered, around 30 days old, heat requirements diminish considerably (Voren and Jordan 1992a). Recommended feeding frequencies per age from captivity are less strict at this stage of development (Clubb et al. 1992c). Hence, when chicks are older than 20 days, chicks that are >5 days apart "look similar" and their parental care requirements, brooding and feeding, are similar. The fact that foster parents were able to fledge chicks that were over 5 days apart is a result of the developmental stage in which the foster chick was placed in the foster nest. Both foster siblings were at the age at which parental care requirements were very similar, and even though foster parents needed time to adjust their food provisioning and allocation, and foster chicks needed to learn how to be fed, death by starvation was no longer a risk.

Conclusions

The technique of macaw foster parents was categorically successful. All relocated foster chicks were successfully accepted by their foster parents (N=28 chicks across 3 seasons) and 89%

of them fledged. Three foster chick fatalities were due to unknow disease (n=1 chick), predation (n=1 chick) and lightening destroying nest (n=1 chick).

Foster chick acceptance by foster parents was a slow process. Foster chicks were initially fed less than resident chicks (daily feeding ratio of 0.37 +/- 0.25 on relocation day, N= 8 chick pairs), but feeding ratio increased progressively until feedings were similar for both chicks 10 days after relocation (daily feeding ratio = 0.8 ± 0.4, N=8 chick pairs). Foster chicks needed on average 4.6 +/- days to consistently have half-full crops when checked (N=23 foster chicks, min= 2 days, max= 15 days).

Growth of foster chicks was similar to wild chicks from previous seasons with no foster chicks' experiments. Growth rate of foster chicks was similar to wild chick (growth rate from logistic equation: all wild chicks combined 0.116 +/- 0.016, N=81, foster chicks 0.120 +/- 0.014, N = 23, Wilcoxon Rank Sum: X^2=0.47 df=1, p=0.5) and both chick groups reached similar maximum weights (asymptotic size from logistic equation: all wild chicks combined: 1014.2 +/- 79.7 g, N=81, foster chicks 1020.3 +/- 81.1 g, N=23, Wilcoxon Rank Sum: X^2= 0.14, df=1, p=0.7). However, foster chicks reached maximum growth rate at a younger age (Age at maximum growth rate from logistic equation: all wild chicks combined 26.3 +/- 3 days, N=81, foster chicks: 23.9 +/- 1.7 days, Wilcoxon Rank Sum: X2= 13.6, N=23, df=1, p=0.0022). I attribute this difference to differences in diet and feeding schedule.

The foster parent's technique increased the reproductive success of my studied population. Fledging success per available nest increased from 23% (1999 – 2016) to 43% (2017-2019) and chick death by starvation decreased from 35% to 6%.

Behind and beyond the success of the foster parents' technique

My ability to produce foster chicks that were successfully accepted and that were very similar to wild chicks by fledgling time, is the result of the integration of three different fields: parrot ecology, avian veterinary medicine, and aviculture. Psittacines have been the heart of aviculture for centuries. There are many well know breeding techniques and procedures that can be easily modify and adjusted for use in the wild (Clubb 1992). In fact, the Scarlet Macaw is considered one of the most productive species of macaws in captivity (Mark Moore, co-owner of Hill Country Aviaries, USA. Personal communications, Clubb and Clubb 1992). In my case, I used information available in the aviculturist literature (Clubb et al. 1992c, Voren and Jordan 1992d, Abramson et al. 1995) and closely worked with well-experienced psittacine breeders that shared their knowledge and expertise from decades of breeding macaws in captivity. I also worked together with avian veterinarians that took care of chick health issues and provided insights from their experiences with captive psittacines. Lastly, I integrated my knowledge on breeding ecology and nesting behavior on the species (Brightsmith 2005, Brightsmith et al. 2010, Vigo et al. 2011b, Olah et al. 2013, Olah et al. 2014).

As other study groups have demonstrated in the past (Puerto Rico Parrot recovery project (Snyder et al. 1987a) and the Spix's macaw Recovery plan (Schischakin 1999, Juniper 2003); my study with macaw foster parents in the wild in Tambopata, demonstrated that the integration of ecologist, vets and especially aviculturists, has great potential to assist management actions in the wild.

Macaw foster parents as a management technique to increase reproductive success

The use of foster parents in the wild has been suggested as a management technique to maximize productivity with harvesting for conservation purposes (Beissinger and Butcher 1992). In the case of the Scarlet Macaw, the increase in the number of young fledged per nest by transferring chicks that would have died by starvation in their natural nests, is a potentially viable management technique that needed to be further tested in the wild. In this species, harvesting later hatching young that would definitely die in the nest has no negative impact in the overall productivity on the natural population (Beissinger and Butcher 1992). Indeed, macaw chicks that starve are “wasted” from a conservation perspective. This research shows that it is possible to use these chicks to increase recruitment and overall reproductive success.

Recommendations

Based on my experience working with macaw foster parents in the wild, I offer some recommendations for those interested in using this technique. (See Chapter V for more details).

1. Place macaw foster chick in receiver nests when ages range from 20 to 69 days old.
2. Use foster parents with proven previous breeding experience
3. Calibrate foster brood size using optimal brood size for the species in the areas
4. Match foster siblings that are in the same developmental stage.
5. Provide supplemental feedings to foster chicks once per day for at least one week after relocation.
6. Monitor health and weight gain of resident chick at the same schedule as foster chick.
7. Monitor health status of foster chick to avoid disease exposure to foster chicks or foster parents.

CHAPTER V

CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS ON HOW TO USE THE FOSTER PARENTS TECHNIQUE IN WILD MACAW POPULATIONS

My study of nestling ecology and behavior on the Scarlet Macaw in Tambopata provides insights from the chick-rearing period in the wild and from the wild foster parents management technique that can be applied to in-situ and ex-situ conservation actions to help recover endangered populations of macaws in the Americas. The Scarlet Macaw is one of the best known of all South American psittacines (Forshaw 2010). It has been studied in many areas throughout its distribution and much about its natural history and ecology has been published in the peer reviewed literature (Brightsmith and Aramburu Munoz-Najar 2004, Brightsmith 2005, Brightsmith et al. 2005, Boyd and McNab 2008, Brightsmith et al. 2010, Vigo et al. 2011b, Olah et al. 2013, Olah et al. 2014, Garcia-Anleu et al. 2017, Brightsmith et al. 2018, Vaughan 2019, Brightsmith et al. In prep). However, the fact that my study includes data for a long period of time (19 consecutive breeding seasons), a good sample size (available nests check per season: mean=29, range= 12 to 47; chicks check per season: mean=15, range: 9-30) and behavioral observations from > 1900 hours of video from inside the nests, allowed me to report different aspects of the nestling ecology and behavior of the species that have not been reported before.

My study is the first that quantifies parental investment inside the nest throughout the whole chick rearing period in a wild macaw. In chapter II, I show that the Scarlet Macaw displays bi-parental care where both nesting female and nesting male feed the chicks. When chicks hatch, the nesting female provides the majority of nest care (in my case chick feedings) and this gradually declines while the nesting male's care increases as nestling rearing progressed. Overall, nest attentiveness patterns reported in other species of psittacines are similar to the chick food allocation pattern I found in this study (Saunders 1982, Gnam 1991, Wilson et al. 1995).

Two novel discoveries of my work are presented in Chapter II. The first one is that that Scarlet Macaw chicks are fed during the night. Feeding schedule patterns showed that the whole morning (from 05:00 to 11:00 hours) is an important feeding time and also late afternoon, right before dusk. However, the two nocturnal feeding peaks are equal in magnitude to the late afternoon peak. Indeed, the last night peak, around 2 am, signifies that adults are able to store food in their crops for over 7 hours. The second discovery is that chicks are fed around the clock all day and night at a rate of 3.6 ± times per hour all throughout the nesting period. Even when chicks are > 65 days old, they are been fed at a very high rate. These findings have a great potential to inform aviculturist practitioners in their psittacine hand-rearing techniques.

My study is the first detailed analysis of weight at hatch in the wild for the Scarlet Macaw. Despite a number of studies on breeding ecology on psittacines, (Snyder et al. 1987c, Rowley and Chapman 1991, Krebs 1998, Beissinger 2008) there is not much information about weight at hatch from wild psittacine chicks. In Chapter II, I show that weight at hatch decreases with hatching order, third and fourth hatched chicks being significantly lighter than first hatched. In Chapter III, I show that chicks that starved (all hatching orders combined) hatched with a significantly lower weight than chicks that fledged but that second chicks that starved did not weigh differently than second chicks that fledge.

This study is the first to document infanticide in the Scarlet Macaw (*Ara macao*). In Chapter II, I report two cases (two broods with two chicks each) where chicks were executed by nest intruders during a fight to take over the nest and one case, where the nesting female threw her own chick out of the nest after she and her pair managed to maintain ownership of their nest. Besides the study on the Eclectus parrot (Heinsohn et al. 2011) that had indirect evidence of fraternal infanticide, my study is the first one that has witnessed such direct evidence of this behavior in wild psittacines.

