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Vanina Dafne Fiorini · Diego Tomás Tuero
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Preface

Behavioral ecology studies the adaptive value (or fitness consequences) of animal behavior. The discipline emerged from ethology in the 1960s and 1970s of the previous century from seminal works of Bill Hamilton, John Maynard Smith, George Williams, and Robert Trivers, among others. Its aim was to understand the behavioral patterns as a result of selective pressures from the physical and social environment in which animals have evolved.

Many studies in behavioral ecology have been conducted in birds, probably because birds are ubiquitous, mostly diurnals, conspicuous, and therefore easy to observe and to study. Thus, birds had a high impact on the development of behavioral ecology, and behavioral ecology has been equally important in the advance of ornithology, as shown in the indexes of the main ornithological journals.

The majority of the studies on bird behavioral ecology have been conducted in the Palearctic and Nearctic biogeographical regions. These regions are relatively poor in bird diversity, with approximately 1000 and 750 species, respectively. On the contrary, relatively few studies on bird behavioral ecology have been conducted in the Neotropical region, which has the richest avifauna of the world, with about 3000 bird species and more than 30 endemic families.

This strong bias toward studies in Palearctic and Nearctic bird species reflects the marked differences in the number of behavioral ecologists and ornithologists working in Europe and North America and those working in South and Central America, likely as a result of the differences in investment in science and technology in developed countries (those in the Palearctic and Nearctic regions) and developing countries (those in the Neotropical region).

One of the consequences of this asymmetry is a north temperate perspective in formulating hypotheses to explain behavioral patterns in birds, hypotheses that in some cases do not provide suitable explanations for the patterns observed in other regions.

The aim of this book is to present studies conducted in the Neotropical region on different aspects of the behavioral ecology of birds. Although our sample is not complete, it includes studies conducted in different groups of birds (i.e., hummingbirds, wrens, swallows, flycatchers, tanagers, cowbirds, cuckoos, and cormorants, among others), at different latitudes (from 58° South to 15° North) and on different subjects, covering social and genetic mating systems, sexual selection, cooperative breeding, brood parasitism, visual and vocal communication, migration, sibling competition, fruit-taking behavior, and foraging and cognition.

We would like to thank all the authors, who not only wrote the chapters but also reviewed other chapters, and João Victor Pildervasser from Springer International Publishing AG, who invited us to edit this book. We also thank Pedro Blendinger, Victor Cueto, Jordan Herman, Bettina Mahler, and Spencer Sealy for reviewing some of the chapters.

We hope that the number of studies on behavioral ecology of Neotropical birds increases in the near future and that the results of these studies provide general explanations for the behavioral patterns observed in birds.

Ciudad Autónoma de Buenos Aires, Argentina

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Chapter 1
Social Mating System Divergence Between North and South Temperate Wrens

Paulo E. Llambías, María M. Jefferies, Paula S. Garrido,
and Gustavo J. Fernández

1.1 Introduction

Social mating systems describe the socio-spatial relationship between members of the opposite sex for the purpose of reproduction (Reichard 2003). Differences in social mating systems are often associated with differences in parental care patterns (Silver et al. 1985; Mock and Fujioka 1990; Webster 1991; Székely et al. 2000). In social monogamy, both sexes cooperate with brood care and usually share parental duties in similar proportions (Lack 1968; Silver et al. 1985; Mock and Fujioka 1990; Cockburn 2006; Leisler and Schulze-Hagen 2011). In contrast, social polygamy is often associated with partial or total desertion by one of the social partners (Searcy and Yasukawa 1989; Webster 1991; Slagsvold and Lifjeld 1994; Møller 2003). The apparent cooperation between socially monogamous pairs in rearing a brood is remarkable since natural selection should favor individuals that increase their fitness by reducing parental care and becoming polygamous (Maynard Smith 1977; Houston et al. 2005; Olson et al. 2008). Social monogamy does not imply sexual fidelity between partners as males and females often pursue extra-pair copulations, hence the social mating system may not reflect the genetic mating system (Gowaty 1996a; Hasselquist and Sherman 2001; Møller 2003).

The study of social mating systems requires time and effort. To adequately characterize a population, it is essential to work with a color-banded population, where territories are mapped carefully, all breeding nests are found and parental care

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patterns are determined. In addition, the description of social mating systems is often considered uninteresting or of limited regional relevance. The study of mating systems in Neotropical passerines has lagged behind when compared to the Nearctic and Palearctic passerines, and today remains undescribed for most species. This has created a temperate zone bias in our understanding of the evolution and maintenance of mating systems of Neotropical passerines (Stutchbury and Morton 2001; Macedo et al. 2008; Ferreira de Souza Dias et al. 2009; Zuk 2016; Xiao et al. 2017).

The Neotropical region extends from the northern edge of the tropical rain forest in Mexico (20° N) southward to Cape Horn (57° S) including both south temperate and tropical climates (Newton 2003). North of the Neotropic, the Nearctic region, with a predominantly temperate climate, extends to the Arctic (Newton 2003). The Nearctic and the Neotropic differ in several abiotic and biotic features that can have profound implications for avian social mating systems. While in the north, harsher winter conditions due to larger land masses result in more migratory bird species with short-term partnerships, in the south, milder winter conditions result in more year-round territorial species with long-term monogamy (Stutchbury and Morton 2001; Ferreira de Souza Dias et al. 2009; Wingfield et al. 2014). For migratory passerines in the north temperate zone, testosterone plasma levels are high during the breeding season and peak during territory establishment; in contrast, several resident Neotropical birds have lower levels of testosterone year round (Wingfield et al. 2014). These differences in testosterone levels may have different effects in the mating system and parental care patterns of Neotropical and Nearctic passerines (Wingfield et al. 2014). Also, Neotropical passerines differ from north temperate species in life-history strategies, having smaller clutch sizes, longer developmental periods, and extended parental care (Moreau 1944; Yom-Tov 1994; Martin 1996; Peach et al. 2001; Russell et al. 2004). Several hypotheses predict greater parental investment per young in the Neotropics (e.g., Russell et al. 2004; Martin 2014, 2015) which in turn should affect social interactions and parental care strategies. Breeding synchrony, which is thought to affect social mating systems (Emlen and Oring 1977), may not differ greatly between north and south temperate zones at equivalent latitudes; however, a greater variation is expected within the tropical zone (Stutchbury and Morton 2001; Macedo et al. 2008). Due to the differences in ecological factors, demography, and life-history strategies, comparisons between hemispheres can shed new light on our understanding of the evolution and maintenance of extant social mating systems.

Lack (1968) noted that although wrens (Troglodytidae) are mostly distributed in the Neotropics, social polygyny only occurs in the Nearctic wren species. Wrens include approximately 85 species, nine of which inhabit North America (Brewer 2001; Kroodsma and Brewer 2005). While 67% of the Nearctic wrens have been frequently reported as being social polygynous, monogamy seems to be the rule in Neotropical wrens (reviewed by Brewer 2001; Kroodsma and Brewer 2005). This pattern, however, may result from bias in number of studies on breeding biology of north temperate species (Stutchbury and Morton 2001; Macedo et al. 2008;

Ferreira de Souza Dias et al. 2009; Xiao et al. 2017). Two species complexes, the Sedge Wren (*Cistothorus platensis*) and the House Wren (*Troglodytes aedon*) are distributed from Canada to Cape Horn and are ideal to evaluate if social polygyny is restricted to northern wrens. *Cistothorus* and *Troglodytes* are closely related taxa (Barker 2004), despite inhabiting different environments (grasslands vs. open forest, respectively), the convergence within and divergence between temperate zones in terms of social mating systems is perplexing.

Here we present a comparative study of the social mating system and parental care patterns of north and south temperate Sedge Wrens and House Wrens. We used a combination of original data and published reports (Table 1.1) to evaluate the divergence in breeding strategies between hemispheres. With this objective we compared social polygyny rates, male contribution to feeding nestlings, and clutch size between south temperate and north temperate populations. This is the first step towards a broad description of the geographical variation patterns in social mating systems; thus, we hope to provide data for future comparative analyses as well as to stimulate much needed researches on mating systems of Neotropical birds.

Table 1.1 Location of study sites for Sedge Wrens and House Wrens

Subspecies	Population	Latitude	Longitude	Environment	Life style	Study period
Cistothorus platensis platensis	Mendoza, Argentina	32°38′ S	69°22′ W	Riparian grassland	Resident	2010–2014
Cistothorus platensis stellaris	Iowa, USA	43°11′ N	94°55′ W	Sedge meadow	Migratory	1974[a]
Cistothorus platensis stellaris	Minnesota, USA	47°40′ N	96°21′ W	Sedge meadow	Migratory	1976[b]
Troglodytes aedon bonariae	Buenos Aires, Argentina	36°25′ S	56°57′ W	Coastal woodland	Resident	2003–2007
Troglodytes aedon chilensis	Mendoza, Argentina	32°38′ S	69°22′ W	Tree plantation	Resident	2011–2014
Troglodytes aedon aedon	New York, USA	42°28′ N	76°29′ W	Deciduous forest	Migratory	2003–2008
Troglodytes aedon parkmanii	Alberta, Canada	49°86′ N 49°56′ N	114°27′ W 114°29′ W	Boreal forest Boreal forest	Migratory Migratory	2011–2014[c] 2011–2012[c]
Troglodytes aedon parkmanii	Wyoming, USA	44°40′ N	106°56′ W	Deciduous forest	Migratory	1987[d]

[a] Field data taken from Crawford (1977)

[b] Field data taken from Burns (1982)

[c] Field data taken from Kaluthota and Rendall (2017)

[d] Field data taken from Johnson and Kermott (1991)

1.2 Methods

1.2.1 *Study Species*

The genera *Cistothorus* and *Troglodytes* belong to a clade of closely related wrens (Troglodytidae, Barker 2004; Mann et al. 2006). Sedge Wrens and House Wrens are broadly distributed from southern Canada to Tierra del Fuego and inhabit tropical and temperate environments in both hemispheres (Brewer 2001; Kroodsma and Brewer 2005; Fig. 1.1). Both species seem to have their origins in Central America and later dispersed to North and South America (Brumfield and Capparella 1996; Robbins and Nyári 2014). A vicariant process caused by the uplift of the Sierra Madre Occidental in southern North America and marine transgressions in the Isthmus of Panama may have contributed to the isolation of subspecies (Brumfield and Capparella 1996; Robbins and Nyári 2014). Both the Sedge Wren and the House Wren are considered as single species (Remsen et al. 2016); however, several genetic lineages have been described (Brumfield and Capparella 1996; Rice et al. 1999; Campagna et al. 2012; Robbins and Nyári 2014).

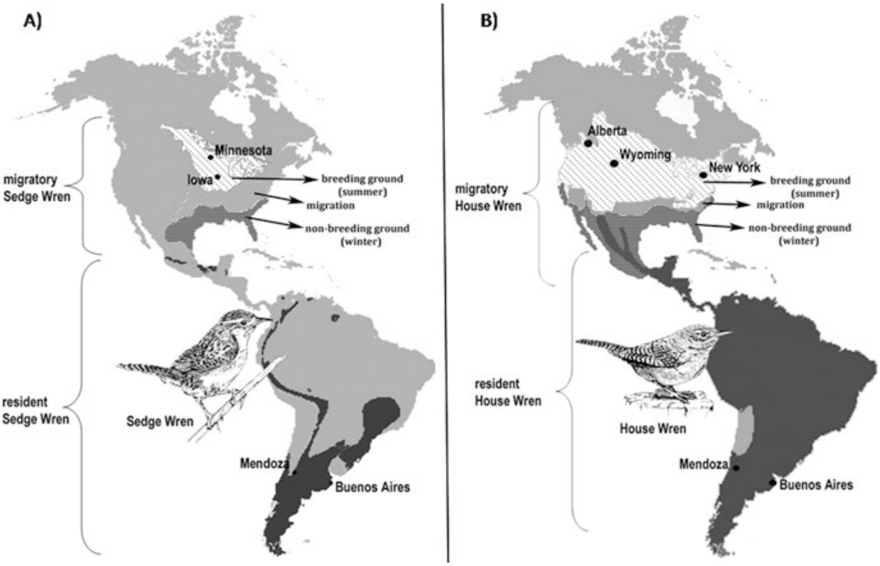

Fig. 1.1 (**a**) Map depicting the distribution of the Sedge Wren (*Cistothorus platensis*) complex. Study sites were located in Mendoza, Iowa (data from Crawford 1977) and Minnesota (data from Burns 1982). (**b**) Map depicting the distribution of the House Wren (*Troglodytes aedon*) complex. Study sites were located in New York, Buenos Aires, Mendoza, Alberta (data from Kaluthota and Rendall 2017), and Wyoming (data from Johnson and Kermott 1991)

1.2.1.1 Sedge Wrens

The Sedge Wren is a small insectivorous passerine that inhabit grasslands, coastal marshlands, and wet meadows (Brewer 2001; Herkert et al. 2001; Kroodsma and Brewer 2005). Males defend multipurpose territories where they forage and build well-concealed dome-shaped nests with grasses amid vegetation (Brewer 2001; Herkert et al. 2001; Kroodsma and Brewer 2005). Males develop complex songs used for territorial defense and mate attraction (Kroodsma et al. 1999a, b). Only females develop a brood-patch and incubate the eggs but both adults can provision the nestlings (Brewer 2001; Herkert et al. 2001; Kroodsma and Brewer 2005).

North American populations (northern Sedge Wrens hereafter) are migratory, breeding in north-central North America and wintering along the Atlantic coasts of the south-eastern USA and north-eastern Mexico (Herkert et al. 2001; Kroodsma and Brewer 2005; Fig. 1.1a). During the breeding season, northern Sedge Wrens are highly nomadic with little site fidelity, apparently producing first broods and second broods in different areas of their breeding range (Bedell 1996; Kroodsma et al. 1999b; Hobson and Robbins 2009; but see Burns 1982). In contrast, Sedge Wrens in Central and South America (southern Sedge Wrens hereafter) are year-round residents (Brewer 2001; Kroodsma and Brewer 2005). Northern Sedge Wren males may attract more than one female to their territories and breed polygynously (Crawford 1977; Burns 1982) while southern Sedge Wrens are thought to be socially monogamous (Kroodsma et al. 1999a).

1.2.1.2 House Wrens

The House Wren is a small insectivorous passerine that inhabit open forests and forest edges (Brewer 2001; Kroodsma and Brewer 2005; Johnson 2014). House Wrens defend multipurpose territories where they forage and build their nests in tree cavities or holes excavated by other birds (Brewer 2001; Kroodsma and Brewer 2005; Johnson 2014). Males develop complex songs which are used to defend the territory or to attract a female (Rendall and Kaluthota 2013; dos Santos et al. 2016). Both sexes contribute to feed and defend the young, but only females incubate the eggs and brood the nestlings (Johnson and Albrecht 1993; Johnson and Kermott 1993; Llambías et al. 2012, 2015; Fernández and Llambías 2013).

North American populations (northern House Wrens hereafter) are mainly migratory (Brewer 2001; Kroodsma and Brewer 2005; Fig. 1.1b), with moderate rates of social polygyny (5–40%; Johnson et al. 1993; Soukup and Thompson 1998; Poirier et al. 2003; Dubois et al. 2006; Llambías et al. 2012). In contrast, populations in Central and South America (southern House Wrens hereafter) are sedentary (Brewer 2001; Kroodsma and Brewer 2005; Fig. 1.1b), with lower rates of social polygyny (1–5%; Freed 1986; Llambías and Fernández 2009; Llambías et al. 2012). Furthermore, while northern House Wrens form short-term social partnerships at the breeding grounds (Drilling and Thompson 1988; Poirier et al. 2003), southern House Wrens maintain year-round monogamous associations (Freed 1987; Carro et al. 2017).

1.2.2 Study Populations

1.2.2.1 Sedge Wrens

We conducted field work on a resident population of southern Sedge Wrens in Mendoza Province, Argentina (Table 1.1, Fig. 1.1a). Our study site was located in a flood plain along the Uspallata Stream dominated by plants of the genus *Cortaderia*, *Tessaria*, and *Juncus*. The riparian grasslands and small swamps are irrigated by local streams and form a fertile corridor surrounded by scrubland vegetation (Carretero 2000). At our southern study site, Sedge Wrens defend a territory and maintain a pair bond year round as confirmed by resighting of banded individuals during the austral winter. We compared our data with published records of two northern Sedge Wren populations from Iowa (Crawford 1977) and Minnesota (Burns 1982; Table 1.1 and Fig. 1.1a).

1.2.2.2 House Wrens

We studied House Wrens breeding in nest-boxes in three temperate populations (Table 1.1, Fig. 1.1b) and in natural cavities in one of the southern temperate sites (see below). To compare polygyny rates between House Wren breeding in natural cavities and nest-boxes we included in our analysis published data from Wyoming (Johnson and Kermott 1991) and Alberta (Kaluthota and Rendall 2017; Table 1.1 and Fig. 1.1b).

We studied a northern House Wren population breeding in nest-boxes during the boreal breeding season (June–August) in New York State, at Cornell Experimental Ponds (Table 1.1, Fig. 1.1b). The study site included three patches of mixed deciduous forest (total area: 18.8 ha). In Argentina, we studied two southern House Wren populations during the austral breeding season (October–February): Buenos Aires and Mendoza (Table 1.1, Fig. 1.1b). In Buenos Aires, the study site was located at a private cattle ranch, and encompassed eight forest fragments of Spiny Hackberry (*Celtis ehrenbergiana*) trees (total area: 9.1 ha). We studied wrens breeding in nest-boxes in three forest plots during the whole study period but monitored wrens breeding in natural cavities in the other five forest patches (total area = 4 ha) for two breeding seasons (2003–2004). However, before the onset of egg laying in 2004, we added two nest-boxes in 50% of the territories ($n = 24$) where House Wrens were breeding in natural cavities. By the end of the 2005 breeding seasons we provided two nest-boxes to all territories. In Mendoza, the study site was located in two forest patches (total area: 5.2 ha) of a White Poplar (*Populus alba*) plantation. We provided all males with at least two nest-boxes.

In all study sites, we constructed nest-boxes of similar dimensions (30.5 × 16.5 × 12.7 cm) with an entrance hole diameter of 38 mm. Boxes were made of wood but materials differed between populations (pine in New York, eucalyptus and pine in Buenos Aires, and poplar in Mendoza). We placed nest-boxes 1.5–1.8 m high attached to greased poles (the USA) or trees (Argentina). To avoid Shiny Cowbird (*Molothrus bonariensis*) brood parasitism in Argentina, we reduced the entrance diameter to 27 mm during the nest building stage or after the first egg was laid.

1.2.3 General Field Procedures

1.2.3.1 Breeding Biology

We located Sedge Wrens nests using both behavioral cues displayed by adults and systematic searching. We used the same technique to locate House Wren nests in tree cavities in Buenos Aires. We checked House Wren nest-boxes every 3 days to detect breeding activity (e.g., addition of nest material).

Once a nest was active, we routinely checked it every 1–3 days, and on a daily basis close to hatching and fledging. We recorded clutch size, number of nestlings hatched, and number of fledglings. We excluded from the analyses southern wren nests where we observed Shiny Cowbird egg destruction.

1.2.3.2 Social Mating Systems

During the breeding season, we captured adults with mist nets and color-banded them for individual identification. We resighted banded individuals every week to map territories and to determine the social mating system.

We calculated social polygyny rates (number of polygynous males/total breeding males) and polygyny type for all populations (see below). We considered a male to be socially polygynous if he was associated with more than one female with overlapping nesting activity. We considered that social polygyny was achieved by territorial usurpation (usurpatory polygyny; *sensu* Freed 1986) when a mated male expanded his territory, replaced a neighbor, and built a nest with the resident female while his mate was building a nest, incubating, or feeding nestlings. We considered that social polygyny was the result of mate attraction when a secondary female started to build a nest in a nest-box (House Wrens) or clump of grasses (Sedge Wrens) where the male was observed signing frequently while the primary female was building a nest, incubating, or feeding nestlings or fledglings.

1.2.3.3 Parental Care Patterns

We used video cameras to record parental behavior at our study sites and evaluate male parental contribution to feeding nestling of socially monogamous pairs. We filmed House Wren nest-boxes with Hi 8 video cameras (Sony Handy-cam) in Buenos Aires and New York, and digital video cameras (Canon Vixia HF R400) in

Mendoza. We set cameras 5–10 m from the nest-box, on tripods 30 cm high, camouflaged with grass and cloth. We filmed southern Sedge Wren nests with digital micro-cameras (Mini 550 resolution button screw micro-camera connected to a PV500 LITE portable mini DVR) disguised with small pieces of camouflaged netting and mounted on *T. absinthioides* stems located 15–20 cm from the nests. We filmed nests continuously for 4–5 h, 1 h after sunrise, when nestlings were 3, 7, 8, or 11 days old (we consider day 0 as the day when the majority of the nestlings in a given nest hatched). When possible, we filmed the same nest at least twice at intervals of 2–3 days between video sessions. For analyses, we compare our results with northern Sedge Wrens male parental care contribution patterns from 12 nests of monogamous pairs reported by Burns (1982) in Minnesota. Burns (1982) monitored nests daily from blinds when nestlings were between 4 and 10 days and pooled sessions of different nestling ages to calculate the per nest total number of trips of males and females to feed nestlings (see Table 3 in Burns 1982). To facilitate comparisons between populations, we pooled our video sessions of different nestling ages when a nest was filmed more than once. We then calculated the total number of trips of both sexes to feed nestlings for each nest (see statistical methods).

1.2.4 Statistical Analyses

We evaluated differences between north temperate and south temperate wrens in social polygyny rate, male parental care (contribution to feeding nestlings), and life-history variables using GLMMs (generalized linear mixed models) and GLMs (general linear models).

To assess differences between temperate zones we classified study sites as north temperate (Alberta, Iowa, Minnesota, New York, and Wyoming) or south temperate (Buenos Aires and Mendoza). We compared polygyny rate between temperate zones using a generalized linear mixed model (GLMM), assuming a binomial distribution of errors and a logit link function. We classified color-banded males as polygynous or non-polygynous and included them in the model as a dichotomous response variable. We included temperate zone, species and species x zone interaction as the predictors, and location as a random variable. We first ran the analysis including polygyny rates of House Wrens breeding in nest-boxes. To control for possible effects of nest-boxes in polygyny rates we then re-ran the analysis including data of House Wrens breeding in natural cavities and excluding data from nest-boxes. Lastly, we also compared the polygyny rate of House Wrens nesting in natural cavities and nest-boxes both in north and south temperate locations. For this analysis, nest type (natural cavity or nest-box) and temperate zone were included as predictors, and location as a random variable.

To evaluate if male contribution to feeding nestlings differs between temperate zones, we used a generalized linear mixed model (GLMM) with the number of male trips to feed the nestlings as the response variable, and temperate zone, species and species x zone interaction as the predictors. To control for lack of independency in the video recordings, we included male identity as a random factor. To control for variation in provisioning rates among breeding pairs we included the logarithm of the total number of visits performed to the nest by both sexes as an offset. For this analysis we assumed a Poisson error distribution and used a logarithmic link function.

We tested for differences in clutch size and number of nestlings fledged between temperate zones initially using a GLMM, with female identity and breeding season as random factors. However, because variance of the random terms was zero in these models (no variance at individual level), we used GLMs to test for effect of temperate zone, species, and the interaction effect. For these analyses, we assumed a Poisson error distribution and used a logarithmic link function.

All analyses were performed in the R language and environment (version 3.3.0; R Core Team 2016). For GLMM and GLM analyses we used the lme4 R package (Bates et al. 2015). Statistical significance of terms was evaluated comparing the deviance of nested models (i.e., with and without the predictor) with a log likelihood ratio test. When interaction was significant, we applied a post hoc Tukey's HSD procedure to explore which pairs of means were significantly different. For these comparisons, we used the multcomp R package (Hothorn et al. 2008).

1.3 Results

1.3.1 Social Systems

Social polygyny rate significantly differed between temperate zones. Although polygyny was low in all wren populations, it was greater in north temperate than in south temperate wrens (15.9% vs. 2.1%; Table 1.2, Fig. 1.2a). There were no significant differences in polygyny rate between Sedge Wrens and House Wrens (8.9% vs. 7.5%, respectively; Table 1.2). When considering only House Wrens breeding in natural tree cavities, social polygyny rate was still significantly higher in the north temperate zone (Table 1.2, Fig. 1.2a). Also, in this analysis we did not detect significant differences in polygyny rate between House Wrens and Sedge Wrens (Table 1.2, Fig. 1.2a). Social polygyny was more frequent in House Wrens nesting in nest-boxes than natural cavities and was also higher in northern hemisphere (Table 1.2, Fig. 1.2a).

All cases of social polygyny in the south temperate zone were the consequence of territorial usurpation (7/7). Of the five cases we observed in southern House Wrens, one was the result of active take-over while in the other four, usurpation seem to have occurred after the territorial male disappeared (usurpation could not be corroborated). The two cases we observed in southern Sedge Wrens were the consequence of the territorial usurpation. In contrast all cases of social polygyny in northern wrens seem to be the consequence of female attraction (Sedge Wrens: five cases (Crawford 1977), one case (Burns 1982); House Wrens breeding in natural cavities: three cases (Johnson and Kermott 1991), six cases (Kaluthota and Rendall 2017); House Wrens breeding in nest-boxes, 20 cases).

Table 1.2 Summary of statistical comparisons of social mating system, male parental care contribution to feeding nestlings in socially monogamous pairs, and life-history traits between southern and northern populations of Sedge Wrens and House Wrens

	Effect	Estimate	SE coeff.	$\chi^2_{(df = 1)}$	*P*
Polygyny rate	Intercept	−1.45	0.50		
	Temperate zone	−2.06	0.88	13.24	<0.01
	Species	−0.38	0.58	0.75	0.39
	Interaction	0.17	1.06	0.03	0.87
Polygyny rate (no nest-boxes)	Intercept	−1.42	0.42		
	Temperate zone	−2.03	0.83	8.33	<0.01
	Species	−0.93	0.54	2.37	0.12
	Interaction	0.92	1.36	0.42	0.52
Polygyny rate (only House Wrens)	Intercept	−1.21	0.25		
	Temperate zone	−2.60	0.52	10.52	<0.01
	Nest type	−1.15	0.43	4.31	0.03
	Interaction	1.50	1.19	1.21	0.27
Parental care	Intercept	−2.95	0.33		
	Temperate zone	2.17	0.37		
	Species	1.86	0.35		
	Interaction	−1.95	0.40	22.43	<0.01
Clutch size	Intercept	1.81	0.03		
	Temperate zone	−0.26	0.04	66.42	<0.01
	Species	0.12	0.07	1.45	0.23
	Interaction	−0.10	0.09	−1.3	0.25
Fledgling number	Intercept	1.63	0.03		
	Temperate zone	−0.27	0.05	26.66	<0.01
	Species	−0.16	0.13	1.87	0.17
	Interaction	0.09	0.16	−0.35	0.56

Reference levels for the estimation of coefficients were: temperate zone: north temperate; species: Sedge Wren

1.3.2 Parental Care

We detected significant differences between populations in male contribution to feeding nestlings of socially monogamous pairs (Table 1.2; Fig. 1.2b). *A posteriori* contrasts indicated that northern Sedge Wren males contributed significantly less in feeding nestlings than males of southern Sedge Wren and northern House Wrens ($z = 16.0$, $p < 0.01$, and $z = 16.5$, $p < 0.01$, respectively; Fig. 1.2b). In contrast, southern Sedge Wren and southern House Wren males did not differ significantly ($z = 0.44$, $p = 0.97$) nor did males of northern and southern House Wrens ($z = 0.60$, $p = 0.92$, Fig. 1.2b).

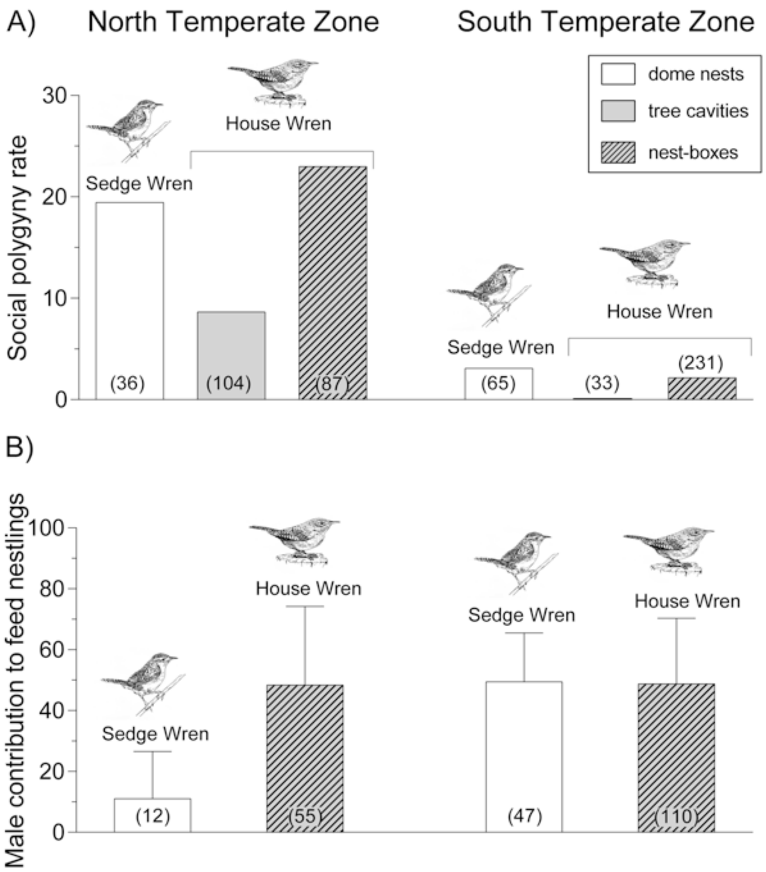

Fig. 1.2 (**a**) Social polygyny rates (polygynous males/monogamous + polygynous males) for temperate populations of Sedge Wrens and House Wrens. Social polygyny was significantly higher in north temperate than in south temperate wrens and for House Wrens breeding in nest-boxes than in natural cavities. Sample sizes (number of males) are given in parenthesis. (**b**) Mean (±SD) percentage of male contribution to feeding nestlings (male provisioning trips/total provisioning trips) 4–11 d nestlings in socially monogmous pairs for temperate populations of House Wrens and Sedge Wrens. North temperate Sedge Wren males contributed significantly less than north temperate House Wrens and south temperate Sedge Wrens. Sample sizes (number of nests) are given in parenthesis

1.3.3 Life-History Traits

Northern wrens had significantly greater clutch sizes (Table 1.2, Fig. 1.3a). Accordingly fledgling number was higher in northern temperate wrens (Table 1.2; Fig. 1.3b) and no differences were found between species (Table 1.2).

1.4 Discussion

Our results suggest convergence within and divergence between hemispheres in social mating system and life-history strategies of Sedge Wrens and House Wrens. Social polygyny was more frequent and clutch sizes were greater in north temperate than in south temperate populations (Figs. 1.2a and 1.3a). Parental care strategies however were not clearly associated with differences in social mating systems. Although social polygyny rates were similar in northern Sedge Wrens and northern House Wrens, northern Sedge Wren males contributed significantly less in feeding nestlings than northern House Wren males (Fig. 1.2b).

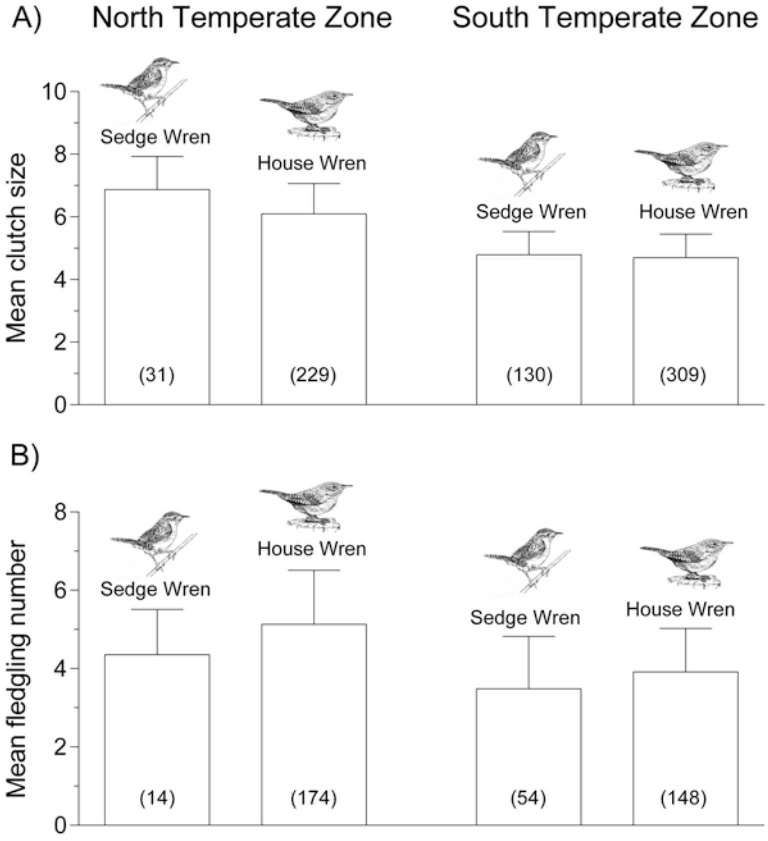

Fig. 1.3 Mean (±SD) clutch size and number of nestlings that fledged for temperate populations of Sedge Wrens and House Wrens. Northern wrens had significantly greater clutch sizes and produced significantly more fledglings than southern wrens. Sample sizes (number of nests) are in parenthesis

1.4.1 Social Mating Systems

In his classic book “Ecological adaptations for breeding in birds,” Lack (1968) noted that social polygyny is more frequent in Nearctic than in Neotropical wrens. Our results show that this pattern is not the result of inter-specific differences between northern and southern wrens. Social polygyny was moderate in north temperate populations of Sedge Wrens and House Wrens, but rare in south temperate populations (Fig. 1.2a). Furthermore, while in the north social polygyny was achieved when a mated male attracted an additional female to his territory, in the south social polygyny occurred only when a mated male replaced a neighboring male and bred with the resident female (usurpatory polygyny).

Although Burns (1982) and Crawford (1977) based their socio-spatial studies of northern Sedge Wrens on detailed maps and monitoring of territories of banded individuals, they did not record usurpatory polygyny. However, at our southern Sedge Wren population, it was easily detected through similar field techniques as it involves the eviction of a resident male with obvious changes in territory size and boundaries. Hence it is unlikely that usurpatory polygyny was not recorded in the northern populations. Further evidence that polygyny is achieved differently between populations is provided by differences in male advertising behavior. In northern Sedge Wrens, males build non-breeding nests from where they sing to attract additional females while the primary female is incubating the eggs and feeding nestlings (Burns 1982). In contrast, at our southern study site, we did not observed males advertising by building non-breeding nests during incubation and rearing of nestlings.