To the best of my knowledge, this is the first study that deeply analyzes the phenomenon of chick starvation associated with in a Neotropical psittacine species. In Chapter III, I focused my chick starvation analysis on just second chicks due to the fact that ~25% of all second chicks starved to death; opposed to third and fourth chicks where nearly 100% starve.

My fist analysis in Chapter III (chick-chick interactions analysis) clearly shows that sibling rivalry was not a cause of starvation of the second chick in Scarlet Macaw nests in Tambopata. The frequency of chick pushing observed was extremely low (0.05 pushes/hour) and was not related to second chick starvation. In addition, chicks pushed adults' beaks while feeding another chick just five times in over 10 000 minutes of video analyzed. In the Scarlet Macaw in Tambopata, parents are apparently not distributing food based on the outcome of chick interactions.

In my second analysis in Chapter III (parent- environment interactions analysis) I found that food availability in the adjacent forest was not significantly associated with death by starvation of the second chick. Not during the first 20 days of life of the broods (older chick that starved to death), not during the first 15 days of life of the broods (average age of starvation of second chicks) and not during the 7-day period pre and post hatching. The lack of relationship between food availability and death by starvation of the second chick in my study could be attributed to: (1) a mismatch between the scale of the area where I quantified food availability and the scale at which the macaws forage, (2) an issue with chick diet specificity, or (3) a true lack of relationship between food and starvation.

My third analysis in Chapter III (chick-parent interaction analysis), shows that the Scarlet Macaw displays a direct control of food distribution within the brood, as was reported in other species of psittacines (Stamps et al. 1985, Krebs et al. 1999, Budden and Beissinger 2009). Parents actively allocated more food to first chicks and less to second chicks. First chicks received more feedings than second chicks; even in broods where second chicks did not starve to death. In addition, difference in feeding of first chicks when second chicks starved was significantly larger than when the second chick fledged. These findings support my hypothesis that chick starvation is due to parental care allocation differences. In addition, I show that second chicks that starved did not weigh differently at hatch than second chicks that fledge, first chicks that fledge, or older sibling from the same brood. This finding suggests that death by starvation of the second chicks is not likely to be related to initial chick body condition.

At the end of this chick-parent analysis, I show that the larger the age difference between brood members the more likely the second chick would starve to death. My results agree with the suggestion from the literature that large chick size differences related to hatching asynchrony is likely the cause of chick starvation associated with (Stoleson and Beissinger 1997b, Koenig 2001, Budden and Beissinger 2009). However, my results from Scarlet Macaw brood manipulations in Chapter IV, showed that big size differences (over 250 gr difference) did not affect survival of the smaller brood members when chicks were older than 20 days because both brood members were in the same developmental stage. I conclude that I have found supporting evidence that second chick death by starvation is driven by brood age differences. However, the differences in chick rearing requirements related to large age differences between chick's resultant from hatching asynchrony are the main driver for death by starvation of second chicks in Tambopata.

My findings from Chapters II and III were used to design and test the foster parent management techniques that I present in chapter IV. The use of wild Scarlet Macaws as foster parents was categorically successful for four reasons: (1) all foster chicks were accepted by new parents with no chick rejection, (2) foster chicks were fed at rates similar to resident chicks, (3) foster chicks' growth was similar to wild chicks' growth, and (4) almost 90% of foster chicks fledged. Moreover, the use of foster parents dramatically reduced chick mortality due to starvation and increased overall reproductive success in the area. I attribute the zero foster chick rejection in my study to the fact that I matched developmental stages between foster chicks and resident chicks. Chicks in the same developmental stage look very similar and have similar feeding and brooding requirements (Voren and Jordan 1992b) consequently, parental investments for feeding and brooding are similar. At the end of Chapter IV, I summarize my recommendations related to the use of wild macaws as foster parents and I expand on those recommendations at the end of the current chapter.

Overall, the studies in my dissertation contribute to both the understanding of the nestling ecology and behavior and the phenomenon of chick starvation of the charismatic and locally endangered Scarlet Macaw. Moreover, the information obtained from my experiments using wild macaws foster parents have a great potential to inform in-situ conservation projects that are working to increase chick recruitment in order to increase population of not only macaws, but other species of psittacines worldwide.

The use of foster parents in avian population management is a technique with great potential to aid in the recovery of highly endangered species in the wild (Cade 1965). Here I provide recommendations based on my experience working with macaw foster parents in the wild, for those interested in using this technique.

Recommendation #1: macaw foster chick age at relocation from 20 days to 69 days

I recommend avoiding the placement of foster chicks during the starvation risk period or 20 first days of life in macaws. According to my investigations on brood reduction by chick starvation, younger chicks in a brood are more likely to die by starvation when they are younger than 20 days old: this is the “starvation risk period” (Vigo In prep CH 3, In prep CH 4). This finding helps calibrate the lower age limit for fostering in wild Scarlet Macaws.

For the maximum age for relocation, I recommend place foster chicks close to fledgling age, which in macaws is older than 69 days. In my experiment, the maximum age I placed a foster chick was 46 days old. Conservationists that work with the Scarlet Macaw in Guatemala have reported a foster chick as old as 65 days, has been successfully accepted (Rony Garcia, per com). Beyond these two maximum values, I have no data to suggest anything other than the recommendation from the literature which is to avoid placing chicks near fledging (Rowley 1980, Snyder et al. 1987a, Sanz and Rojas-Suárez 1997). In the case of *Ara macao* in Tambopata, near fledging could be considered 69 days old (fledgling age: mean=88 days old, range= 79 to 99 day old, n=104 chicks, Vigo Trauco 2007).

Recommendation #2: use as foster parents macaws with previous breeding experience

I strongly recommend to use as foster parents individuals that have proven evidence of effective chick care and have successfully raised at least 1 chick in previous breeding seasons. As recommended in the Yellow-shouldered Amazon foster parents research (Sanz and Rojas-Suárez 1997) it is imperative to avoid using novice nesting pairs as foster parents. We have evidence from my studies which indicate that new breeders are not good parental care providers. In two cases, I registered two different breeding pairs (banded individuals, ages between 7 & 8 years old) that most likely were first breeding attempts. Both pairs had failed to hatch eggs the previous breeding season. In the current breeding season, they hatched one chick but parental care provisioning was poor and feeding frequency was very low. The adults were also very rough when they fed the chick, shaking the chick more than normal during feeding. In one case, the solo chick died the day after hatching. In another case, the solo chick died in three days.

Recommendation # 3: calibrate foster brood size using optimal brood size of the species in the area

I recommend to calibrate foster brood size using as a general indicator the optimal brood size of the species in the area. It was also recommended in the Yellow-shouldered Parrot foster parent research (Sanz and Rojas-Suárez 1997) not to create foster broods that were bigger than the optimal brood size of the species. According to my investigations on Scarlet Macaw breeding biology and natural history in Tambopata, the maximum number of chicks that fledge is 2 chicks per nest. Indeed, just 37% of nesting pairs managed to fledge 2 chicks and 1.3 chicks per nest is the average chick production per nest in the area (Vigo In prep CH 2). Therefore, in my first two seasons of experimentation, I did not create foster broods bigger than 2 chicks because that is their optimal brood size as a species in the area. However, in my third season of chick relocation experiments I did create a triple brood. Even though all chicks fledged, all required intense monitoring and all three chicks required additional supplemental feeding because they were not gaining weight as expected for their ages. Parents were feeding all three chicks but it seemed they could not provide enough to feed three chicks.

Recommendation #4: match foster siblings in same developmental stage

Because my relocations were so successful I suggest that future projects use developmental stages for matching foster and resident chicks for relocations. Previous studies with psittacine foster parents suggest that foster chicks need to be of similar age to chicks already in foster nests (Rowley 1980, Snyder et al. 1987a, Sanz and Rojas-Suárez 1997, Krebs et al. 1999, Romer 2000). Instead of this, I decided to match foster and resident chicks that were in the same developmental stage. Based on my previous studies I defined my developmental stages in the following way: Stage 1 hatchling (from 0 to 2 days old); Stage 2A from 3 days old to light pinfeathers & eyes open; Stage 2B from light pinfeathers to heavy pinfeathers; Stage 3 from heavy pinfeathers to well-feathered, Stage 4 from well feathered to fully feathered (See full explanation about developmental stages in *Ara macao* in (Vigo In prep CH 4)). Given the evidence that chick growth curve shape and development are quite consistent across the family Psittacidae (Vigo Trauco 2007), my general description of developmental stages should be useful across a wide array of parrot species.

Recommendation # 5: provide supplemental feeding after relocation of foster chick

I recommend to provide supplemental food to foster chicks for at least 10 days after relocation or until foster chick is found with more than half a full crop. I recommend to syringe-fed once per day in the late afternoon, as close as possible to dusk. This single supplementation will allow the foster chicks to maintain weight but will let them get hungry enough to solicit food from foster parents the next day. In the case of nesting individuals that get disturbed by human intervention, foster nests will have to be observed for days before foster chick relocation in order to determine the nesting pair visiting schedule and adjust supplemental feeding accordingly.

Providing supplemental food to foster parrot chicks after placement was a novel aspect of this study. It was a technique used in a few cases in Puerto Rican Amazon work (Snyder et al. 1987a) in order to give more time to foster parents to adjust to the foster chick, but mainly in egg for chick swaps and not in a systematic way as I did in my study. However, their idea to give the chicks time to get used to being in the nest was the main justification for my supplemental feeding plan. Adult psittacines in captivity display a combination of curiosity and caution when new situations and objects are presented (Fox and Millam 2007). A new chick appearing in the nest will require adjustment time for the parents, especially when this new chick implies that their parental care provisioning duties were doubled so quickly.

In the case of chick, aviculturists know that chicks (not only psittacines) take time to adjust when switching feeding techniques (Clubb et al. 1992c, Voren and Jordan 1992d). There is no reason to believe a hand raised foster chick will immediately know how to receive food from a beak when it was fed by a syringe all its life. The study with Yellow-shouldered Amazon mentioned that foster chick rejection on the day of relocation could have been attributed to the fact that the foster chick was syringe fed in captivity, and didn't know how to receive food from foster parents (Sanz and Rojas-Suárez 1997, Styles 2001). Moreover, I have evidence that not all chicks naturally raised in wild nests grow healthy enough to successfully fledge. I have recorded one case of a Scarlet Macaw pair raising two chicks until fledgling age (around 86 days old): the first chick was properly fed and fledged normally, but the second one grew extremely stunted and jumped from the nest to its death when it reached fledging age. For these three reasons, I recommend providing supplemental food to foster chicks when researchers suspect they are not been fed adequately. A good indicator to spot inadequately feeding is weight gain per age, so I do recommend to use it when available. Otherwise, crop size can be used as a surrogate.

Recommendation # 6: monitor health status of foster chicks to avoid disease exposure to other birds

I do not recommend relocating foster chicks directly from a donor nest. I recommend keeping foster chicks in a controlled environment (nursery) and monitoring for about 10 days for disease symptoms. I also recommend monitoring the original nest, to make sure biological siblings are pathogen free.

Disease transmission while moving wildlife for restoration is a risk that can potentially diminish success of manipulations (Kock et al. 2010). This needs to be considered when relocating foster chicks, especially when placing chicks in foster nests that already have resident chicks.

One of my two foster chick mortalities was due to an unknown disease that killed not only the foster chick while in the foster nest but also its biological siblings in the original nest. The foster chick was placed as a solo chick. It was relocated the very same day it hatched, directly from the original nest to the foster nest. At that time, the biological siblings in the original nest did not present symptoms and appeared to be healthy and gaining weight as expected. Disease symptoms (red hematomas) started appearing when chicks were 2 days old in all three sick chicks, in the foster nest and the original nest. At the time, I didn't have a nursery available to raise the foster chick.

Other studies with Amazon parrot foster chicks recommended not to use foster nests that had chick mortalities due to unknown reasons to avoid potential disease problems for foster chicks and also mentioned the importance of maintaining sanitary considerations to avoid foster chicks introducing pathogens to foster families (Sanz and Rojas-Suárez 1997). It is known that psittacines are susceptible to a variety of diseases (Derrickson and Snyder 1992) and that many of them can be problematic to manage because they can exist in a carrier state for months without detection and they are incurable by current methods (Harrison and Lightfoot 2006). Therefore, the ability to control or even detect diseases in foster chicks is very limited.

The use of foster parents in the wild has been suggested as a management technique to maximize productivity with harvesting for conservation purposes (Beissinger and Butcher 1992). In this study, it has been intensively tested and refined to such an extent that it shows that it is possible to use it as a viable management technique that utilizes chicks that would definitely die in the nest to increase overall reproductive success.

REFERENCES

Abramson, J. 1995. Incubation. Pages 177-186 *in* J. Abramson, B. L. Spear, and J. B. Thomsen, editors. The large macaws: their care, breeding and conservation. Raintree Publications, Fort Bragg, California.

Abramson, J., B. L. .Spear, and J. B. Thomsen. 1995. The Large Macaws: Their Care, Breeding and Conservation. Raintree Publications, Ft. Bragg, CA.

Alastair, F., P. Galipeau, and L. Nikolaiczuk. 2013. Brood reduction by Infanticidae in Peregrine Falcon. Artic **66**:226-229.

Arroyo, R., A. Arce, F. Dear, and C. Vaughan. 2004. Conceptual model of a strategy for Scarlet Macaw (*Ara macao*) protection in the Central Pacific Conservation Area (ACOPAC), Costa Rica., La Asociación para la Protección de Psitácidos del Área, Garabito, Costa Rica.

Beers, M. H., MD, , and M. Robert Berkow. 2004. Starvation. The Merck Manual of Diagnosis and Therapy. Whitehouse Station., NJ: Merck Research Laboratories.

Beissinger, S. 2008. Long term studies of the Green Rumped Parrotlet. Hatching asynchrony, social system and population structure. Ornitologia Neotropical **73**:11.

Beissinger, S., and S. Stoleson. 1991. Nestling mortality patterns in relation to brood size and hatchingasynchrony in Green-rumped Parrotlets.*in* Acta XX Congressus Internationalis Ornithologici.

Beissinger, S., S. Tygielski, and B. Elderd. 1998. Social constraints on the onset of incubation in a Neotropical parrot: a nestbox addition experiment. Behavioral Ecology and Sociobiology **55**:21-32.

Beissinger, S. R., and E. H. Butcher. 1992. Sustainable harvesting of parrots. Pages 73-115 *in* S. R. Beissinger and N. F. R. Snyder, editors. New World Parrots in Crisis. Smithsonian Institution Press, Washington DC.

Beissinger, S. R., and N. F. R. Snyder. 1992. New World Parrots In Crisis. Smithsonian Institution Press, Washington, D.C.

Beissinger, S. R., and J. R. Waltman. 1991. Extraordinary clutch size and hatching asynchrony of a Neotropical parrot. Auk **108**:863–871.

Bentin, M., and J. C. Leyva. 2018. Model of assisted breeding of two *Primolious couloni* chicks by *Ara macao* adults. Pages 23-29. AFA Watchbird magazine. American Federation of Avicutlure.

Berkunsky, I., P. Quillfeldt, D. J. Brightsmith, M. C. Abbud, J. M. R. E. Aguilar, U. Alemán-Zelaya, R. M. Aramburú, A. Arce Arias, R. Balas McNab, T. J. S. Balsby, J. M. Barredo Barberena, S. R. Beissinger, M. Rosales, K. S. Berg, C. A. Bianchi, E. Blanco, A. Bodrati, C. Bonilla-Ruz, E. Botero-Delgadillo, S. B. Canavelli, R. Caparroz, R. E. Cepeda, O. Chassot, C. Cinta-Magallón, K. L. Cockle, G. Daniele, C. B. de Araujo, A. E. de Barbosa, L. N. de Moura, H. Del Castillo, S. Díaz, J. A. Díaz-Luque, L. Douglas, A. Figueroa Rodríguez, R. A. García-Anleu, J. D. Gilardi, P. G. Grilli, J. C. Guix, M. Hernández, A. Hernández-Muñoz, F. Hiraldo, E. Horstman, R. Ibarra Portillo, J. P. Isacch, J. E. Jiménez, L. Joyner, M. Juarez, F. P. Kacoliris, V. T. Kanaan, L. Klemann-Júnior, S. C. Latta, A. T. K. Lee, A. Lesterhuis, M. Lezama-López, C. Lugarini, G. Marateo, C. B. Marinelli, J. Martínez, M. S. McReynolds, C. R. Mejia Urbina, G. Monge-Arias, T. C. Monterrubio-Rico, A. P. Nunes, F. Nunes, C. Olaciregui, J. Ortega-Arguelles, E. Pacifico, L. Pagano, N. Politi, G. Ponce-Santizo, H. O. Portillo Reyes, N. P. Prestes, F. Presti, K. Renton, G. Reyes-Macedo, E. Ringler, L. Rivera, A. Rodríguez-Ferraro, A. M. Rojas-Valverde, R. E. Rojas-Llanos, Y. G. Rubio-Rocha, A. B. S. Saidenberg, A. Salinas-Melgoza, V. Sanz, H. M. Schaefer, P. Scherer-Neto, G. H. F. Seixas, P. Serafini, L. F. Silveira, E. A. B. Sipinski, M. Somenzari, D. Susanibar, J. L. Tella, C. Torres-Sovero, C. Trofino-Falasco, R. Vargas-Rodríguez, L. D. Vázquez-Reyes, T. H. White, S. Williams, R. Zarza, and J. F. Masello. 2017. Current threats faced by Neotropical parrot populations. Biological Conservation **214**:278-287.