Similarly to northern Sedge Wrens, northern House Wren males achieved social polygyny by advertising a surplus nesting site and attracting a secondary female while the primary female is incubating the eggs (Johnson 2014). In a study in Wyoming, Johnson and Kermott (1991) reported that 47% of the males that bred in natural cavities repeatedly advertised for secondary mates. Similarly in Alberta, Kaluthota and Rendall (2017) reported that 32% of the males breeding in tree cavities try to attract a secondary mate while their first nest was active. In contrast, in southern House Wrens, we did not observe males advertising additional cavities nor nest-boxes during incubation and caring of the nestlings. Furthermore, although southern females prefer to mate with males with nest-boxes on their territories, addition of two nest-boxes to plots where males were breeding in natural cavities failed to produce polygyny (Llambías and Fernández 2009; Llambías 2012). However, experimental removal of territorial males increases the rate of usurpatory polygyny, strongly suggesting that territory take-over is the main strategy to achieve polygyny for southern House Wrens (Llambías 2012). Similarly, Freed (1986) reported that polygyny is infrequent in tropical House Wrens breeding in nest-boxes in Panama, and that all cases resulted from territorial usurpation.

The pattern of geographical variation in social mating systems of Sedge Wrens and House Wrens described here suggests that social polygyny is facultative in both hemispheres. Three main questions arise from this pattern: (1) Why is social polygyny more frequent in the northern than in the southern hemisphere? (2) Why is social polygyny mainly achieved by female attraction in the north but by territorial usurpation in the south? (3) Can the same variables that explain differences in polygyny rates also explain differences in polygyny type? The fact that Sedge Wrens inhabit grasslands and House Wrens open forests suggests an underlying common factor within hemispheres that shapes social mating systems.

The most obvious difference between hemispheres is the migratory behavior: while north temperate Sedge Wrens and House Wrens are migratory, south temperate populations are residents (Brewer 2001; Kroodsma and Brewer 2005). Migration is thought to affect several aspects of the breeding biology of birds, including breeding synchrony, life histories, social stability, and genetic mating systems (Stutchbury and Morton 2001; Ramenofsky and Wingfield 2006; Macedo et al. 2008; García-Peña et al. 2009; Wingfield et al. 2014). In migratory Sedge Wrens and House Wrens, males arrive first to the breeding grounds and establish a territory; females arrive later, settle on a territory, and form a pair bond with a resident male (Schramm et al. 1986; Demory et al. 2010). Migratory females may be time-constrained to either evaluate the social status of a potential partner and/or locate a bachelor male (Møller 1985; Stenmark et al. 1988; Ferretti and Winkler 2009). Furthermore, as females continue arriving at the breeding grounds and, settling on territories, the social status of males changes rapidly and social information becomes unreliable. Hence, northern migratory females may not be able to make optimal choices of social mates. Migratory males may take advantage of this constrain by advertising nesting sites to achieve polygyny.

In resident southern wrens, males and females remain on their territories year round and pair formation can occur before the onset of the breeding season. Social information is available during the non-breeding season, allowing females plenty of time to evaluate the social status of potential partners. At our south temperate Sedge Wren site, we often resighted social partners together on their territories during the non-breeding season, and we found most females paired several weeks before egg laying started in the population. We observed a similar pattern in southern House Wrens at our study site in Buenos Aires. Also, southern House Wren females initiate divorce more frequently than males, their decision is affected by mate availability and divorce is more frequent between breeding seasons than within breeding seasons (Carro et al. 2017). This suggests that female choice of social mates is based on social information and that these decisions are less constrained during the non-breeding season than during the breeding season. Considering this scenario, resident females are more likely to resist manipulation and control of their reproduction by males than migratory females (Gowaty 1996b). This in turn should select for different male strategies to exert control over females (advertising in migratory populations and usurpation in resident populations).

Differences in breeding synchrony may also explain differences in social polygyny rates between hemispheres. The female breeding synchrony hypothesis states that if female fertility is synchronous within the population, males will be unable to monopolize multiple mates because, after courtship and mating have occurred with the primary female, potential secondary females will have already paired with bachelor males (Emlen and Oring 1977). For House Wrens, this hypothesis is unlikely to explain differences between temperate populations as breeding synchrony in New York and Buenos Aires does not differ significantly (LaBarbera et al. 2010).

Given the broad distribution of Sedge Wrens and the reduced number of study sites (Table 1.1, Fig. 1.1), future research at other locations will be needed to confirm the generality of our results. Social polygyny may be frequent in other North American populations, as suggested by low male participation in feeding nestlings reported at other sites (e.g., Montreal, Mousley 1934; Michigan, Walkinshaw 1935). In contrast, biparental care was observed in three additional sites in south temperate Argentina (Córdoba, Salvador 2012; Jujuy, Salvador 2015; Buenos Aires, P. Llambías, unpublished data) and in a tropical site in Costa Rica (Kroodsma et al. 1999a). Similar geographical differences in social mating systems are observed when comparing other *Cistothorus* wrens. In North America, social polygyny is moderate in most Marsh Wren (*C. palustris*) populations studied (12.5–54%, Welter 1935; Verner 1965; Leonard and Picman 1987; but see Kale 1964). In contrast, in the Andean highlands of tropical South America, field observations of year-round associations between pairs suggest long-term monogamy in the Merida Wren (*C. meridae*, Kroodsma et al. 2001) and Apolinar's Wren (*C. apolinari*, Morales-Rozo 2005).

1.4.2 Parental Care Patterns

Differences in food availability, which in turn should affect male parental care contribution, can explain geographic variation in mating systems (Halupka et al. 2014). It has been proposed that social monogamy should be obligatory when biparental care is essential to rear a brood, as it maximizes the fitness of both sexes (Lack 1968; Bart and Tornes 1989; Ligon 1999; Reichard 2003). This hypothesis is unlikely to explain differences between hemispheres in House Wren social mating systems, as in Buenos Aires and New York females are able to rear at least some nestlings with reduced male care, even though they are unable to fully compensate for the lack of male help (Llambías et al. 2012).

Although northern wrens showed moderate rates of social polygyny, northern Sedge Wrens males contribute significantly less to feeding nestlings than northern House Wren males (Fig. 1.2b). The differences in paternal care patterns between northern wrens are probably due to differences in benefits of biparental care which in turn may be associated with differences in productivity between northern ecosystems. Indeed northern Sedge Wrens inhabit damp grasslands while House Wrens breed in open forest. It has been suggested that north temperate marshlands and grasslands are characterized by more food productivity than forests, reducing the benefits of biparental care (Verner and Willson 1966; Møller 1985; Leisler and Schulze-Hagen 2011). Accordingly, partially deserted northern House Wren females are unable to compensate for the lack of male help and produce fewer and lighter fledglings than fully aided females (Johnson and Kermott 1993; Llambías et al. 2012;

but see Bart and Tornes 1989). However, the costs of reduced male care in northern Sedge Wrens remain to be evaluated.

1.4.3 Life-History Traits

Southern wrens have smaller clutch sizes and fledge fewer nestlings than northern wrens, also suggesting an underlying common factor within hemispheres that shapes life-history strategies irrespectively of habitat type. Young (1996) proposed that survival in resident populations is influenced mainly by territory acquisition and intraspecific competition, while migratory species are subject to extrinsic mortality, caused by unpredictable weather conditions during migration. Hence, resident birds should invest more in offspring quality, whereas migratory species should invest in quantity. It has also been proposed that higher predation risks of nestlings and fledglings in the tropical and south temperate zone selects for higher parental effort per nestling in order to enhance wing development that increases fledgling survival (Martin 2015; Lloyd and Martin 2016). Accordingly, southern House Wrens in Buenos Aires have higher provisioning rates per nestling and longer developmental periods than northern House Wrens in New York (Llambías et al. 2015). If southern wrens invest more in offspring quality while northern wrens invest more in offspring quantity, southern males should invest less in attracting secondary females which in turn should be less likely to accept social polygyny.

1.5 Conclusions

A comprehensive theory of the evolution and maintenance of social mating systems should be able to explain geographic variation, including the interaction between migratory behavior, life-history strategies, parental care patterns, extra-pair fertilizations, and demography. Our research is the first step towards identifying differences in social mating systems between Neotropical and Nearctic wrens. The study of social mating systems requires time and effort, as detailed field descriptions of breeding biology, parental care patterns, and socio-spatial relationships between males and females are needed. Given the greater diversity on avian species in the Neotropic, the study of mating systems of Neotropical birds is essential for developing a general theory of avian mating systems.

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Ethical Approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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Chapter 2
Understanding Variation in Extra-Pair Paternity in Birds: A Focus on Neotropical Birds

Valentina Ferretti

2.1 Introduction

Since 1987 when DNA molecular techniques were first applied to behavioral and ecological studies of mating systems in birds (Burke and Bruford 1987), the long-standing assumption that 90% of avian taxa are monogamous (Lack 1968) has steadily become less tenable. Now, it is difficult to speak of avian mating systems without distinguishing between social and genetic mating systems. While genetic monogamy refers to the association of a male and a female for breeding purposes that results in the exclusive parentage by the breeding pair, social monogamy accompanied by genetic polygamy refers to a situation in which a male and a female breed and raise young together but some, or all, of the offspring in the nest are sired by other adults in the population as a result of a mixed reproductive strategy by the social parents.

The first studies that came out on this subject applied molecular techniques to the study of wild bird populations to evaluate the incidence of mixed reproductive strategies by males and females (e.g., Quinn et al. 1987). Early contributors to the study of extra-pair mating systems proposed the existence of a latitudinal cline, with tropical birds having lower extra-pair paternity rates (EPP rates) than birds breeding at higher latitudes (Stutchbury and Morton 2001, 2008; Macedo et al. 2008). We have now come to a point where, instead of asking *what* is the incidence of EPP or *what* is the pattern of variation in EPP, research questions are focused on *why* there is variation in this incidence both within and between populations and species (e.g., Bennett and Owens 2002; Griffith et al. 2002; Westneat and Stewart 2003; Griffith and Immler 2009). This shift resulted in the proposal by various authors of different

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factors that could account for the observed variation in genetic mating systems and the publication of several review papers on the subject in the last two decades (Petrie and Kempenaers 1998; Griffith et al. 2002; Westneat and Stewart 2003; Neudorf 2004; Akçay and Roughgarden 2007).

Several hypotheses have been proposed to explain interspecific variation in EPP rates (Griffith et al. 2002; Neudorf 2004). Emlen and Oring (1977) proposed that monopolization of resources by members of one of the sexes would lead to increased variance in that sex's reproductive success. This perspective suggests that breeding synchrony and nest density can explain interspecific variation in EPP rates. That is, EPP should be the result of opportunistic events benefited by spatial or temporal variation of resources (i.e., number of fertile mates at any given time, nest density). For example, higher breeding synchrony has been suggested to facilitate comparisons of displaying males by females and, thus, lead to a higher rate of EPP (Stutchbury and Morton 1995; Stutchbury 1998a, b; but see also Weatherhead and Yezerinac 1998) on one hand. On the other hand, a higher degree of breeding synchrony has been proposed to constrain male behavior, reducing the opportunities for extra-pair copulations: mate-guarding males will face a trade-off between seeking extra-pair copulations and guarding their fertile mates to avoid being cuckolded (Birkhead and Biggins 1987; Westneat et al. 1990). In fact, Hammers et al. (2009) found that mate-guarding behavior increased with breeding synchrony in the colonial fairy martin (*Petrochelidon ariel*), probably as a result of an increase in the perceived risk of loss of paternity. The controversy in the direction of the relationship between breeding synchrony and paternity rates is matched by inconclusive and contradictory empirical results. This same controversy across studies is apparent in the relationship between breeding density and rates of EPP (Westneat and Sherman 1997; Griffith et al. 2002; Neudorf 2004). Greater breeding densities may provide more opportunities for extra-pair copulations (Bennett and Owens 2002), but empirical results to support this have been ambiguous (see Appendix S2 in Mayer and Pasinelli 2013). It has also been suggested that EPP rates are the result of a transaction between mates in which each sex maximizes the benefit-cost difference of engaging in extra-pair copulations (e.g., Shellman-Reeve and Reeve 2000; Chapman 2006). Birkhead and Møller (1992) proposed that the maintenance of a given EPP rate is driven by the benefits it carries for males and females engaging in such tactics. Particularly, EPP can act as insurance against the social partner's infertility (e.g., Vedder et al. 2010) or as a means of increasing the genetic quality or diversity of the offspring (e.g., Petrie and Kempenaers 1998; Petrie et al. 1998). Given these potential advantages, why don't all birds engage in extra-pair behavior? The answer to this question can be explored by studying evolutionarily stable strategies and game theory (Maynard Smith 1982; Dugatkin and Reeve 2000). Particularly, high EPP rates should be associated with little need for paternal care (because females should be more likely to engage in extra-pair behavior when they can bear the cost of reduced male parental care; Mulder et al. 1994; Gowaty 1996), and to low adult survival (high EPP rates will only be evolutionarily stable in species with high adult mortality rates, because of the high chance, for males, of not breeding otherwise; Mauck et al. 1999; Bennett and Owens 2002). Then, the final breeding outcome will depend upon male and female individual adaptive decisions. Despite all the attention received and some careful comparative analyses (e.g., Arnold and Owens 2002) there still does not seem to be a unified understanding of the causes of variation in EPP, and geographic patterns of variation are by and large debatable (Martin 2004; Neudorf 2004; Macedo et al. 2008; Ferretti 2010).

What are we still missing? Lack of unified understanding may be due to (1) insufficient sampling of EPP rates for taxa inhabiting particular regions, with certain life-histories (e.g., tropical, south-temperate taxa), and across groups of recent divergence (below the taxonomic level of family), (2) a north-temperate biased perspective in formulating hypotheses (Zuk 2016), and/or (3) inadequate understanding of the links between EPP and other life-history traits. I review these topics below and then briefly describe some of the findings of my research that illustrate how north-temperate assumptions and insufficient sampling can lead us to formulate hypotheses that do not provide general explanations for the patterns observed in nature.

2.1.1 Insufficient Sampling

As noted in previous reviews on mating systems of tropical birds all the data available on paternity rates in birds today represent a very small minority of bird species in the world (Neudorf 2004; Macedo 2008). Neotropical birds (those inhabiting not only the American tropics, but also the regions that include the southern tips of Mexico, Florida and Baja peninsulas, Central America, and all South America) account for about 37% of the world's avian biodiversity with more than 3700 species, representing 90 families (Kricher 1997; Stotz et al. 1997), but only a small fraction of them have been studied, with direct measures of extra-pair paternity rates in 33 socially monogamous species (Table 2.1). With most bird diversity concentrated in the tropics and the southern hemisphere (Hawkins et al. 2003) and almost all studies performed in northern hemisphere birds, it should come as no surprise that, as we start looking at non-northern populations in more detail the patterns of variation in mating systems become unclear, making it almost impossible to predict extra-pair mating strategies.

Comparative work by Arnold and Owens (2002) and Bennett and Owens (2002) found that more than 50% of the diversification in EPP rates occurs at the level of family and order, and may therefore be explained by ancient diversification in mating systems. However, in these analyses the authors used studies describing only 88 species of birds—of the nearly 10,000 extant species—from 36 different taxonomic families, where only two families had two or more species in the same genus for which there was paternity information (*Falco* and *Parus*); and all of these were on populations inhabiting Europe and/or North America. This is mainly due to the fact that there are few studies south of the tropic of cancer, and the paucity of data on closely related groups, both of which can obstruct the interpretation of historical and contemporary data.

Table 2.1 Rates of extra-pair paternity in Neotropical birds

#	Species name	Family	Latitude of study	EPP (% broods)	EPP (% young)	Reference
1	*Buteo ridgwayi*[a]	Accipitridae	19° N	0%	0%	Woolaver et al. (2013)
2	*Ardea alba egretta*[b]	Ardeidae	16°26′ S to 16°46′ S	0%	n/a	Miño et al. (2011)
3	*Ardea alba egretta*[b]	Ardeidae	30°16′ S	0%	n/a	Miño et al. (2011)
4	*Habia fuscicauda*[a]	Cardinalidae	9° N	52.63%	41.46%	Chiver et al. (2015)
5	*Jabiru mycteria*[b]	Ciconiidae	19°57′ S to 16°23′ S	7.69%	n/a	Lopes et al. (2013)
6	*Mycteria americana*[b]	Ciconiidae	16°25′ S to 16°43′ S	0%	n/a	Miño et al. (2011)
7	*Mycteria americana*[b]	Ciconiidae	0°27′ N to 1°56′ N	0%	n/a	Miño et al. (2011)
8	*Zonotrichia capensis*[a]	Emberizidae	0°21′ S	64%	42%	Eikenaar et al. (2013)
9	*Zonotrichia capensis*[a]	Emberizidae	0°37′ S	60%	52%	Eikenaar et al. (2013)
10	*Tachycineta albilinea*[a]	Hirundinidae	9°10′ N	26%	15%	Moore et al. (1999)
11	*Tachycineta albilinea*[a]	Hirundinidae	17°36′ N	18%	8%	Ferretti (2010)
12	*Tachycineta leucorrhoa*[a]	Hirundinidae	35°34′ S	78%	56%	Ferretti et al. 2011)
13	*Tachycineta leucorrhoa*[a]	Hirundinidae	36°25′ S	61%	35%	Ferretti (2010)
14	*Tachycineta meyeni*[a]	Hirundinidae	54°44′ S	13.5%	6.8%	Ferretti et al. (2016)
15	*Agelaioides badius*[a,c]	Icteridae	35°7′ S	38%	13%	Ursino et al. (2017)
16	*Agelaius xanthomus*[a]	Icteridae	17°57 ′N	37%	23%	Liu (2015)
17	*Colaptes campestris*[a,c]	Picidae	15°56′ S	0%	0%	Dias et al. (2013)
18	*Cyanoliseus patagonus*[a]	Psittacidae	41°3′ S	0%	0%	Masello et al. (2002)
19	*Forpus passerines*[a]	Psittacidae	8°34′ N	14.4%	7.7%	Melland (2000)
20	*Myiopsitta monachus*[b]	Psittacidae	31°40′ S to 32°55′ S	40%	n/a	Martínez et al. (2013)
21	*Cercomacra tyrannina*[a]	Thamnophilidae	9°04′ N	0%	0%	Fleischer et al. (1997)
22	*Thamnophilus atrinucha*[a]	Thamnophilidae	8°59′ N	4%	3%	Tarwater et al. (2013)

(continued)

Table 2.1 (continued)

#	Species name	Family	Latitude of study	EPP (% broods)	EPP (% young)	Reference
23	*Geospiza fortis*[a]	Thraupidae	0°15′ S	35.5%	19.7%	Keller et al. (2001)
24	*Geospiza scandens*[a]	Thraupidae	0°15′ S	15%	8%	Petren et al. (1999)
25	*Neothraupis fasciata*[a,c]	Thraupidae	15°32′ S	39.4%	27.9%	Moreira (2014)
26	*Poospiza torquata*[a]	Thraupidae	28°03′ S	42.86%	20.65%	Sanchez et al. (2017)
27	*Ramphocelus costaricensis*[a]	Thraupidae	8°42′ N	55%	49%	Krueger et al. (2008)
28	*Volatinia jacarina*[a]	Thraupidae	15°57′ S	63%	50%	Carvalho et al. (2006)
29	*Platalea ajaja*[b]	Threskiornithidae	16°27′ to 16°76′	14.28%	n/a	Miño et al. (2011)
30	*Platalea ajaja*[b]	Threskiornithidae	1°09′ N to 1°56′ N	0%	n/a	Miño et al. (2011)
31	*Platalea ajaja*[b]	Threskiornithidae	32°29′ S	5.88%	n/a	Miño et al. (2011)
32	*Cantorchilus leucotis*[a]	Troglodytidae	9°7′ N	3%	4%	Gill et al. (2005)
33	*Thryothorus pleurostictus*[a]	Troglodytidae	10°40′ N	10%	4.5%	Cramer et al. (2011)
34	*Thryothorus rufalbus*[a]	Troglodytidae	10°40′ N	6%	2%	Douglas et al. (2012)
35	*Troglodytes aedon*[a]	Troglodytidae	36°26′ S	32.5%	15.66%	LaBarbera et al. (2010)
36	*Turdus albicollis*[a]	Turdidae	24°04′ S	36.4%	30%	Biagolini et al. (2016)
37	*Turdus grayi*[a]	Turdidae	9°7′ N	53%	38%	Stutchbury et al. (1998)
38	*Elaenia chiriquensis*[a]	Tyrannidae	9°7′ N	67%	37%	Stutchbury et al. (2007)
39	*Elaenia flavogaster*[a]	Tyrannidae	9°7′ N	8%	4%	Stutchbury et al. (2007)
40	*Pyrocephalus rubinus*[a]	Tyrannidae	19°18′ N	62.5%	41%	Ríos-Chelen et al. (2008)

EPP (% broods) = percent of broods in the population that had at least one extra-pair young; EPP (% young) = percent of extra-pair young in the population. n/a = data not available. It is important to consider that some of these studies have low sample sizes, which may have important implications in the error of the estimate (Griffith et al. 2002). Only reports of socially monogamous species were included in this review

[a] Paternity calculated with molecular markers using complete family information

[b] Paternity inferred using molecular markers through relatedness coefficients of offspring

[c] Species with facultative cooperative breeding, extra-pair paternity rate of socially monogamous pairs

In my expanded review of EPP rates in Neotropical birds one thing that strikes the attention is the existing variation among the taxa studied to date (Table 2.1). Birds in the Neotropics exhibit rates that range from 0 to 78% of broods having at least one extra-pair young. This is not surprising, as the Neotropical realm comprises a broad and diverse collection of environments and habitats (Kricher 1997), and the differences in physical geography pose differences in the selective pressures individuals inhabiting the different regions experience. For example, the extreme daily weather variation experienced by birds in Tierra del Fuego might select for a tight social pair bond in aerial insectivores like Chilean swallows (*Tachycineta meyeni*), which are highly dependent on weather, as both adults are needed to bring food to the nestlings to successfully fledge young, and both adults sit on the eggs during incubation (Ospina et al. 2015), presumably to keep the eggs above the physiological zero while the other adult is out foraging (Webb 1987). This tight bond, in turn, will restrict extra-pair forays and behavior that might result in lower EPP rates at the population level, as seen in Ferretti et al. (2016). On the other hand, the laxity and more benign weather of the Pampas might allow for a more flexible pair bond which may result in higher rates of EPP, as found in white-rumped swallows, *Tachycineta leucorrhoa* (Ferretti et al. 2011, 2018).

The other striking result stemming from the review of these studies of Neotropical birds is that EPP rates do not follow a latitudinal gradient of increase towards higher latitudes (Fig. 2.1a, b; but, please, note that this rough analysis did not take into

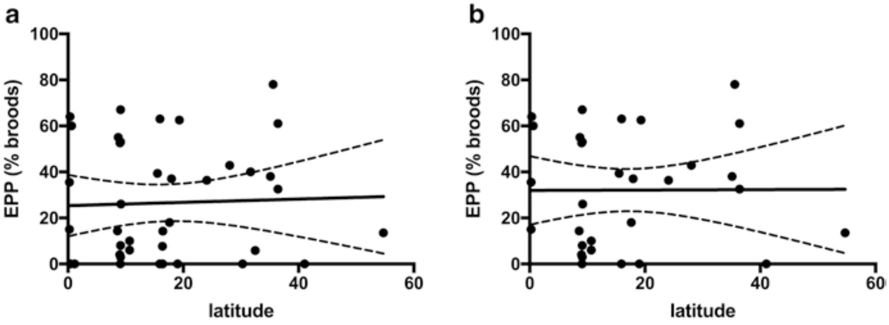

Fig. 2.1 Latitudinal variation in extra-pair paternity rates for the Neotropical species studied to date. *X*-axis represents the absolute value of the latitude at which the study was conducted (latitude); *Y*-axis represents the percent of broods with at least one extra-pair young in the population (EPP % broods). (**a**) All studied species/populations were included in this plot. Pearson's correlation $r = 0.037$, $p = 0.408$, $N = 40$. The solid line represents the linear regression $Y = 0.07135 \times X + 25.36$ (R squared = 0.001, slope does not deviate significantly from zero: $F = 0.054$, $p = 0.818$), the dashed lines are the 95% confidence intervals. (**b**) Only species/populations with complete molecular marker information for families from which extra-pair paternity was calculated were included in this plot. Pearson's correlation $r = 0.004$, $p = 0.490$, $N = 31$. The solid line represents the linear regression $Y = 0.008347 \times X + 31.98$ (R squared <0.001, slope does not deviate significantly from zero: $F < 0.001$, $p = 0.980$), the dashed lines are the 95% confidence intervals. (Data from Table 2.1)

consideration species' relatedness), and even taxa of recent divergence differ markedly in their genetic mating system (Table 2.1; i.e., *Geospiza scandens* vs. *Geospiza fortis*; *Tachycineta meyeni* vs. *Tachycineta leucorrhoa*; *Troglodytes aedon* vs. *Thryothorus pleurostictus, Thryothorus rufalbus, Cantorchilus leucotis; Elaenia flavogaster* vs. *Elaenia chiriquensis*; *Turdus grayi* vs. *Turdus albicollis*). With such low numbers of Neotropical species sampled, generalizations about the different factors that might affect geographic variation in EPP, as well as any evaluations on the diversification in EPP rates from a historical and a contemporary ecological standpoint, are doomed to fail. In sum, we don't understand *why* there is variation in EPP rates because we have a partial sample of taxa and thus inadequate sampling of the ecological/evolutionary factors that may have shaped, and may still be shaping, EPP rates. So the shift from asking *what* EPP rates are to asking *why* they are variable may be premature.

2.1.2 A North-Temperate Biased Perspective

As Stutchbury and Morton (2008) state in their review "[...] studies of temperate latitude species dominate our world view of avian biology." The scientific literature is full of examples that come from the work of researchers based in Europe and North America, that, at most, ventured to the northern half of the tropics (i.e., to the area between 0° and 23°26′N of latitude). Much of the scientific theory and the hypotheses proposed to explain variation in mating strategies are, thus, based on this research, which might distort our interpretations. Concomitant with this biased sampling in research studies is a biased perspective of the world in which we live (Zuk 2016). The notion that the patterns found in north-temperate latitudes are the norm is widespread, and continues to flood the scientific literature. Hypotheses explaining variation in EPP rates do not escape this north-temperate biased model. This is what has probably contributed to the plethora of discussion forums, contradicting responses to papers, and heated arguments among members of the ornithological community (e.g., Stutchbury 1998a, b; Weatherhead and Yezerinac 1998; Westneat and Stewart 2003; Akçay and Roughgarden 2007; Macedo et al. 2008, just to name a few).

Fortunately, we are starting to see an increase in awareness of this bias, and it is being acknowledged more often than not, as evidenced by the American Society of Naturalists' Vice Presidential Symposium at the Evolution meeting in 2015, organized by Zuk (2016). Studies on variation in EPP rates need to incorporate Neotropical species. While it is often more difficult to gather these data than those of species that inhabit the Nearctic and Palearctic realms, largely because of the lower bird breeding densities and logistic complications of working in Neotropical habitats/countries, detailed databases on these species will provide the backcloth for new, more inclusive, hypotheses and studies of variation in mating systems.

2.1.3 Understanding Links Between EPP and Other Life-History Traits

Insufficient and/or unbiased sampling might not be the only issues to consider. Mate choice, both genetic and social, can be directly affected by selection acting on other life-history traits. While this does not impact our understanding of EPP rates among Neotropical birds per se, it is something to consider, as it can have direct consequences on our understanding of variation in mating systems. Understanding the interplay between intra-individual and inter-generational trade-offs, the relationship among life-history traits, and between these and ecological variables, might help shed some light on the expected variation in EPP. While mapping these interactions might seem daunting at first sight, I believe it will provide a better understanding of the links and trade-offs between variables, and the expectations of variation under different conditions.

Different species, even those closely related, exhibit substantial variation in their life cycles. Some species migrate and some are year-round residents, some roost in the same places where they breed, some form long-term partnerships; and there is variation in the rates of within- and extra-pair copulations, variation in the number of eggs they lay, and in the length of the periods in which birds incubate or during which nestlings stay at the nest. When we parameterize all this information we end with a complex network of interactions among traits (Fig. 2.2). For example, adult survival can have an effect on the duration of the pair bond and can impact the reproductive share that the adults put into each breeding attempt, which has the potential of affecting parental care tactics, and thus, mating systems (i.e., the degree

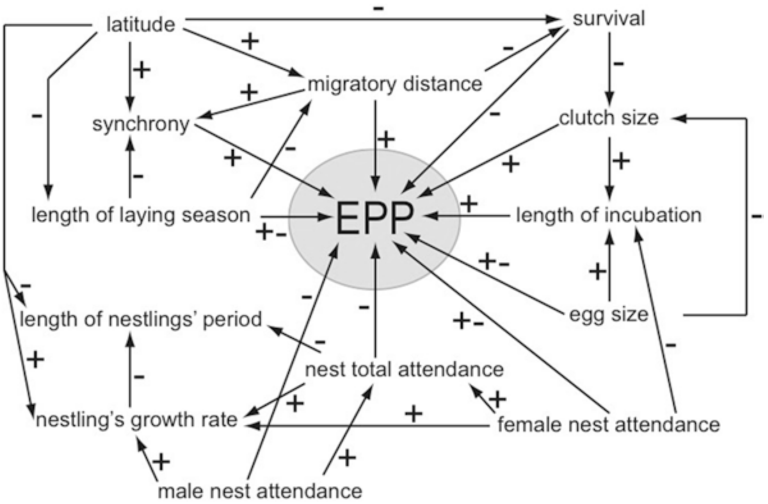

Fig. 2.2 Hypothesized relationships among life-history and other ecological traits. The sign and direction of the arrows represent the expected relationship between the trait where the arrow starts and the trait where it ends. (Taken from trade-offs and relationships addressed in Griffith et al. 2002; Martin 2004, as well as personal observation of hypothesized relationships among traits)

of EPP). Survival may in turn be influenced by migratory behavior and migratory distance, a factor that will likely be related to latitude. Similarly, male nest attendance should be inversely related to EPP at the nest, and increased attendance by both adults should have a positive effect on the rate of growth of nestlings (Griffith et al. 2002; Martin 2004). These are just two examples of a much larger and complex network of interactions and trade-offs, where, in fact, correlated suites of traits (e.g., adult survival and reproductive rate) could also be linked to high EPP.

For example, Stutchbury et al. (2007) in their study of extra-pair mating system in two tropical flycatchers found that resident and migrant Elaenia flycatchers breeding at the same site exhibited contrasting rates of EPP (see Table 2.1 for EPP values for these two species). These two species are closely related, breed at the same latitude, and yet, have very different genetic mating systems, likely due to the differences in life cycles. In their study the authors explained these differences exclusively in terms of the species' breeding synchrony. However, an alternative plausible explanation for this difference can be found in the relationships and trade-offs among life-history and ecological traits (Fig. 2.2). The lesser Elaenia (*Elaenia chiriquensis*) is a migratory species that defends seasonal territories, breeds during a shorter period of time, and has high rates of EPP, while yellow-bellied Elaenias (*E. flavogaster*) are residents that defend their territories year round, and have low EPP rates (Stutchbury et al. 2007). Migration can affect survival, which in turn can have an effect on the rates of EPP, as lower adult survival has been found to be associated with increased rates of EPP (Bennett and Owens 2002; Griffith et al. 2002).

The need for comprehensive comparative studies in life-history theory is imperative. Studies of variation in other traits, such as variation in clutch size or survival, have already taken this approach (e.g., Martin 2004, 2014, 2015; Martin et al. 2018). Understanding variation in traits such as EPP requires integrating across different levels and a detailed understanding of life-history traits and their population-level and evolutionary drivers. Research addressing the relationships in this network will untangle what seems like an overwhelmingly complicated set of arrows, traits, and variables, and give insights into the main drivers of variation in mating systems.

2.1.4 Breeding Synchrony and Extra-Pair Paternity in Birds: Why the South Matters in Swallows of the Genus *Tachycineta*

I have explained above what are, in my opinion, the reasons for our inability to predict rates of EPP in birds, in general, and among Neotropical birds, in particular. It was my research on variation in mating systems in *Tachycineta* swallows that got me thinking about this, and made me look into other research where the patterns of variation were similar to the ones observed in *Tachycineta*, or where the empirical results were not explained by theory. In this section I will first test the idea that EPP rates are lower at lower latitudes and that breeding synchrony is the main driver of this pattern of variation in this closely related group of birds, and will show you that the breeding synchrony hypothesis is not well supported when we include in the analysis species from the Neotropics. I will then discuss other possible explanations for the variation observed in this genus.

2.1.5 Hypotheses and Objectives

As mentioned earlier in this chapter, several hypotheses have been proposed to explain variation in EPP in birds (reviewed in Griffith et al. 2002), two of which address the importance of ecological facilitation on mating decisions—female breeding synchrony and nest density (Bennett and Owens 2002). In these hypotheses, direct interactions between the sexes affect breeding behavior, as increasing numbers of interactions between males and females allow for increased opportunities for copulations. In this way, through spatial or temporal concentration of mates, both hypotheses explain variation in EPP rates within and between species.

Originally proposed by Stutchbury and Morton (1995), the breeding synchrony hypothesis states that high breeding synchrony leads to high EPP rates, because females will be better able to compare the quality of potential mating partners when these display synchronously, facilitating extra-pair copulations. Since its proposal this hypothesis has generated a turmoil among behavioral ecologists and ornithologists, particularly from studies using the comparative method to control for possible phylogenetic effects (Westneat and Sherman 1997; Stutchbury 1998a, b; Weatherhead and Yezerinac 1998; Stutchbury and Morton 2001; Griffith et al. 2002; Neudorf 2004). The main points of this debate are centered around the fact that the comparative analyses performed by Stutchbury (1998a, b), although phylogenetically robust, are based on a limited database—34 species—and have not taken into account factors such as the magnitude of errors around the EPP estimate due to small sample sizes (Griffith et al. 2002). In addition, intraspecific studies testing the correlation between within-season synchrony and paternity rates have found conflicting results and no clear trend (reviewed in Griffith et al. 2002; Macedo et al. 2008). Then again, within-season studies have been suggested to be weak tests for this relationship because females might be evaluating males in periods of high breeding synchrony and then base later decisions on these prior evaluations (Stutchbury 1998b). Overall, the present conclusion seems to be that there is currently little empirical evidence to support or reject the hypothesis of breeding synchrony influencing rates of EPP (Neudorf 2004; Macedo et al. 2008).

Nonetheless, in their review, Stutchbury and Morton (2008) argue that differences in the length of the breeding seasons between temperate and tropical species account for differences in breeding synchrony, which in turn help explain the latitudinal differences in EPP rates, and they point out that low breeding synchrony is associated with low EPP rates in tropical birds. I review here the results of some of my previous work (Ferretti 2010; Ferretti et al. 2011, 2016, 2018) where I sampled a set of closely related species and tested whether breeding synchrony can explain intra and interspecific variation in EPP rates, as suggested by Stutchbury and Morton

(1995). To do this: (1) I studied EPP rates of five species, distributed in North, Central, and South America, in the swallow genus *Tachycineta*—a monophyletic group (Whittingham et al. 2002) already known for its extreme tropical/north-temperate variation in genetic mating system (Moore et al. 1999); (2) I calculated population-wide synchrony indices (Kempenaers 1993; Marsden and Evans 2004) for the species studied; and (3) I thereby tested for an association between EPP rates and synchrony index. If female breeding synchrony has an effect on the rates of EPP, interspecific differences in EPP rates among *Tachycineta* species should be positively associated with the substantial differences in the length of the breeding seasons reflected in the synchrony index (Stutchbury and Morton 1995), when all five species are included in the analysis.