Berkunsky, I., L. N. Segura, R. M. Aramburu, R. A. Ruggera, W. S. Svagelj, and J. C.Reboreda. 2016. Nest survival and predation in Blue-fronted Parrots *Amazona aestiva*: effects of nesting behavior and cavity characteristics. BioOne Complete **104**:8.

Birdlife International. 2019a. Handbook of the Birds of the World and BirdLife International digital checklist of the birds of the world., http://datazone.birdlife.org/userfiles/file/Species/Taxonomy.

Birdlife International. 2019b. Species factsheet: *Ara macao*., http://www.birdlife.org.

Bjork, R., and G. V. N. Powell. 1995. Buffon's Macaw: some observations on the Costa Rican population, its lowland forest habitat and conservation. Pages 387-392 *in* J. Abramson, B. L. Spear, and J. B. Thomsen, editors. The Large Macaws: Their Care, Breeding and Conservation. Raintree Publications, Ft. Bragg, CA.

Bonebrake, T. C., and S. Beissinger. 2010. Predation and infanticide influence ideal free choice by a parrot occupying heterogeneous tropical habitats. Population Ecology **163**:9.

Boyd, J., and R. B. McNab. 2008. The Scarlet Macaw in Guatemala and El Salvador: 2008 status and future possibilities. Findings and Recommendations from a Species Recovery Workshop 9–15 March 2008. Wildlife Conservation Society - Guatemala Program, Guatemala City and Flores, Peten, Guatemala.

Braun, B., and G. L. Hunt. 1983. Brood Reduction in Black-Legged Kittiwakes. The Auk **100**:469-476.

Brightsmith, D., J. Boyd, and E. A. Hobson. In prep. Satellite telemetry reveals complex movement patterns of large macaws in the western Amazon basin.

Brightsmith, D., E. A. Hobson, and G. Martínez. 2018. Food availability and breeding season as predictors of geophagy in Amazonian parrots. Ibis **160**:17.

Brightsmith, D. J. 2001. The Tambopata Macaw Project: developing techniques to increase reproductive success of large macaws. AFA Watchbird **28**:24 - 32.

Brightsmith, D. J. 2004. Effects of diet, migration, and breeding on clay lick use by parrots in Southeastern Peru. Pages 13-14 *in* Annual Convention Proceedings 2004, American Federation of Aviculture. American Federation of Aviculture, San Francisco, CA.

Brightsmith, D. J. 2005. Parrot nesting in southeastern Peru: seasonal patterns and keystone trees. Wilson Bulletin **117**:296-305.

Brightsmith, D. J. 2006. Diets of wild psittacines in Tambopata, Peru. A report to the Wildlife Protection Foundation. Schubot Exotic Bird Health Center, Texas A&M University, College Station, Texas.

Brightsmith, D. J., and R. Aramburu Munoz-Najar. 2004. Avian geophagy and soil characteristics in southeastern Peru. Biotropica **36**:534-543.

Brightsmith, D. J., and A. Bravo. 2006. Ecology and management of nesting Blue-and-yellow Macaws (*Ara ararauna*) in *Mauritia* palm swamps. Biodiversity and Conservation **15**:4271-4287.

Brightsmith, D. J., J. Hilburn, A. Del Campo, J. Boyd, M. Frisius, R. Frisius, D. Janik, and F. Guillén. 2005. The use of hand-raised Psittacines for reintroduction: a case study of Scarlet Macaws (*Ara macao*) in Peru and Costa Rica. Biological Conservation **121**:465 - 472.

Brightsmith, D. J., K. M. Holle, and A. Stronza. 2008. Ecotourism, conservation biology, and volunteer tourism: a mutually beneficial triumvirate. Biological Conservation **141**:2832-2842.

Brightsmith, D. J., D. Matsufuji, D. McDonald, and C. A. Bailey. 2010. Nutritional content of free-living Scarlet Macaw chick diets in southeastern Peru. Journal of Avian Medicine and Surgery **24**:9–23.

Brightsmith, D. J., D. McDonald, D. Matsufuji, and G. Matuzak. 2006. Diets of wild psittacines in Tambopata, Peru. A progress report to South Lakes Wildlife Animal Park. Duke University Dept. of Biology, Durham, NC.

Brightsmith, D. J., and E. Villalobos. 2011. Parrot behavior at a Peruvian clay lick. Wilson Journal of Ornithology **123**:595-602.

Britt, C., R. G. Anleu, and M. J. Desmond. 2014. Nest survival of a long-lived psittacid: Scarlet Macaws (*Ara macao cyanoptera)* in the Maya Biosphere Reserve of Guatemala and Chiquibul Forest of Belize. The Condor Ornithological Applications **116**:10.

Britt, C. R. 2011. Nest survival and nest-site selection of Scarlet Macaws (*Ara macao cyanoptera*) in the Maya Biosphere Reserve of Guatemala and Chiquibul Forest of Belize. New Mexico State University, Las Cruces New Mexico.

Browne, T., C. Lalas, T. Matterns, and Y. Vann Heezik. 2011. Chick starvation in yellow-eyed penguins: Evidence for poor diet quality and selective provisioning of chicks from conventional diet analysis and stable isotopes. Austral Ecology **36**:99-108.

Budden, A. E., and S. Beissinger. 2009. Resouce allocation varies with parental sex and brood size in the asynchronously hatching green-rumped parrotlet. Behavioral Ecology and Sociobiology **63**:11.

Cade, T. J. 1965. Relations between Raptors and Columbiform Birds at a Desert Water Hole. The Wilson Bulletin **77**:340-345.

Cade, T. J. 1980. The husbandry of falcons for return to the wild. International Zoo Yearbook **20**:3.

Cantor, E., T. Lewis, M. Louter, K. Smith, D. Schmitke, C. Moore, and S. Kleindorfer. 2019. Nest site attributes and nesting outcome in the vulnerable eastern Regent Parrot (*Polytelis anthopeplus monarchoides).* Transactions of the Royal Society of South Australia **143**:18.

Carabias, J., J. De la Maza, and R. Cadena. 2015. Conservacion y desarrollo sustentable en la selva Lacandona: 25 años de actividades y experiencias, Mexico.

Clark, A. B., and D. S. Wilson. 1981. Avian Breeding Adaptations: Hatching Asynchrony, Brood Reduction, and Nest Failure. Quarterly Review of Biology **56**:253-277.

Clubb, K. J., and S. L. Clubb. 1992. Status of macaws in aviculture.*in* R. M. Shubot, K. J. Clubb, and S. L. Clubb, editors. Psittacine Aviculture: perspectives, techniques and research. Avicultural Breeding and Research Center, Loxahatchee Florida.

Clubb, K. J., D. Skidmore, R. Schubot, and S. L. Clubb. 1992a. Growth rates of handfed psittacine chicks.*in* R. M. Shubot, K. J. Clubb, and S. L. Clubb, editors. Psittacine Aviculture: perspectives, techniques and research. Avicultural Breeding and Research Center, Loxahatchee Florida.

Clubb, S. L. 1992. The role of private avicultre in the conservation of Neotropical psittacines. Pages 117-132 *in* N. F. R. Snyder and S. R. Beissinger, editors. New World Parrots in Crisis. Smithsonian, Washington DC.

Clubb, S. L., K. J. Clubb, D. Skidmore, S. Wolf, and A. Phillips. 1992b. Psittacine neonatal care and hand-feeding. Page Chapter 11 *in* R. M. Shubot, K. J. Clubb, and S. L. Clubb, editors. Psittacine Aviculture: perspectives, techniques and research. Avicultural Breeding and Research Center, Loxahatchee Florida.

Clubb, S. L., K. J. Clubb, D. Skidmore, S. Wolf, and A. Phillips. 1992c. Psittacine neonatal care and hand-feeding.*in* R. M. Shubot, K. J. Clubb, and S. L. Clubb, editors. Psittacine Aviculture: perspectives, techniques and research. Avicultural Breeding and Research Center, Loxahatchee Florida.

Clubb, S. L., and A. Phillips. 1992. Pssitacine embryonic mortality.*in* R. M. Shubot, K. J. Clubb, and S. L. Clubb, editors. Psittacine Aviculture: perspectives, techniques and research. Avicultural Breeding and Research Center, Loxahatchee Florida.

Clubb, S. L., S. Wolf, and A. Phillips. 1992d. Psittacine pediatric medicine.*in* R. M. Shubot, K. J. Clubb, and S. L. Clubb, editors. Psittacine Aviculture: perspectives, techniques and research. Avicultural Breeding and Research Center, Loxahatchee Florida.

Cockburn, A. 2006. Prevalence of different modes of parental care in birds. Proceedings of The Royal Society B **273**:9.

Cornejo, J. 2012. Insights on psittacine nutrition through the study of free-living chicks. PhD Dissertation Texas A&M University, College Station, Texas.

Cornejo, J., E. Dierenfeld, C. A. Bailey, and D. J. Brightsmith. 2011. Predicted metabolizable energy density and amino acid profile of the crop contents of free-living scarlet macaw chicks (*Ara macao*). Journal of Animal Physiology and Animal Nutrition.