I used the genus *Tachycineta* in my analysis for a couple of reasons. First, and most important, this genus has been previously used to test the breeding synchrony hypothesis by its proponents and co-authors (Moore et al. 1999). In their study the authors compared the north-temperate tree swallow (*T. bicolor*) with the tropical mangrove swallow (*T. albilinea*) and found that differences in EPP rates and synchrony followed the direction predicted by their hypothesis. They suggested that the difference observed in mating system between the two species was likely a result of the difference in female breeding synchrony—the longer breeding season in the tropics resulted in a lower degree of overlap, and thus lower breeding synchrony, among breeding birds, which in turn resulted in lower rates of EPP (Stutchbury and Morton 1995, 2008; Stutchbury 1998a, b; Moore et al. 1999). By adding more data on north-temperate and south-temperate species in this same genus I am increasing the strength of this comparison. Second, by using standardized protocols in nest-box colonies (i.e., similar cavity size, box availability, etc.), I can control nesting conditions to some extent, and nesting birds are easy to follow with samples easy to collect. I will argue that by adding Neotropical species from the southern hemisphere to the analysis, the pattern of geographic variation in EPP becomes unclear, with North and South hemisphere birds exhibiting contrasting patterns of latitudinal variation.

2.2 Methods

Tachycineta is a New World genus with nine species of swallows distributed from Alaska to Tierra del Fuego. Swallows in this genus are typically found in open habitat near water, often close to woodland and houses (Turner and Rose 1989), and they readily use nest-boxes for breeding. Co-authors/collaborators and I collected new data from four species—two different breeding populations of white-rumped swallow (*T. leucorrhoa*) in Buenos Aires Province, Argentina, Chilean swallow (*T. meyeni*) in Tierra del Fuego, Argentina, violet-green swallow (*T. thalassina*) in California and Oregon, and mangrove swallow (*T. albilinea*) in Belize—and used previously published data for the fifth species, Tree Swallow (*T. bicolor*), considered in this analysis (Dunn et al. 1994, 2009; Kempenaers et al. 1999; Moore et al. 1999;

Whittingham and Dunn 2001; Whittingham et al. 2006; O'Brien and Dawson 2007; Stapleton et al. 2007; Crowe et al. 2009), as well as for a second population of mangrove swallows nesting in Panama (Moore et al. 1999).

Field protocols included capturing both breeding adults at the nest-boxes, taking a blood sample from both of them and the nestlings (if nestlings were found dead before we could take a blood sample, then we collected a sample of pectoral tissue), and monitoring nest activity. For each active nest we recorded lay date, length of the laying period, and clutch size, for calculations of a synchrony index. Methodological details of paternity analyses can be found in Makarewich et al. (2009), Ferretti (2010), and Ferretti et al. (2011, 2016). Paternity analyses were based on microsatellite patterns of allelic variation. For all species sampled, the combined exclusion probability with one known parent (the mother) was >0.9999. To study the effect of breeding synchrony on extra-pair behavior among species and populations I used a measure of synchrony (synchrony index or SI) following the formula presented by Kempenaers (1993). This synchrony index represents the average of the proportion of fertile females in the population that overlapped with each female's fertile period. Latitude was measured at each site using a GPS (±3 m).

As a first crude approach to analyzing the pattern of latitudinal variation in EPP and synchrony, and their relationship, I conducted three correlations. I examined geographic variation in EPP in the genus *Tachycineta* by testing the correlation between the absolute value of latitude of the colonies sampled and the rate of EPP. To explore whether interspecific differences in EPP rates could be explained by female breeding synchrony, I tested for a correlation between synchrony indices and EPP rates. In addition I looked at the latitudinal pattern of variation in synchrony by examining the correlation between the synchrony indices and the absolute latitudes of the populations sampled. This rough analysis allowed me to use the average values for all the species/sites published, in addition to my own data. I then used generalized linear mixed models (GLMM, Zuur et al. 2013) with data collected by my collaborators and myself to assess the relationship between EPP and the explanatory variables absolute latitude, hemisphere, and SI. In this model we considered the interactions between absolute latitude and the other two variables. Each data point represents a female in a specific population; therefore we considered population of origin as a random factor in the analyses.

2.3 Results

Figure 2.3 shows the geographic variation in EPP rates (measured as percent of broods in a population with at least one extra-pair young). *Tachycineta* swallows present a range of EPP variation of 13–87%, and the synchrony index (SI) follows this same pattern (8–64%, Ferretti 2010). One interesting thing to note is that the two sister species, white-rumped swallow and Chilean swallow, are the two species in both extremes of this range of variation. On a first analysis it seems that EPP and breeding synchrony do not follow a latitudinal gradient of variation (EPP Pearson's

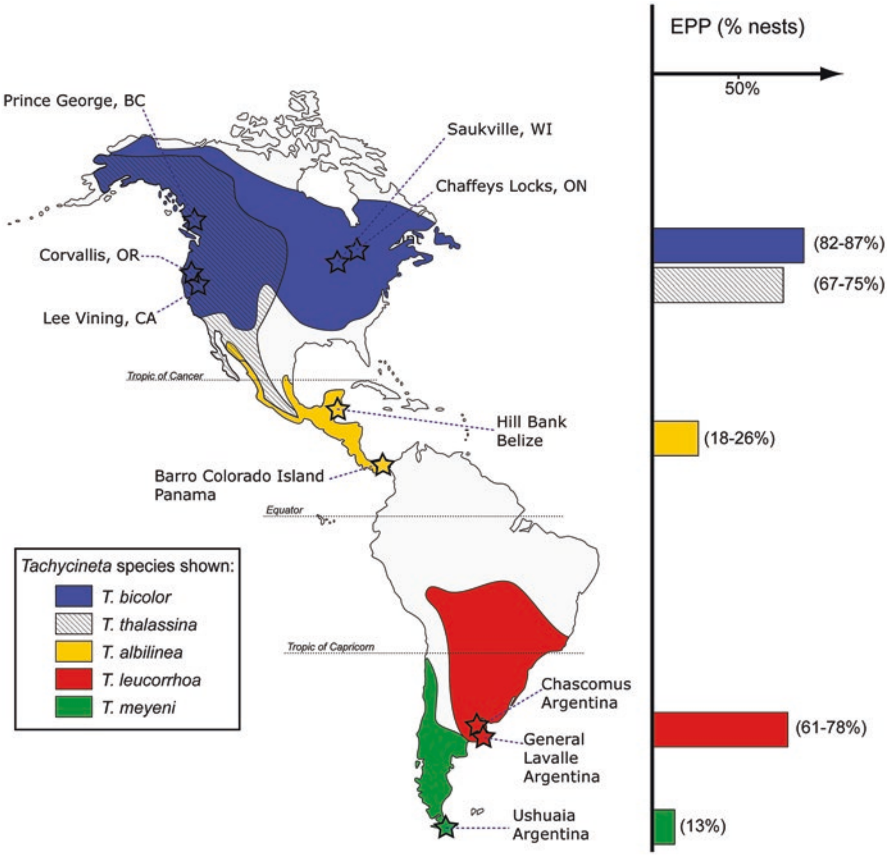

Fig. 2.3 Geographic variation in extra-pair paternity rates in five species of *Tachycineta* swallows studied (Ferretti 2010 and the references therein, Ferretti et al. 2011, 2016). EPP rates based on % of broods in the population with at least one extra-pair young

correlation $r = 0.47$, $p = 0.17$, $N = 10$; SI Pearson's correlation $r = 0.52$, $p = 0.23$, $N = 7$), and breeding synchrony and EPP are not related (Pearson's correlation $r = 0.51$, $p = 0.24$, $N = 7$).

The results of the GLMM show a similar result: EPP rates are not explained by variation in SI, but the interaction between latitude and hemisphere is statistically significant, (Table 2.2), Ferretti V unpublished data). By separating the data in North and South hemispheres a contrasting pattern emerged: EPP shows a positive pattern of increase in the North (coefficient associated with latitude is 0.11) and a negative relationship with latitude in the South (coefficient associated with latitude is –0.14).

Table 2.2 Results of GLMM with beta binomial (SI) and binomial (EPP) error distributions for final models, assessing the effects of latitude (Lat) and hemisphere (Hem, S = south), and their interaction on SI and EPP

	EPP final model			
	Coefficient	SE	*z*	*P*
Intercept	–3.40	1.09	–3.12	<0.01
Lat	0.11	0.03	3.20	<0.01
Hem_S	9.25	1.75	5.27	<0.0001
Lat:Hem_S	–0.24	0.05	–4.98	<0.0001

2.4 Discussion

I tested the female breeding synchrony hypothesis by examining interspecific differences in EPP rates and breeding synchrony in five species in the genus *Tachycineta*. The populations of the five species used in this analysis breed at markedly different latitudes, from high northern and southern latitudes throughout the tropics, and present extensive variation in the rates of EPP (Fig. 2.3). The results show that differences in EPP rates among species of *Tachycineta* are not explained by differences in their breeding synchrony (Figs. 2.3 and 2.4). Moreover, differences in the length of the breeding season, and the correspondingly large variation in their breeding synchrony, are not related to latitude. In a previous study, Moore et al. (1999) compared the north-temperate tree swallow with the tropical mangrove swallow and found that differences in EPP rates and synchrony followed the direction predicted by the breeding synchrony hypothesis (Stutchbury and Morton 1995; Moore et al. 1999). They suggested that the longer breeding season in the tropics resulted in a lower degree of overlap among breeding birds, and thus lower breeding synchrony, which in turn resulted in lower rates of EPP (Stutchbury and Morton 1995, 2008; Stutchbury 1998a, b; Moore et al. 1999). When south-temperate species are included in the analysis, as well as additional data from other populations in the North we are presented with a different scenario, where EPP and SI are not related and where neither SI nor EPP follow the expected latitudinal pattern of variation.

This work reminds us of the importance of comparative studies that span different latitudes and different life-history strategies. The addition of southern hemisphere species revealed a different pattern that the one expected, and broke the seeming correlation between breeding synchrony and paternity when only tropical and northern hemisphere species were used for comparison (Moore et al. 1999). Had we not added these southern representatives, we would have been left with a spurious result. This is not to say that current ecological factors such as breeding synchrony are not playing an important role in determining the behavior of birds and influencing the evolution of variation in mating systems; in fact I believe they might. But we need to have a closer look at the relationships among the different variables and life-history traits (e.g., Fig. 2.2), and we need to be aware of north-temperate biases in our assumptions and construction of hypotheses (Zuk 2016), as well as the dearth of information for species breeding in the Neotropics. Synchrony

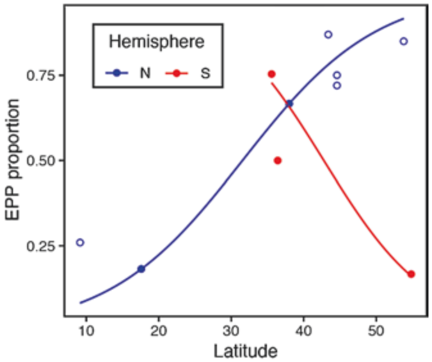

Fig. 2.4 Latitudinal variation in extra-pair paternity. *y*-axis: proportion of broods with at least one extra-pair young (EPP proportion), *x*-axis: absolute latitude. Data points are average values from North (N) and South (S) hemisphere sites/species and are distinguished by color. Open circles represent data taken from previously published studies (Ferretti 2010 and references therein), filled circles represent data from my own work (Ferretti V et al. unpublished data)

is linked to seasonality, but seasonality does not always vary with latitude. Seasonality is related to a combination of weather patterns, dependent on the geography of the area surveyed (i.e., altitude, continentality, and/or distance to the ocean), that in turn might have an effect on other life-history traits such as survival and clutch size (Martin 2004). Life-history traits are interconnected by a complex array of relationships (e.g., Fig. 2.2) and the resulting life-history strategies are believed to be adaptive outcomes of the trade-offs among the different traits and the selective nature of different ecological variables (see Figs. 2 and 3 in Martin 2004). Isolating one trait and one ecological variable will not provide further enlightenment in life-history theory or the evolution of avian mating systems.

2.5 Conclusion and Future Directions

The Neotropical realm has the most biodiverse avifauna on Earth (Kricher 1997; Stotz et al. 1997). Studies of mating systems, behavior, and evolutionary ecology should focus on the birds that breed at these latitudes. Our better understanding of the Neotropics will likely provide the data and observations to propose new and more integrative hypotheses that will shed light on such fascinating aspects of the evolution of behavior in birds.

In this review I showed how our perspective of variation in mating systems can change when we add species breeding in the Neotropics. *Tachycineta* swallows are aerial insectivores and as such they are highly dependent on daily weather patterns. It is possible that this strong dependence is acting as a selective pressure on the social interaction of the breeding pair, which in turn selects for a specific outcome of parentage. This is clearly observed in Chilean swallows breeding at 54° South that have the lowest rates of EPP in the group, likely because the largely unpredictable weather of Tierra de Fuego requires both members of the breeding pair to attend the nest at all times during the breeding cycle (Ospina et al. 2015; Ferretti et al. 2016). This link between extreme weather conditions and low EPP might be unique to aerial insectivores, as birds in other foraging guilds might not suffer the same pressures with the ever-changing weather. I strongly believe that the idiosyncrasies of the geography play a major role in shaping life-history strategies, but may be too complex to address with standard/older methods of analysis and the proposal of hypotheses that address only one aspect of the complicated life-histories of the taxa under consideration. Modeling approaches like the use of phylogenetic generalized least-squares (e.g., Boyce et al. 2015) or non-standard applications of software programs such as Maxent (v. 3.4.1., Phillips et al. 2018) can illuminate our way on the hierarchization of the different parameters and ecological variables, and make specific predictions for the outcome of the ongoing tug-of-war of the different parameters in the systems under study.

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Chapter 3
Cooperative and Communal Breeding

Christina Riehl

3.1 Introduction

The study of cooperative breeding in birds has a long history in the New World tropics—in fact, it began there over 80 years ago with the publication of Alexander F. Skutch's classic 1935 paper, "Helpers at the Nest." Decades before the evolutionary paradox of cooperation captured the attention of biologists, Skutch (1935) described social nesting behaviors in a variety of Neotropical species, especially brown jays (*Psilorhinus morio*), bushtits (*Psaltriparus minimus*), and band-backed wrens (*Campylorhynchus zonatus*), in which he carefully observed several individuals caring for the nestlings at a single nest. He noted that in most cases, so-called helpers—unmated attendants who assisted at the nest of a breeding pair—were young birds, probably immature offspring from a past brood, and he speculated that this type of family cooperation might be widespread. Skutch's (1987) book *Helpers at Birds*' *Nests* confirmed this impression, collating dozens of instances of cooperative breeding worldwide. The review documented cooperative breeding in several Neotropical taxa, primarily based on Skutch's own observations, including parakeets, cuckoos, hoatzins, swifts, todies, puffbirds, araçaris, woodpeckers, ovenbirds, flycatchers, fruitcrows, jays, wrens, mockingbirds, tanagers, blackbirds, and grosbeaks. The number of Neotropical birds thought to breed cooperatively has since increased to well over 200 species, representing more than one-quarter of all cooperative breeders worldwide. This is likely an underestimate, given that the breeding systems of most Neotropical birds remain undescribed (Cockburn 2006).

Cooperative breeding has arisen independently in several lineages of Neotropical birds, and the diversity of social structures across species reflects these different evolutionary histories. Some species follow the simple "helper at the nest" model

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first described by Skutch (1935), in which non-breeding offspring from a previous brood assist their parents in rearing younger nestlings. For example, the cooperatively breeding ovenbirds (Furnariidae), tanagers (*Neothraupis*, *Cypsnagra*, and *Tangara* spp.), bicolored wren (*Campylorhynchus griseus*), and some mimic thrushes (*Ramphocinclus brachyurus*, *Nesomimus trifasciatus*) all appear to nest in small family groups consisting of a breeding pair and related, non-breeding helpers (reviewed in Riehl 2013). Genetic relatedness between helpers and the offspring they care for is presumably high and helping behavior is likely to be favored by a combination of kin selection and ecological constraints on independent breeding (reviewed in Koenig and Dickinson 2004). In other species, however, social groups contain complicated combinations of breeders, non-breeders, relatives, and immigrants that defy easy categorization. Both related and unrelated helpers of both sexes are common in white-throated magpie-jays (*Calocitta formosa*; Berg 2005), Española mockingbirds (*Nesomimus macdonaldi*; von Lippke 2008), campo flickers (*Colaptes campestris*; Dias et al. 2013), and grayish baywings (*Agelaioides badius*; Ursino et al. 2017), to highlight a few examples; and these exhibit reproductive strategies ranging from cooperative polygamy to extra-group mating to conspecific brood parasitism. Competitive and cooperative tactics clearly co-exist in these societies, reflecting the mutual fitness benefits of social nesting as well as the conflicts that arise between group members over reproduction and parental care.

This interesting juxtaposition of cooperation and conflict is evident in the anis (*Crotophaga* spp.) and the related guira cuckoo (*Guira guira*), which together compose a monophyletic lineage within the cuckoo family (Cuculidae: subfamily Crotophaginae). This small clade is exclusively Neotropical: the guira cuckoo and greater ani (*C. major*) are largely confined to South America, while the groove-billed ani (*C. sulcirostris*) and smooth-billed ani (*C. ani*) reach Mesoamerica, the Caribbean, and the subtropical US (Sorenson and Payne 2005). The anis are black, long-tailed, and somewhat ungainly in appearance and movement. Their West Indian nicknames of “witch bird” and “black parrot” capture some of their odd charm, as does Archie Carr’s (1956) description of their “disjointed way of alighting in a bush as if thrown there.” All four species breed in social groups containing several reproductive females which lay eggs in a shared nest (sometimes referred to as “communal” nesting), but groups may also include young birds that have remained with their natal group and act as non-breeding helpers (in what is traditionally referred to as “cooperative” nesting). Patterns of social bonds vary across species—groove-billed and greater anis are socially monogamous with strong pair-bonds and small, highly organized social groups, whereas smooth-billed anis and guira cuckoos lack strong pair-bonds and nest in larger, loosely organized groups—but they share fundamentally similar breeding habits.

Two aspects of crotophagine breeding behavior are especially perplexing. First, adults in breeding groups are typically unrelated to one another: young birds of both sexes usually disperse from their natal group before breeding, leading to an apparent lack of kin structure in social groups. Second, breeding females consistently destroy the eggs (and sometimes the nestlings) of fellow group members, leading to severe reproductive competition that can cause nest failure. Understanding the selective pressures that maintain cooperation in this bizarre reproductive system has been the focus of several long-term field studies, beginning with Sandra Vehrencamp's classic studies of groove-billed anis in Costa Rica in the 1970s and 1980s (Vehrencamp 1977, 1978; Vehrencamp et al. 1986; Bowen et al. 1989). Subsequent study populations of smooth-billed anis were established in Puerto Rico by James Quinn and his research group (Schmaltz et al. 2008; Quinn et al. 2010; Grieves et al. 2014) and of guira cuckoos in Brazil by Regina Macedo and colleagues (Macedo 1992; Macedo and Bianchi 1997; Macedo et al. 2001, 2004).

In this chapter I review recent studies of the fourth crotophagine cuckoo, the greater ani, at a field site in central Panama. Whereas the other three species inhabit open savannah and scrubby pastureland, greater anis nest exclusively along lake and river edges in tropical forest—a habitat that poses challenges as well as advantages for the field worker. It is also the only species for which relatively complete genetic data are available, enabling quantification of mating patterns, kinship, and reproductive success. These tools have enabled many advances in our understanding of the breeding habits of these unique birds—in many cases confirming patterns recorded in earlier studies, and in others revealing behaviors that would have otherwise gone unnoticed.

3.2 Natural History and Methods

Greater anis are locally abundant in eastern Panama and the Amazon basin, but they are not always easy to observe: the large, bulky stick nests are always built over water, often in marshy vegetation, and are impossible to access without a boat. Davis (1941) provided the first description of their habits and behavior, complaining that "even though using a canoe at all times, it is frequently impossible to keep up with the birds or to follow them when they go into the thick brush or flooded lands along the river course." Although Davis found only one greater ani nest in his brief study (curtailed, in part, by malaria) he provided valuable and perceptive descriptions of their social behavior, all of which have withstood the test of time.

Detailed field studies of the greater ani began in 2006, when my colleagues and I began establishing a color-banded population at the Barro Colorado Nature Monument in central Panama (BCNM). This lowland tropical forest reserve is operated by the Smithsonian Tropical Research Institute and contains the 1500-ha Barro Colorado Island as well as several adjacent mainland peninsulas. The region receives approximately 2600 mm of rain each year, 90% of which falls between May and November (Windsor 1990). Greater anis, like many animals, time their reproduction to coincide with the flush of young leaves and insects that emerge in the middle of the rainy season. The first eggs are typically laid in early July, with reproductive activity peaking in August and rapidly tapering off in early September when increasingly heavy rainfall makes foraging difficult. Greater anis occur in large numbers along the shoreline of the island and peninsulas, most frequently nesting in the small tree *Annona glabra*, the large aquatic fern *Acrostichum danaeifolium*, and the prickly shrub *Montrichardia arborescens*, all of which grow in shallow water along the shoreline. Nests are also built in low branches of large trees that extend out from the shoreline, or in thick curtains of lianas hanging over the water. Small islands of emergent vegetation—clusters of *Annonas*, isolated aquatic ferns, and <1-ha forested islands—are favored nesting sites, and nearly every tiny islet along the shore is home to at least one nesting group. Anis tend to avoid windy or exposed areas, and prefer to nest in the deep, sheltered coves that pocket the shoreline.

With an outboard motorboat—an advantage that Davis (1941) lacked—greater ani nests are easy to locate and monitor. Groups are noisy and conspicuous, typically spend most of the day in the vicinity of the nest, and make no attempt to conceal their frequent visits. The large basket-shaped nests are typically built just a few meters above the water's surface and are usually accessible, though sometimes requiring the use of a stepladder and a flat-bottomed boat. Furthermore, groups establish nesting territories and construct their nests early in the rainy season (late May and June), weeks or even months before egg-laying commences. It is therefore possible to monitor nests well in advance of reproduction, enabling complete data collection through the breeding season. As part of our long-term monitoring project, we attempt to locate each nesting group in the study area every year and record the size of the breeding group, the fate of each egg and nestling, and when possible, the identity of the adult breeders. Eggs are numbered with a waterproof pen to track the position and fate of each egg in the communal clutch, and a sample of maternal DNA is taken from the surface of the shell using a swabbing technique originally developed by Schmaltz et al. (2006) and refined by our research team over the years (Riehl 2010a). Like most cuckoos, greater anis have extraordinarily short incubation and nestling periods: although the eggs weigh up to 35 g, they hatch in less than 12 days, and the agile nestlings are able to scramble out of the nest, swim, and climb to avoid predators at 5–6 days of age (Riehl and Jara 2009). As a result, we take blood samples from nestlings at 2–3 days and band them with individually unique combinations of anodized metal color bands at 4–5 days of age.

Between 2007 and 2009, a substantial proportion of the adult nesting population was mist-netted, color-banded, and genetically sampled (Riehl 2011). Trapping adults along the shoreline became increasingly dangerous as the population of American crocodiles (*Crocodylus acutus*) in the Panama Canal continued to rise, recovering from years of crocodile population control by the US administration that ended when operation of the Canal was transferred to Panama in 1999. We ceased netting adults in 2010, so knowledge of adult identity and reproductive success is drawn primarily from genetic sampling of eggs and nestlings. Since only maternal DNA is deposited on eggshell surfaces, our data set is far more complete for females than males and our studies have primarily focused on questions relating to female fitness.

3.3 Group Structure and Stability

In the Barro Colorado study population, greater ani breeding groups always consist of two, three, or, rarely, four socially monogamous pairs, sometimes attended by 1–2 non-reproductive “helpers” (often, though not always, sons from a previous brood). Social pair-bonds are obvious to the observer: within a group, each pair allopreens, forages together, and often separates from the rest of the group. Interestingly, the greater ani is the only one of the four crotophagine cuckoos that appears to be obligately social. Single pairs virtually never attempt to nest alone, preferring to join other breeding groups or to skip reproduction entirely. The modal group size is two pairs (70–80% of nesting groups per year), with groups of three pairs representing a significant minority (15–30% of nesting groups per year) and groups of four pairs being rather rare (0–3% of nesting groups per year; Riehl 2011; Riehl and Strong 2019). Of more than 600 total nesting attempts, we have observed just three instances in which single pairs tried to nest alone. In all three cases, the pair had originally been part of a larger group which was reduced by the disappearance and/or desertion of other group members; and none of the three pairs succeeded in raising young. The proportion of groups with unpaired “helpers” varies substantially across years, but has never been more than 15%. In about half of these cases, the helper was a banded male from a previous nesting attempt (i.e., a son of one of the breeding pairs in the group); but in the remaining instances, the unpaired helper was not banded and the genetic relationships with other group members were not known.

Ani breeding groups are highly stable and well-organized, with strong social bonds between same and opposite-sex group members as well as between mates. During the breeding season, members of the nesting group tend to remain near the nest for most of the day, rarely leaving the nest unattended (even before eggs are laid) and typically foraging within sight of the nest. This high rate of nest attendance may be related to competition among groups for high-quality nesting sites, since neighboring groups occasionally attempt to evict each other from nest sites on particularly high-quality territories (Strong et al. 2018). One pair often remains at the nest while another pair forages nearby, but the foraging birds return quickly upon hearing alarm calls at the nest. Extra-group individuals are quickly recognized and chased away from the nest itself, though nesting groups will overlap in their foraging areas and do not defend extensive foraging territories. Perhaps the most unusual aspect group behavior is their habit of performing loud, conspicuous calling displays—stereotyped vocal choruses in which all of the group members gather in a circle, bills pointing towards the center, and give a prolonged gurgling call that can last up to several minutes (Riehl and Jara 2009). Individuals sometimes touch bills within the circle or jockey for position, scrambling around to face one another while giving a monotonous gurgling call. Davis (1941) described the sound of this collective vocalization as a “curious…gurgling, bubbling *brrrr* resembling the sound of boiling water” and indeed it is this vocalization that has given the greater ani its South American nickname of *hervidor*, the water-boiler. The functions of this remarkable display remain unknown, but it is possible that it serves to reinforce social bonds and recognition between group members, and/or to advertise the group's presence on the nesting territory. Immature birds and non-breeding helpers do not participate in these choruses. Early in the season, communal chorusing displays may also involve individuals from different breeding groups, but participation in choruses is eventually restricted to only the members of the nesting group as the breeding season approaches.

Greater anis in central Panama are sedentary. Groups remain on their nesting territories year-round, although individuals from many nesting groups come together to form huge communal roosts during the non-breeding season, which can number over 100 individuals. Breeding groups typically separate again during the day and return to their nesting territory several times during the day. Although nesting group members remain in close association during the non-breeding season, group membership is more fluid at this time of year and several different groups may coalesce into larger foraging flocks for part of the day.

Perhaps due to their year-round presence on territories, breeding groups can be extraordinarily stable and long-lasting. The current record is a decade—several of the original groups first recorded in 2006 were still on the same territories in 2016, containing the same individuals—but this will doubtless increase as we accumulate more years of data. The average "lifespan" of an ani social group is approximately 3.5 years, but the distribution of group longevity is bimodal: many groups form, nest for 1 year, and dissolve after a single unsuccessful attempt, whereas others last upwards of 7 or 8 years. Exactly why group stability varies so much is unknown, but most groups that last only 1 year are composed of young birds (<6 years old) and fail to fledge offspring. Mark-resighting analyses of banded adults indicate that the average adult ani lives 15–17 years, so most individuals probably change groups at least once in their lifetimes, and probably 2–3 times. One female was found nesting in 4 different groups over 8 years, but this degree of restlessness is unusual (Riehl and Strong in preparation).

How do ani social groups form in the first place? Due to the difficulty of tracking immature birds from fledging through dispersal to a breeding territory, we lack a full understanding of this phenomenon, but there appear to be several routes to joining a group. After dispersing from their natal group, immature anis range widely for 1–2 years before first breeding at the age of 2–3 years. As mentioned previously, some male offspring delay dispersal and act as helpers at their natal nest for 1 year, but only very rarely do these birds inherit a breeding position within the group. Microsatellite analyses of relatedness among 341 offspring in 58 breeding groups revealed only one instance in which a male nestling stayed with his natal group and became a breeder (his mother was still in the same natal group, but his social mate was an unrelated female), and two instances in which a male nestling dispersed to breed in groups containing close kin (Riehl 2011). In no cases were females found to breed in the same group as relatives. The vast majority of young birds then disperse considerable distances from the natal group before settling on a breeding territory with unrelated group members. Only 6 of approximately 300 banded fledglings have been recorded breeding in the nature monument, so most must die before breeding, or breed outside the study area.

It seems likely that social bonds between group members initially form in the non-breeding season, potentially in the large communal roosts that contain many breeding groups as well as immature birds and immigrant “floaters.” In some instances, pairs have been observed to form in these pre-breeding roosts, then join another pair (or group of two pairs) on an already-established nesting territory. In other instances, groups appear on a nesting territory as a unit, apparently having already established their identity as a breeding group before settling on the site. And in yet other cases, single birds join an already-established breeding group, replacing a same-sex group member who has died or left the group. Transitions in group membership are sufficiently infrequent, and sufficiently difficult to observe, that we do not yet know which of these routes (if any) is most common. Nor do we know how groups of two pairs “decide” to allow another pair to join, or how two pairs coalesce to form a group; but observations of chasing and communal displays during the pre-breeding period suggest that group displays play some role in group formation. Once on a territory, groups vigorously chase extra-group individuals if they approach the nest site too closely, suggesting that certain individuals or pairs can indeed be prevented from joining a breeding group.

In all three *Crotophaga* species, most group members are genetically unrelated to one another, a pattern suspected by earlier observations of groove-billed ani fledglings dispersing from their natal groups before breeding (Bowen et al. 1989). Microsatellite analyses in greater anis confirmed that coefficients of relatedness among both same-sex and opposite-sex group members are not significantly greater than random chance would predict (Riehl 2011). More recent genetic analyses using single-nucleotide polymorphisms have confirmed that relatedness among group members is effectively zero; furthermore, the study population is outbred and panmictic, so the lack of kin structuring within groups is not an effect of a recent population bottleneck or high local relatedness (Riehl and Sin in preparation).

3.4 Intra-Group Competition: Egg Ejection and Infanticide

Watching a group of anis at their communal nest is a fascinating experience. In some respects, the breeding group appears to be a wholly cooperative team, working together towards a shared goal. The large stick nest is built by all of the group members—typically, by two pairs taking turns, as though in a relay. One female often stays at the nest, arranging twigs brought by her mate and occasionally contributing a stick of her own. After a period ranging from several minutes to over an hour, the second pair arrives at the nest and the first pair leaves abruptly, as though by mutual agreement. The second pair takes over and continues the building process, and only rarely do both pairs attempt to contribute sticks to the nest simultaneously. In response to an alarm call by any group member, though, all quickly gather to mob potential threats, often displaying in a communal chorus on the nest platform itself or on a perch nearby.

It is only when the first egg appears in the nest that group members cease to act in each others' best interests. Regardless of which female in the group lays the first egg into the shared nest, it is always rolled out by another female in the group—a female who, by definition, has not yet started laying. Several video-recordings of this behavior, obtained in 2013, reveal how the egg removal is accomplished. The female stands over the egg and pulls it towards her with her bill, such that the underside of the bill is in contact with the egg. After several false starts, the egg is rolled up out of the nest cup and onto the rim of the nest, sometimes between the female's legs. Using her bill, she then nudges the egg off the rim of the nest and onto the ground (or into the water) directly below. The female who laid the egg neither attempts to guard her egg nor retaliates against the female that evicted it: a series of experiments confirmed that, having laid at least one egg into the communal nest, females immediately cease the eviction behavior, even if they have observed that their first egg was removed (Riehl et al. 2015). This pattern implies that females remove eggs only before they have started to lay, and that physiological and hormonal changes are probably responsible for the switch in behavior after a female starts laying. Interestingly, however, this switch can be over-ridden if group members (either male or female) perceive that something is wrong with an egg. Cracked or broken eggs, artificial wooden eggs (which are not as heavy as real ani eggs), or eggs that are laid after incubation has already begun are swiftly removed even if all of the group's females have laid (Riehl 2010a; also see "Conspecific brood parasitism" below).

This rule of thumb—evict eggs before laying, then accept eggs after laying—leads to predictable patterns of egg loss. The first female to start laying (female A) always loses at least one egg, and sometimes several. If the group consists of only two females, and if the second female (B) lays her first egg immediately after the first female does, then the first female loses only one egg. Eggs begin to accumulate in the nest once female B begins laying, and she loses no eggs (because at that point, both females have laid one egg). But the costs of "going first" increase if the two females are not in reproductive synchrony: female A may lay two, three, or (rarely) up to eight eggs before female B starts to lay. In these cases, the eggs laid by female A are not allowed to accumulate in the nest, but are rolled out one by one by the other female, usually within a day or two of their appearance. Egg loss is even more costly if the group contains three females, since females A and B may each lose several eggs before the third female (C) begins laying (Fig. 3.1a). Two factors, then, determine the extent of egg loss: the number of females in the group, and the degree of reproductive synchrony between the females. In highly synchronized groups with two females, only one egg may be evicted, whereas in asynchronous groups with three or more females, up to 19 eggs may be evicted. The early laying females often abandon the nest in these extreme cases, and sometimes the rest of the group follows suit.