Cornejo, J., E. S. Dierenfeld, C. A. Bailey, and D. J. Brightsmith. 2013. Nutritional and physical characteristics of commercial hand-feeding formulas for parrots. Zoo Biology.

Cotton, P. A., J. Wright, and A. Kacelnik. 1999. Chick begging strategies in relation to brood hierarchies and hatching asynchrony. The American Naturalist **153**:412-420.

Dahlin, C., B. Chlesea, R. Jake, and T. Wright. 2018. Long-term monitoring of Yellow-naped Amazons (*Amazona auropalliata*) in Costa Rica: breeding biology, duetting and the negative impact of poaching. Journal of Field Ornithology **89**:11.

De la parra Martinez, S. M., K. Renton, A. S. Melgoza, and L. G. M. Lacy. 2015. Tree cavity and selection by a large bodied secondary cavity nester: the Military Macaw. Journal of Ornithology **156**:10.

Derrickson, S. R., and N. F. R. Snyder. 1992. Potentials and limits of captive breeding in parrot conservation. Pages 133-164 *in* N. F. R. Snyder and S. R. Beissinger, editors. New World Parrots in Crisis. Smithsonian, Washington DC.

Dingle, S. 1998. Olde Tymer Bill Rattray: King of the King Parrots. AFA Wathcbird. American Federation of Aviculture.

Drummond. 1987. A review of parent-offspring conflict and brood reduction in the Pelicaniformes. Colonial Waterbirds **10**:1-15.

Drummond, and C. G. Havelas. 1989. Food shortage influences sibling aggresion in the blue-footed booby. Animal Behavior **37**.

Eberhard, J. R. 2002. Cavity Adoption and the Evolution of Coloniality in Cavity-Nesting Birds. The Condor **104**:240-247.

Enkerlin-Hoeflich, E. C. 1995. Comparitive Ecology and Reproductive Biology of Three Species of *Amazona* Parrots in Northeastern Mexico. PhD Dissertation. Texas A&M University College Station, TX.

Enkerlin-Hoeflich, E. C. 1998. Status, ecología y conservación de loros Amazona en el Noreste de México. Instituto Tecnológico y de Estudios Superiores de Monterrey. Centro de Calidad Ambiental. Informe final SNIB-CONABIO proyecto No.B115. México D. F.

Fentzloff, C. 1984. Breeding, artificial incubation and release of White-tailed sea eagles. International Zoo Yearbook **23**:17.

Fernandes Seixas, G. H., and G. d. M. Mourão. 2002. Nesting success and hatching survival of the Blue-fronted Amazon (*Amazona aestiva*) in the Pantanal of Mato Grosso do Sul, Brazil. Journal of Field Ornithology **73**:399-409, 311.

Forshaw, J. M. 1989. Parrots of the world. Third edition. Landsdowne Editions, Melbourne, Australia.

Forshaw, J. M. 2010. Parrots of the world. Princeton University Press, Princeton, NJ.

Fox, R. A., and J. R. Millam. 2007. Novelty and individual differences influence neophobia in orange-winged Amazon parrots (Amazona amazonica). Applied Animal Behaviour Science **104**:107-115.

Garcia-Anleu, R., G. Onze-Santizo, S. Gulick, J. Boyd, D. Brightsmith, and R. B. McNab. 2017. Predation on Scarlet Macaw (*Ara macaw cyanoptera)* chicks by Collared Forest Falcons (*Micrastur semitorquatus)* in the Maya Biosphere Reserve, Guatemala. Ornitologia Neotropical **2017**:5.

Gilardi, J. D. 1996. Ecology of Parrots in the Peruvian Amazon: Habitat Use, Nutrition, and Geophagy. Ph.D. dissertation. UC Davis, Davis, California.

Gish, E. 2009. The case for bio-centric development: an ethnographic study of the Tambopata Macaw Project, ecotourism and volunteer tourism in the Peruvian Amazon. MSc Dissertation. Wageningen University.

Gnam, R. S. 1991. Breeding biology of the Bahama parrot (*Amazona leucocephala bahamensis*). the City University of New York, New York.

Gregory, N. G., and J. K. Robins. 1998. A body condition scoring system for layer hens. New Zealand Journal of Agricultural Research **41**:4.

Grenier, J. L., and S. R. Beissinger. 1999. Variation in the onset of incubation in a Neotropical parrot. Condor **101**:752-761.

Guedes, N. M. R. 2003. Sucesso reproductivo das araras-vermelhas (*Ara chloroptera*), em dez estacões reproductivas no Pantanal Ensaios e ciencia, Campo Grande - MS **7**:961-968.

Guedes, N. M. R., and L. H. Harper. 1995. Hyacinth Macaws in the Pantanal. Pages 395-421 *in* J. Abramson, B. L. Spear, and J. B. Thomsen, editors. The Large Macaws: Their Care, Breeding and Conservation. Raintree Publications, Fort Bragg, California.

Guittar, J. L., F. Dear, and C. Vaughan. 2009. Scarlet Macaw (*Ara macao*, Psittaciformes: Psittacidae) nest characteristics in the Osa Peninsula Conservation Area (ACOSA), Costa Rica. Revista de Biología Tropical **57**:387-393.

Harper, R. G., S. A. Julianho, and C. THompson. 1992. Hatching asynchrony in the house wren. Behavioral Ecology and Sociobiology **3**:76-83.

Harrison, G. L., and T. L. Lightfoot. 2006. Clinical Avian Medicine, Palm Beach, FL.

Hart, J. 1995. The Lear's Macaw. Pages 469-483 *in* J. Abramson, B. L. Spear, and J. B. Thomsen, editors. The Large Macaws: their care, breeding and conservation. Raintree Publications, Fort Bragg, California.

Heinsohn, R., N. Langmore, A. Cockburn, and H. Kokko. 2011. Adaptative Secondary Sex Ratio adjustments via sex-specific Infanticidae in Birds. Current Biology **21**:4.

Huber, w. 1933. Birds collected in northern Nicaragua in 1922. Prod. Acad. nat. Sci. Philad **84**:44.

Iñigo-Elias, E. E. 1996. Ecology and breeding biology of the Scarlet Macaw (*Ara macao*) in the Usumacinta drainage basin of Mexico and Guatemala. Ph.D. dissertation. University of Florida, Gainesville, Florida.

IUCN. 2019. The IUCN Red List of Threatened Species., www.iucnredlist.org.

Jones, C. G., K. Swinnerton, M. Thorsen, and A. Greenwood. 1998. The biology and conservation of the echo parakeet *Psittacula eques* of Mauritius. Pages 110-121 *in* IV International Parrot Convention. Loro Parque, Puerto de la Cruz, Tenerife, Canary Islands, Spain.

Juniper, T. 2003. Spix's Macaw: the race to save the world's rarest bird. Fourth Estate, London.

Kattan, G. H., and N. Gómez. 1992. Boby temperature of spectacled parrotlet nestlings in relation to body mass and brood size. 94 **94**:280-282.

Kock, R. A., M. H. Woodford, and P. B. Possiter. 2010. Disease risks associated with the translocation of wildlife. Revue Scientifique Et Technique De L Office Internatinal Des Epizities **29**:21.

Koenig, S. E. 2001. The breeding biology of Black-billed Parrot *Amazona agilis* and Yellow-billed Parrot *Amazona collaria* in Cockpit Country, Jamaica. Bird Conservation International **11**:205 - 225.

Krebs, E. 1998. Breeding biology of crimson rosellas (*Platycercus elegans*) on Black Mountain Australian Capital Territory. Australian Journal of Zoology **46**:17.

Krebs, E. 2001. Begging and food distribution in Crimson Rosella (*Platycercus elegans*) broods: why dont hungry chicks beg more? Behavioral Ecology Sociobiology **50**:10.

Krebs, E. 2002. Sibling competition and parental control: patterns of begging in parrots. Pages 319-336 *in* J. W. a. M. L. Leonard, editor. The evolution of begging. Kluwer Academic Publishers, Netherlands.

Krebs, E., and R. Margrath. 2000. Food allocation in Crimson Rosella broods: parent differ in their responses to chick hunger Animal Behavior **59**:739-751.

Krebs, E. A. 1999. Last but not least: nestling growth and survival in asynchronously hatching Crimson Rosellas. Journal of Animal Ecology **68**:266-281.

Krebs, E. A., R. B. Cunningham, and C. F. Donnelly. 1999. Complex patterns of food allocation in asynchronously hatching broods of Crimson Rosellas. Animal Behavior **57**:753-763.

Lack, D. 1947. The significance of clutch-size. Ibis **89**:302-352.

Lack, D. 1954. The Natural Regulation of Animal Numbers. Clarendon, Oxford, UK.

Lanning, D. V. 1991. Distribution and breeding ecology of the Red-fronted Macaw. Willson Bull **103**:357 - 365.