Egg loss should be energetically costly to female anis because the eggs are unusually large—approximately 17% of female body mass, at the upper extreme of the ratio for birds that fly (Rahn et al. 1975). In fact, ani eggs are so large that gravid females are easily identified by their bulging abdomens and labored flight! First-laid

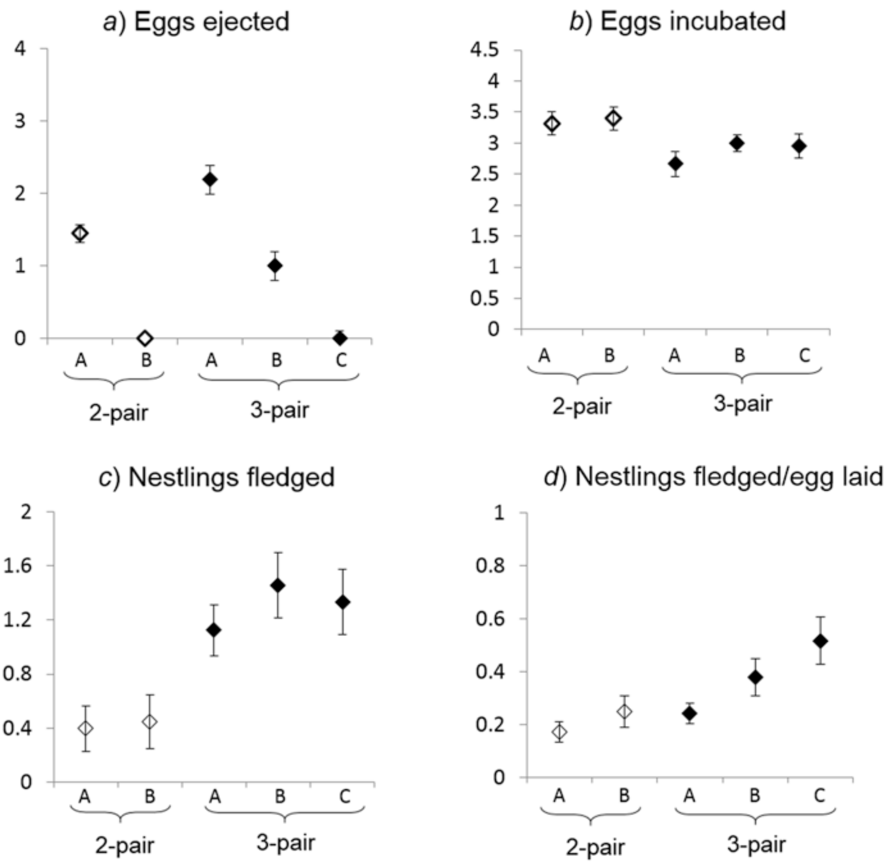

Fig. 3.1 Four measures of reproductive output for females nesting in groups containing two pairs (open diamonds) or three pairs (filled diamonds). Letters indicate the female's position in the laying order of the communal clutch (A = first-laying female, B = second-laying female, C = third-laying female). Means ± standard errors are shown. (**a**) Eggs ejected. (**b**) Eggs incubated. (**c**) Nestlings fledged. (**d**) Nestlings fledged/egg laid. Redrawn from Riehl (2011) data collected from 2007 to 2010. The scale of the vertical axis differs on the four graphs

eggs are, on average, slightly smaller than eggs in the middle of a female's clutch, and this difference is especially pronounced for females that are the first in their group to lay (Riehl 2010b). Which unfortunate female goes first, though, seems to be a toss-up. Her position in the laying order of the communal clutch is not correlated with her age, experience, body condition, or tenure in the group; and if the first clutch is destroyed and the group re-nests, another female may take the lead in the new clutch (Riehl 2011). At this point, a random die roll is our best-fit model for predicting which female in a group is the first to lay.

Although a female's position in the laying order is unpredictable, preliminary analyses of long-term data suggest that the degree of reproductive synchrony between females is not. In groups with two females, pairs of females that have previously nested together tend to be much better synchronized than are females that have never been part of the same social group, and egg loss is consequently lower. However, the degree of reproductive synchrony does not continue to increase with the number of years that females nest together (Riehl and Strong 2018). This indicates that social familiarity may play a role in reproductive synchrony, and that there is a cost to switching groups and nesting with an unfamiliar "partner." What role the males play in all of this (if any) is completely unknown.

Once all of the females in the group have laid at least one egg, the rest of the laying period is peaceful. Eggs appear in the nest at regular intervals: each female lays one egg every 2 days, so in a group of two females the eggs may appear alternately (one egg per day) or both females may lay on one day, skip a day, and both lay again on the third day. Incubation begins after each female has laid 3–5 eggs in the communal clutch, so the final incubated clutch size ranges from 6 to 17 eggs, depending on group size. Large clutch sizes come with a cost: the overall hatching rate of non-depredated eggs is 86%, and hatching failures increase with clutch size, especially above 9 eggs (Riehl and Jara 2009). Group members are not vigilant at the nest during this time, often leaving it unattended for several hours per day. However, mate-guarding is obvious during the laying period, with members of mated pairs foraging and roosting together. This social monogamy is reflected in the genetic mating system: the majority of nestlings are produced by monogamous pairs, with just 8–15% of nestlings resulting from extra-pair copulations within the social group. The rate of extra-pair copulations does not seem to depend on group size, although statistical differences may simply be difficult to detect with our limited sample sizes (Riehl 2012). Extra-pair copulations with males outside the group are even rarer (<5%), as are instances of quasi-parasitism (when a male group member mates with an extra-group female and she lays her egg in the group's nest; Riehl 2012). Vehrencamp (1977) found that the egg ejection system of groove-billed anis led to slight inequity in each female's contribution to the communal clutch, with last-laying females contributing an average of one extra egg. We have not found this to be the case in greater anis; there seems to be no systematic bias in clutch size depending on a female's position in the laying order, apparently because early laying females lay more eggs to compensate for those that are ejected (Fig. 3.1b; Riehl 2011).

All group members participate to some extent in defense, incubation, and feeding of the shared clutch, but the burden of incubation, in particular, is unequal. As in groove-billed and smooth-billed anis, a single male performs all incubation at night and the majority of daytime incubation. In groove- and smooth-billed anis, this male also fathers a disproportionate number of nestlings in the communal clutch because he is often mated to the last-laying female; but in greater anis, the last-laying female does not gain a consistent advantage so the nocturnal incubator enjoys no apparent fitness advantage for his extra work (Riehl 2012). It seems likely that the ancestral pattern in anis is for reproduction to be unequally shared among males, such that one male fathers the majority of nestlings and acts as the nocturnal incubator. In greater anis, the role of nocturnal incubator has apparently been retained even though reproduction is relatively egalitarian. We still lack information on whether the role of nocturnal incubator is consistent over different reproductive attempts by the same group, or whether, like a female's position in the laying order, it changes over time.

After the nestlings hatch, all group members appear to participate more or less equally in food delivery to the clutch. Cross-fostering experiments confirmed that adults cannot recognize their own nestlings in the communal clutch (Riehl and Strong 2015), so adults are apparently unable to preferentially feed their own nestlings. As with nest-building, pairs in the group seem to take turns feeding the young; rarely do all of the group members deliver food simultaneously, though all will assemble quickly if a predator threatens the nest.

Given that group members cannot recognize their own young and vigorously defend the communal clutch against predators, it came as a surprise to discover that adults occasionally kill nestlings in their own nest (Riehl 2016). Infanticide is rare, accounting for just 13% of nestling deaths, and it was more common in 2007 and 2008 (years with extremely high rates of nest success) than in subsequent years. We discovered dead and maimed nestlings in a few nests, and on one occasion actually observed an adult male group member killing a nestling by striking it on the head and back with its bill. Interestingly, infanticide is most likely to occur at nests with high hatching asynchrony—when nestlings hatch over a period of several days rather than all at once—and the first-hatched nestlings are most likely to be killed. Hatching asynchrony occurs when one adult begins incubating before all of the females have completed laying, and moderate hatching asynchrony (1–2 days) is common in the study population. Although we lack direct evidence on the identity of killers in most cases, several lines of evidence support the hypothesis that early hatched nestlings are killed by group members whose own eggs have not yet hatched—a situation parallel to that of egg ejection, in which early laid eggs are evicted by females who have not yet laid (Riehl 2016). Just as egg ejection ensures reproductive synchrony among laying females, infanticide (though much rarer) appears to favor hatching synchrony among nestlings. Starvation of last-hatched nestlings favors synchronous hatching, too, since late-hatched nestlings in asynchronous clutches exhibit reduced rates of growth and are sometimes outcompeted by older nest-mates (Riehl 2016).

3.5 Predation, Group Size, and Individual Fitness

Although egg ejection, infanticide, and starvation take a toll on the survivorship of greater ani eggs and nestlings, the real threat is from predation. Nest predation accounts for the vast majority of egg and nestling mortality: up to 90% of all of the eggs laid in the study population are eaten by predators each year, and between 60% and 82% of nests fail to fledge any young at all due to predation. Although rates of predation vary substantially across years, predation has consistently been the primary factor limiting reproductive output in every year of the study. Snakes, especially the tiger rat snake (*Spilotes pullatus*) and the bird-eating snake (*Pseustes* *poecilionotus*) are the primary egg predators, with individual snakes often returning to the same nest over the course of several days and eating eggs one or two at a time (Riehl and Jara 2009). White-faced capuchins (*Cebus capucinus*) will eat eggs and nestlings as well, although most nests are protected to some extent by being built in fragile, marshy vegetation that monkeys usually avoid. The majority of nest predation occurs during the egg stage, although nestlings are also eaten by rat snakes and yellow-headed caracaras (*Milvago chimachima*). Caracara predation on ani nestlings has increased in the study area between 2006 and 2016, especially in the western portion of the nature monument. This area borders on an unprotected region of degraded farmland and open pastureland, the caracara's preferred habitat; our observations of increased nest predation may reflect an increase in the caracara population as forested areas around the nature monument continue to be cleared.

Nests built in emergent clumps of aquatic vegetation, such as isolated *Annonas* standing in the water, or on small islets, are less likely to be accessed by terrestrial predators like snakes and monkeys. On average, over 60% of nests built in these emergent sites fledge at least one offspring each year, compared to just 11% for nests built in vegetation along the shoreline (Riehl 2011). The dramatic difference in nest predation between emergent and shoreline sites is not unique to this study area: Lau et al. (1998) found a nearly identical pattern in a nesting population of greater anis along the banks of the Guárico River in Venezuela. There, as at Barro Colorado, anis nest in low, partly inundated vegetation along the water's edge, and nests built in emergent bushes were substantially more successful than those built on the shoreline. Lau et al. (1998) suspected that shoreline nests in Venezuela were more vulnerable to terrestrial predators, just as we have found at Barro Colorado.

Lau et al. (1998) did not record the sizes of the nesting groups on emergent and shoreline sites, but we have found that large (three-pair) groups are more likely to nest in emergent sites than are small (two-pair) groups (Riehl 2011). One possible explanation for this pattern is that these sites are limited and that larger groups are better able to outcompete smaller groups to acquire them. We have little direct evidence to support this, although it seems likely that emergent nest sites are indeed limited due to their high rate of occupancy: nearly every islet in the study area has a resident ani group. Larger groups appear to be better able to defend eggs and nestlings against predators, too: even controlling for differences in nest-site type (emergent vs. shoreline), three-pair groups still experience lower rates of nest predation than do two-pair groups (Riehl 2011). Footage from nest cameras supports this hypothesis, showing that adult group members cooperatively mob nest predators, and are even capable of killing small snakes. Although mobbing usually doesn't eliminate the risk of predation entirely—snakes are especially persistent, returning day after day until the nest is empty—it can delay or discourage the predator long enough for at least some nestlings to fledge.

The combination of safer nest sites and better defense against predators translates into a significant fitness advantage for individuals in larger groups. On average, each female in a three-pair group can expect to fledge 1.3 offspring in a given year, whereas her counterpart in a two-pair group fledges just 0.4 offspring (Fig. 3.1c). The drawback of being in a larger group, of course, is that more eggs are ejected during the early laying period. These costs can be significant for the early laying female(s), as outlined above, and the net result is that early laying females must lay more eggs in order to fledge the same number of young (Fig. 3.1d). Longitudinal data suggest that most groups do not attempt to nest every year, and that females in large groups may lay fewer clutches of eggs over the course of their lifetimes. Careful calculations of lifetime reproductive fitness are still needed in order to test this hypothesis, but it appears likely that the benefits of nesting in a large group are partially balanced by the long-term physiological costs of egg ejection. This may even explain why small two-pair groups are the modal group size in the population, despite having lower rates of nest success than three-pair groups. It must be remembered, though, that the physiological costs of egg ejection are borne only by females. As far as we can tell, nesting in a three-pair group should always be the best option from the fitness perspective of a male. Whether these differential costs lead to an evolutionary conflict of interest between the sexes is an open, and intriguing, question.

The difference in reproductive success between three-pair and two-pair groups has been even more pronounced in El Niño years, when rainfall in Panama is below average and the water levels in Gatún Lake drop far below their usual levels. During the 2015 El Niño, the strongest in over two decades, we recorded the lowest rate of reproductive success of the 10-year study period. Most groups built nests, but did not lay eggs at all. Just 5 of 52 nests fledged at least one offspring (9.6%), and just 11 of 127 eggs laid survived to fledging (8.7%). Remarkably, all of the successful groups contained at least three pairs, whereas none of the two-pair groups fledged young. Similar trends (though not as extreme) were observed in the moderate El Niño event of 2009. The low reproductive output in El Niño years appears to be driven by both top-down and bottom-up ecological factors: fewer groups attempted to lay eggs, the onset of laying across the study area was unusually late, and those that did lay eggs experienced unusually high predation rates. We are continuing to investigate the possibility that food is scarcer and predation is higher in El Niño years, and, more broadly, that variation in rainfall may play a role in maintaining variation in group size.

3.6 Conspecific Brood Parasitism

Cuckoos are notorious brood parasites (see Chap. 6), and anis are no exception. Even though cooperative parental care is by far the most common reproductive tactic in our study population, conspecific brood parasitism is a relatively common alternative. Prior to our study, two different types of parasitic behaviors had previously been documented in the other *Crotophaga* species. In his study of smooth-billed anis, Loflin (1983) observed that one pair in a breeding group sometimes deserted the nest after laying, abandoning the clutch to be cared for by the remaining members of the breeding group. This behavior—essentially, parasitism by desertion—appeared to be rare, and Loflin (1983) did not record whether the remaining birds were able to rear the clutch to fledging. The more common type of parasitism is parasitic laying by extra-group females, which has been recorded in both smooth-billed and groove-billed anis (Loflin 1983; Bowen 2002). As many as 20% of groove-billed ani nests may be parasitized by extra-group females, based on the appearance of eggs of different sizes in communal nests (Bowen 2002). Perhaps not surprisingly, parasitism by extra-group females is also common in greater anis (Riehl 2010a), accounting for 5–30% of eggs genotyped in the study population each year. We first suspected brood parasitism when we observed irregularities in the laying sequence (i.e., when more eggs appeared in the communal nest than would be predicted by the number of female group members), and later confirmed it through microsatellite genotyping (Riehl 2010a).

Parasitic eggs are at a disadvantage in greater ani nests, primarily because they tend to be laid at the wrong time. As outlined above, the timing of laying in communal nests is fairly stereotyped and reproductive synchrony among female group members is essential to a successful breeding attempt. Extra-group females do not time their laying to coincide with the host group; instead, parasitic eggs tend to appear at random—sometimes before any of the group's females have started to lay, sometimes during the laying period, or, most frequently, after incubation is already underway. Parasitic eggs that are laid before the host females have started to lay are always ejected, just as the first-laid egg in any communal clutch is ejected by females that have not yet laid. Those that are laid during the laying period are accepted by the host group, and may hatch and fledge along with the rest of the clutch.

The majority of parasitic eggs, though, are laid after the onset of incubation at the host nest, and these are usually removed by adult group members. Experiments in 2008 and 2009 confirmed that group members can recognize late-laid, asynchronous eggs by the appearance of the shell: freshly laid eggs are coated with vaterite, a polymorph of calcium carbonate, and appear chalky and white, whereas eggs that have already been incubated are scratched and abraded, revealing the blue calcite shell underneath the vaterite coating (Fig. 3.2). Freshly laid white eggs are obvious misfits in a clutch of blue, incubated eggs, and group members will eject late-laid eggs even if they are laid by another female in the group (Riehl 2010a). It therefore seems likely that removal of parasitic eggs is not a response to parasitism itself, but is instead a general response to the presence of eggs that are unlikely to hatch (cracked or broken eggs are also removed). From the host group's perspective, it is advantageous to remove these eggs because, due to large clutch sizes, the presence of parasitic eggs reduces the hatching rate of the hosts' own eggs even if the parasitic egg never hatches.

Why, then, do females lay parasitically, and why don't they time their laying to coincide with the host group? Detailed genetic data from over 200 females in the study population suggest that brood parasitism is a best-of-a-bad-job strategy: the majority of parasitic eggs are laid by communally nesting females whose own nests were depredated (or completely destroyed) during the laying period. Rather than searching for nests that are still in the laying phase, these females seem to simply dump their eggs in the nearest available nest, almost always on an adjacent territory. Loflin (1983) described an identical instance in his study population of smooth-

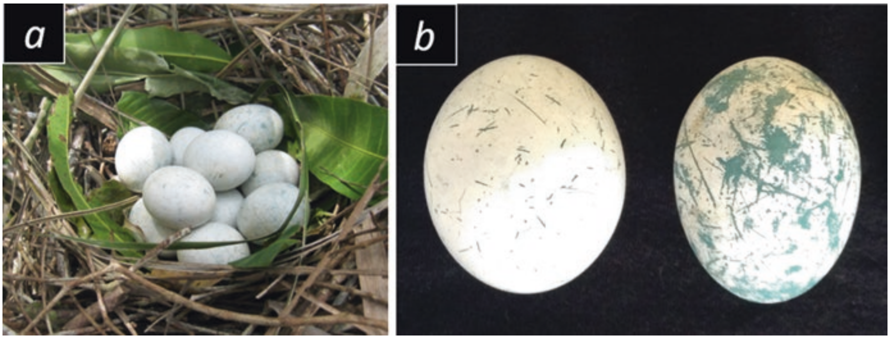

Fig. 3.2 (**a**) Greater ani nest, Barro Colorado Nature Monument, Panama, 2008, showing 10 eggs laid by 3 females. Note the layering of eggs in the nest, characteristic of large clutches. (**b**) Two greater ani eggs at different stages of incubation, showing the mostly intact white vaterite coating of a freshly laid egg (left) and the patchy appearance of an incubated egg (right) in which the vaterite coating has been scratched to reveal the blue calcite shell underneath. Photo: Christina Riehl

billed anis in Florida, in which a gravid female whose nest was destroyed in a storm entered a neighboring territory and laid several eggs into that group's nest. We have observed several instances in which the "parasitic" female appeared to try to join the nesting group that she parasitized, staying at the communal nest and attempting to incubate and participate in communal displays. This is rarely successful, since group members recognize extra-group individuals and prevent them from attending the nest. In one instance, though, a female laid parasitically in one nesting attempt, then joined the group and participated fully in parental care in the subsequent nesting attempt. Similar behaviors have been observed in groove-billed anis, leading to the suspicion that the so-called parasitic behaviors were actually attempts to join a nesting group late in the laying cycle (Vehrencamp and Quinn 2004). This strategy makes sense, given that communally nesting females have far higher reproductive success than parasites. Not only is the survival probability of parasitic eggs rather low, but parasitic females usually manage to lay just one or two eggs into host nests, rather than the normal clutch size of 3–5 eggs for a communal nester. Interestingly, only a small minority of females ever act as parasites, though nest predation during the laying period is extremely common. Most groups cease laying entirely following predation, and a few lay a second clutch on the same territory. The latter option is usually unsuccessful, since re-nesting attempts by the same group are typically found and destroyed by the same predator. From an individual fitness perspective, it seems likely that brood parasitism yields a lower payoff than successful communal nesting, but a higher payoff than failing to lay at all—or, potentially, than attempting to re-lay in the same risky location.

3.7 Evolutionary Origins

Every field researcher who has studied anis, beginning with David E. Davis and continuing right down the line, has noticed the similarities between the anis' communal breeding system and the intraspecific brood-parasitic behaviors that I described above. Consider the parallels: in both cases, two or more females lay their eggs in the same nest. The only difference is that a brood parasite abandons parental care to the other female, whereas a communal breeder remains at the nest to help raise the young (Lyon and Shizuka 2010). Seven decades ago, Davis (1942) hypothesized that the ani is essentially a brood parasite that, as he put it, "has become host-specific on itself." Loflin (1983) and Vehrencamp (2000) agreed, suggesting that the competitive behaviors seen in ani groups—such as egg ejection and high variance in parental investment—might be vestiges of intraspecific parasitic behavior. In many non-cooperative bird species, for example, a host female will eject conspecific parasitic eggs if they are laid before she lays her first egg, but not afterwards (Stouffer et al. 1987; Pinxten et al. 1991). This generates a pattern of egg ejection that is virtually identical to that seen in anis, except that the "parasitic" ani remains at the "host" nest, continues to lay eggs, and subsequently contributes to parental care. Therefore, one potential scenario for the evolution of communal nesting would require conditions under which a parasitic female would maximize her reproductive output by providing parental care to the mixed clutch rather than abandoning it (Vehrencamp and Quinn 2004). If shared benefits accrue to both partners, then the relationship shifts from a parasitism to a mutualism. Our recent data on the relative fitness of females that lay parasitically or communally supports this scenario: cooperation is clearly favored over parasitism, and parasitism persists only as a best-of-a-bad-job strategy when no other options are available (Riehl and Strong 2019).

3.8 Conclusions

What can anis reveal about the evolution of cooperative breeding, and how does their peculiar life history fit in with that of other Neotropical birds? At the ultimate level, phylogeny and evolutionary history have clearly influenced the crotophagine breeding system. Cuckoos share many ancient physiological and behavioral traits that appear to have set the stage for the evolution of their diverse reproductive systems: unusually flexible habits of mating and parental care, the ability to lay a huge number of eggs in a short period of time, and a propensity towards brood parasitism. The signal of phylogenetic history is strong in this clade; communal nesting has been maintained in all four crotophagine lineages over considerable evolutionary time scales. But after 10 years of studying greater anis in the field, I have been equally impressed by the role of tropical ecology in shaping their life history. Like many tropical birds—and unlike their temperate-zone counterparts—anis typify the "slow" end of the life-history spectrum, exhibiting low adult mortality, delayed reproductive maturity, long-term pair-bonds, and year-round territory defense (Ricklefs and Wikelski 2002). Could communal breeding evolve in a temperate-zone cuckoo, one with a hazardous seasonal migration, high adult mortality, and yearly re-establishment of breeding territories? Perhaps, but it is hard to imagine that it would look much like the ani system, with its elaborate communal displays and decades-long social bonds. It is equally hard to ignore the importance of snake predation on eggs and nestlings, which is extremely high and apparently favors cooperative nest defense—another classic tropical paradigm, hearkening back to Alexander Skutch's observation that, in tropical forests, snakes are "by far the worst enemies of nesting birds" (cited in Lewis 2004). Contrary to the old belief that tropical environments are a seasonal and unchanging, recent meta-analyses have shown that the unpredictable rainfall typical of many tropical habitats may be an important correlate of cooperative breeding, with social nesting acting as a buffer in harsh years and allowing increased reproductive output in benign years (Jetz and Rubenstein 2011; Rubenstein 2011). Our data on the effects of El Niño on ani population demographics offer a remarkably good match to these predictions, suggesting that cooperation allows bumper crops of ani nestlings in wet years and prevents total failure in dry years. We could not have foreseen these results at the outset of the study, but new patterns emerge with each year of data, and each new pattern leads to new questions. After 10 years of research on the witch birds of Barro Colorado, we are only beginning to scratch the surface.

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Chapter 4
Sexual Selection and Mating Systems: Contributions from a Neotropical Passerine Model

Regina H. Macedo and Lilian T. Manica

4.1 An Introduction to Sexual Selection

In his seminal book on natural selection, *The Origin of Species*, Charles Darwin (1859) suggested, almost as an aside, that sexually dimorphic and highly variable traits in animal species evolved through a distinct process that he termed sexual selection. Twelve years later he published an expanded account of sexual selection (Darwin 1871), with copious evidence supporting his conclusion that secondary sexual traits regulate the bearers' chances of leaving descendants in the next generation. According to his theory, members of one sex compete for access to the other sex, and competitors in better condition or bearing more extravagant ornaments should gain a mating advantage. Such an advantage can be transmitted to the offspring of the competing sex (usually males), setting the perfect scene for sexual selection to produce sexual dimorphism (Andersson 1994). Darwin's ideas led to the foundation of modern theory describing animal breeding systems (Trivers 1972; Emlen and Oring 1977; Reynolds 1996; Owens and Bennet 2002) and are still inspiring ongoing studies seeking to understand reproductive phenomena in animals (Beani and Zuk 2014; Miller and Svensson 2014; West-Eberhard 2014; Zuk et al. 2014; Schaefer and Ruxton 2015).

Darwin (1871) suggested that pronounced sexual dimorphism should be more common among polygamous species, such as hummingbirds, birds of paradise, peacocks, and pheasants, when compared to monogamous ones (see also Owens and Hartley 1998; and Dunn et al. 2001). Polygamy can be distinguished from monogamy by the ability of one sex to monopolize the other sex, and prevails when one of

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the sexes (males in polygyny and females in polyandry) deserts the current mate to seek additional mates (Emlen and Oring 1977; Reynolds 1996). Despite the risk of reducing offspring survival after desertion, multiple mating behavior should increase individual fitness when polygamy potential is high (i.e., when mating partners or limiting resources are economically defendable; Emlen and Oring 1977). Because only individuals in superior condition, holding better territories, or bearing stronger armaments should be able to attract multiple partners, only few individuals can thus maximize their reproductive potential (Andersson 1994). Resulting reproductive skew leads to a higher variance in reproductive success in polygamous systems, increasing the strength of sexual selection (Emlen and Oring 1977). In contrast, social alliances between males and females in monogamy are maintained throughout or across breeding seasons due to few opportunities for exclusive possession of multiple sexual partners, and the possible fitness costs of mate and offspring desertion (Emlen and Oring 1977; Owens and Bennet 2002). Monogamy should prevail when chances of finding a mate and producing offspring are more evenly distributed among individuals and across the sexes, resulting in less intense competition and more comparable mating opportunities. Monogamy should also evolve when both sexes are needed to care for the offspring, making the fitness costs of desertion too high (Trivers 1972). In theory, in monogamous systems, traits increasing survival have a greater adaptive value than do secondary sexual traits that increase mating success. However, we still lack a clear understanding of the relationship between sexual selection and mating systems, since recent new perspectives have been incorporated in the underlying theory, as discussed below.

The need for a better classification of animal mating systems was highlighted by the discovery that the social mating behavior of animals often does not correspond squarely to their actual sexual choices (Reynolds 1996). Conjectures regarding the role and frequency of female multiple mating among monogamous birds began in the 1950s, based on observations of extrapair copulations (EPCs; von Haartman 1951; Bray et al. 1975). With the development of molecular methods (e.g., DNA fingerprinting, Burke and Bruford 1987), extrapair fertilization (EPF) came to be documented widely, with intriguing consequences for sexual selection theory. Additional evidence was based upon the finding that morphological characters, such as tarsus length, often did not coincide with expectations of heritability of traits from the social father (Alatalo et al. 1984). A study of zebra finches *Taeniopygia guttata* in a semi-natural aviary, for example, showed that EPCs by females were indeed leading to EPFs (Birkhead et al. 1988). This study also showed that behavioral responses of social males to female “infidelity” favored their own reproductive success: copulations within the breeding pair right after EPC decreased the cuckolded males’ chances of EPF and paternity loss (Birkhead et al. 1988). Investigations regarding the characteristics of social partners (e.g., male age and experience) and pair bond duration were also a focus of early studies (Wetton and Parkin 1991). Reports of female multiple mating among socially monogamous birds and mammals flourished in the literature, indicating that the pattern is widespread (Griffith et al. 2002).

The discovery, particularly in birds, of widespread EPF suggested that mating systems evolution is influenced by postcopulatory, prezygotic selection more than previously realized (Birkhead and Møller 1992). In females, multiple mating behavior may trigger sperm competition within the reproductive tract, where sperm can be stored from 6 to 45 days (10 days in most species, Birkhead and Møller 1992), resulting in female control of paternity. Comparative studies have suggested that cryptic female choice can be more important than the mating system itself for the evolution of secondary sexual traits, such as plumage dimorphism in birds (Møller and Birkhead 1994; Owens and Hartley 1998). However, the relationship between mating systems and sexual traits is complicated by the observation that mating systems may influence the evolution of other types of traits, such as size dimorphism, which can have secondary influences on sexual trait structure (Owens and Hartley 1998). The scenario can be even more complicated given that multiple environmental factors, such as climate, nesting site distribution, and altitude, also appear to influence sexual selection and should thus not be dismissed (Badyaev and Hill 2003). In general, very few bird studies have been able to generate comprehensive tests of the relationships between sexual selection, mating systems, and sperm competition. One of the most frequently cited studies showed that both plumage and body size dimorphism are influenced by the social mating system (mainly when comparing monogamous to polygynous systems), whereas the influence of sperm competition appeared to be minimal (Dunn et al. 2001). A relationship between sexual dimorphism and mating system has also been documented for other taxonomic groups (e.g., Lindenfors and Tullberg 1998), as well as in comparisons limited to closely related bird taxa (e.g., Price and Whalen 2009; Carmona-Isunza et al. 2015).

Since Darwin's (1871) publication on sexual selection, numerous studies have provided exciting new results that have consolidated the theoretical framework he proposed. It is now recognized that sexual selection not only promotes adaptations in behavior, morphology, and physiology, but is also in itself an agent of speciation (Andersson 1994). However, most of the empirical work that has been conducted about sexual selection has focused on species restricted to temperate regions of the world. Thus, information about tropical animals is critically underrepresented in the literature. Because animal diversity reaches its peak in tropical regions of the world, this gap in knowledge undermines the concepts and generalizations associated with sexual selection theory (Stutchbury and Morton 2001; Macedo 2008; Macedo and Machado 2013; Zuk 2016). Divergences from classical sexual selection models may very possibly occur for the tropical avifauna, given that sexual selection pressures should differ between the temperate and tropical realms. Numerous hypotheses have been advanced to explain the evolution of mating systems in conjunction with occurrence of EPF, especially for birds (e.g., breeding synchrony, rapid pair formation, breeding density, adult mortality, female constraints, etc.; reviewed in Macedo et al. 2008). Yet, few comparative studies have been conducted to examine the outcome of contrasting selective pressures between the temperate and the tropical avifaunas. It is thus imperative that experimental, hypothesis-based, and data-rich behavioral ecology studies be conducted targeting the tropical fauna to decrease this bias in sexual selection theory (e.g., see Chap. 1).

In this chapter, we present work that we have developed within the scope of sexual selection theory, using as a model a small Neotropical passerine, the blue-black grassquit (*Volatinia jacarina*). This body of work, developed in the Animal Behavior Laboratory of Universidade de Brasilia, integrates long-term data from both captive and wild populations, to detail the natural history of the species. These data allowed us to develop multifaceted hypotheses covering numerous aspects of the biology of the species, including mating system evolution, genetic paternity, hormonal basis for ornamentation, predator, and parasite-mediated responses, among many others. We hope that this approach will help and encourage other researchers in the Neotropics to develop analogous frameworks targeting many other interesting species!

The rest of the chapter starts with a general descriptive overview of the blue-black grassquit, followed by a synopsis of field and laboratory methods applied in our studies. We then subdivide questions that we have addressed into four sections covering the following conceptual frameworks: (1) parasite-mediated sexual selection; (2) social and sexual mating systems; (3) female choice; and (4) the evolution of sexual ornamentation.

4.2 The Blue-Black Grassquit Study Model

The blue-black grassquit is a small (approximately 9–11 g) seed-eating passerine with a broad geographic range, extending from Mexico southwards to most of South America, with its southernmost limits in Northern Chile and Northern Argentina. It prefers grasslands and disturbed habitats and is a common inhabitant of rural areas. In central Brazil, where we conduct our studies, this species is migratory and arrives each year at the beginning of the rainy season, in October, and departs around April, purportedly bound for northern regions of South America (Sick 2001). Grassquits depend on the yearly abundance of grass seeds produced during the rainy season in central Brazil. They use small shrubs and dense patches of grasses to support their small (ca. 7.5 cm), cup-shaped nests at heights of about 40–50 cm, and lay clutches that vary from 2 to 3 eggs (Carvalho et al. 2007; Macedo et al. 2012). Nest predation rates are very high (approximately 80%), and the incubation and nestling periods last approximately 10 days each (Carvalho et al. 2007).

We started conducting research on blue-black grassquits nearly two decades ago. Several life-history and reproductive traits have made this species a useful model system for testing questions about sexual selection and mating systems. First, the species is sexually dichromatic, facilitating the identification of adult males and females in the field (Fig. 4.1). Adult females have a dull, brownish plumage, while adult males molt, prior to the breeding season, into a blue-black iridescent nuptial plumage with distinct white underwing patches. The acquisition of iridescent nuptial plumage by males is likely a product of sexual selection, and more specifically

Fig. 4.1 Adult male (left) and female (right) blue-black grassquits from central Brazil. Photo: Regina Macedo and Lilian Manica

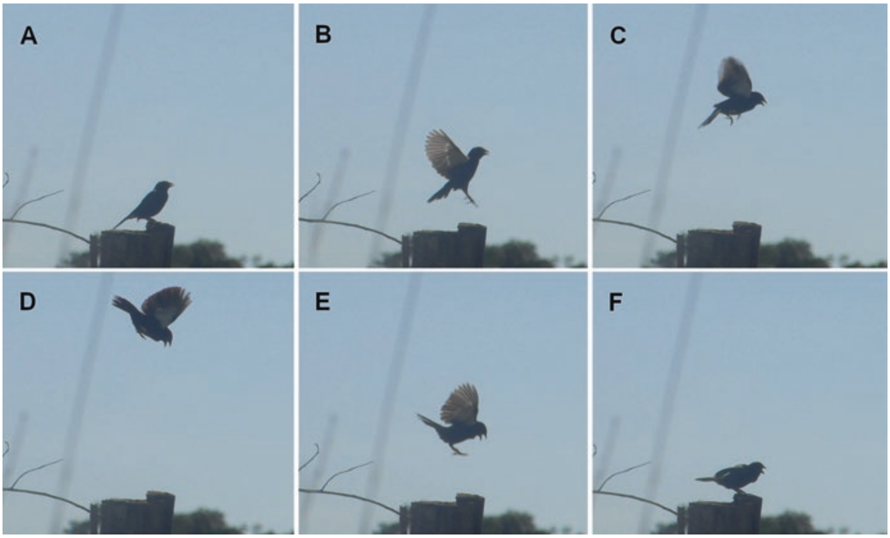

Fig. 4.2 Acrobatic vertical flight that composes the blue-black grassquit sexual display. Photo: Lilian Manica

of female choice for plumage ornamentation (see Hill and McGraw 2006). Furthermore, males vary widely in the coverage and expression of this ornamentation (Maia and Macedo 2011), such variation being a common feature for sexually selected traits.

Males also exhibit a conspicuous and highly repetitive behavioral display during the breeding season. This display consists of repeated acrobatic vertical flights (i.e., leap display). Each flight is generated using high-speed wing beats, at the peak of which birds rotate their bodies forward, and then land on the same perch (Fig. 4.2).

Upon descending they emit a buzzy, short call, which can also be produced uncoupled with the leap display. Acoustically, these calls are fairly stereotyped within males (retaining much of their structure within and across years; Dias 2009; Manica et al. 2017), yet highly variable among males (Fig. 4.3; Fandiño-Mariño and Vielliard 2004; Dias 2009). The complexity and persistence of the leap display (discussed in more detail below) have been of enormous interest from the very beginning of our studies on sexual selection. The fact that males execute what appears to be an energetically costly physical display with remarkable zeal and persistence for long periods in the morning and afternoon (Carvalho et al. 2007; Manica et al. 2017) suggests that sexual selection in these birds may be particularly influential.

Finally, another intriguing detail is that due to their very small territories, males display in very close proximity. The lack of information about the social and genetic mating system and parental roles led to suggestions that the species had lek-like characteristics (Carvalho 1957; Murray 1982; Webber 1985). However, our initial studies showed that grassquit males, in contrast to true lekking males (see definition by Höglund and Alatalo 1995), defend multipurpose territories within which females nest, and also engage in paternal care. However, both males and females also forage outside their territories. All of these biological elements generated the intriguing possibility that the blue-black grassquit was a socially monogamous species under intensive sexual selection, raising all sorts of interesting questions, which we discuss in more detail below.

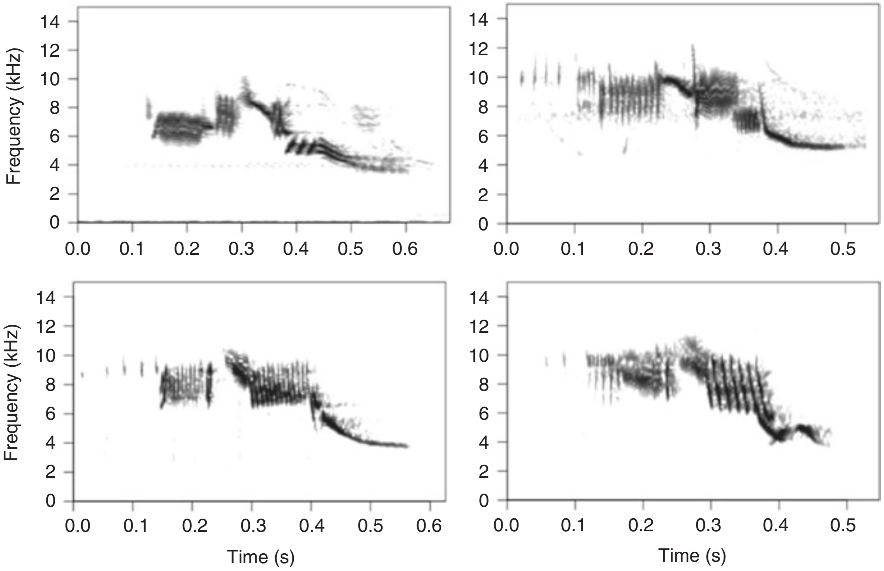

Fig. 4.3 Sonograms of calls of four different males, exhibiting individual variability yet retention of call structure within and across years for each individual (Dias 2009)

4.3 Methodological Approaches

4.3.1 Field Areas and General Procedures

Our primary study populations occupy two sites separated by approximately 40 km. The more rural population is located in Fazenda Água Limpa, a property of the University of Brasília (15°56’S 47°56’W), approximately 30 km from the city center. This field site, approximately 7 ha, is a mosaic of native grasses of the *Cerrado* biome (roughly 300 species; Almeida 1995), cultivated crop areas, pastures, and orchards. The second field site, of about 9 ha, is located in a savanna fragment in an urban matrix, within the campus of the University of Brasília (15°44’S, 47°52’W), and near busy streets and residential areas.

For experimental studies, we have also maintained a small population of birds (from 50 to about 100 individuals) in two outdoor aviaries, within which we have housed birds either separately in smaller cages or in groups of different sizes in larger compartments. Birds in captivity are provided with an *ad libitum* diet of mixed seeds (green, red, and yellow millet and birdseed), water, and a vitamin complex. In one study (Aguilar et al. 2008) we treated a subgroup of these birds with vermifuge (mebendazole) and medication to control for endo- and ectoparasites. We enrich compartments with grasses, artificial nests, calcium stones, and water baths. Long-living individuals have been in the aviary for up to eight years.

We have employed traditional methods yearly to capture and process birds in the field, with small variations depending upon the specific objectives of ongoing studies. We capture the birds with mist nets, and mark them with a combination of colored plastic bands and uniquely numbered aluminum bands provided by the Brazilian banding agency (CEMAVE/ICMBio). We take typical phenotypic measurements and collect blood samples via brachial venipuncture.

For some of our studies we have needed to determine territory ownership, size, and quality. To define territory boundaries we usually mark all perches birds use during displays, and then outline a maximum-sized polygon. We then calculate territory areas by measuring the sides of the polygon and the angles between them. This method for calculating territory area is somewhat crude but perhaps more precise than using a GPS, given systemic imprecision in GPS readings combined with the often very small sizes of these birds’ territories (as small as 13 m^2 and average of 72 m^2; Almeida and Macedo 2001; Carvalho et al. 2006). We have also assessed the quality of territories in various studies. This is done by estimating seed density within 1 × 1 m quadrats, by counting the number of grass stalks bearing seeds and those with empty culms. This methodology has varied somewhat across different studies, using different numbers of quadrats established either linearly or at short distances from nests (e.g., Dias and Macedo 2011; Manica et al. 2014).

4.3.2 Nest Monitoring and Parental Activities

We conduct nest checks every 2–3 days and with minimum disturbance. Distinct studies over the years have demanded different approaches for gathering data on parental activities after nestlings hatch. Some observations of parental activities were carried out through focal nest observations using binoculars, while at other times we have employed camouflaged video cameras set on tripods close to nests. The data collected include provisioning behavior by both parents (e.g., frequency and types of food delivered), time spent at the nest, timing of visits, and general behaviors, which take into account the style of approach to the nest and execution of displays or song upon leaving. For some studies we have monitored chick growth through periodic measurements.

4.3.3 Plumage Coloration

The structural, nuptial plumage of the blue-black grassquit can be considered a sexually selected secondary character under female choice. It varies considerably among males and is condition dependent (Doucet 2002); additionally, the iridescent coloration reflects investment in the prenuptial molt (Maia and Macedo 2011). We have thus strived to measure properties of male plumage coloration in various ways. We estimate the proportion of the body that is covered by blue-black plumage relative to the more cryptic brownish plumage that precedes the prenuptial molt. This is done by overlaying a small transparent plastic disc, subdivided into eight segments, over the plumage on various parts of the body, and counting the number of segments that are black or brown, thus calculating a general percentage of nuptial plumage. We also investigate color production by using reflectance spectrometry to measure spectral properties of feathers, which include brightness, contrast, and blue and ultraviolet chromas. Reflectance measures are conducted using an Ocean Optics USB 4000 portable spectrometer attached to a PX-2 pulsed xenon light source (Ocean Optics, Dunedin, Florida).

4.3.4 Male Courtship Display and Song

Above we briefly described the motor displays executed by males, which comprise a vertical leap with wing beats associated with a short song. Initial evaluations of this motor performance were generally unsophisticated and based on behavioral observations, with the main parameter measured being display rate (the number of displays per unit time). We have used a translucent scale held at arm's length, through which we estimated the height of the leap relative to that of the perch. We then measured real perch height with a tape measure, to calibrate the measures estimated through the translucent scale. Currently, with modern techniques, we have more recently been using high-speed digital cameras followed by analyses of computerized images. Analyses of video clips using ImageJ® v. 1.45s (Schneider et al. 2012), calibrated to objects of known size in the video frame (including the birds themselves), allowed us to measure several male motor display parameters, including precise leap height, forward body rotation angle, and launch velocity (Manica et al. 2017; Fig. 4.4).

Acoustic variables are also collected during male display bouts. For this purpose, we record songs of focal males using digital recorders (typically Marantz model PMD 660) and unidirectional (Sennheiser K6/ME66) or omnidirectional (Sennheiser/ME62) microphones. Analyses are subsequently conducted with acoustic analysis software programs (e.g., Cool Edit v.2.1 or Raven Pro® 1.4), to determine parameters such as song duration, minimum and maximum frequencies (kHz), and frequency bandwidths. From recordings we have also been able to quantify song output (number of songs per minute) and the consistency of song structure across multiple renditions sung by each male. A main question we have been addressing is whether these parameters indicate some aspects of male quality.

4.3.5 Body Condition, Parasitism, and Immune Status

When we capture blue-black grassquits, we take several classic body measurements as well as use the opportunity for sampling blood (see below), and to examine the bird for other particularities. We have used several criteria to determine the overall condition of the birds (see Costa and Macedo 2005), but the simplest of these is a size index calculated by dividing mass by tarsal length. This index is applicable because in our data we do not find a correlation between mass and tarsus, one of the

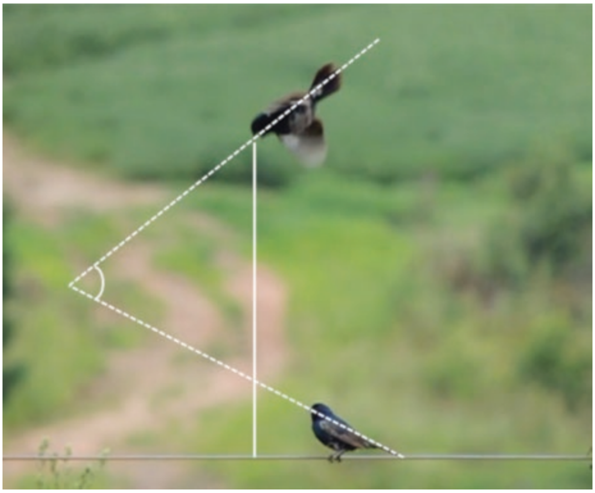

Fig. 4.4 Male motor display showing parameters measured using sequential video frames. The vertical continuous line represents the leap height and the angle between the two dashed lines represents the forward body rotation angle. Photo: Lilian Manica

prerequisites to calculate a scaled mass index (Peig and Green 2009). This size index has allowed us to explore associations between the overall health condition of an individual and other aspects of its phenotype, taking into consideration the possible energetic tradeoffs that may be involved.

In several studies, we have assessed what types of effects parasites may impose upon blue-black grassquit morphology, health, and behavior, always in a context associated with sexual selection. When we capture blue-black grassquits, we determine the presence and number of feather mites by examining both wings against the light (Koop and Clayton 2013). To date, all of the mites we have identified belong to the genus *Trouessartia* (Magalhães et al. 2014), which are common avian ectoparasites in the central Brazilian savanna region (Kanegae et al. 2008). Coccidian intestinal parasites are also important in a sexual selection context, as we have determined that they can strongly affect secondary sexual characters as well as behavior (Costa and Macedo 2005; Aguilar et al. 2008). The degree of coccidian infestation can be assessed by analyzing the extent of oocyst occurrence in the birds' feces. To collect fecal samples we place the birds in paper bags for approximately 15 min during the afternoon period, when there is maximum excretion of oocysts (Brawner and Hill 1999). Fecal samples are then preserved in a 2.2% solution of potassium dichromate (McDougald and Reid 1997). In the laboratory we have applied protocols that use either sedimentation (Sloss et al. 1999) or a standard flotation test (Greve 1996). We use aliquots taken from individual fecal samples to produce slides, which are then scanned under 340–400× magnification to estimate oocyst quantity. Because of the difficulty of identifying different coccidian species based upon visual inspection, we consider observed oocysts as a single group (Buchholz 1995). Depending on the concentration of oocysts, they can be either counted directly or estimated in groups of tens or hundreds per field.

Stressors in an animal's environment may result in physiological responses that disrupt the animal's delicate internal hormonal balance (Wingfield et al. 1998). We have endeavored to assess how certain stressors (e.g., predation risk and captive conditions) may result in altered physiological responses, primarily by examining the leukocyte profile, which reflects circulating glucocorticoid levels (Maxwell 1993). In birds, measurements that include total leukocyte count and the ratio of blood heterophils to lymphocytes (*H/L* ratio) have been used in other studies that have evaluated stress levels (Gross and Siegel 1983; Ots et al. 1998; Hõrak et al. 2002; reviewed in Maxwell 1993). The laboratory protocol is simple, and involves the collection of small blood samples and production of blood smears fixed in absolute methanol. The results of the hemogram and cell counts are provided by specialized veterinary clinics, and allow us to calculate the *H/L* ratio.

4.3.6 Genetic Analyses for Parentage Determination

A primary goal associated with our studies of the blue-black grassquit's mating system has been to determine parentage. In the field, we collect blood samples via brachial venipuncture not only from all adults captured, but also from nestlings.

Laboratory methods for molecular determination of parentage are changing at a fast pace, so there has been no constant protocol. In our work on grassquits, we have used microsatellite genotyping and the development of microsatellite sequences (Carvalho et al. 2006; Manica et al. 2016). We have used up to 15 microsatellites for parentage assignment, and also estimated relatedness between mating partners by calculating Queller and Goodnight's (1989) *r* relationship coefficient. The results of these genetic analyses, as described below, transformed our theoretical outlook and interpretation of the behavior of the blue-black grassquit, which at first appeared to be that of a typical socially monogamous passerine.

4.4 Results and Discussion

4.4.1 Parasite-Mediated Sexual Selection

Females may base their choice of mates upon male attributes or upon the resources males defend (Andersson 1994). In the first case, females may be choosing mates using physical or behavioral cues indicating a high fitness potential, that if heritable, could be passed on to their offspring (Trivers 1972). These indirect mechanisms of female choice are grouped under the denomination of "good genes models" of sexual selection, and are based on the assumption that evolution should favor female preference for males whose genes are viable. Based upon these general patterns of female choice, one hypothesis, known as the handicap principle (Zahavi 1975, 1977), suggests that exaggerated ornamental attributes borne by males should be costly and hinder survival, and could be targeted by female choice. By favoring males bearing costly ornaments, females would likely be selecting mates of better quality, to the extent that such attributes serve as honest signals of a male's viability.

A notable extension of the handicap principle was proposed by Hamilton and Zuk (1982), and involves the co-adaptive cycles between parasites and their hosts. This hypothesis suggests that parasites are selective agents for more resistant male genotypes. Higher quality males would be less likely to suffer the negative effects inflicted by parasites and pathogens, and their resistance would be reflected in cues indicating their better health, when compared with less resistant males. These cues could include enhanced plumage color and brightness and more elaborate or active displays. Females choosing males using such cues would produce offspring that could inherit the male's parasite-resistant genotype. Additionally, by associating with the healthier males, females would avoid contagion by parasites (Borgia and Collis 1989), and perhaps have access to better resources provided by such males (Hamilton 1990). These collective advantages and their impacts on female choice comprise what has been termed the parasite-mediated sexual selection model.

Two key predictions for birds generated by the Hamilton–Zuk parasite hypothesis of sexual selection are that: males with lower levels of parasite/pathogen infestation should exhibit brighter plumage or more ornamented phenotypes, relative to infested males; and second, females should mate preferentially with males of the former type. Many theoretical models have tested the Hamilton–Zuk hypothesis, although their results remain controversial (Kirkpatrick 1986, 1987; Pomiankowski 1987; Read 1988; Møller 1990; Kirkpatrick and Ryan 1991; Møller et al. 1999). Additionally, numerous studies have also empirically examined the predictions generated by the hypothesis, with varying levels of data lending support (reviewed in: Endler and Lyles 1989; McClennan and Brooks 1991; Clayton et al. 1992).

We have tested some of the key concepts generated by the parasite-mediated sexual selection model, for birds in both free-living and captive conditions. In a first study, conducted with wild grassquits, we examined potential links between intestinal parasite infestation levels (coccidian oocysts) and extravagance of secondary sexual characters and body condition (Costa and Macedo 2005). We expected that as parasite levels increased, males would exhibit a lower body condition, which was assessed using body mass and size, hematocrit levels, and total plasma protein levels. We also expected that a male with a lower body condition due to parasitism would have a less exuberant phenotype in terms of ornamental traits. These included percentages of coverage of nuptial plumage and spectral characteristics, and courtship display attributes. Our results supported one of the predictions of the parasite-mediated sexual selection hypothesis, which proposes that individuals with higher levels of parasite infestation should have less extravagant ornaments. We found a negative correlation between the number of oocysts and nuptial plumage coverage, as well as display leap frequency. Encouraged by these results, we conducted a follow-up study with a captive population to examine the second key prediction of the parasite-mediated sexual selection hypothesis that females would prefer males with lower parasite infestation levels that showed more exuberant ornamentation (Aguilar et al. 2008). In this study, we used a captive population consisting of two groups of birds, one of which was medicated and thus free from coccidian parasites, while the other group was non-medicated, with resultant high levels of parasites. We found that the parasite-free males developed a higher body condition index compared with the baseline group, and also exhibited enhanced courtship behavior, with displays that were more persistent, produced at higher rates and higher leap heights. So this specific prediction of the parasite-mediated sexual selection hypothesis was upheld. In female-choice trials we evaluated whether females would favor parasite-free males over males with baseline parasite levels. We measured female preference by time spent close to a male, within a testing apparatus where females could see and hear two males simultaneously. However, our data did not provide support for this second prediction of the hypothesis; females showed no detectable preference for healthy males overall, despite their superior body condition and more energetic displays. These results were surprising, given that studies with several different species have reported female choice for healthier, non-parasitized males (Clayton 1990; Milinski and Bakker 1990; Shawkey et al. 2009; Bosholn et al. 2015). However, results from laboratory mate choice experiments should be interpreted with caution, because in such conditions, individuals are frequently not exposed to the full range of sensory and social stimuli that occur in wild conditions (Byers and Kroodsma 2009). While in our published paper we discuss the various possibilities that consider the outcome of this experimental study (Aguilar et al. 2008), it is also clear that since the Hamilton–Zuk hypothesis was proposed, studies have often failed to report conclusive and supporting evidence for the entire model and its predictions (reviewed in: Endler and Lyles 1989). The parasite-mediated mechanism of sexual selection is one of the several possible mechanisms that modulate female choice and we speculate that this type of selection should be found in specific circumstances, such as in years of higher incidence of parasitism or when chances for being infected by contagion are higher.

4.4.2 Social and Sexual Mating System

As previously mentioned, it is well established that just observing social alliances and copulations is not sufficient for understanding animal sexual behavior. More comprehensive views can be gained by combining field observations with molecular techniques revealing biological parentage (as well exemplified in birds, Griffith et al. 2002). A rich body of literature concerning cryptic sexual behavior of animals is presently available, but many questions regarding its relation to sexual selection remain unanswered. The study of the blue-black grassquit has allowed us to deeply investigate mechanisms and consequences of pair formation and fertilizations, by describing both social and sexual (genetic) patterns of parentage. Our data have provided a more transparent understanding of this passerine's behavior, although the interpretation of data has frequently been challenging. Here, we briefly describe our main findings and how they have enhanced our understanding about this small passerine's breeding behavior.

Sexual behavior of the blue-black grassquit remained an enigma for decades. Despite bearing characteristics typical of monogamous birds (Alderton 1963; Almeida and Macedo 2001), it was repeatedly suggested as a lekking species (Carvalho 1957; Murray 1982; Webber 1985). Reasons for this were due to several peculiar features of this bird: accentuated dichromatism, exuberant male courtship behavior, and spatially aggregated patterns of breeding. Our initial studies concluded that the species did not fulfill assumptions of a traditional lek (Höglund and Alatalo 1995), and that social monogamy was unequivocal because males and females participate in nest building, nestling feeding, brooding, and defense (Almeida and Macedo 2001; Diniz et al. 2015, in agreement with Alderton 1963). We thus proposed an alternative explanation for blue-black grassquits, a mating system that falls under Wagner's (1998) "hidden-lek" definition (Almeida and Macedo 2001; Macedo et al. 2018). According to this hypothesis, tight territorial clustering may occur when socially monogamous individuals seek EPCs, and not because of underlying resource distribution (Wagner 1998). In blue-black grassquits, small territories are highly clumped, which may facilitate potential mate comparisons by females, since males vary largely in their display attributes (Almeida and Macedo 2001; Maia and Macedo 2011; Diniz et al. 2015; Manica et al. 2016). Aggregated patterns may also enhance females' chances of finding and assessing extrapair mates, and thus of obtaining direct or indirect benefits (see "Female choice: direct or indirect benefits?"). In fact, intruding males often interrupt display bouts of territory owners, suggesting strong competition for territories and copulations within "arena-like" aggregations. Several of our studies were designed to discern how well the hidden-lek hypothesis might apply to blue-black grassquits. Although we found a relationship between aggregation occurrence and territory quality in one study population (Aguilar et al. 2008; Dias et al. 2009), we considered that EPC could still drive clustering in this model species, but only genetic parentage analyses would provide further understanding.

Our subsequent study, which used molecular techniques to assess parentage, provided the evidence needed to reinforce the hidden-lek hypothesis: female blue-black grassquits do engage in extrapair forays (Carvalho et al. 2006). This study reported high rates of EPF, occurring in 64% of nests and 50% of genotyped nestlings, although sample size was very limited (11 nests and 20 nestlings). Distribution of genetic parentage in different nests was highly variable, such that males losing paternity in their own nests were still biological fathers of at least one nestling in their nests ($n = 7$), or gained EPF in other males' nests ($n = 3$, Carvalho et al. 2006). More recently, we have expanded our understanding of the social and genetic mating systems of the grassquits using data from a three-year study that comprised a much larger sample, of 95 nests and 208 nestlings (Manica et al. 2016). Rates of EPF were lower than previously reported by Carvalho et al. (2006), found in 30.5% of nests and 21.1% of nestlings, but are still high considering birds in general (Griffith et al. 2002). We also found broods composed entirely of extrapair nestlings ($n = 13$, 13.7%) as well as mixed broods (including extrapair and within pair young, $n = 16$, 16.8%, Manica et al. 2016), suggesting that mating strategies vary greatly among individuals.

Interestingly, both studies investigating genetic parentage in blue-black grassquits presented cases where females were not the genetic parents of offspring in their own nests. Such patterns result from alternative female mating strategies: intraspecific brood parasitism (when the nestling is unrelated to either social parent), or quasi-parasitism (when at least the social father is also the biological parent, Yom-Tov 2001; Griffith et al. 2004). However, we found low rates of these strategies, only three cases of intraspecific brood parasitism (27%, Carvalho et al. 2006) and seven cases of quasi-parasitism (5%, Manica et al. 2016), as is usually the case for altricial species (Yom-Tov 2001). These low rates indicate that these behaviors may not result in high fitness gains for females. Among possible explanations, parental care may be costly in blue-black grassquits (Almeida and Macedo 2001; Dias and Macedo 2011), such that selection favored the evolution of social parent strategies to detect other females attempting to parasitize their nests (Lyon and Eadie 2008). However, this hypothesis remains to be tested.

In our 3-year study, rates of EPF varied broadly across years sampled (23.5%, 34.7%, and 8.2% of nestlings genotyped, respectively; Manica et al. 2016). We still lack explanations for this pattern, because a robust method to understand the relation between EPF and time-dependent variables requires data from a longer period of sampling. Nonetheless, we suspect that environmental fluctuations, such as precipitation, resource availability, or distribution, or even the social environment (e.g., sex ratio or mating partner availability, Maia et al. 2012), may have influenced individual body condition and, consequently, attractiveness and mate choice (Cornwallis and Uller 2010; Botero and Rubenstein 2012). Despite these open questions, we now have a better understanding of mechanisms of intersexual selection (mate choice) that occur in blue-black grassquits, and how females benefit from choosing within pair and extrapair fertilizations, an idea we develop in the next topic.

4.4.3 Female Choice: Direct or Indirect Benefits?

Encountering appropriate individuals and mating are not always easy tasks for sexually reproducing organisms. While sex is a crucial mechanism of gene transmission to future generations in animals, selection has favored behaviors that can hinder such achievement: mate preference and choice. Specific circumstances, such as the ready availability of potential sexual partners varying in quality attributes, may lead individuals to neglect some opportunities of social and sexual pairing in favor of only a subset of potential mates (Andersson 1994). Indeed, selective reproductive behavior is widespread across taxonomic groups, from neurologically simpler organisms (e.g., horned beetles, Kotiaho 2002; spiders, Elias et al. 2006) to animals with complex social organizations and cognitive abilities (e.g., birds: DuVal and Kempenaers 2008; Karubian et al. 2009; mammals: Galimberti et al. 2000; Drickamer et al. 2003). Being overly choosy can be costly to individual fitness because searching and sampling involve risk, time, and energy investment (Jennions and Petrie 1997). However, benefits from being choosy must explain its evolution and maintenance, encompassing behaviors that may influence the individual's own survival and fecundity (direct benefits) to those increasing genetic quality of the offspring (indirect benefits) (Reynolds and Gros 1990; Andersson 1994). Alternatively, choice can also occur as a byproduct of a sensorial bias to specific traits of potential partners that stimulate behavioral responses associated with activities other than reproduction (e.g., foraging and predator avoidance, Ryan 1990).

The female is the choosy sex in most bird species, which is typical of most animals. Given the high payoffs, increased investment in egg production, and wide availability of sexually active males (namely, a "male-biased operational sex ratio"), choice is often adaptive for females (Kokko et al. 2006). By evaluating male secondary sexual traits (such as ornaments, displays, and morphological specializations), females can benefit directly by choosing good fathers for their offspring (Buchanan and Catchpole 2000; Pickett et al. 2013). Male mating partners may share parental duties and allow females to save energy for other activities, such as foraging, feeding additional nestlings, offspring protection, and future breeding attempts (Hoelzer 1989; Moreno et al. 2013). Female choice can favor more fertile males (Sheldon 1994), or physically vigorous or skilled mates (Byers et al. 2010), which may also hold resource-rich territories (Bensch and Hasselquist 1992). Females can obtain indirect benefits for their offspring by fertilizing their eggs with sperm from males with good genetic quality, which are more genetically compatible or diverse, thus decreasing the deleterious risks of inbreeding (Griffith et al. 2002; Neff and Pitcher 2005; Kempenaers 2007). Sexual attributes of males are often related to these genetic advantages, although in some circumstances they do not necessarily indicate condition, but rather attractiveness (Fisher 1915; Kirkpatrick and Ryan 1991; Prum 2017).

Understanding mechanisms and outcomes of female choice in blue-black grassquits has been our objective in both observational and experimental studies. We have examined whether males bearing more extravagant characteristics were more likely to obtain matings, form social alliances, and build a nest or fertilize eggs (Carvalho et al. 2006; Dias et al. 2014; Manica et al. 2016). We know that at least a few males are unable to attract a mate (22% of 31 males: Manica et al. 2016). Studying birds in the field, our focus has been on male traits that indicate a possible influence of sexual selection: leap display attributes (leap height, rate and forward body rotation angle) and song parameters (song duration and frequency bandwidth). We also quantified behaviors indicating male investment in courtship, such as percentage of time spent displaying, presence in territories, chasing or fighting with potential rivals, and male morphological dimensions. Two independent studies (Carvalho et al. 2006; Manica et al. 2016) produced converging results that led us to conclude that, in blue-black grassquits, leap height is the most important trait influencing female choice. We found that this leap parameter is related to male pairing success (a binomial variable indicating whether a male is socially paired and owns a nest), indicating that females favor those leaping higher (i.e., bearing a more exaggerated trait). In addition, males that paired successfully with a female spent more time on their territories and executed leaps at higher rates (Carvalho et al. 2006), although this latter parameter was not confirmed in the second study (Manica et al. 2016). None of the other parameters measured provided evidence for female preference. Leaping higher and repeatedly in long bouts of displays is challenging for males, as suggested by a tradeoff in the two parameters (Manica et al. 2017), and birds in worse health in terms of parasite load are negatively affected (Aguilar et al. 2008). While these results suggest that females choose social males carrying good genes, the conclusion that this choice leads to indirect benefits is not straightforward. Social pairing does not necessarily imply fertilization success in blue-black grassquits, as chances of extrapair fertilization are high (Carvalho et al. 2006; Manica et al. 2016, see “Social monogamy and extrapair paternity”). Nonetheless, social males may be chosen due to other attributes as well, since they cooperate intensively with parental care and territory defense (Almeida and Macedo 2001; Diniz et al. 2015). Therefore, selection may have favored females that choose social partners by assessing important male signals about their paternal role, which can generate direct benefits to female fitness (Manica et al. 2016). Additionally, the vigor implicated in higher leaping could also be an indication of male quality at some level, and heritable to a certain degree. Possibly, leap height may also serve as a good genes cue in female choice.

Inferences regarding fertilization success in Manica et al. (2016) were shown with more precision through genetic parentage analyses. Using this approach, we tested whether male display traits also guided female sexual choice. We used two measures of male fertilization success as proxies for female choice: paternity lost within each male's social brood to an extrapair male, and extrapair paternity gained in any other brood. Despite the clear influence on social pairing, neither leap height nor any other measured male display trait appeared to influence sexual choice, and these included leap rate, song duration, and frequency bandwidth. Pairwise comparisons between social and extrapair males did not distinguish them by motor and song parameters nor in the quality of their territories in terms of seed availability, thus supporting the absence of biased female choice in fertilizations. To test for non-additive genetic benefits of female choice, we also quantified male genetic quality as genetic diversity (heterozygosity by locus, Aparicio et al. 2006) and compatibility (relatedness with female, Queller and Goodnight 1989). However, we found that social and extrapair males did not differ with regard to these parameters. Hence, sexual choice in extrapair matings in blue-black grassquits is not likely to be determined by indirect benefits.

A complementary, experimental study of captive birds was designed to understand the importance of plumage coloration and body condition for female choice. We evaluated female behavioral responses in the presence of a novel male (i.e., a potential extrapair male) after being paired with a first male ("social male," an individual that displayed to the female and with whom she copulated and shared a cage for at least five months, Dias et al. 2014). Tests included the comparison of plumage and condition traits of social and extrapair males and an experimental manipulation. In the latter, the social male observed his mate interacting with a potential extrapair rival, after which he was profiled in terms of aggressiveness and stress level (steroid hormonal assay). Results indicated that females actively approached novel males and indeed spent more time closer to these males rather than their social mates (Dias et al. 2014). Despite this interest of the female, however, we did not find that any of the novel male's characteristics influenced female behavior. Additionally, social males, after observing their mates' response to novel males, did not exhibit aggressive behavior or higher steroid levels (Dias et al. 2014). In conclusion, our three studies of female choice in blue-black grassquits indicate that social mate choice is clearly guided by male leap height, but there is no evidence for selection of specific male traits in an extrapair context. The experience in captivity suggests that females may seek unfamiliar males, and respond to this more than to specific quality attributes when seeking extrapair mates. Taken together, results from the field and in captivity provide support for the hypothesis of direct benefits (good father) and, more weakly, for indirect (genetic) benefits, where in females use leap height as a cue for choosing their social mates.

4.4.4 The Where, When, and How of Sexual Ornamentation: Costs and Tradeoffs

The blue-black grassquit is also a good model species for understanding mechanisms mediating the evolution of secondary sexual characteristics. Sexual signals carry essential information about signaler attributes, such as health condition, social status, body size, and strength (Andersson 1994). While individuals can gain fitness benefits in expressing these characteristics, they often face limitations when producing and maintaining ornaments and displays. Such limitations can result from a wide variety of factors, for instance, resource availability (Ritschard and Brumm 2012), predator risk (Abbey-Lee et al. 2016), social context (O'Loghlen and Rothstein 2010), and mechanical or physiological constraints (Clark 2012; Sewall et al. 2013). In this sense, several of our methods were designed to understand how biotic or abiotic environmental variables constrain or favor the production or expression of specific male attributes.

As noted previously, leap display is important for mate choice in blue-black grassquits (Carvalho et al. 2006; Manica et al. 2016), but equally important for the male is finding a good spot to execute displays. The act of choosing an adequate display perch can be decisive for successful reproduction. We have shown that habitat selection is non-random in blue-black grassquits: males establish clustered territories within areas covered with taller and more productive grasses and with smaller and more numerous shrubs (Almeida and Macedo 2001; Dias et al. 2009). These choices could reflect survival requirements, female preference, or both; therefore, spatial decisions may favor individual settlement and survival within an area. Beyond providing adequate display perches, these vegetation requirements may provide suitable nesting sites (Aguilar et al. 2008) as well as enough food for nestlings. However, the benefits of courtship displays in prominent perches and territories come at a cost, as we found that individuals are also probably more exposed to predators. Support for this hypothesis is based on the high predation rates of artificial nests within territories of displaying males versus predation rates in territories without displaying males (Dias et al. 2010).

Costs are also evident when comparing males that differ in body condition (mass to tarsus rate, a body mass index), in relation to their leap heights and proportion of displays produced that include the leap component. Males with lower body mass index lack the ability to produce exaggerated forms of both parameters, resulting in a tradeoff such that they reduce one parameter when the other is increased (Manica et al. 2017). Repetition of leap displays is energetically demanding for individuals, since they often execute many leaps in succession (and even up to 300 or more in sequence). While individuals are able to produce highly repeatable vocal and motor signals despite their challenging nature, our results indicate a quantity–quality tradeoff. With this finding, we suggest that males with depleted fat reserves or decreased muscle tissue experience additional obstacles in communicating with females or potential rivals. Our study also revealed that signals can be redundant because other components of the displays, including both motor (leap duration, launch velocity, and number of wing beats) and vocal parameters (song duration), are positively correlated and transmit similar information about individual condition (Manica et al. 2017).

Also critical for attracting females are behaviors and physiological mechanisms in males that influence the blue-black plumage's iridescence. Every breeding season, males molt into the blue-black nuptial (or alternate) plumage, a melanin-based coloration, while females remain brownish and cryptic (Maia and Macedo 2011). Our studies led to a greater understanding of the male iridescent plumage, allowing us to conclude that this coloration is likely an honest quality signal. We know that molting speed is an important factor regulating coloration quality, as males investing in faster or earlier plumage acquisition produce more saturated, UV-shifted coloration (Maia and Macedo 2011). While costs for production of melanin-based plumage are still under debate (Roulin 2016), barb cells' demand of melanin to produce iridescence is also probably high, imposing indirect energetic costs to organisms that produce this pigment (Maia et al. 2012). Indeed, we showed that nuptial coloration is a condition-dependent trait, because males with high incidence of intestinal parasites (coccidian oocysts) exhibited reduced blue-black feather coverage (Costa and Macedo 2005). Similar data from birds in captivity (which have greater fat deposits), however, did not support this hypothesis (Aguilar et al. 2008), indicating that results based on experimental conditions should be interpreted cautiously when translated to free-living contexts.

We have also found that the timing of leaping and the display site are important in how male plumage ornamentation is exhibited. Individuals gain an advantage when displaying bathed directly by sunlight, because of increased conspicuousness of their iridescent plumage coloration (Sicsú et al. 2013). Both the achromatic (brightness) and chromatic (hue and saturation) contrasts between feather reflectance and the background are higher when light incidence upon males is higher, as we revealed using visual models (Sicsú et al. 2013). Undeniably, males produce their displays (including both leaps and vocalizations while perched) more frequently under this lighting condition, while the effects of other environmental parameters (ambient temperature, relative humidity, and sun height) are negligible. Therefore, males with few opportunities to find and defend a display perch that emphasizes their iridescent plumage (e.g., noticeable perches, under direct incidence of sunlight for longer periods) may be limited in their capacity to attract sexual partners.

Social conditions likewise influence the conspicuousness of grassquits' plumage. In our experiments with social contexts, males maintained in cages together with other males molted faster and earlier, and also produced more UV-shifted feather coloration, in comparison to males held in paired condition with a female or in mixed-sex cages (Maia et al. 2012). All-male contexts also led individuals to engage in more aggressive interactions, and correspondingly, their testosterone levels differed from males in other social conditions (Lacava et al. 2011). Testosterone levels in these males rose earlier and faster in the beginning of the breeding season, and remained higher for a longer period than for males in two other treatments (Lacava et al. 2011). Male–female social interactions during parental activity are also reflected in male plumage condition, as we observed when studying the nestling feeding period. We found support for the hypothesis that there is a tradeoff between parental and mating efforts, because there is a reduction in male provisioning rate when their reflectance in the UV chroma is higher (Diniz et al. 2015). This likely occurs because attractive males benefit more by investing in mating activities through EPC than by investing in current offspring. Nonetheless, female provisioning rate increases with male blue-black coverage, supporting the positive differential allocation hypothesis. Females paired with males with higher nuptial plumage coverage are more likely to obtain good genes for their offspring and, in such conditions, it is advantageous for females to increase their investment.