Lee, A. T. K., D. J. Brightsmith, M. P. N. Vargas, K. Q. Leon, A. J. R. Mejia, L. Y. Q. Huanca, A. K. Lee, and S. J. Marsden. 2014. Diet and geophagy across a western Amazonian parrot assemblage. Biotropica **46**:322-330.

Marc, B. 1983. Food suply and the occurence of Brood Reduction in Swainson's Hawk. The Wilson Bulletin **95**:233-242.

Marineros, L., and C. Vaughan. 1995. Scarlet macaws in Carara. Pages 445-468 *in* J. Abramson, B. L. Spear, and J. B. Thomsen, editors. The Large Macaws: their care, breeding and conservation. Raintree Publications, Ft. Bragg, CA.

Marks, H. L. 1974. Relationship of embrionatic developemnet to egg weight, hatch weight and growth in Japanese Quail. Poultry Science **54**:6.

Masello, J. F., and P. Quillfeldt. 2002. Chick growth and breeding success of the burrowing parrot. Condor **104**:574-586.

McDonald, J. H. 2014. Handbook of Biological Statistics (3rd Edition), Baltimore, Maryland.

Mock, D. W. 1987. Parent-offspring conflict, an unequal parental investment by egrets and herons. Behavioral Ecology and Sociobiology **20**:247-256.

Morandini, V., and M. Ferrer. 2015. Sibling agression and brood reduction: a review. Ethology, Ecology and Evolution **27**:2-16.

Moreno, J. 2012. Parental infanticide in birds through early eviction from the nest: rare or under-reported. Journal of Avian Biology **43**:43-46.

Munn, C. A. 1992. Macaw biology and ecotourism, or when a bird in the bush is worth two in the hand. Pages 47-72 *in* S. R. Beissinger and N. F. R. Snyder, editors. New World Parrots in Crisis. Smithsonian Institution Press, Washington, D.C.

Munn, C. A. 1998. Adding value to nature through macaw-oriented ecotourism. Journal of the American Veterinary Medical Association **212**:1246 - 1249.

Navarro, J. L., M. B. Martella, and E. Bucher. 1992. Breeding season and productivity of monk parakeets in Cordoba, Argentina. Wilson Bulletin **104**:413-424.

Nycander, E., D. H. Blanco, K. M. Holle, A. d. Campo, C. A. Munn, J. I. Moscoso, and D. G. Ricalde. 1995. Manu and Tambopata: nesting success and techniques for increasing reproduction in wild macaws in southeastern Peru. Pages 423-443 *in* J. Abramson, B. L. Spear, and J. B. Thomsen, editors. The Large Macaws: their care, breeding and conservation. Raintree Publications, Fort Bragg, California.

O'Gorman, T. 1987. Applied adaptative statistical methods: test of significance and confidence intervals (ASA-SIAM Series on Statistics and applied probability).

Olah, G., S. Butchart, A. Symes, I. Medina Guzman, R. CUnningham, D. Brightsmith, and R. Heinsohn. 2016. Ecological and socio-economic factors affecting extinction risk in parrots. Biodiversity Conservation **25**:205-223.

Olah, G., R. G. Heinsohn, J. R. Espinoza, D. J. Brightsmith, and R. Peakall. 2015. An evaluation of primers for microsatellite markers in Scarlet Macaw (*Ara macao*) and their performance in a Peruvian wild population. Conservation Genetics Resources **7**:157-159.

Olah, G., G. Vigo, R. Heinsohn, and D. J. Brightsmith. 2014. Nest site selection and efficacy of artificial nests for breeding success of Scarlet Macaws (*Ara macao*) in lowland Peru. Journal for Nature Conservation **22**:176-185.

Olah, G., G. Vigo, L. Ortiz, L. Rozsa, and D. J. Brightsmith. 2013. Philornis sp. bot fly larvae in free living scarlet macaw nestlings and a new technique for their extraction. Veterinary Parasitology.

Pacifico, E. C., E. A. Barbosa, T. Filadelfo, K. G. Oliveira, L. F. Silveira, and J. L. Tella. 2014. Breeding to non-breeding population ratio and breeding performance of the globally Endangered Lear’s Macaw Anodorhynchus leari: conservation and monitoring implications. Bird Conservation International **24**:466-476.

Perry, D. R. 1978. A method of access into the crowns of emergent and canopy trees. Biotropica **10**:155-157.

Perry, D. R., and J. Williams. 1981. The tropical rain forest canopy: a method providing total access. Biotropica **13**:283-285.

Pinho, J. B., and N. F. M. B. 2003. Hyacinth Macaw (*Andorhunchus hyacinthinus*) reproduction in the northern Pantanal, Matto Grosso, Brazil. Neotropical Ornithology **14**:29 - 38.

Portillo Reyes, H. 2005. Distribucion actual de la guara (lapa) roja (*Ara macao*) en Honduras. Zeledonia **9**:3.

Raso, T. D., G. H. F. Seixas, N. M. R. Guedes, and A. A. Pinto. 2006. Chlamydophila psittaci in free-living Blue-fronted Amazon parrots (Amazona aestiva) and Hyacinth macaws (*Anodorhynchus hyacinthinus*) in the Pantanal of Mato Grosso do Sul, Brazil. Veterinary Microbiology **117**:235-241.

Renton, K. 2002. Influence of environmental variability on the growth of Lilac-crowned Parrot nestlings. Ibis **144**:331-339.

Renton, K. 2004. Agonistic interactions of nesting and nonbreeding macaws. Condor **106**:354-362.

Renton, K., and D. J. Brightsmith. 2009. Cavity use and reproductive success of nesting macaws in lowland forest of southeast Peru. Journal of Field Ornithology **80**:1-8.

Renton, K., and A. Salinas-Melgoza. 1999. Nesting behavior of the Lilac-crowned Parrot. Wilson Bulletin **111**:488-493.

Renton, K., and A. Salinas-Melgoza. 2004. Climatic variability, nest predation and reproductive output of Lilac-crowned Parrots (*Amazona finschi*) in tropical dry forest of western Mexico. Auk **121**:1214-1225.

Ricklefs, R. 1965. Brood reduction in the Curve-billed Thrasher. Condor **67**:505-510.

Ricklefs, R. 1969. An analysis of nesting mortality in birds. Smithsonian Institution Press, City of Washington.

Ricklefs, R. E. 1968. Patterns of growth in birds. Ibis **110**:419-451.

Robertson, I. 1960. Some factors effecting hatchability in the domestic fowl. University of Edinburgh.

Robinet, O., and M. Salas. 1999. Reproductive biology of the endangered Ouvea Parakeet Eunymphicus cornutus uvaeensis. Ibis **141**:660-669.

Romer, L. 2000. Management of the Double-eyed or Red-Browed fig parrot. The Zoological Society of London **37**:6.

Rowley, I. 1980. Parent-offspring Recognition in a Cockatoo, the Galah Cacatua roseicapilla. Australian Journal of Zoology **28**:9.

Rowley, I. 1990. The Behavioral Ecology of the Galah *Eolophus roseicapilus* in the Wheatbelt of Western Australia, Sydney.

Rowley, I., and G. Chapman. 1991. The breeding biology, food, social organization, demography and conservation of the Major Mitchell or Pink Cockatoo, *Cacatua leadbeateri*, on the margin of the Western Australian wheatbelt. Australian Journal of Zoology **39**:211-261.

Ruiz, J., and C. A. Lunam. 2010. Effect of pre-incubation storage conditions on hatchability, chick weight at hatch and hatching time in broiler breeders. British Poultry Science **2002**:3.

Saint Jalme, M. 1999. Endangered Avian Species Captive Propagation: An overview of Functions and Techniques. Avian and Poultry Biology Reviews **13**:16.

Sanz, V., and A. Rodriguez-Ferraro. 2006. Reproductive parameters and productivity of the Yellow-shouldered Parrot on Margarita Island, Venezuela: A long-term study. Condor **108**:178-192.

Sanz, V., and A. Rodríquez-Ferraro. 2006. Reproductive parameters and productivity of the Yellow-shouldered Parrot on Margarita Isalnd, Venezuela: a long-term study. Condor **108**:178-192.

Sanz, V., and F. Rojas-Suárez. 1997. Los nidos nodriza como técnica para incrementar el reclutamiento de la cotorra cabeciamarilla (*Amazona barbadensis*, Aves: Psittacidae). Vida Silvestre Neotropical **6**:8-14.

SAS Institute Inc. 2019. JMP, Version 15. Cary, NC.

Saunders, D. A. 1982. The breeding behaviour and biology of the short-billed form of the White-tailed Black Cockatoo *Calyptorhynchus funereus*. Ibis **124**:422-455.

Schew, W. A., and R. E. Ricklefs. 1998. Developmental plasticity. Pages 288 -303 *in* M. Starck and R. E. Ricklefs, editors. Avian growth and development - Evolution within the altricial - precocial spectrum, New York - Oxford.