4.5 Conclusions and Future Directions

Across almost two decades of field and laboratory studies, we have attempted to answer questions associated with the operation of sexual selection using a Neotropical bird as our study model. Initial studies showed that although the species exhibited several lek-like characteristics, it defied the traditional lek model criteria. We used paternity testing to assess the possibility that sexual selection in this species could operate via Wagner's (1998) "hidden-lek" model. Indeed, we found that the species has one of the highest rates of EPF found to date for a passerine, suggesting that strong sexual selection pressures should be in operation within the scope of a socially monogamous system. Working within this paradigm, we developed further studies designed to understand the mechanisms of both inter- and intrasexual selection in the blue-black grassquit.

We examined male traits that could influence female choice, including morphological and ornamental plumage attributes, motor exhibitions, song parameters, and interactive and parental behaviors in general. Of all traits investigated, leap height during the courtship display turned out to be the most important characteristic influencing female choice, especially in the social pairing context. Additionally, we found that novel males may be attractive to females, irrespective of how their attributes compare to those of a more familiar mate. In general, our data support the idea that females may choose males for the quality of the direct benefits they may provide (e.g., paternal care) and, more weakly, for indirect (genetic) benefits, when they choose social mates based on leap height. In assessing the outcome of sexual selection in the production of ornamentation and courtship displays, our data point to the fact that nuptial coloration is a condition-dependent trait that may be influenced by the level of endoparasites in individuals. We also found that the timing of leaping and the display site are important: males bathed in direct sunlight increase their leaping frequency, presumably to take full advantage of the augmented conspicuousness of their iridescence under sunlight. Finally, our data also reveal that plumage ornamentation is influenced by the social context of males. Those confined to male-only laboratory conditions molt faster and earlier and produce more UV based plumage when compared to other males in other social contexts.

We continue to pursue explanations about how sexual selection may have shaped reproductive behaviors and the phenotype of the blue-black grassquit. Currently, we are exploring how predation pressure may affect both male display behaviors and female choice. In particular, we are interested in how predation risk, by affecting male and female behaviors, may influence the rates of extrapair paternity (e.g., Yuta and Koizumi 2016). This should be especially relevant given the extremely high predation rates found for blue-black grassquit nests in our study populations. At present, we are also testing some specific premises of the hidden-lek hypothesis to elucidate whether sexual selection may be driving the clustered spatial distribution of breeding pairs.

We believe that by applying a multifaceted approach to the study of the blue-black grassquit, as illustrated in the various studies described above, we have contributed to the empirical evidence that further clarifies mechanisms of sexual selection. We hope that this chapter shows that the study of other model systems, among the abundant and diverse Neotropical avifauna, is a realistic and feasible goal.

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Chapter 5
Brood Reduction in Neotropical Birds: Mechanisms, Patterns, and Insights from Studies in the Imperial Shag (*Phalacrocorax atriceps*)

Walter S. Svagelj

5.1 Introduction

5.1.1 Brood Reduction: Classifications and Mechanisms

One of the most stimulating topics in avian research has been the study of the evolution of clutch and brood size (Lack 1947, 1954; Charnov and Krebs 1974; Temme and Charnov 1987; Forbes 1990). Ornithologists have realized long time ago that several bird species lay more eggs than fledglings they can rear until independence (Lack 1954). In addition to extrinsic causes that can reduce the size of the family before independence (e.g., partial predation), the reduction of the brood size is usually an intrinsic consequence of the family dynamics itself (Mock and Forbes 1995; Mock and Parker 1997).

The term brood reduction was coined by Robert Ricklefs in their study in curved-billed thrashers (Ricklefs 1965). Brood reduction—in narrow sense—is defined as a within-brood partial mortality due to sibling rivalry (Mock 1994; Mock and Parker 1997) and asynchronous hatching is the main mechanism facilitating this process. In brood-reducer species, asynchronous hatching determines offspring roles in two statuses: advantaged core offspring (i.e., subset of eggs or chicks that parents can normally raise) and disadvantaged marginal offspring (i.e., eggs or chicks that hatch later in the hatching sequence and suffer higher mortality rates, Mock and Forbes 1995; Mock and Parker 1997).

Brood reduction systems are very diverse in terms of the frequency and mechanism causing the offspring elimination (Forbes and Mock 1994). According to the frequency of death events observed across the nests, brood reduction can be classified as facultative or obligate (Simmons 1988; Mock and Parker 1997). In facultative

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brood-reducer species, marginal offspring have a reasonable chance of surviving alongside core siblings, while in obligate ones the death of at least one sibling occurs in more than 90% of nests (Simmons 1988; Mock and Parker 1997). Also, brood reduction can be classified considering the mechanism causing the offspring death (Mock and Parker 1997; Zieliński 2002). In both facultative and obligate systems, offspring death can be caused by fatal starvation, resulting from either direct competition for food between siblings or by selective starvation of one of the competing chicks by its parents, by siblicide (i.e., chick mortality is caused by aggressive behavior of elder siblings), or by parental infanticide (i.e., chick mortality is caused by a parental behavior that makes a direct and significant contribution to the immediate death of own offspring) (Mock 1984; Mock and Parker 1997; Zieliński 2002). In the last 50 years, a large number of bird species from diverse taxa have been recognized as brood reducers, with most of the detailed studies focusing on siblicidal species (Edwards Jr and Collopy 1983; Simmons 1988; Anderson 1990; Mock and Parker 1997). Parental infanticide and obligate brood reduction by fatal starvation are among the rarest forms of brood reduction and were only reported in a few species (Mock and Parker 1997; Zieliński 2002).

5.1.2 Why Lay More Eggs than Offspring That Can Be Actually Raised?

For both facultative and obligate systems, under special circumstances, marginal chicks may enhance fitness of their parents (Mock and Forbes 1995; Mock and Parker 1997; Forbes and Mock 2000). David Lack (1947, 1954) was the first to propose an explanation for consistent differences between clutch sizes and brood sizes at fledging, suggesting that parents laying an enlarged clutch size would take advantage of years with unusually rich resources. The "Resource-tracking Hypothesis" (Lack 1947; Ricklefs 1965; Temme and Charnov 1987; Kozlowski and Stearns 1989) states that marginal offspring can survive (in addition to core offspring) in years where resources are unusually available; if resources are not sufficient, the marginal offspring are either neglected, eliminated or outcompeted by their larger siblings (Lack 1954; Ricklefs 1965). Thus, the presence of surplus offspring may allow parents to track variable resources that may change unpredictably, reducing brood size only when resources are not adequate.

Two main hypotheses have been proposed for the benefits of a replacement for failed or defective core offspring: the "Insurance Egg Hypothesis" (Dorward 1962) and the "Progeny Choice Hypothesis" (Kozlowski and Stearns 1989; Forbes and Mock 1998). The first hypothesis proposes that the production of excess young is an adaptation to uncertain offspring viability, providing insurance against early failures of the core offspring. Surplus offspring are thought to serve an insurance function in diverse animal taxa (Mock and Parker 1997), being extensively documented in birds (Dorward 1962; Anderson 1990; Forbes 1990; Wiebe 1996; Forbes et al. 1997), and experimentally confirmed in American White Pelicans (*Pelecanus erythrorhynchos*, Cash and Evans 1986) and Nazca Boobies (*Sula granti*, Clifford and Anderson

2001a). The second hypothesis states that competition between marginal and core chicks would reveal deficiencies in the core chicks (as congenital or developmental disorders), and predicts that sometimes core chicks can lose in the competition with the marginal chick.

Two hypotheses are framed within the developmental facilitation of the core offspring. The "Offspring Facilitation Hypothesis" (Mock and Forbes 1995) proposes that although surplus offspring may ultimately die, they may aid to core offspring to survive. For example, if parents adjust food supplies to brood size (Ploger 1997), the core offspring may take advantage of the enhanced level of parental stimulation through the begging calls made by the marginal offspring, eventually outcompeting it and appropriating those extra resources (Forbes 2007; Ostreiher and Heifetz 2016). Also within the developmental facilitation logic, the "Icebox Hypothesis" (Ingram 1959; Alexander 1974) proposes that marginal offspring may represent a fresh store of food to the rest of the family, dying and being consumed during food shortages. This hypothesis was mainly proposed for species exhibiting within-family cannibalism (Bortolotti et al. 1991; Stanback and Koenig 1992).

Finally, the "Adoption Hypothesis" (Holley 1981) proposes that occasionally other families could accidentally adopt some offspring. Consequently, parents producing marginal offspring have a higher probability of producing a low-cost offspring through adoption than do parents producing only core offspring. Although such adoptions appear as low-frequency mistakes made by parents, at least 150 bird species exhibit adoption of young from outside the family (Riedman 1982; Pierotti and Murphy 1987; Pierotti 1991). For ground-nesting species, both eggs and chicks may be feasible to be adopted. Adoption is the only viable option for marginal chicks expelled from the nest by core chicks, while eggs may be adopted if displaced downhill into or near another nest (Clifford and Anderson 2001a; Humphries et al. 2006). Likelihood of adoption by foster parents depends on a variety of factors as characteristics of breeding habitat (i.e., predators, soil, vegetation, slope, and nest density), offspring age, and also by inherent breeding behavior and life-history characteristics of particular species.

Clearly, these hypotheses are not mutually exclusive. For example, by generating an extra egg, parents can cover against infertility and fails in egg-hatching, and also enhance survival of core offspring through facilitation. As many authors suggested (Mock and Forbes 1995; Mock and Parker 1997; Forbes and Mock 2000; Humphries et al. 2006), a multi-hypothesis approach must be considered to identify and decompose the different types of benefits, where experimentally manipulated conditions are indicated to control for possible confounding factors.

5.1.3 Phenotypic Handicap in the Offspring

Altricial birds usually produce a within-brood variation in the offspring phenotype (i.e., body size or age) through the onset of incubation and the manipulation of egg characteristics. Such manipulations impair the competitive status of nestlings, conferring phenotypic handicaps upon some and advantages upon others (Forbes and

Mock 1994; Mock and Forbes 1995; Mock and Parker 1997; Glassey and Forbes 2002). These phenotypic handicaps differentially affect growth, survival, and ultimately, fitness of siblings (Glassey and Forbes 2002). Phenotypic handicap within broods is a consequence of at least four main factors: variation in the timing of hatching, differences in egg size, differences in egg composition, and brood sex composition.

Asynchronous hatching is a widely observed pattern among birds occurring as a result of the onset of incubation before clutch completion (Magrath 1990; Stoleson and Beissinger 1995). It leads to the establishment of a within-brood hierarchy in age, size, and competitive abilities that affect sibling dynamics (Mock and Parker 1997). A large number of adaptive and non-adaptive hypotheses have been proposed for this phenomena (extensively reviewed in Magrath (1990) and Stoleson and Beissinger (1995)). In the context of brood reduction, hatching asynchrony has been usually considered as the main mechanism favoring adaptive reduction as it facilitates the elimination of marginal offspring and the reduction of interactions with core offspring.

Egg size is highly correlated with hatchling mass for many bird species (Williams 1994; Christians 2002). Also, egg size could affect survival of the unfed hatchlings, as yolk is the main food store for the hatchling (Williams 1994). Even though differences in egg size do not appear to be translated into differences in fledgling quality or adult size, they may make a substantial difference early in the nestling period (Williams 1994; Christians 2002). It has been proposed that variation in egg size within clutches may be an adaptive response to mitigate or reinforce sibling competition through hatchling-size hierarchy (Howe 1976; Clark and Wilson 1981; Slagsvold et al. 1984). Howe (1976) suggested that an increase in egg size with laying sequence is an adaptation to counteract the effect of asynchronous hatching ("brood-survival strategy"; sensu Slagsvold et al. 1984), whereas a decline with laying sequence would accentuate the effect of hatching asynchrony, facilitating brood reduction ("brood-reduction strategy"; Slagsvold et al. 1984). An alternative hypothesis is that egg-size variation within clutches may be an adaptive response to modulate sibling competition through increasing or decreasing hatching asynchrony (Parsons 1972). If the incubation period is longer for larger eggs (Parsons 1972; Aparicio 1999), the last egg laid, usually the smallest, may reduce the hatching asynchrony and therefore offspring size hierarchy within the brood. In this case, the smaller size of chicks hatched from small eggs would be compensated by postnatal growth (Parsons 1972; Aparicio 1999).

Egg composition and particularly the hormonal levels in the eggs may affect both begging behavior and competitive abilities of siblings (Lipar and Ketterson 2000; Schwabl and Lipar 2002). For example, high levels of testosterone temporarily improve the competitive ability of hatchlings increasing both mobility and rate of begging (Schwabl 1996; Schwabl and Lipar 2002). In the last years many studies found that females deposit hormones in their eggs in varied patterns. Cattle Egrets (*Bubulcus ibis*) and Zebra Finches (*Taeniopygia guttata*) deposit more testosterone in first-laid eggs (Schwabl et al. 1997; Gil et al. 1999), while domestic Canaries (*Serinus canaria*), American Kestrels (*Falco sparverius*), and Red-Winged

Blackbirds (*Agelaius phoeniceus*) deposit more testosterone into later-laid eggs (Schwabl 1993, 1996; Lipar et al. 1999; Sockman and Schwabl 2000).

In birds with sexual size dimorphism, the largest sex is usually both the most expensive to rear and the one that exhibits the highest growth rate (Anderson et al. 1993; Krijgsveld et al. 1998). Consequently, brood sex composition (i.e., brood sex ratio and sex according to laying order) may affect growth and survival of competing siblings, and hence, parental fitness (Mock and Parker 1997). The effect of brood sex composition on the dynamic of nestling size hierarchy would depend on the degree of sexual size dimorphism of the particular species. Furthermore, sex-specific interactions could also explain patterns of within-brood sex ratio (e.g., in relation to laying order; Uller 2006). Also, interactions between offspring could lead to selection on maternal traits, such as when to initiate incubation or to terminate parental care (Mock and Parker 1997). Because maternal return on reproductive investments depends on the reproductive value of her offspring, this will in turn lead to selection on maternal sex ratio.

The dynamics and consequences of sibling interactions will depend on within-brood variation in offspring traits (Mock and Parker 1997; Ricklefs 2002). Hatching asynchrony is by far the primary source of handicap, while differences in egg size, egg composition, and brood sex ratio usually play secondary roles unless offspring hatch synchronously (Williams 1994; Glassey and Forbes 2002; Ricklefs 2002; but see Lamey 1990).

5.1.4 Brood Reduction in Neotropical Birds

Most studies in brood reduction were conducted in Nearctic and Palearctic regions (Mock and Parker 1997). Even so, some of the most comprehensive characterizations of brood reduction systems correspond to the Neotropical region. Here, I present a brief overview of some of them to illustrate the diversity of systems.

The Blue-Footed Booby (*Sula nebouxii*) is a seabird that lays 1–3 eggs and raises 1–3 chicks (Drummond et al. 1986). In the colony of Isla Isabel, off the Pacific Coast of Mexico, this species adjusts brood size to food availability by facultative siblicidal brood reduction (Drummond et al. 1986). The modal clutch size is two eggs that hatch 4 days apart due to a 5-day laying interval and immediate incubation of the first egg (Drummond et al. 1986; Osorno and Drummond 1995). Senior chicks grow faster than their sibs in years of good or poor growth, maintaining the initial size disparity for at least 65 days (Drummond et al. 1986). Junior nestlings have higher mortality than seniors because dominant chicks respond to parental underfeeding by killing their siblings (Drummond and García Chavelas 1989). Drummond et al. (1986) found a differential mortality of junior chicks not associated with their own growth, but with a 20–25% weight deficiency of the senior sib, implying siblicidal brood reduction triggered at a weight threshold. From roughly 5 days of age through at least 10 weeks of age juniors are pecked, bitten, and threatened by their elder siblings (Drummond et al. 1991), with aggression peaking when the aggressive dominance is finally established at 16–21 days of age. After 3 weeks of aggressive subordination, juniors become trained subordinates that submit promptly to roughly 90% of aggressions (Drummond and Osorno 1992; Valderrábano Ibarra et al. 2007). Compared with their siblings, subordinates received 17% less fish during the first 7 days of life and 13% less fish between 12 and 35 days of age (Anderson and Ricklefs 1995; Guerra and Drummond 1995), making juniors 11% lighter than seniors at age 20 days (Drummond et al. 1986). In the second half of the nestling period, juniors largely catch up in mass and size (Drummond et al. 1991, 2003) and at 70 days of age they are only 3% lighter than seniors (Drummond and Rodríguez 2013). Due to food deprivation, corticosterone levels are two-times higher in subordinate chicks than in dominant chicks (Nuñez de la Mora et al. 1996). An analysis of 20 cohorts using multi-state mark recapture models showed that after fledging, juniors and seniors have similar probabilities of survival and recruitment at all ages up to 20 years of age (Drummond et al. 2011). However, Drummond and Rodríguez (2013) found that the cost of growing up as a subordinate sibling is passed to the next generation, because the offspring produced by (formerly) junior chicks are less likely to recruit into the breeding population than offspring of seniors.

The Nazca Booby (*Sula granti*) is a seabird exhibiting obligate brood reduction by siblicide. At the colony of Punta Cevallos of Galápagos Islands, Ecuador, this species lays one or two egg per clutches but usually raise single chick broods (Dorward 1962; Anderson 1989). Eggs hatch asynchronously 5–6 days apart and the second chick is typically ejected from the nest scrape by the elder sibling few days after hatching (Anderson 1989). Overall hatching success in two-egg clutches is relatively low (48%), and second eggs contribute a surviving hatchling after the failure of first eggs in 19% of two-egg clutches (Anderson 1990). The insurance value of marginal eggs was demonstrated by Clifford and Anderson (2001a) in an experimental study manipulating clutch size. In line with the predictions of the insurance hypothesis (Dorward 1962), natural one-egg clutches that were enlarged to two eggs produced more hatchlings and fledglings than control one-egg clutches did, and natural two-egg clutches that were reduced to one egg produced fewer hatchlings and fledglings than control two-egg clutches did (Clifford and Anderson 2001a). Despite the insurance value of marginal eggs, almost half of Nazca Booby females lay only one egg. To elucidate that, Clifford and Anderson (2001b) tested if one-egg clutches are result of food limitation in this species. Females were provided with supplemental food, and a higher proportion of supplemented females produced two-egg clutches than did control females (Clifford and Anderson 2001b). Also, Humphries et al. (2006) used 12 years of breeding and band re-sighting data to evaluate the several potential benefits of the marginal offspring in a multi-hypothesis approach. This study revealed that marginal and core offspring are functionally equivalent in the absence of sibling interactions, and that core offspring incur no detectable costs from siblicide (Humphries et al. 2006). The authors found no evidence for the resource-tracking hypothesis (99.95% of two-chick broods were reduced to one chick before fledging), no evidence that marginal offspring provide a food resource for other family members, and very limited evidence of progeny choice and adoption benefits.

The Green-Rumped Parrotlet (*Forpus passerinus*) is a small parrot that lays a large clutch that hatches very asynchronously. In the llanos of Venezuela, this species lays clutches of 5–10 eggs over a period of 7–16 days (Beissinger and Waltman 1991). Incubation starts with the first egg and clutches hatch over a period of 2–14 days, averaging 4.7 (range 1–8) fledglings per successful nest (Beissinger and Waltman 1991). Fledging success is uniformly high for all chicks in small broods, decreases slightly for the last two chicks in medium-sized broods, and decreases sharply for the last two chicks in large broods. The last two nestlings in the medium- and large-sized broods frequently die by starvation (Beissinger and Waltman 1991). If survives, however, these nestlings show both extra reproductive value (fledging alongside core siblings) and insurance value (replacing core eggs that failed to hatch; Beissinger and Waltman 1991).

The three examples showed above illustrate the diversity of brood reduction systems in Neotropical birds. In addition to these amply characterized systems, several studies have been conducted in the Neotropics where brood reduction was evaluated directly or analyzed indirectly through hatching asynchrony or other breeding traits (*cormorants*: Snow 1966; Harris 1979; Kalmbach and Becker 2005; *grebes*: Nuechterlein and Johnson 1981; Fjeldså 1986; Roesler 2016; *gulls*: Urrutia and Drummond 1990; *passerines*: Duré Ruiz et al. 2008; *parrots*: Berkunsky et al. 2017; *penguins*: Barrionuevo and Frere 2017). Considering the richness in taxonomic groups and the diversity in life-history strategies of Neotropical bird species, much remains to be done in the study of brood reduction.

Below, I review some aspects of the brood reduction in Imperial Shags (*Phalacrocorax atriceps*), illustrating the mechanisms, consequences, and benefits of this breeding strategy.

5.2 Model Species and Study Site

The Imperial Shag (Fig. 5.1) is a medium-sized seabird that preys on fish and invertebrates by foot-propelled diving (Nelson 2005). This colonial seabird inhabits southern South America on both the Atlantic and Pacific coasts (Nelson 2005). Imperial Shags are sexually dimorphic in size with males being larger and heavier than females (males: 2317 g, females: 1966 g; Svagelj and Quintana 2007). Dimorphism in size mostly arise from 15 days of age onward (Svagelj and Quintana 2017). Using four DNA microsatellites originally developed for Great Cormorants (*P. carbo*) and successfully cross-amplified in Imperial Shags, Calderón et al. (2012) assessed the parentage of 110 chicks from 37 broods sampled during two breeding seasons. No evidence of extra-pair paternity or intraspecific brood parasitism was detected (Calderón et al. 2012). Data on Imperial Shags banded as chicks and re-sighted as breeders showed that adults start to breed at an age of 2 years (Svagelj and Quintana 2011a).

At the north of Patagonia, the breeding season typically lasts from September to December (Svagelj and Quintana 2011a). Both parents play an active role in nest

Fig. 5.1 Imperial Shag, *Phalacrocorax atriceps*, brooding two nestlings. Photo: Carolina Pantano

defense, incubation, brood care, and chick feeding duties throughout the breeding cycle (Quintana et al. 2011; Svagelj and Quintana 2011a, b; Svagelj et al. 2012). This bird usually lays three-egg clutches with an incubation time of ~29 days, while chick-rearing period lasts for more than 2 months (Svagelj and Quintana 2011a, b, 2017). Imperial Shags raise a single brood per year and exhibit a very limited renesting potential with <1% of pairs attempting to breed twice in a season, always as a consequence of early breeding failures (Svagelj and Quintana 2011a). The number of days elapsed between the completion of the first and last clutches in a breeding season is usually 6 weeks (Svagelj and Quintana 2011a).

All results discussed here are derived from data analyzed in several studies conducted at the Punta León colony (43°05’S, 64°30’W), Chubut, Argentina, during multiple breeding seasons since 2004. The Punta León colony is located in a flat and elliptical area ~130 m long by 15 m wide, without vegetation inside (Yorio et al. 1994). The colony size when studies started comprised ~3200–3400 breeding pairs, with nests distributed at a homogeneous density of ~2 nests m^2 (Svagelj and Quintana 2011a).

5.3 Main Objectives, Nest Monitoring Protocol, and Particular Methods

In the next section, I discuss information about: (1) basic breeding parameters and frequency of brood reduction, (2) hatching asynchrony and chick survival, (3) relationship between intra-clutch egg-size variation and brood reduction, (4) parental food allocation during the first week after hatching, and (5) the effect of sibling asymmetries on brood reduction.

As a general nest monitoring protocol, nests were checked throughout the breeding cycle. Nests were checked every 1–3 days from egg laying to clutch completion. Eggs were labelled with the nest number and laying order using a permanent marker and measured (length and width) using digital calipers. Egg mass was calculated from egg-length and width measurements (Svagelj and Quintana 2011b). During the hatching period, nests were checked every 1–3 days to establish the hatching success of individual eggs according to laying order. Hatchlings were marked on the tarsus using tape bands labelled with the associated hatching order. Those chicks that survived until day 20 of age were ringed using numbered metal rings. During the chick-rearing period, nests were visited every 3–5 days to measure and determine the fate of chicks until it proved impossible to capture them further (approx. 40 days old), see Svagelj and Quintana (2007, 2011a, b, 2017) and Giudici et al. (2017) for more details of the methodology. The intra-clutch egg-size variation was evaluated as the deviation in egg size (DES) between the third and the other eggs in the clutch, and was calculated as DES = C – (A + B)/2, where A, B, and C are the masses of A-, B-, and C-eggs, respectively (Svagelj and Quintana 2011b). Because most of brood reduction events typically occurs within the first week after hatching of the marginal chick (Svagelj 2009), parental food allocation was evaluated when marginal chicks were up to 7 days old (Giudici et al. 2017). To quantify the amount of food received by each chick during a feeding event, nestlings were weighed before and after the event (Giudici et al. 2017). To evaluate the effect of sibling-size asymmetries on brood reduction, breeding success, and chick growth, Giudici et al. (2017) manipulated this variable by swapping hatchlings and chicks between nests. The authors generated two types of symmetrical broods containing three similar-sized chicks resembling ages at the beginning of chick-rearing (three chicks of ~3 days old) and close to the day when most brood reduction events occur (three chicks of ~8 days old) that contrast with the natural asymmetrical brood (see below; Giudici et al. 2017).

5.4 Brood Reduction in the Imperial Shag

5.4.1 *Clutch Size, Egg Size, and Breeding Success*

Mean clutch size is 2.8 eggs per nest with a range of 1–4 eggs (Svagelj and Quintana 2011a). The modal clutch size is three eggs (75% of clutches), and clutches of two and three eggs represent 95% of clutches (Svagelj and Quintana 2011a). In three-egg clutches, egg size decreases with laying order (55.2 g, 54.8 g, and 52.6 g for first (A), second (B), and third (C) eggs, respectively; Svagelj and Quintana 2011b). Average breeding success is 1.24 fledglings per nest, ranging from 0 to 3 fledglings (Svagelj and Quintana 2011a). Modal brood size at independence is 2 fledglings (43% of breeding attempts), while three-fledgling broods represent less than 1% of clutches (3/471, Svagelj 2009; Svagelj and Quintana 2011a).

5.4.2 Hatching Asynchrony and Chick Survival According to Hatching Order

Three-egg clutches hatch asynchronously over 4–5 days (Svagelj 2009; Svagelj and Quintana 2011a, b). On average, B- and C-eggs hatch 1.7 days and 4.3 days after the A-egg, respectively (Svagelj 2009). The asynchronous hatching pattern creates an important asymmetry of age and size between core and marginal chicks (Fig. 5.2, Svagelj 2009). When C-chick hatches, A- and B-chicks are already 148% and 60% heavier, respectively (Fig. 5.2). Those asymmetries progressively increase as chicks grow, with A- and B-chicks being 249% and 152% heavier than C-chicks by day 5 (Fig. 5.2). As a consequence of that asymmetry, probability of fledging drastically decreases with hatching order in three-hatchling broods (85.3%, 60.1%, and 6.7% for A-, B-, and C-chicks; Svagelj 2009; Svagelj and Quintana 2011b). Marginal chicks die from starvation with a median time of 6 days (Svagelj and Quintana 2011b). Overall, 69.2%, 52.4%, and 15.5% of A-, B-, and C-eggs from three-egg clutches become fledglings (Svagelj 2009). Remarkably, 14.6% of C-eggs fledged from broods where at least one core member failed (Svagelj 2009). Summarizing, Imperial Shags exhibit obligate brood reduction with last-hatched chicks from three-hatchling broods usually starving to death within the first week of life. Also, the marginal offspring have mainly an insurance value, while the extra reproductive value (resource-tracking hypothesis) appears to be negligible as the marginal chick rarely fledges alongside core siblings.

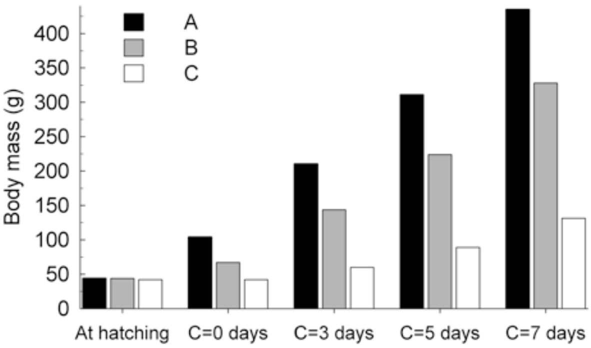

Fig. 5.2 Body mass of first-(A), second-(B), and third-(C) hatched chicks of the Imperial Shag at different ages of the marginal chick for three-hatchling broods (modified from Svagelj 2009)

Imperial Shags belong to the "blue-eyed shag" complex, a group of closely related species inhabiting the Southern Hemisphere (Nelson 2005). Like the Imperial Shag, other blue-eyed shag species also exhibit considerable asynchronous hatching (4–5 days on average), a decrease in survival probabilities according hatching order, and strong brood reduction (South Georgia Shag, *P. georgianus*: Shaw 1985; Crozet Shag, *P. melanogenis*: Derenne et al. 1976; Williams and Burger 1979).

5.4.3 Effect of Intra-Clutch Egg-Size Variation on Brood Reduction

Average deviation in egg size between C-egg and the other eggs in the clutch is –2.3 g ranging from –8.6 g to 3.3 g. Deviation in egg size is not related to survival time of the C-chick (Svagelj and Quintana 2011b). Considering the large effect that hatching asynchrony has on the hierarchy in size among nestlings (see Fig. 5.2), the net effect of intra-clutch variation in egg size is negligible. Thus, this data does not support an adaptive value for intra-clutch variation in egg size (Parsons 1972; Howe 1976) in the Imperial Shag.

5.4.4 Parental Food Allocation and Brood Reduction

The amount of food received by chicks during a feeding event—in the first week after hatching—progressively decreases with hatching order (25 g, 13 g, and 5 g for A-, B-, and C-chicks, respectively; Giudici et al. 2017). Also, the probability of being fed of C-chicks is lower than those for A- and B-chicks (0.80, 0.57, and 0.20 for A-, B-, and C-chicks, respectively; Giudici et al. 2017). During the first week after hatching, begging behavior is mostly circumscribed to nestlings lifting their heads but without displacements within the nest (Giudici et al. 2017). At that early age, parents down their head toward a particular chick and regurgitate food. Thus, the death of marginal chicks is caused by selective starvation by their parents, which mostly ignore the begging behavior of marginal chicks.

5.4.5 The Effect of Sibling Asymmetries on Brood Reduction

As expected, survival time of marginal chicks is higher in broods where sibling asymmetry is lower (brood with natural asymmetry: 6 days, symmetric brood with 3-day-old chicks: 10 days, and symmetric brood with 8-day-old chicks: 14.5 days; Giudici et al. 2017). Despite this, overall breeding success is unrelated to sibling asymmetry levels (Giudici et al. 2017). Interestingly, obligate brood reduction occurs irrespective of the level of sibling asymmetry, with only two of 124 broods fledging three chicks (Giudici et al. 2017). Thus, hatching asynchrony or within-brood asymmetries at the beginning of the chick-rearing period are not needed for obligate brood reduction to occur in Imperial Shags. Also, asymptotic mass of fledglings from 8-day-old broods is lower than those for natural and 3-day-old broods, suggesting that hatching asynchrony favors early brood reduction and improves fledging condition (Giudici et al. 2017). These results are in line with several experimental studies demonstrating that fledglings from asynchronous broods are heavier than those from synchronous ones (Amundsen and Slagsvold 1991a, b).

5.5 General Conclusions and Avenues for Future Research

In this chapter, I summarized some of the main findings about brood reduction in the Imperial Shag. At the Punta León colony, Imperials Shags are obligate brood reducers with marginal chicks usually starving to death within the first week of life. Marginal chicks have mainly an insurance value replacing core offspring that fails. Hatching asynchrony generates an asymmetry in age and size among nestlings that facilitates the elimination of the marginal chick. However, obligate brood reduction occurs even in symmetrical broods. Beyond this basic characterization, future studies analyzing sex-specific survival and variation in hormonal levels are needed to acquire a deeper comprehension of the brood reduction in this species. In addition, it must be noted that this great picture of the Imperial Shag brood reduction corresponds to a single colony. Considering the widespread distribution of the species, more studies at different places, with different ecological conditions and selective pressures, are needed to evaluate the generality of this pattern.

Here, I presented a brief review of the hypotheses accounting for the adaptive value of marginal offspring, also discussing different factors modulating brood reduction. Some brood reduction systems in the Neotropical region are incredibly rich and extensively documented. However, most studies correspond to seabirds or species with small clutch sizes. Considering the diversity of taxa and life-history strategies in Neotropical birds, the currently studied species only provide a narrow representation of brood reduction systems in the region. Thus, more studies in new families and species are needed to acquire a comprehensive picture of brood reduction in the Neotropics.

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Chapter 6
Obligate Brood Parasitism on Neotropical Birds

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6.1 Introduction

Obligate brood parasites do not build their nests nor do feed and take care of their nestlings. Instead, they lay their eggs in nests of individuals of other species (hosts) that rear the parasitic progeny. For behavioral ecologists interested in coevolution, obligate brood parasites are pearls of the avian world. These species represent only 1% of all the living avian species, and their peculiar reproductive strategy imposes on them permanent challenges for successful reproduction. At the same time, the hosts are under strong selective pressures to reduce the costs associated with parasitism, such as the destruction of eggs by parasitic females and the potential fitness costs of rearing foreign nestlings. These selective pressures may result in parasites and hosts entering in a coevolutionary arms race, in which a broad range of defenses and counterdefenses can evolve. Females of most species of parasites have evolved behaviors such as rapid egg laying and damage of some of the host's eggs when they visit the nest (Sealy et al. 1995; Soler and Martínez 2000; Fiorini et al. 2014). Reciprocally, as a first line of defense, hosts have evolved the ability to recognize and attack adult parasites (Feeney et al. 2012). Parasitic eggs typically hatch earlier than host eggs decreasing host hatching success and nestling survival (Reboreda et al. 2013), but several host species have evolved recognition and rejection of alien eggs, which in turn selected for the evolution of mimetic eggs in the parasite (Brooke and Davies 1988; Gibbs et al. 2000). Parasitic young are often morphologically and behaviorally adapted to manipulate host's parental effort, but sometimes host parents are able to discriminate against them (Liang et al. 2017). In addition to tricking hosts into raising them by mimicking gape markings (Payne et al. 2001), plumage

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color (Langmore et al. 2011), and begging calls (De Mársico et al. 2012), brood parasites also face the challenge of recognizing their conspecifics to interact and reproduce in the future. Yet, how parasitic juveniles identify and join their own kind is poorly understood.

Over the past 50 years, avian brood parasitism has been the focus of a plethora of studies that have substantially contributed to our understanding of the evolution of adaptations between parasites and their hosts, encompassing all the stages of the parasites' lifecycle (for a recent and comprehensive review, see Soler 2017). There are about 100 obligate brood-parasitic species worldwide distributed in seven phylogenetically independent groups (Sorenson and Payne 2002). In the Neotropics, eight species have been described in three of these groups: four cowbirds (*Molothrus*, Icteridae), three New World cuckoos (*Dromococcyx* and *Tapera*, Cuculidae, subfamily Neomorphinae), and the black-headed duck (*Heteronetta atricapilla*, Anatidae), which is the only precocial obligate brood parasite (Table 6.1). In this chapter, we present a compendium of the characteristics and behaviors of these species that aid our understanding of how natural selection shapes the interactions between parasites and their hosts.