Schischakin, N. 1999. The Spix's Macaw recovery project: a non-extinction story. AFA Watchbird **Nov-Dec**.

Schubot, R. M., K. J. Clubb, and S. L. Clubb. 1992. Psittacine Aviculture: Perspective, Techniques and Research. Avicultural Breeding and Research Center, Loxahatchee, FL.

Simmons, R. E. 1988. Offspring quality and the evolution of cainism. Ibis **130**.

Smith, G. A. 1975. Systematics of parrots. Ibis **117**:99.

Smith, G. T. 1991. Breeding ecology of the Western Long-billed Corella, *Cacatua pastinator pastinator*. Wildlife Research **18**:91-110.

Smith, G. T., and D. A. Saunders. 1986. Clutch size and productivity in three sympatric species of cockatoo (Psittaciformes) in the south-west of Western Australia. Australian Wildlife Research **13**:275-285.

Snyder, N., J. Wiley, and C. Kepler. 1987a. The Captive Program.*in* M. Morrison, editor. The parrots of Luquillo: Natural History and Conservation of the Puerto Rican Parrot. The Western Foundation of Vertebrate Zoology, California.

Snyder, N., J. Wiley, and C. Kepler. 1987b. Reproductive Biology.*in* M. Morrison, editor. The parrots of Luquillo: Natural History and Conservation of the Puerto Rican Parrot. The Western Foundation of Vertebrate Zoology, California.

Snyder, N. F. R., and H. Snyder. 2000. The California condor: a saga of natural history and conservation. Academic Press, New York.

Snyder, N. R. R., J. W. Wiley, and C. B. Kepler. 1987c. The parrots of the Luquillo: natural history and conservation of the Puerto Rican Parrot. Western Foundation of Vertebrate Zoology, Los Angeles, California.

Speer, B. L. 1995. Stunting in the large macaws. Seminars in Avian and Exotic Pet Medicine **4**:9-14.

Stamps, J., A. B. Clark, P. Arrowood, and B. Kus. 1985. Parent-offspring conflict in Budgerigars. Behavioral Ecology and Sociobiology **94**:40.

Stojanovic, D., G. Olah, M. Webb, R. Peakall, and R. Heinsohn. 2018. Genetic evidence confirms severe extinction risk for critically endangered swift parrots: Implications for conservation management. Animal Conservation **21**:313-323.

Stoleson, S., and S. Beissinger. 1995. Hatching asynchrony and the onset of incubation in birds, revisited. Pages 191-271 *in* D.M.Power, editor. Current Ornithology. Springer Science - Business Media, New York.

Stoleson, S., and S. Beissinger. 2001. Does risk of nest failure of adult predation influence hatching patterns of the Green-rumped parrotlet. The Condor **103**:85-97.

Stoleson, S. H., and S. R. Beissinger. 1997a. Hatching asynchrony in parrrots: boon or bane for sustainable use? Pages 157-180 *in* J. R. Clemmons and R. Buchholz, editors. Behavioral approaches to conservation in the wild. Cambridge, New York.

Stoleson, S. H., and S. R. Beissinger. 1997b. Hatching asynchrony, brood reduction, and food limitation in a Neotropical parrot. Ecological Monographs **76**:131-154.

Stoodley, A. A. 1986. Surrogate Parents. Page 6 AFA Watchbid. American Federation of Aviculture.

Styles, D., K. 2001. Captive psittacine behavioral reproductive husbandry and management: socialization, aggression control, and pairing techniques. Pages 3 - 14 *in* The Association of Avian Veterinarians. The Association of Avian Veterinarians, Orlando, Florida.

Tortosa, F., and T. Redondo. 1992. Motives for Parental Infanticide in White Storks *Ciconia ciconia*. Ornis Scandinavica (Scandinavian Journal) **23**.

Tosi, J. A. 1960. Zonas de vida natural en el Perú. Memoria explicativa sobre el mapa ecológico del Perú. Instituto Interamericano de las Ciencias Agricolas de la Organización de los Estados Americanos, Lima, Peru.

Vaughan, C. 2019. Conservacion de la lapa roja (*Ara macao)* con manejo in situ en el Pacifico Central de Costa Rica. Revista de Ciencias Ambientales **53**:166-188.

Vaughan, C., M. Bremmer, and F.Dear. 2008. Scarlet Macaw (*Ara macao*) Parental nest visitation in Costa Rica. Rev.Biol.Trop. **57**:6.

Vaughan, C., F. Dear, N. Nemeth, and L. Marineros. 2006a. Cavidades de nidos de la Lapa Roja (*Ara macao*) en Costa Rica e implicaciones para su manejo. Mesoamericana **10**:11-18.

Vaughan, C., J. Gack, H. Solorzano, and R. Ray. 2003a. The effect of environmental education on schoolchildren, their parents, and community members: a study of intergenerational and intercommunity learning. The Journal of Environmental Education.

Vaughan, C., N. Nemeth, J. Cary, and S. Temple. 2005. Response of a Scarlet Macaw *Ara macao* population to conservation practiced in Costa Rica. Bird Conservation International **15**:119-130.

Vaughan, C., N. Nemeth, and L. Marineros. 2003b. Ecology and management of natural and artificial scarlet macaw (*Ara macao*) nest cavities in Costa Rica. Ornithologia Neotropical **14**:381 - 396.

Vaughan, C., N. Nemeth, and L. Marineros. 2006b. Scarlet macaw, Ara macao, (*Psittaciformes : Psittacidae*) diet in Central Pacific Costa Rica. Revista De Biologia Tropical **54**:919-926.

Vigo, G. In prep CH 2. Nesting behavior and ecology of the Scarlet Macaw in Tambopata, Peru.

Vigo, G. In prep CH 3. Death by starvation in Scarlet Macaw chicks.

Vigo, G. In prep CH 4. Increasing survival of wild macaw chicks using foster parents.

Vigo, G., M. Williams, and D. Brightsmith. 2011a. Growth of Scarlet Macaw (Ara macao) chicks in Southeastern Peru. Ornitologia Neotropical **22**:143-153.

Vigo, G., M. Williams, and D. J. Brightsmith. 2011b. Growth of Scarlet Macaw (*Ara macao*) chicks in southeastern Peru. Neotropical Ornithology **22**:143-153.

Vigo Trauco, G. 2007. Crecimiento de pichones de Guacamayo Escarlata, *Ara macao* (Linneus: 1758) en la Reserva Nacional Tambopata - Madre de Dios - Perú. Professional thesis. Universidad Nacional Agraria La Molina, Lima, Peru.

Viñuela, J. 2000. Opposing selectie pressures on hatching asynchronoy: egg viability, brood reduction and nestling growth. Behavioral Ecology and Sociobiology **48**.

Voren, H., and R. Jordan. 1992a. Feeding Page 24 Parrots: hand feeding & nursery management. Mattachione, Silvio, & Company.

Voren, H., and R. Jordan. 1992b. Maintenance of Nestlings (Brooding). Parrots: hand feeding & nursery management. Mattachione, Silvio, & Company.

Voren, H., and R. Jordan. 1992c. Maintenance of nestlings (Brooding). Page 17 Parrots: hand feeding & nursery management. Mattachione, Silvio, & Company.

Voren, H., and R. Jordan. 1992d. Parrots: hand feeding & nursery management. Mattachione, Silvio, & Company.

Voren, H., and R. Jordan. 1992e. Potential health problems in the nursery. Parrots: hand feeding & nursery management. Mattachione, Silvio, & Company.

Waltman, J. R., and S. R. Beissinger. 1992. Breeding behavior of the Green-rumped Parrotlet. Wilson Bulletin **104**:65-84.

White, T., H., and F. J. Vilella. 2004. Nest Management for the Puerto Rican Parrot (*Amazona vittata*): gaining the technological edge. Ornitologia Neotropical **15 (Suppl.)**:467-476.

White, T. H., G. G. Brown, and J. A. Collazo. 2006. Artificial Cavities and Nest Site Selection by Puerto Rican Parrots: a Multiscale Assessment. Avian Conservation and Ecology - Écologie et conservation des oiseaux **1**.

Wiedenfeld, D. A. 1994. A new subspecies of Scarlet Macaw and its status and conservation. Ornitologia Neotropical **5**:99-104.

Wilson, K. A., R. Field, and M. H. Wilson. 1995. Successful nesting behavior of Puerto Rican Parrots. Wilson Bulletin **107**:518-529.

Xenoulis, P. G., P. L. Gray, D. J. Brightsmith, B. Palculict, S. Hoppes, J. M. Steiner, I. Tizard, and J. S. Suchodolski. 2010. Molecular characterization of the cloacal microbiota of healthy wild and captive parrots. Vet Microbiol **15**:320-325.

Yantz, J. 1986. Notes on fostering finches. AFA Watchbird Magazine. American Federationof Aviculture.