Neotropical parasites reflect a wide range of strategies, from specialization to extreme generalization in host use, from nestmate tolerant to nestmate killing, and the unique nidifugous brood parasite. Unfortunately, most of these species have been incompletely studied and the extension devoted to each one in this chapter reflects this unbalance in the available information.

6.2 Family Icteridae

*6.2.1 Shiny Cowbird (*Molothrus bonariensis*)*

6.2.1.1 Species Characteristics

Shiny cowbirds are widespread throughout much of South America and the Caribbean. They occur from southern Argentina (Chubut province) to eastern Panama, with the exception of most areas above 2000 m and extensively forested regions such as the Amazon rainforest. They are also found in Chile, from Aysén to Atacama. During the early 1900s, they expanded their range to include the West Indies, and were first recorded in Peninsular Florida in 1987, where they are considered permanent residents since 1991 (Cruz et al. 1998; Lowther 2011).

This species occurs in open or semi-open habitats and are attracted to deforested areas like fields and pastures with scattered patches of trees and shrubs, or tree groves near farms, gardens and plantations (Cavalcanti and Pimentel 1988; Mason 1985). They also may be found in undisturbed habitats such as mangroves (Post and Wiley 1977). Their diet includes a wide variety of arthropods and seeds. Adults feed on the ground, usually in association with cattle and other large grazing mammals, and pick insects from the backs of grazers (Ortega 1998). Shiny cowbirds may show seasonal variation in diet, depending on the most readily available items. For example, they can consume mainly arthropods during the breeding season and then feed on grains and feed-mixtures in feedlots during the winter (Cruz et al. 1990; Lowther 2011).

Shiny cowbirds are sexually dimorphic in plumage coloration and body size. Males are entirely glossy black with blue and purple iridescence (Ortega 1998). Females are dull brown throughout most of the species' distribution, but in some areas they are dark brown or black (Friedmann 1929; Mahler et al. 2010). Males are larger than females, but body size varies geographically across subspecies (Table 6.1).

Table 6.1 Characteristics of the Neotropical obligate brood parasites

Parasite family	Species	Adult body mass	Incubation period	Number of hosts	Range of host body mass	Nestling/ chick behavior
Icteridae	*Molothrus bonariensis*	Smallest subspecies: *M.b. minimus*[a] Female: 34.1–36.4 g Male: 37.9–40.0 g Largest subspecies: *M.b. cabanissi*[a] Female: 45.2–55.6 g Male: 49.0–63.7 g Argentinean subspecies: *M.b. bonaerensis*[b] Female: 46.8 g Male: 51.6 g	12–13 days[c]	268 victims 97 effective hosts[d]	10–80 g[e]	Nestmate tolerant[f]
	Molothrus rufoaxillaris	Female: 43.6–55 g[g,h] Male: 50.8–65 g[g,h]	12 days[i,j]	5[d]	40–90 g[k,l,m]	Nestmate tolerant[n]
	Molothrus oryzivorus	Female: 74–129 g[o], 156 g[n] Male: 120 g[o], 212 g[n]	10–13 days[a]	11[d]	40–232 g[m]	Nestmate tolerant[n]
	Molothrus aeneus	Female: 57 g[o], 59 g[n] Male: 69 g[n,o]	11–13 days[a]	102[d]	20–222 g[m]	Nestmate tolerant[n]

(continued)

Table 6.1 (continued)

Parasite family	Species	Adult body mass	Incubation period	Number of hosts	Range of host body mass	Nestling/chick behavior
Cuculidae	*Tapera naevia*	Females and males: 52 g[p]	15 days[q]	22[d]	7–37 g[m]	Nestmate killing[q]
	Dromococcyx pavoninus	Females and males: 48 g[p]	No information	7[d]	No information	Nestmate killing[o]
	Dromococcyx phasianellus	Females and males: 80 g[p]	No information	No information	No information	Nestmate killing[o]
Anatidae	*Heteronetta atricapilla*	Female:565 g[n] Males: 513 g[n]	21–22 days[r]	23[s]	394–1080 g[m]	Nidifugous[p]

[a] Lowther (2011)
[b] Reboreda et al. (1996)
[c] Fiorini et al. (2005)
[d] Lowther (2018)
[e] De Mársico et al. (2010a, b)
[f] Gloag et al. (2012)
[g] Mason (1987)
[h] Cabezas et al. (2011)
[i] Fraga (1998)
[j] De Mársico et al. (2010b)
[k] Fraga (1992)
[l] Mermoz and Reboreda (2003)
[m] Dunning (1993)
[n] Ortega (1998)
[o] Payne (2005)
[p] Davies (2000)
[q] Morton and Farabaugh (1979)
[r] Lyon and Eadie (2004)
[s] Cabrera et al. (2017)

The shiny cowbird is the most generalist parasite of the *Molothrus* clade, parasitizing more than 260 species of 26 families (Lowther 2018). Less than half of these species have reared parasitic nestlings (Table 6.1). Hosts vary broadly in body mass, from the tiny house wren (*Troglodytes aedon*) to the large brown-and-yellow marshbird (*Pseudoleistes virescens*) (Table 6.1). At individual level, host use by shiny cowbird is not random. In eastern Argentina, some genetic differences exist between females that parasitize the house wren, which is a cavity-nester, and those parasitizing three other common hosts that build open nests (Mahler et al. 2007). This result suggests that host preference of shiny cowbird females might be mainly guided by host's nest type (Mahler et al. 2007), although some individual females in the population parasitize both cavity- and open-nesting hosts (Gloag et al. 2014; de la Colina et al. 2016).

6.2.1.2 Behaviors and Adaptations of the Shiny Cowbird and Host Antiparasitic Defenses

Adults

During the breeding season, female shiny cowbirds use relatively constant areas, in which they search for nests to parasitize (Gloag et al. 2013; Scardamaglia and Reboreda 2014). They are also faithful to one communal roost throughout the breeding season, which is located near their diurnal home-range (Scardamaglia et al. 2018). Daily and cumulative morning ranges of females are about half the size of those of males (22 *vs.* 45 ha and 70 *vs.* 185 ha, respectively), which is consistent with males mating with multiple females and a socially polygynous or promiscuous mating system (Scardamaglia and Reboreda 2014). Nevertheless, information on the genetic mating system is needed to confirm this observation.

Most parasitism occurs before sunrise (90% of parasitic events) but there are parasitic events until 30 min after sunrise (Gloag et al. 2013). Females make at least one prelaying visit to a nest that they parasitize (range 1–8 visits), which is normally located within the area that they used on previous days (Scardamaglia and Reboreda 2014; Scardamaglia et al. 2017). On the laying day, females fly directly from the roost to the target nest, which indicates that they have already acquired information about where to lay through previous prospecting visits (Scardamaglia and Reboreda 2014; Scardamaglia et al. 2017, 2018). Video recording of shiny cowbird females visiting nests of a primary host, the chalk-browed mockingbird (*Mimus saturninus*), revealed that laying visits last less than 30 s on average. During this time, the female first punctures the eggs before laying quickly while being mobbed by the hosts (Gloag et al. 2013; Fiorini et al. 2014). Mobbing does not reduce the probability of parasitism, but it decreases the chance of host eggs being punctured (Gloag et al. 2013). Experiments performed in several host species consisting in the presentation to breeding pairs of taxidermic models of female shiny cowbirds and a control species show that they are able to recognize the parasite as a threat (for a review see Reboreda et al. 2013).

In chalked-browed mockingbird and house wren nests, female shiny cowbirds lay their eggs either standing in the nest, with the legs partially or fully extended, or perched on the rim of the nest. These positions result in cowbird eggs being dropped from about 4–7 cm to the nest floor or onto the other eggs (Ellison et al. in press). This laying behavior may benefit the female cowbird, as a thickly shelled egg laid from a certain height can damage existing eggs in the nest and therefore reduce the competition at the nestling stage (López et al. 2018; Ellison et al. in press).

Female shiny cowbirds do not defend exclusive territories. Individual females overlap in their ranges (Scardamaglia and Reboreda 2014) and two or more females laying eggs in the same nest are common (Mason 1986a; Mermoz and Reboreda 1999; Gloag et al. 2012). Moreover, in chalk-browed mockingbird nests, almost 40% of the parasitic events recorded were cases of same-day multiple parasitism (Gloag et al. 2014). Evidence of other parasite–host systems shows that brown-headed and bronzed cowbirds also present same-day multiple parasitism

(Ellison et al. 2006). For shiny cowbirds, around one-third of these events involved a second female closely tailing a preceding female to the nest (Gloag et al. 2013). This "tailing" behavior might have arisen as a strategy used for the second female to evade mockingbird attacks when approaching the nest. Another possibility is that tailing females, lacking information on suitable nests to parasitize, follow a conspecific from the communal roost (Gloag et al. 2013).

Once a female shiny cowbird parasitizes a nest, she does not visit it again (Gloag et al. 2014; Scardamaglia and Reboreda 2014; but see de la Colina et al. 2016). This pattern is consistent with a “bookkeeping” mechanism (Clayton et al. 1997), that is, the cowbird female has a mental inventory of suitable nests to parasitize and this inventory is updated periodically by eliminating the nests she already has parasitized. In this way, the parasite benefits by remembering the location and status of each nest and her own act of laying in them, avoiding the costs of repeated parasitism, such as sibling competition and damaging her own previously laid eggs (Gloag et al. 2014). Nevertheless, as in brown-headed cowbird, whereby females sometimes return to parasitize the same nest (McLaren et al. 2003), de la Colina et al. (2016) found that in an area of low density of nests of its main host, female shiny cowbirds did not avoid laying in the same nest they had parasitized (i.e., repeated parasitism).

Shiny cowbirds spend morning hours on breeding grounds watching host behavior and use the host’s nest building activity as a cue for finding nests (Wiley 1988). Female cowbirds may also locate host nests by using conspicuously noisy searching (i.e., flushing the host from its nest) (Wiley 1988) or by searching systematically through the habitat (Kattan 1997; Svagelj et al. 2003; Fiorini and Reboreda 2006). Hosts could reduce the risk of nests being detected by choosing more concealed nesting sites. Nevertheless, increased nest concealment seems not to decrease the probability of shiny cowbird parasitism (Svagelj et al. 2003; Fiorini et al. 2009a, 2012). The host laying sequence itself is not a cue for eliciting parasitism and shiny cowbirds need to observe host activity at the nest before parasitizing it (Fiorini and Reboreda 2006).

Shiny cowbirds synchronize parasitism with laying of the host. Nevertheless, the degree of the synchronization varies across host species. In medium- and large-sized and open-nester hosts, the percentage of synchronized parasitic events is high (70–80%; Massoni and Reboreda 1998; Mermoz and Reboreda 1999; Fiorini and Reboreda 2006; Astié and Reboreda 2009), whereas in nests of the small-sized and close-nester house wren, synchronization decreases (47–57% of parasitism events during host’s laying period; Kattan 1998; Fiorini et al. 2009b; Tuero et al. 2007). In hosts whose eggs have longer incubation period than cowbird eggs, laying synchronization secures that they will hatch first, thereby giving a head start to the parasitic nestlings (Mermoz and Reboreda 1999; Fiorini et al. 2005). This advantage is critical in nests of larger hosts, where parasitic nestlings are more likely to be outcompeted for food, than in nests of small-sized hosts (Mermoz and Reboreda 2003; Fiorini et al. 2009b; Gloag et al. 2012).

Shiny cowbird females peck eggs during nest visits to puncture them and render them unviable. In chalk-browed mockingbird nests, such egg-pecking behavior begins immediately upon arrival and continues, on average, for about 12 s, though the duration depends on whether cowbirds are mobbed (mean: 2.6 s) or not (15.9 s) (Fiorini et al. 2014). Egg puncturing reduces host's clutch size and, in cases where the host is larger than the parasite, it increases the survivorship of the parasitic nestlings (Mermoz and Reboreda 2003; Sackmann and Reboreda 2003; Astié and Reboreda 2009; Fiorini et al. 2009b; Gloag et al. 2012). Indeed, there is some evidence that shiny cowbird females strategically modulate their puncturing behavior according to the clutch size and eggshell thickness (Cossa et al. 2017). For example, they peck more at larger mockingbird clutches (Tuero et al. 2012; Fiorini et al. 2014), in which parasitic nestlings are more likely to be outcompeted for food (Fiorini et al. 2009b). In addition, under both natural and laboratory conditions, females peck more frequently at clutches containing thicker-shelled cowbird eggs than at those containing less resistant host eggs (Fiorini et al. 2014; Cossa et al. 2017). In brown-headed and bronzed cowbirds, the puncture behavior is used by females that found host nests late in the nesting cycle, to induce host to renest and create new opportunities for parasitism (i.e., nest farming) (Arcese et al. 1996; Peer and Sealy 1999a; Swan et al. 2015). On the contrary, females of shiny and screaming cowbird puncture eggs in association with parasitism (De Mársico and Reboreda 2014; Fiorini et al. 2014) and do not puncture all the eggs at complete clutches (Cossa et al. 2017), supporting the hypothesis of reduction of competition with host nestlings. Therefore, the puncture behavior seems to have different functions depending on the parasitic species and probably on the ecological context (Peer 2006).

Eggs

The eggs of the shiny cowbird are adapted to their brood-parasitic lifestyle. Eggshells are thicker than expected for the egg volume and thicker than the eggshells of their hosts (Spaw and Rohwer 1987; Mermoz and Ornelas 2004; López 2013; López et al. 2018). Increased eggshell thickness provides greater resistance against puncturing by other parasitic females (Hudson 1874; Mermoz and Ornelas 2004; Gloag et al. 2012; Fiorini et al. 2014) and decreases the probability of cowbird eggs being damaged when laid from an elevated position, meanwhile inflicting damage to host eggs (López et al. 2018). Moreover, the thicker eggshell protects cowbird eggs from being damaged by eggs that are laid in the nest by subsequent female cowbirds (López et al. 2018). It has been hypothesized that this increased resistance is an adaptation of cowbird eggs to minimize the ejection of hosts that need to puncture the egg before rejecting it (puncture-ejecters) (Spaw and Rohwer 1987). Nevertheless, ejection of parasitic eggs is rare among shiny cowbird hosts (9 species; Mason 1986b, Reboreda et al. 2013); and only two host species are known to puncture-eject foreign eggs: the red-crested cardinal, *Paroaria coronata* (Segura and Reboreda 2012), and the fork-tailed flycatcher, *Tyrannus savana* (Tuero et al. unpublished data).

Each shiny cowbird female lays eggs of consistent appearance (Gloag et al. 2014), but at the population level, the eggs vary widely in background color and spotting pattern, from unspotted to highly spotted (Ortega 1998; Mahler et al. 2007; Hanley et al. 2019). Shiny cowbird eggs mismatch in size and coloration of the eggs of most of their hosts. Therefore, it would be expected that hosts eject parasitic eggs. However, among hosts tested, only two species ejected the spotted and unspotted (white) shiny cowbird eggs, and four species only ejected the unspotted eggs (Reboreda et al. 2013). Besides, hosts smaller than shiny cowbirds are non-ejectors, probably because they are unlikely to remove parasitic eggs from their nests (but see Underwood and Sealy 2006 for a small host that grasp-eject brown-headed cowbird eggs). Small hosts do not usually desert their nests in response to parasitism either (Mason 1986b; Reboreda et al. 2013).

Nestlings and Fledglings

Shiny cowbird nestlings do not evict host eggs or nestlings; therefore, the number and relative size of their nestmates affect their survival and growth dynamics. In nests of small-sized hosts, the major problem faced by cowbird nestlings is to elicit sufficient parental provisioning to meet their needs (Massoni and Reboreda 1998; Tuero et al. 2007). Under this scenario, cowbird nestlings benefit from the presence of host nestlings because, collectively, they induce higher provisioning rates and parasitic nestlings monopolize the extra food (Fiorini et al. 2009b; Gloag et al. 2012, Fig. 6.1). By contrast, in nests of large hosts where competition for food is more intense, cowbird nestlings often grow more slowly with lower survival when reared alongside host nestmates (Astié and Reboreda 2009; Fiorini et al. 2009b; Gloag et al. 2012). Unlike other brood parasites (Payne 1973), the shiny cowbird

Fig. 6.1 Shiny cowbird (*Molothrus bonariensis*) nestling sharing the nest with four smaller house wren (*Troglodytes aedon*) nestlings. Photo: Vanina D. Fiorini

has not evolved shorter incubation periods or faster growth rates than expected by allometric regressions (Mermoz and Ornelas 2004). Nevertheless, their incubation period is shorter than that of many of their hosts (Kattan 1995; Mermoz and Reboreda 1994; Fiorini et al. 2005; but see Astié and Reboreda 2009). In large-sized hosts, such as brown-and-yellow marshbird and the chalk-browed mockingbird, hatching ahead of host young enhances the survival (Fig. 6.2). This is because early hatching decreases the size difference relative to the larger host nestlings or allows the cowbird to be the largest nestling in the brood during most of the nestling period (Dure Ruiz et al. 2008; Mermoz and Reboreda 2003; Fiorini et al. 2009b).

Shiny cowbird nestlings do not mimic the appearance or begging calls of any particular host (Gloag and Kacelnik 2013; Tuero et al. 2016; Bortolato et al. in preparation). Nevertheless, they appear to be highly efficient in stimulating provisioning in a wide range of host species. This ability is partly due to their relatively long and tremulous begging calls that can stimulate parental feeding, even in non-host species (Gloag and Kacelnik 2013). Moreover, shiny cowbird nestlings modulate the intensity of their begging behavior based on their perceived level of intrabrood competition. Tuero et al. (2016) experimentally showed that shiny cowbird nestlings reared in chalk-browed mockingbird nests begged more intensively, faster, and for longer periods of time than those reared in house wren nests. The body condition of cowbird nestlings was similar in both host species; hence, the authors suggested that they adjusted their begging effort to allow them to secure sufficient provisioning without incurring extra energetic costs (Tuero et al. 2016). Gochfeld (1979) and Lichtenstein (1997) also described the begging calls of shiny cowbirds as louder and longer than host's begging calls. A drawback of such exaggerated behavior is that noisy cowbird nestlings may render host nests more detectable to potential

Fig. 6.2 One shiny cowbird (*Molothrus bonariensis*) exhibiting its red gape and three chalk-browed mockingbird (*Mimus saturninus*) nestlings. The parasitic cowbird has hatched before host nestlings and all have a similar body size. Photo: Vanina D. Fiorini

predators (Massoni and Reboreda 1998) as it also happens in brown-headed cowbirds (Dearborn 1999).

Most shiny cowbird hosts do not discriminate against parasitic nestlings. An exception is the firewood-gatherer (*Anumbius annumbi*), which seems to reject shiny cowbird nestlings shortly after hatching (Delhey et al. 2011). Cowbird nestlings in firewood-gathered nests were found dead inside the nest within the first 48 h post-hatching, probably due to insufficient feeding, whereas host nestlings that hatched later were raised until fledging or predation. Hosts may have recognized the parasitic nestlings as foreign and rejected them. Alternatively, it could be a case of "discrimination without recognition" (*sensu* Grim et al. 2003). In this host, shiny cowbird eggs hatched 4–5 days before host eggs; thus, it is possible that host parents begin to provision their young after a certain incubation period and failed to feed nestlings that hatch too early (Delhey et al. 2011). These alternatives remain to be tested.

There is little information for shiny cowbirds pertaining to the fledgling stage, particularly how parasitic fledglings begin to associate with adult conspecifics and disperse away from the natal territory. Recent observations of shiny cowbirds fledged from chalk-browed mockingbird and house wren nests show that survival rate until independence is 45–60% (Crudele et al. unpublished data). Fledglings departed from the host's territory at about 35 days of age and occasionally they associate with adult conspecific females within the natal range (Crudele et al. unpublished data). Adult females could facilitate the socialization of parasitic juveniles (Soler and Soler 1999), but this idea has not been tested and it is not known whether shiny cowbird juveniles disperse solitarily or in groups.

*6.2.2 Screaming Cowbird (*Molothrus rufoaxillaris*)*

6.2.2.1 Species Characteristics

The screaming cowbird is the most specialized of the five *Molothrus* species (Table 6.1). It inhabits savannahs, grasslands, and suburban areas throughout most parts of Argentina (excluding central-south Patagonia and the Andean region), Uruguay, Paraguay, southeastern Bolivia, and southeastern Brazil (Ortega 1998). Its geographic distribution overlaps completely that of the closely related shiny cowbird and the two species frequently forage together in mixed flocks. Adult screaming cowbirds are readily recognizable by their glossy black plumage that lacks the iridescence of male shiny cowbirds. Sexual dichromatism is subtler in the screaming cowbird than in other cowbird species. Males and females are alike in plumage except for the rufous axillary patch that is more noticeable in males. They do show sexual dimorphism in body size, with males being visibly larger than females. Screaming cowbirds are also characterized by their vocalizations, a harsh and loud call note uttered by both sexes as a contact call. Contrary to shiny cowbirds, they are suspected to be socially monogamous. Males and females are typically seen in pairs and both capture–recapture and radio-tracking data suggest that pair bonds last the entire breeding season (Mason 1987; Scardamaglia and Reboreda 2014). It is still unclear why they form stable sexual associations in the absence of parental care (see Hauber and Dearborn 2003).

6.2.2.2 Host Use at Population and Individual Level

The screaming cowbird has four known effective hosts, grayish baywing (*Agelaioides badius*; Hudson 1874), chopi blackbird (*Gnorimopsar chopi*; Sick 1985; Di Giacomo and Reboreda 2014), brown-and-yellow marshbird (Mermoz and Reboreda 1996; Mermoz and Fernández 2003), and austral blackbird (*Curaeus curaeus*; Lowther 2018). Two other species are suspected hosts in Brazil based on online photographic records, yellow-rumped marshbird (*Pseudoleistes guirahuro*; Sessegolo 2014) and the pale baywing (*Agelaioides fringillarius*; Mota 2010), yet these reports require confirmation. These species differ in body size, incubation period, and nest characteristics, but all breed cooperatively (Orians et al. 1977; Fraga 1991; Mermoz and Fernández 2003; Ursino et al. 2011; Di Giacomo and Reboreda 2014). This suggests a non-random association of screaming cowbird parasitism and the presence of helpers-at-the-nest that deserves further inquiry (Feeney et al. 2013). The scarlet-headed blackbird (*Amblyramphus holosericeus*) was added to the host list based on a single record (Lowther 2018), which, if confirmed, would be the first non-cooperatively breeding host species. Screaming cowbird parasitism also has been reported in nests of solitary cacique (*Cacicus solitarius*) and cattle tyrant (*Machetornis rixosa*), but that parasitism is attributed to recognition errors made by laying females attempting to parasitize baywing or chopi blackbird nests (Di Giacomo et al. 2010). Interestingly, such “recognition errors” reveal a potential mechanism through which screaming cowbird females may have colonized their hosts, or could switch to new host species in the future. Using mtDNA, Mahler et al. (2009) reported in an area of sympatry that haplotype frequency distribution differed between screaming cowbird eggs laid in baywing and chopi blackbird nests, which suggested females are host-specific and host switches would have occurred more than once over evolutionary time.

From the host species reported so far, the grayish baywing (hereafter baywing) is the primary host across most of the screaming cowbird’s geographic range. This cavity-nester breeds mostly in bulky stick nests constructed by many furnariid species (e.g., *Anumbius annumbis*, *Phacellodomus* sp.), domed nests of rufous horneros (*Furnarius rufus*) and great kiskadees (*Pitangus sulphuratus*), and excavated nest holes of woodpeckers (e.g., *Colaptes melanochloros and C. campestris*). In eastern Argentina, baywings breed later than most other passerines, from late November to mid-February. It is quite common to see pairs of screaming cowbirds arriving at or departing from baywings’ nesting sites throughout the breeding season. Each season, more than 90% of baywing nests are parasitized by screaming cowbirds, with a mean of about five parasitic eggs per parasitized nest (De Mársico et al. 2010a).

Despite such heavy parasitism pressure, the costs of screaming cowbird parasitism to baywing's reproductive success seem to be relatively benign, and baywings usually fledge all or most of their own young alongside one or two screaming cowbird nestlings (De Mársico and Reboreda 2014). Screaming cowbirds are so tightly linked to baywings that it would be almost impossible to understand many aspect of their biology without considering how they interact with each other. What follows is an overview of the screaming cowbird's parasitic behavior and various reciprocal adaptations undergone by screaming cowbirds and baywings at different stages of the nesting cycle.

6.2.2.3 Parasitic Behaviors of Screaming Cowbirds and Host Antiparasitic Defenses

Laying Period

Brood parasites must locate suitable host nests and parasitize them at the right time to produce offspring. If parasitism occurs too early, parasitic eggs are more likely to be rejected, and if it occurs too late, the eggs may not hatch or the parasitic nestlings may be outcompeted by their older nestmates. For screaming cowbird females, synchronizing parasitism with baywing's egg-laying period is not straightforward because this host may start to lay eggs at virtually any time, between 1–2 days and 2–3 weeks, following nest completion (Fraga 1998; De Mársico and Reboreda 2008). During this prelaying period baywings defend the nest as aggressively as would after laying eggs; thus, they do not provide any obvious behavioral clue for screaming cowbirds (or researchers!) to reliably assess when egg laying will commence (De Mársico and Reboreda 2008). As a result, nearly one-third of all screaming cowbird eggs laid in baywing nests appear before the hosts have initiated laying and are almost invariably rejected by baywings, i.e., they are literally kicked out from the nest (De Mársico and Reboreda 2008; De Mársico et al. 2013). In addition, baywings often reject the entire clutch when parasitic eggs outnumber their own and lay a replacement clutch in the same nest after, again, a variable prelaying period (De Mársico et al. 2013). These prelaying and clutch rejection strategies allow baywings to limit the number of parasitic eggs they ultimately incubate and, thus, potential fitness costs of parasitism (De Mársico et al. 2010a). Interestingly, screaming cowbirds synchronize parasitism better in nests of their alternative host species than in baywing nests and, conversely, the host-generalist shiny cowbirds synchronize parasitism well in their primary hosts but not in baywing nests. This further supports the role of baywing's egg-laying behavior as an evolved defense against brood parasitism (De Mársico and Reboreda 2008).

Synchronizing parasitism with an unpredictable host correlates with the screaming cowbird's nest prospecting behavior. Studies involving monitoring of radio-tagged screaming cowbird females revealed that they maintain constant areas to search for host nests, and that parasitism of baywing nests occurs within a narrow time-window, from roughly 30 to 60 min before sunrise (Scardamaglia and Reboreda

2014; Scardamaglia et al. 2017). Consistent with multiparasitism in baywing nests, parasitic females overlap extensively in their individual morning ranges, which confirms non-exclusive use of breeding territories (Scardamaglia and Reboreda 2014). Scardamaglia et al. (2017) used a novel digital radio-tracking technology to record nest visits by screaming and shiny cowbird females prior and during the host's egg-laying period. For both species, parasitism events were always preceded by at least one visit to the targeted nest, providing direct evidence that cowbird females prospect host nests before laying eggs. The frequency of nest visits was higher among screaming than shiny cowbird females, suggesting that the former required more prospecting visits to gather information about the status of baywing nests (Scardamaglia et al. 2017). Furthermore, screaming cowbird females often revisited the nest where they had laid an egg and occasionally parasitized the nest twice, contrary to shiny cowbirds that seldom revisit nests and typically avoid parasitizing already parasitized nests (Gloag et al. 2014; Scardamaglia et al. 2017; but see de la Colina et al. 2016). These differences likely reflect adaptive strategies of the host-specialist screaming cowbird for synchronizing egg laying with its unpredictable host and keeping track of baywing nests for new opportunities of parasitism.

During nest visits, screaming cowbirds, like shiny cowbirds, may puncture host eggs, a behavior that presumably serves to reduce competition among parasitic offspring (Fiorini et al. 2009b; Cossa et al. 2017). The most obvious host defense against egg puncturing would be to prevent parasitic females from accessing the nest in the first place, but apparently this is seldom achieved. Although baywings recognize adult screaming cowbirds as a specific threat and respond aggressively to them (De Mársico and Reboreda 2008), the high frequency of parasitism on baywing nests clearly indicates that screaming cowbirds are able to overcome host nest defense. Video recordings of baywing nests show that when screaming cowbird females arrive to lay, the host female is almost always inside the nest, sitting tightly on the nest chamber (De Mársico et al. 2013). This "tight sitting" behavior is useless to prevent parasitism because, despite host efforts, screaming cowbird females manage to lay their egg, and they do so quickly, sometimes on the head or back of the host. Instead, tight sitting may serve to protect host eggs from being punctured by blocking access of cowbird females to the nest contents, but this hypothesis needs to be tested (De Mársico et al. 2013; see also Hobson and Sealy 1989). Moreover, parasitic females may have difficulty puncturing baywing eggs, due to these species' thicker eggshells than expected from allometry, which has been proposed as an adaptation to increase egg resistance against cowbird attacks (Hudson 1874; Spaw and Rohwer 1987; Mermoz and Ornelas 2004).

Nestling and Fledging Periods

Host–parasite interactions encompass the entire nesting cycle, but it is during the nestling and fledgling stages that the most striking adaptations of screaming cowbirds become apparent. Unlike their cowbird relatives, young screaming cowbirds mimic their hosts (Hudson 1874). They resemble baywings so closely that, by the age of 4–5 days, nestlings of the two species are almost impossible to distinguish, even for the trained eye (Fraga 1979). The parasitic juveniles retain their baywing-like plumage until well after they have attained nutritional independence, by the age of 37 days post-hatching (Ursino et al. 2012). At that time, they initiate molt into the adult black plumage and reveal their true identity. Hudson (1874) was the first to note the parasitic habit of screaming cowbirds after identifying molting juveniles in a flock of baywings. He was astonished by the sight of those birds that “appeared to be undergoing the process of transmutation into another species” (p. 162). An adaptive explanation for the remarkable similarity between screaming cowbird and host fledglings came much later from a series of field observations and cross-fostering experiments that show that adult baywings refuse to care for non-mimetic fledglings of the shiny cowbird as soon as they leave the nest, but provision screaming cowbird fledglings until independence (Fraga 1998; De Mársico et al. 2012).

Screaming cowbirds also precisely match the begging call structure of baywing nestlings. Recent cross-fostering experiments suggest that the development of baywing’s species-specific acoustic signals occurs independently of the social experience of parasitic nestlings (Rojas Ripari et al. 2018). Ursino et al. (2017) tested the response of adult baywings to begging calls of screaming cowbird (mimetic), shiny cowbird (non-mimetic), and conspecific nestlings. They supplemented six-day-old broods with playbacks of each call type and found that baywings increased nest provisioning rates in response to screaming cowbird and conspecific begging calls, but not in response to non-mimetic calls. These results provide support of the adaptive value of vocal similarity between screaming cowbird and baywing nestlings and its role in manipulating host parental behavior (Ursino et al. 2017). In addition, screaming cowbird nestlings beg more intensely than host nestlings at similar hunger levels, which might also serve to effectively compete for food (Lichtenstein 2001; Ursino 2016). Some recent experiments further suggest that host-specific call structure and exaggerated begging displays are critical for parasitic fledglings to capture the attention of adult baywings after leaving the nest (Lama et al. unpublished data).

At some point after attaining nutritional independence, parasitic fledglings must abandon their foster parents and join their conspecifics to find potential mates, but very little is known about this transition in cowbirds and other brood parasites (reviewed recently in De Mársico et al. 2017). This knowledge gap is likely due to the difficulties inherent in following mobile juveniles. Preliminary data from radio-tagged fledglings suggest that screaming cowbird juveniles remain with their foster parents for 40–60 days after fledging, and that they come in contact with conspecifics before dispersing (Rojas Ripari et al. unpublished data). Interactions with conspecific adults could facilitate natal dispersal and socialization of cowbird juveniles, but this hypothesis has not been tested (e.g., Hahn and Fleischer 1995; Lorenzana and Sealy 1998). Also not known is the mechanism of conspecific recognition, although species-specific vocal cues are presumably involved (e.g., Hauber et al. 2001). Clearly, more work is needed to disentangle how young parasites join their own after having been reared by heterospecific hosts.

*6.2.3 Giant Cowbird (*Molothrus oryzivorus*)*

6.2.3.1 Species Characteristics

As its name denotes, the giant cowbird is the largest species in the genus *Molothrus* and one of the larger New World blackbirds. It has a long rounded tail, black feet, and has a conspicuous ruff of feathers around the neck that makes the head look small (Jaramillo and Burke 1999). The bill is long and black with a shape unlike to the bill of other cowbirds. The maxilla expands into a flat frontal shield rounded at the base, which is absent in the other cowbird species, but occurs in the giant cowbird's hosts. Males are larger and heavier than females (Table 6.1) and this sexual dimorphism extends to the plumage. The male is black with a violet iridescence, whereas the female is dark brown to black. The neck ruff is more conspicuous in males (Ortega 1998).

The giant cowbird is quiet, though noisy in flight (Jaramillo and Burke 1999). Its geographic range is wide, from southern Mexico south to northern Argentina. It is associated with open woodlands and cultivation, but it is also the only cowbird species found deep in the forest (Jaramillo and Burke 1999). It usually forages in flocks and consumes arthropods, fruit, and nectar (Robinson 1998). Giant cowbirds feed on the ground, near water, on top of trees (branches and foliage), and on the back of large herbivores such as capybaras (*Hydrochoerus hydrochoerus*) (Robinson 1998).

Eleven host species are known for this parasite (Lowther 2011; Table 6.1). Its better-known hosts are colonial nesting blackbirds: two species of caciques (*Cacicus* sp.) and four species of oropendolas (*Psarocolius* sp.) (Friedmann 1929; Robinson 1998; Jaramillo and Burke 1999). These species are the same size or larger than giant cowbirds. Most host species remain unstudied and little is known about host–parasite interactions, possibly because host nests are difficult to access as most colonies are placed on top of very tall, isolated trees (Fraga 2011).

6.2.3.2 Host–Parasite Interactions

Contrary to other cowbird species that approach nests stealthily and lay eggs around sunrise, giant cowbirds lay in host nests during the day and visit colonies in groups, where males appear to distract hosts while females enter the nests. It has also been observed that single females or pairs visit host colonies at times of the day when caciques and oropendolas were most likely to be absent (Robinson 1998). Hosts aggressively defend the nest when giant cowbirds approach their colonies (Webster 1994; Robinson 1998).

Giant cowbird's eggs are oval and have the largest relative volume among those of the parasitic cowbirds. They vary from immaculate white to dark-spotted on white, pale or green backgrounds (Fleischer and Smith 1992). Most hosts have not been studied yet, but their eggs are apparently not mimetic to any particular host. Fraga (2011) suggested some resemblance in color, but not in size, between the spotted egg morph and cacique's eggs in northeastern Argentina; in this area, the unspotted white egg was the more common morph.