APPENDIX 1

DIET DETAILS FOR SCARLET MACAW WILD CHICKS IN THE NURSERY

Formula for neonates (< 4 days old) was prepared as 1-part Zupreem formula to 4 parts water. For chicks ≥ 4 days old regular chick formula was 1-part Zupreem formula to 3 parts water plus peanut butter in the majority of the cases. For chicks ≥ 12 days old a mix of shredded raw Brazil nuts, pecans, and peanuts was added to the regular chick formula (Table 1 Supplemental materials). The majority of the time chicks were fed when their crops were empty or close to empty resulting in a feeding frequency of about once every 2.7 hours when they were under 4 days of age to about once every 5 hours when they were between 15 and 20 days old (modified from Voren and Jordan 1992d). This protocol was followed for 21 chicks. For one chick I experimented adding shredded peanuts and peanut butter to the neonate formula starting at age 2 days and four chicks that had additional health problems received customized feeding regimes.

One underweight third chick was fed neonatal formula until it was 11 days old because its digestion was slow. From 12 days on it was fed regular chick formula. By age 15, it showed slower growth and slower development for its age but by 24 days old, its weight was as expected for its age. A similar situation happened with the underweight forth chick that arrived to the nursery right after hatching. The chick was fed neonatal emergency formula on its first day of life and neonate formula its second day of life. Subsequently it was moved up to neonate formula plus until it was 11 days old. At age 7 and age 8 chick showed early signs of slow digestion and it was given a mix of warm papaya juice and cinnamon added to its usual food until crop size increased to half crop full, once per day. From hatch, this chick showed a slower growth and slower development for its age but by age 25, it weighed as expected for its age. A second chick with signs of starvation, was given a special neonatal emergency formula (1 part Formula One by Avitech and 4 parts water;

(http://www.avitec.com/Formula-One-for-hand-feeding-hatchlings-s/70.htm) and subcutaneous fluids for its first 12 hours in the nursery. In these first 12 hours it gained 78% of its arrival weight and after that the chick was fed accordingly to its age.

One chick with a large botfly infection and low weight received two feedings that were a mix of neonatal emergency food and regular neonatal formula.

One first chick that was brought as part of the acclimation process to create a triple brood, had food aspiration problems in its second day in the nursery, when it was 19 days old. The chick was under antibiotics, anti-inflammatory and antifungal oral treatment for the following 20 days (15 days in the nursery, 5 days after nest relocation). This chicks weight gain was always as expected for its age. All of the remaining chicks were fed normally according to their age.

APPENDIX 2

FOSTER CHICK FATALITIES

During my three years of experimentations with wild macaws as foster parents, three foster chicks perished in their foster nests.

The first one died five days after being placed possibly because of an unknown disease. This foster chick had half-full crop by the day after relocation but just ¼ full on the following days. On those days, it was supplemental fed. Starting on the day after relocation, this foster chick showed small red hematomas, first on the right flank, then the left flank, next to the keel with a scratch-like wound on the right leg. The foster chick was the third chick in its original nest. Both chicks in the original nest died with the same type of hematomas: second hatch at 6 days of age and the first hatch at 12 days.

The second case of a foster chick dead was due a combination of predation and a lightning hitting the video cable systems installed in artificial nest (PVC pipe). Nest was found with cable system burn and the human-access door blow up. Foster chick (39 days old) and resident chicks (41 days old) were not found inside nest or surroundings. Marks of large claws were found around the door of an artificial PVC nest and on the tree branches from where nest was hung.

A third case of a foster chick death was due to lightning hitting the artificial nest (wooden box) that blow up the base and top off the nest. The foster chick was 36 days old. Both foster and resident chick were found on the ground, below nest tree, right after the thunderstorm stopped. Necropsy showed that foster chick death was due to electrocution and resident chick due to the fall.

APPENDIX 3

SUMMARY OF DIET OF WILD MACAW CHICKS IN THE NURSERY

Food names were assigned to differentiate among five different types of food provided. Neonate food was given to younger chicks (under 4 days old) and Regular food to older ones (over 4 days old). Emergency food was given to chicks showing signs of starvation. PLUS foods contain peanut butter and EXTRA PLUS foods contain peanut butter plus shredded raw Brazil nuts, pecans, and peanuts. Chick age is given in days. Formulas used are well-known commercial formulas use to raised macaw chicks in captivity: Zupreem Embrace (https://www.zupreem.com/products/birds/embrace-plus/) and Formula One by Avitech (http://www.avitec.com/Formula-One-for-hand-feeding-hatchlings-s/70.htm). Proportion used to prepare formula was the recommended by the manufacture.

Food Name	**Age Range**		**Ingredients**					**Formula / Water Proportion**
	Min (days)	**Max (days)**	**Formula Zupreem Embrace Baby Bird**	**Formula One Avitech**	**Peanut Butter**	**Sheered Seeds**	**Water**	
Neonates Formula	0	9	Yes	No	No	No	Yes	1 to 4
Neonates Formula Plus	2	20	Yes	No	Yes	No	Yes	1 to 4
Regular Formula	4	43	Yes	No	No	No	Yes	1 to 3
Regular Formula Plus	4	74	Yes	No	Yes	No	Yes	1 to 3
Regular Formula Extra Plus	12	28	Yes	No	Yes	Yes	Yes	1 to 3
Special Emergency Formula	7	13	No	Yes	No	No	Yes	1 to 4

APPENDIX 4

VIDEO OBSERVATIONS OF SCARLET MACAW BEHAVIOR IN FOSTER NESTS

Video observations done using surveillance cameras inside wild macaw nests in Southeastern Peru. Field observations were done by a mix of 20 different assistants watching live video feeds in the field. Recorded observations were done by one experienced observer using video recordings and include recordings of both diurnal and nocturnal activity. A total of 10 chicks were observed with video, 3 in 2017 and 7 in 2018.

	Seasons	**# Total Chicks**	**# Observers**	**Total hours observed**	**Hours observed per day**			
					Max	**Min**	**Average**	**St Dev**
Field Observations	2018	7	20	**417.9**	12.0	4.3	8.4	2.8
Recorded Observations	2017 & 2018	10	1	**573.4**	23.6	3.7	9.0	4.2

APPENDIX 5

PSITTACIFORMES SPECIES WITH REPORTS OF BROOD REDUCTION LINK TO CHICK STARVATION

English Name	Scientific Name	Area Reported	Reference
Hyacinth Macaw	*Anodorhunchus hyacinthinus*	Brazil	(Guedes and Harper 1995)
Green-wing Macaw	*Ara chloropterus*	Peru	(Vigo & Brightsmith unpublished data)
Scarlet Macaw	*Ara macao*	Mexico	(Iñigo-Elias 1996)
		Guatemala	(Boyd and McNab 2008)
		Costa Rica	(Vaughan et al. 2008, Vaughan 2019)
		Peru	(This study, Nycander et al. 1995, Vigo Trauco 2007)
Blue-and-yellow Macaw	*Ara ararauna*	Peru	(Brightsmith unpublished data)(Brightsmith and Bravo 2006)
Yellow-headed Amazon	*Amazona oratrix*	Mexico	(Enkerlin-Hoeflich 1995)
Red-crowned Amazon	*Amazona autumnales*	Mexico	(Enkerlin-Hoeflich 1995)
Red-lored Amazon	*Amazona viridiginales*	Mexico	(Enkerlin-Hoeflich 1995)
Black-billed Amazon	*Amazona agilis*	Jamaica	(Koenig 2001)
Yellow-billed Amazon	*Amazona collaria*	Jamaica	(Koenig 2001)
Puerto Rican Amazon	*Amazona vittata*	Puerto Rico	(Snyder et al. 1987b)
Yellow-Shouldered Amazon	*Amazona barbadensis*	Venezuela	(Sanz and Rodríquez-Ferraro 2006)
Red-spectacle Amazon	*Amazona petrei*	Brazil	(Elenise A. B. Sipinski personal communications)
Red-tailed Amazon	*Amazona brasilensis*	Brazil	(Elenise A. B. Sipinski personal communications)
Blue-fronted Amazon	*Amazona aestiva*	Brazil	(Fernandes Seixas and Mourão 2002)
Monk Parakeet	*Miopsitta monachhus*	Argentina	(Navarro et al. 1992)
Burrowing Parrot	*Cyaniliseus patagonus*	Argentina	(Masello and Quillfeldt 2002)
Green-rumped Parrotlet	*Forpus passerinus*	Venezuela	(Beissinger and Waltman 1991, Stoleson and Beissinger 1997b)
Black-cockatoo	*Zanda sp*	Australia	(Saunders 1982)
Red-tailed black cockatoo	*Calyptorhynchus magnificus*	Australia	(Smith and Saunders 1986)
Long-billed Corella	*Cacatua pastinator*	Australia	(Smith 1991)
Galah	*Cacatua roseicapilla*	Australia	(Smith and Saunders 1986, Rowley 1990)
Crimson Rosella	*Platycercus elegans*	Australia	(Krebs 1999)
Ouvea Parakeet	*Eunymphicus cornutus uvaeensis*	New Caledonia	(Robinet and Salas 1999)