In general, nests are parasitized with a single egg, but multiparasitism is also common (Fraga 2011). Giant cowbirds damage host eggs, which may have selected for increased clutch size in the Montezuma oropendola (*P. montezuma*) (Cunningham and Lewis 2006; Fraga 2011). This host is an obligate brood-reducer that does not raise more than one chick per brood; however, most clutches are of two eggs (Cunningham and Lewis 2006). Montezuma oropendolas apparently benefit from laying this "extra" egg because cowbird females often remove or damage one host egg when they parasitize the nest. Therefore, hosts are more likely to fledge their own nestling in two-egg clutches (Cunningham and Lewis 2006). This host species rejects up to 72% of model giant cowbird eggs placed in their nests, regardless of whether there were own eggs present for comparison (Cunningham and Lewis 2006).

Giant cowbird nestlings have white bills and a pale frontal casque like those of their oropendola hosts. Bills turn to the usual cowbird-black after fledglings become independent (Redondo 1993). The pale bill may be a phylogenetically retained feature because it is found in the closely related screaming cowbird (Fraga 1979). The casque is retained in adult giant cowbirds, but it becomes smaller and black. Due to the resemblance between the casque of giant cowbirds and oropendolas, Webster (1994) proposed this could be a case of mimicry. However, the evolutionary origin of the frontal casque as well as its potential fitness benefit to giant cowbird nestlings remains to be studied.

A controversial study proposed that parasitism by the giant cowbird is advantageous for the host species (Smith 1968). Nevertheless, results of other studies have not supported this hypothesis (Robinson 1998; Webster 1994). Moreover, Cunningham and Lewis (2006) described a giant cowbird nestling unable to remove *Philornis* larvae from host nestlings, which was the main benefit proposed for this parasitic system (Smith 1968). Finally, giant cowbirds infested with *Philornis* spp. were observed in Argentina (Fraga 2011).

*6.2.4 Bronzed Cowbird (*Molothrus aeneus*)*

6.2.4.1 Species Characteristics

The bronzed cowbird owes its common name to the plumage color of the males; they are dark bronzed-brown with iridescent black on the wing and tail. Like giant cowbirds, males have elongated feathers in the neck forming a conspicuous ruff. Females are brownish black and lack the males' distinctive bronze color, but its color varies among the three subspecies. Bronzed cowbirds are also known as red-eyed cowbirds due to the red iris that males exhibit in summer. Female's iris color is brownish orange, similar to males in winter (Ortega 1998). The bill is one of the longest among cowbirds.

The geographic range extends from the southern United States to Mexico, western Panamá, and northeast Colombia. There are three subspecies and an isolated population on the Caribbean coast of Colombia that is sometimes treated as a separate species, the bronze-brown cowbird (*M. armenti*) (Ortega 1998; Fraga 2016). The bronzed cowbird occurs in open and semi-open fields, agricultural fields, and forest parches (Ortega 1998). It often forages alone, but also with conspecifics in small flocks or in mixed flocks with other blackbirds. They are omnivorous and search for food on tree branches, the ground, and on the back of large grazing mammals (Carter 1986).

This is a generalist parasite with more than 100 known host species (Table 6.1), mainly icterids and flycatchers (Sealy et al. 1997; Lowther 2018). Hosts are smaller and larger than the cowbird (Table 6.1). Eggs are immaculate pale blue, bluish green, greenish blue, and white and, like other cowbird species, the shells are thick (Carter 1986; Ortega 1998).

6.2.4.2 Host–Parasite Interaction

Females parasitize host nests a few minutes before sunrise with egg laying lasting a few seconds (Peer and Sealy 1999b). Small hosts, like the hooded oriole (*Icterus cucullatus*) and orchard oriole (*I. spurius*), are frequently at their nests when cowbird females arrive to lay, and attempt to remain there defending the nest while bronzed cowbirds peck their eggs. However, host nest defense often does not prevent parasitism (Ellison and Sealy 2007). Bronzed cowbirds, similar to shiny and screaming cowbirds, pierce host eggs during laying visits. Egg puncturing may have different functions but the evidence suggests that it serves to force renesting, when bronzed cowbird females locate a nest that is too advanced for successful parasitism (Peer and Sealy 1999b). In addition, egg puncturing may decrease competition when parasitizing larger hosts (Peer and Sealy 1999b). Multiparasitism is common and same-day laying at a single nest has been observed, indicating that more than one female can lay an egg in the same nest (Carter 1986; Peer and Sealy 1999b). Through genetic analyses, Ellison et al. (2006) confirmed that multiparasitism is the result of different females laying in the same nest and that most females did not parasitize nests again. Some females parasitized more than one host species, acting as generalists (Ellison et al. 2006).

This species generally synchronizes laying with the host's laying, but parasitism after the onset of incubation sometimes occurs (Carter 1986; Ellison et al. 2006). Egg rejection has been documented in several host species (Sealy 1999; Sealy and Underwood 2004); Rasmussen et al. 2012). An interesting case is that of grackles (*Quiscalus* spp.), many of which have retained a 100% of rejection behavior towards bronzed cowbird eggs in the absence of parasitism (Peer and Sealy 2004). Conversely, rejection occurs only in 18% of nests of clay-colored thrushes (*Turdus grayi*) in Costa Rica, where reports about parasitism by bronzed cowbirds are infrequent, suggesting the existence of a mixture of acceptor and ejector individuals in this population (Rasmussen et al. 2012).

There are few descriptions of the nestling stage of bronzed cowbirds. The cowbird egg can hatch before, on the same day, or after the host's eggs. If the parasitic nestling hatches before or within 36 hs after the host eggs, it has a better chance of fledging than if it hatches later (Carter 1986). Bronzed cowbirds have a rapid development that allows them to outcompete its host nestmates and to become alone in the nest of small-sized hosts. On the other hand, large-sized hosts can raise the parasitic nestling alongside its own nestlings, but cowbirds that hatch too late, generally die (Carter 1986).

6.3 Family Cuculidae, Subfamily Neomorphinae

*6.3.1 American Striped Cuckoo (***Tapera naevia***)*

6.3.1.1 Species Characteristics

The striped cuckoo owes its common name to its striped blackish and rufous shaggy crest. Adult females and males are similar in appearance. The upper parts are brown streaked buff and black. The alula is long and black and it is exhibited during courtship. The wings are brown to rufous with a white base noticeable in flight. It has a long tail and its face has a white streak above the eyes and a black whisker line (Payne 2005).

This cuckoo occurs in open habitats as pastures and llanos from southern Mexico to northern Argentina. This is a solitary and shy species, which uses counter-singing and duets in reproduction and territory defense. Individuals are often heard singing from bushes and trees, but are difficult to find. They forage amid vegetation or near the ground, where they feed primarily on large insects (Howell and Webb 1995). The striped cuckoo is a generalist parasite with 22 known host species (Table 6.1). Its hosts are small passerines that build open or domed nests, especially the ovenbirds (Furnariidae). The breeding biology of the striped cuckoo is little known (Payne 2005; Mark 2013).

6.3.1.2 Host–Parasite Interaction

The intensity of parasitism is usually one egg and sometimes two. Among the New World cuckoos, only the striped cuckoo lays eggs that mimic host eggs in color. Eggs may be white, bluish white, or greenish blue, depending on the geographic area (Payne et al. 2005). In most of South America, striped cuckoos lay white eggs that are identical to those of its host species. In Central America, however, striped cuckoos lay blue eggs that mimic those of a different suite of hosts. There is an area where the ranges of these two-host groups overlap and striped cuckoo eggs are polymorphic. The other cuckoo species in the striped cuckoo's clade lay white eggs. Therefore, white eggs were probably the ancestral condition for striped cuckoos and blue color may have evolved as courter-defense to the host egg rejection (Payne 2005). However, the defense and counterdefense between striped cuckoo and its hosts have been poorly studied. There is only one experimental study that has explored host defenses against striped cuckoo eggs (Mark 2013). Using reflectance spectrometry, Mark (2013) showed that cuckoo eggs matched the coloration of the immaculate blue-green eggs of its host, the rufous-and-white wren (*Thryophilus rufalbus*). Visual mimicry of host eggs would be adaptive for the cuckoo because it reduces host rejection of parasitic eggs (Mark 2013). Another infrequently used host species that lays white eggs, the plain wren (*Cantorchilus modestus*), accepts both mimetic and non-mimetic eggs (Mark 2013). Curiously, striped cuckoo's eggs accurately match the blue-green appearance of rufous-and-white wren eggs despite differences in pigment composition and concentration, suggesting that egg mimicry can arise from alternative chemical pathways (Dainson et al. 2018).

As in most of the Old World cuckoos, the striped cuckoo kills its nestmates (Table 6.1) but, unlike its relatives, striped cuckoo nestlings slash host nestlings to death with a sharp bill hook, soon after hatching (Morton and Farabaugh 1979). As a result, the parasitic nestling is reared alone in the nest, losing the bill hook as it grows (Morton and Farabaugh 1979).

The young cuckoo leaves the nest at 16–18 days of age, remains flightless for a week, and may be cared for the hosts until it is one month of age (Payne 2005). Brood parasitism by the striped cuckoo leads to changes of rufous-and-white wren host behaviors because parasitic fledglings move away from the center of the host territory, towards forest edges and open areas that are not used by the host (Mark and Gamez-Rugama 2015). Moreover, there is evidence that parasitized parents are more stressed than non-parasitized ones (Mark and Rubenstein 2013). The physiological costs of being parasitized can carry over into subsequent nesting attempts, as suggested by the positive association between parasitism status and the latency to renest in the same breeding season and the negative association between parasitism and the likelihood of nesting in the subsequent breeding season (Mark and Rubenstein 2013).

The post-fledging stage is poorly studied in birds in general and even less so in brood parasites. An observational study involving three radio-tracked striped cuckoo fledglings discovered that juveniles might associate with adult conspecifics. Adults often initiate the social interactions; the resulting juvenile–adult pairs move and forage together, and even counter-singing and duetting (Mark and Gamez-Rugama 2015).

*6.3.2 Pavonine Cuckoo (*Dromococcyx pavoninus*)*

6.3.2.1 Species Characteristics

Female and male are alike. The face is rufous with a short rufous crest. The back is brown with feathers edged in white and the long graduated tail is spotted with white. The pavonine cuckoo also has a long alula and wing covers edged with whitish tinge. Its belly is white. The bill is black above and gray below and the feet are gray to gray brown (Payne 2005).

This species is solitary and uncommon, and their distribution is discontinuous in South America east of the Andes, from Colombia, Venezuela, Guyana, and French Guyana south to eastern Ecuador, eastern Peru, Bolivia, Brazil, and northeastern Argentina. Its habitats include understory forests, mountain forests, and thickets with dense secondary woodland at height elevations (Payne 2005). Pavonine cuckoos seem to be sensitive to human avoiding their settlements.

This cuckoo is a generalist brood parasite with seven known host species of suboscine passerines, mainly of the Tyrannidae family (Table 6.1). Its hosts build small closed or bag-shaped nests with a side entrance (Payne 2005; Lowther 2009). Given its large size, it is not clear how pavonine cuckoo females manage to lay their egg in such small host nests.

6.3.2.2 Host–Parasite Interaction

Dromococcyx species are the most poorly studied Neotropical parasites. Available information is mainly restricted to species lists and records of its presence. Recently, Sanchez-Martınez et al. (2017) looked for evidences of pavonine cuckoo parasitism in many potential hosts in the Peruvian Amazon. Over the seven-year-study, they found pavonine eggs in only nine out of 74 nests of three host species. Nests were parasitized in synchrony with host laying, with only one egg in each nest. There was no evidence for egg mimicry because pavonine cuckoo eggs were white with brown spots and host eggs were white and smaller in size. Some evidences of antiparasitic defenses were found in two host species: the ochre-bellied flycatcher (*Mionectes oleagineus*) and the sepia-capped flycatcher (*Leptopogon amaurocephalus*), where the hosts deserted one and three parasitized nests, respectively. However, in three nests, these species accepted cuckoo eggs. The reasons that hosts accept or desert parasitized nests have not been explored.

As in most other cuckoo species, pavonine cuckoo nestlings apparently are infanticidal (Table 6.1), based on the observation that host nestlings disappeared after the cuckoo hatched, or they were found dead under the nest (Payne 2005; Sanchez-Martınez et al. 2017). Nestling skin color differed substantially between one host, the sepia-capped flycatcher (pink), and the parasitic cuckoo (black). However, nestling plumage coloration is similar in both species (Sanchez-Martınez et al. 2017), suggesting a potential coevolutionary arms race that awaits study.

*6.3.3 Pheasant Cuckoo (*Dromococcyx phasianellus*)*

6.3.3.1 Species Characteristics

Similar to the other Neotropical parasitic cuckoos, the pheasant cuckoo is neither sexually dichromatic nor dimorphic. It has a small head, thin neck, and a long fan-shaped tail with white spots. Its face shows a white line through the eye. Its back is blackish-brown, the wing covers have white margins, and the alula is long. The tail covers end with a subterminal black band and a white spot (Payne 2005).

The pheasant cuckoo ranges from south Mexico through Central and South America to Paraguay, northeastern Argentina, and southeastern Brazil. It is a forest bird, frequently described as easy to hear but difficult to see. It often forages on the ground, feeding on insects and lizards (Davies 2000).

This species is among the most poorly understood cuckoo species in the world. It is a generalist with at least 5 documented host species (Table 6.1). Its hosts are small passerines birds, mainly tyranid flycatchers that construct open or closed nests (Davies 2000). The breeding biology, laying behavior, and egg characteristics of this parasite are unknown (Johnsgard 1997; Davies 2000; Payne 2005; Lowther 2010).

6.4 Family Anatidae, Subfamily Oxyurinae

*6.4.1 Black-Headed Duck (*Heteronetta atricapilla*)*

6.4.1.1 Species Characteristics

The black-headed duck (*Heteronetta atricapilla*) is unique in that it is the only precocial obligate brood parasite described. Black-headed ducks are able to care for themselves just a few hours after hatching (Davies 2000). It is a small, dark duck and females are larger and heavier than males (Table 6.1) (del Hoyo et al. 2011). The male has a black head, whereas the female is pale brown overall.

It is distributed in the central region of Argentina to Uruguay, southeastern Brazil, Paraguay, and Bolivia, and also, the central region of Chile (Carboneras 1992). Black-headed ducks inhabit swamps, lakes, pools, and marshes of permanent fresh waters with abundant emergent vegetation (Weller 1968; Carboneras 1992).

The black-headed duck is a generalist parasite with more than 20 known host species (Cabrera et al. 2017) (Table 6.1), mainly coots (*Fulica* spp.), but also swans and gulls (Madge and Burn 1988; Lowther 2011; Lyon and Eadie 2013). There are very few data on parasitism of black-headed ducks and most of the accounts are from central-east Argentina (Weller 1968; Rees and Hillgarth 1984; Carboneras 1992; Lyon and Eadie 2004, 2013).

6.4.1.2 Host–Parasite Interaction

Hosts of the black-headed duck provides incubation and protection for the parasitic eggs during the 24–25 days of the incubation period. Because black-headed ducks do not damage host eggs like other brood-parasite species, sophisticated host defensive behaviors are not expected during the laying and prelaying stages. Black-headed duck eggs are whitish to buff in color and unmarked, similar to those of the rosy billed pochard (*Netta peposaca*) (Davies 2000), but unlike other hosts' eggs

(Lyon and Eadie 2013, 2004). There is no evidence for egg rejection by rosy billed pochards but this behavior was described in other three main host species in the east-central Argentina: the red-gartered coot (*F. armillata*), red-fronted coot (*F. rufifrons*), and brown-hooded gull (*Chroicocephalus maculipennis*) (Lyon and Eadie 2013). Coots buried parasitic eggs in their nests (Lyon and Eadie 2004), whereas gulls eject eggs or often move them off to the side, so that duck eggs were not incubated.

The parasitic eggs hatch before host eggs. One or two days after hatching, black-headed ducks leave their brood mates because they are able to care for themselves without any assistance from the hosts (Weller 1968; Lyon and Eadie 2004).

6.5 Final Conclusions

Throughout this chapter, we presented the main characteristics and behaviors of Neotropical obligate brood parasites. These species show a wide range of adaptations to their exciting lifestyle but some of them have characteristics that do not fit any particular host. The nestling morphology and the behavior of female shiny, giant, and bronzed cowbirds allow them to succeed in a variety of hosts. Others, such as the screaming cowbird, that has a tight relation with its main host, mimics the appearance of their nestling and fledging and also their begging calls. Whereas cowbird species are nestmate tolerant, the New World cuckoos kill their nestmates. The black-headed duck is an outlier in the brood-parasite world, as it is the only precocial species and only needs the host for the incubation of the eggs. The asymmetry of the information available on the different species is marked. Shiny and screaming cowbirds were studied for the first time more than 130 years ago, by Hudson (1874), followed by Friedmann (1929) and Hoy and Ottow (1964). Later, research by Fraga (1979, 1985, 1998) and Ortega (1998) expanded the information on these cowbird species. During the last two decades there have been very many studies on the behavioral ecology of these species. Although there are still several questions to be answered, the advance of the last years has been evident.

The reasons why the other Neotropical parasitic species have not been extensively studied yet could be related to the difficulty to reach the areas of distribution of these species and to the low density of some of their populations. On the other hand, the lack of resources in the countries where these species are distributed may also limit the possibility to study them, due to low numbers of researchers and the lack of adequate equipment and funding to carry out investigations.

The information on Neotropical obligate brood-parasites species is subrepresented compared to Old World or North American species and this may skews the interpretations and conclusions on the adaptiveness of parasitic behaviors and on the results of the coevolutionary processes between them and their hosts. To better understand the variety of adaptations of the parasites, it is crucial to increase our knowledge on Neotropical parasites, which will give more comprehensive understanding of how species solve problems through different strategies.

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Chapter 7
Bird Migration in South America: The Fork-tailed Flycatcher (*Tyrannus savana*) as a Case Study

Diego Tomás Tuero, Alex E. Jahn, and Maggie MacPherson

7.1 Introduction

7.1.1 General Patterns of Bird Migration in South America

One of the first descriptions of bird migration in South America comes from the nineteenth century when the Argentinean naturalist Williams E. Hudson wrote: "… when the great wave of bird-life set northwards, and all through March and April the birds were visible in flock succeeding flock from dawn to dark, until the summer visitants were all gone, to be succeeded in May by the birds from the far south…" (Hudson 1918). Scenes such as this can still be seen in South America, where bird migration is comprised of three major systems:

1. Nearctic–Neotropical migration, in which birds that breed in North America spend the boreal wintering the tropics (e.g., *Dolichonyx oryzivorus*, Renfrew et al. 2013; *Catharus fuscescens*, Heckscher et al. 2015).
2. Intra-tropical migration (Fig. 7.1), in which migratory birds breed and spend the non-breeding season wholly within tropical latitudes. This includes longitudinal migration, in which birds make east-west movements within the tropics, as occurs in the Atlantic Rainforest (e.g., Shear-tailed Gray-Tyrant, *Muscipipra*

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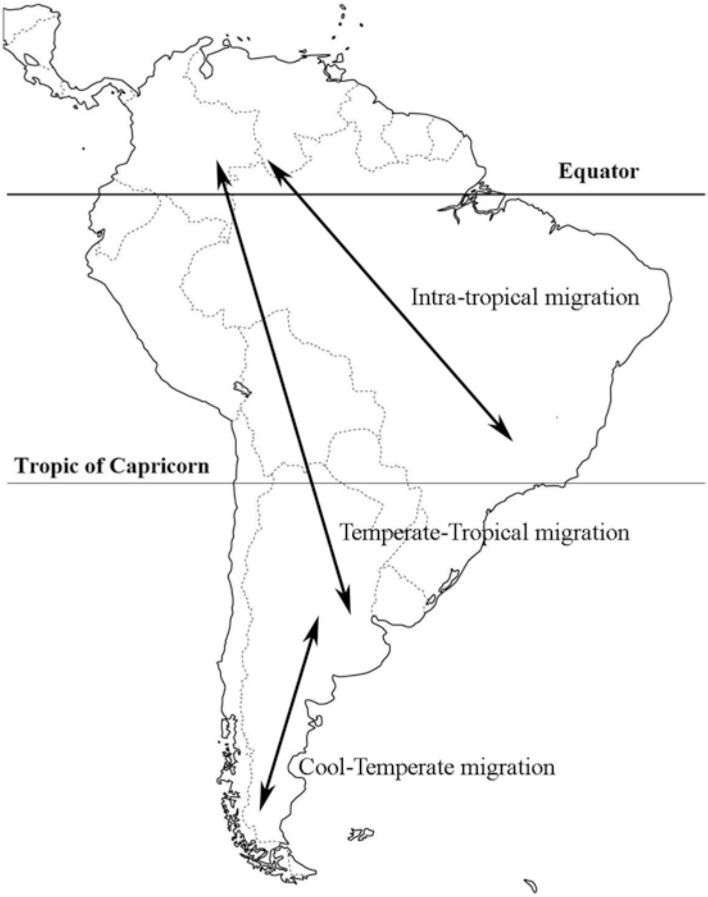

Fig. 7.1 Major patterns of bird migration in South America

vetula, Areta and Bodrati 2008; Yellow-legged Thrush, *Turdus flavipes*, Areta and Bodrati 2010). Intra-tropical migration can also consist of altitudinal migration, in which birds perform seasonal movements across different elevations. Such movements are common in the Andes Mountains (e.g., Hobson et al. 2003; Merkord 2010) and the Atlantic Rainforest (e.g., Galetti 2001; Areta and Bodrati 2010; Bczuska 2017).

3. Neotropical austral bird migration (Fig. 7.1), in which birds breed at south-temperate latitudes of South America, then overwinter closer to the Equator (Chesser 1994), but also includes those that do not leave the south-temperate latitudes of South America during the winter (Cueto and Jahn 2008). This represents the third largest bird migration system in the world and the most extensive in the Southern Hemisphere (Chesser 1994), comprising at least 230 species (Chesser 1994; Stotz et al. 1996). Approximately half of the species in this system are passerines (Chesser 1994), with 33% belonging to the family Tyrannidae

(Chesser 1994). Birds in this system may be either South American Temperate-Tropical migrants if they breed at south-temperate latitudes and overwinter within the tropics (i.e., north of the Tropic of Capricorn, Fig. 7.1), or South American Cool-Temperate migrants if they spend their entire lives within south-temperate latitudes of South America (Fig. 7.1) (Joseph 1997). An example of the former is the White-crested Elaenia (*Elaenia albiceps*), which migrates >5500 km between its Patagonian breeding grounds and northern Brazilian wintering grounds (Jiménez et al. 2016; Bravo et al. 2017), whereas an example of the latter is the Rufous-collared Sparrow (*Zonotrichia capensis*), which breeds in Patagonia and overwinters as far north as northern Chile and Argentina (Ortiz and Capllonch 2011).

Despite the significance of bird migration in South America at a global scale, the annual cycle of birds migrating within South America has seldom been studied. Although numerous studies exist on the biology of migratory birds in South America during either breeding or wintering periods, few studies describe their migratory routes or life-history strategies in detail. The migratory patterns of individual birds have been described for only a handful of bird species in South America (*Neochen jubata*, Davenport et al. 2012; *Tyrannus savana*, Jahn et al. 2013a; *Rynchops niger*, Davenport et al. 2016; *Elaenia albiceps*, Jiménez et al. 2016; Bravo et al. 2017; Barn Swallow, *Hirundo rustica*, Winkler et al. 2017). This represents a significant gap in information, since a broader understanding of seasonal life-history strategies of migratory birds in South America would allow testing of evolutionary hypotheses regarding the origin and evolutionary drivers that shape migratory behavior of bird species in general (Jahn and Cueto 2012).

7.1.2 Continental Features of South America

Other globally unique features of how and why birds migrate in South America are due to the unique geography of the continent. Unlike the Nearctic–Neotropical and Palearctic–Paleotropic migratory systems, in which birds must cross major geographic barriers (i.e., the Gulf of Mexico in the former and the Sahara Desert in the latter), few major geographic obstacles exist to bird migration in South America. The largest mountain range on the continent is the Andes, which have a north-south orientation and are therefore not an obstacle to most migratory species because migratory routes run parallel to this mountain chain (Chesser 1994). The Amazon forest could be another barrier to some migratory species that inhabit unforested habitats, as this huge tropical forest ecosystem separates the breeding and wintering areas of species that breed in grasslands at south-temperate latitudes (i.e., the "*Pampas*"), then overwinter in the grasslands of the Orinoco River Basin (i.e., the "*Llanos*"; e.g., some *Sporophila* seedeaters, Stotz et al. 1996). However, we lack sufficient understanding of how these species cross or potentially use this forest during either spring or fall migration to be able to classify the Amazonian forest as a geographical barrier.

Another geographical feature unique to South America is that the southern land areas in South America where austral migrants breed are significantly smaller than their northern wintering areas (Chesser 1994). As a result, the breeding density of migratory birds in temperate South America is likely to be higher than in the wintering areas, such that an increase in intra- and possibly inter-specific competition is expected during the reproductive period (Chesser 1994; Chesser and Levey 1998). Finally, the shape of South America results in a remarkable climatic pattern, in that the relatively narrow portion of southern South America is buffered from extreme seasonal changes in temperature by the large ocean area surrounding it (Dingle 2008). This reduces the seasonality of the south-temperate breeding grounds and offers a unique opportunity to test hypotheses about how seasonality affects the life-history strategies of migratory birds that breed there. Thus, the geographical particularities of South America that make the challenges to bird migration there unique among global migratory systems offer a unique test bed of the mechanisms underlying the evolution of bird migration.

7.1.3 Life-History Traits: Migration, Reproduction, and Molt

The substantial energetic demands that a bird faces during the breeding period results in a tradeoff between reproduction and growth, or reproduction and survival (Stearns 1992). This tradeoff, which has been broadly documented in numerous species during the last 25 years, is exhibited through a strong negative relationship between longevity and annual breeding investment. For example, experimental research, in which reproductive effort has been artificially increased, has shown dramatic reductions in adult survival (Monaghan and Nager 1997; Visser and Lessells 2001; de Heij et al. 2006). This tradeoff has also been observed among migratory and sedentary individuals, as well as between migratory and resident populations belonging to the same species (Rappole 2013), with migrants laying larger clutches than residents (Rappole 2013). However, we lack longitudinal research to clarify the causal links between clutch size and migratory versus sedentary life-history strategies, or the mechanisms driving variation in longevity between species living in tropical and temperate latitudes.

For migratory birds in general, tradeoffs also likely exist in the timing of the three major life-history events that occur on an annual basis: migration, reproduction, and molt. Although geographical barriers to migration within South America are lacking, migratory birds there must balance the timing and rate of migration with the timing and energetic requirements of reproduction and molt. One of the major challenges that migrants face is acquiring sufficient energy to fuel these energetically expensive activities, which some species accomplish by a diet shift between seasonally ephemeral arthropod, fruit, or nectar resources (e.g., Levey and Stiles 1992). These seasonal dietary preferences are typical of the migratory Tyrannidae, reflecting seasonal patterns of resource availability in the open habitats occupied by this family, and may provide the essential fuel for long-distance flights of these species (MacPherson 2017).

Annual feather molt is one of the least understood events that migrants must undertake on an annual basis. Yet, mounting evidence shows that it is energetically costly across various species (Lustick 1970; Lindström et al. 1993; Murphy 1986; Murphy and King 1992), resulting in an increased basal metabolic rate (Lindström et al. 1993), and requiring increased foraging effort and food intake (Hedenström 2003; Bonier et al. 2007; Echeverry-Galvis and Hau 2012). Due to the essential role that feathers play, other collateral costs of feather growth and wear also exist. Thermoregulation is affected when birds begin feather molt (Dawson and Maloney 2004) and flying during molt or on worn feathers also increases energetic demands of flight (predicted to be more costly for migratory individuals; Swaddle and Witter 1997; Chai et al. 1999; Hedenström and Sunada 1999; Hedenström 2003). Thus, the timing of feather molt rarely overlaps with migration, often occurring during a short period at the end of the breeding season (e.g., Foster 1975; Jenni and Winkler 1994; Rappole 2013; Mumme 2018). Thus, research on tradeoffs in timing and resource demands of major life-history events of birds migrating within South America is particularly needed to better understand how migration evolved in the geographical context of South America and why the Tyrannidae is such a prevalent family in this system.

In this chapter, we discuss the annual cycle of the Fork-tailed Flycatcher (*Tyrannus savana*), a widespread, common bird that migrates across South America. We describe the current state of knowledge about the annual cycle of the Fork-tailed Flycatcher, analyze the potential tradeoffs between breeding, molt, and migration in this species, and offer future directions for research on the annual cycle of this and other migratory birds in South America.

7.2 Model Species and Study Sites

The Fork-tailed Flycatcher (*Tyrannus savana*) is an especially conspicuous species of open habitats in South America (Fig. 7.2). Among the many wonderful Neotropical bird species, Fork-tailed Flycatchers are highly distinguishable due to their elongated outer tail feathers and aggressiveness in attacking potential aerial predators such as hawks and falcons. Although this species is one of the most widely known migratory bird species in South America, as is true of many Neotropical birds, the details of their annual cycle remained unknown until recently. The nominate subspecies, *T. s. savana* (Vieillot 1808; Zimmer 1937; Mobley 2004), is a long-distance migrant and one of the four subspecies recognized by various systematists. The other three subspecies are *T. s. circumdatus* (Zimmer 1937), *T. s. monachus* (Hartlaub 1844; Zimmer 1937), and *T. s. sanctaemartae* (Zimmer 1937). Morphological differences distinguish subspecies such as wing morphology (presence and extension of notch at the wing tips, Zimmer 1937) and back feather coloration (migratory subspecies is slightly darker, Zimmer 1937) (Fig. 7.2). Specifically,

Fig. 7.2 Fork-tailed Flycatcher males of two subspecies. Left: *T. s. savana* (Photo: Diego T. Tuero). Right: *T. s. monachus* (Photo: José I. Giraldo)

the migratory subspecies *T. s. savana* has a notch in all three outer primaries, whereas the sedentary *T s. monachus* and *T. s. circumdatus* have notches in only two outer primaries (the notches of *T. s. circumdatus* are shorter than *T. s. monachus*; Zimmer 1937; Pyle 1997).

Many aspects of the life history of the migratory *T. s. savana* have been well studied in recent years (e.g., reproductive strategies, Jahn et al. 2014; Tuero et al. 2018; migratory routes, Jahn et al. 2013a; molt strategies, Jahn et al. 2016a, 2017; migratory timing, Bejarano and Jahn 2018; MacPherson et al. 2018). *T. s. savana* is a long-distance migrant that breeds in Argentina, Bolivia, Brazil, and Paraguay, and overwinters at tropical latitudes in northern South America, primarily Colombia, Venezuela, Guyana, and Suriname (Fig. 7.3; Jahn et al. 2013a), where they often use multiple winter sites (Jahn et al. 2013a, b). Populations breeding at south-temperate latitudes migrate >3000 km northwards to arrive at their wintering grounds (Jahn et al. 2013a). However, some individuals from a Brazilian breeding population (see Fig. 7.4) migrated to the southwest after breeding, later migrating north to overwinter (Jahn et al. 2016b). As this was only observed in a population breeding at tropical latitudes, it suggests that different breeding populations of this subspecies have evolved unique migratory strategies, providing an ideal opportunity to evaluate the tradeoffs between migratory strategy, reproduction, and molt.

We studied 4 breeding populations of this subspecies across South America: 2 temperate populations in Argentina and 2 tropical populations in Brazil (Fig. 7.4). Temperate populations in Argentina were from two study sites: Reserva Natural El Destino, Buenos Aires Province (hereafter "El Destino"; 35.1°S, 57.4°W), and Reserva Provincial Parque Luro and surrounding properties in La Pampa Province (hereafter "Parque Luro"; 36.8°S, 64.3°W). Habitat at El Destino is primarily composed of temperate grasslands and marshes grazed by cattle, including tracts of woodland dominated by *Celtis ehrenbergiana* and *Scutia buxifolia*. Parque Luro is composed primarily of tracts of *Prosopis caldenia* trees and grasslands with scattered bushes. Tropical populations in Brazil were studied at two study sites: Parque da Alvorada and the campus of the Universidade de Brasília within the city

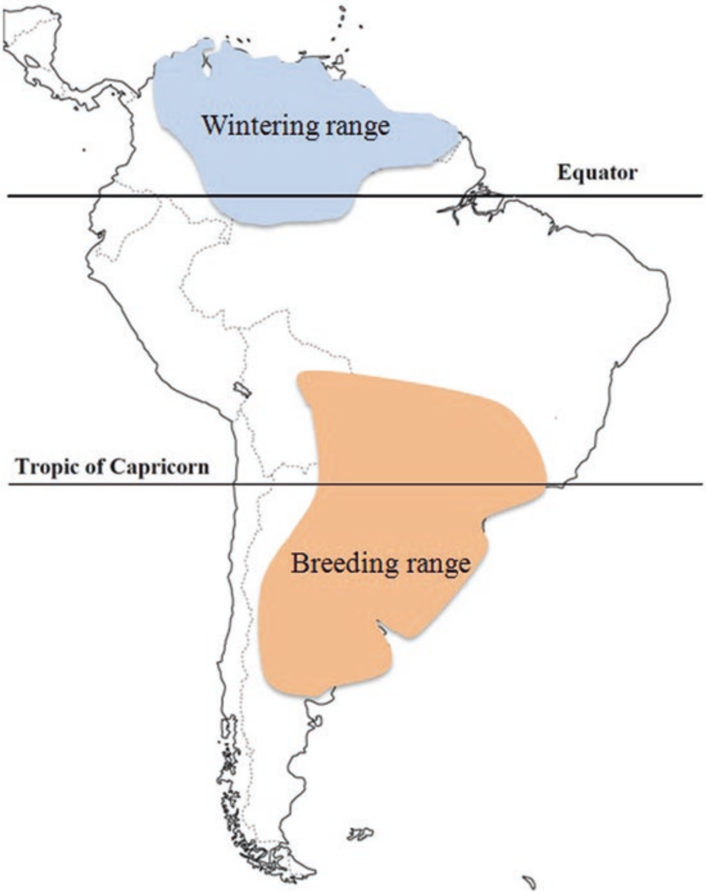

Fig. 7.3 *T. s. savana* breeding and wintering range

limits of Brasília (hereafter “Brasília”; 15.8°S, 47.8°W), and at Estação Ecológica de Itirapina in São Paulo State (hereafter “Itirapina”; 22.3°S, 47.9°W). The habitat in Brasília is primarily short, mowed grass and scattered trees, while habitat at Itirapina it is primarily composed of low campo and cerrado grassland. The sedentary population of *T. s. monachus* that we studied in Colombia was in Meta Department at the Reserva Indigena Wakoyo (hereafter “Wakoyo”; 4°22’N, 71°59’W; Fig. 7.4) and at Arrocera Carimata (hereafter “Carimata”; 4°04’N, 73°08’W; Fig. 7.4). At Wakoyo, flycatchers roosted in a bamboo grove located in a tropical grassland with scattered human dwellings. At Carimata, a roost of several thousand flycatchers was located at a rice farm with a surrounding landscape of mostly rice fields, intersected by windbreaks consisting of low bushes and trees.

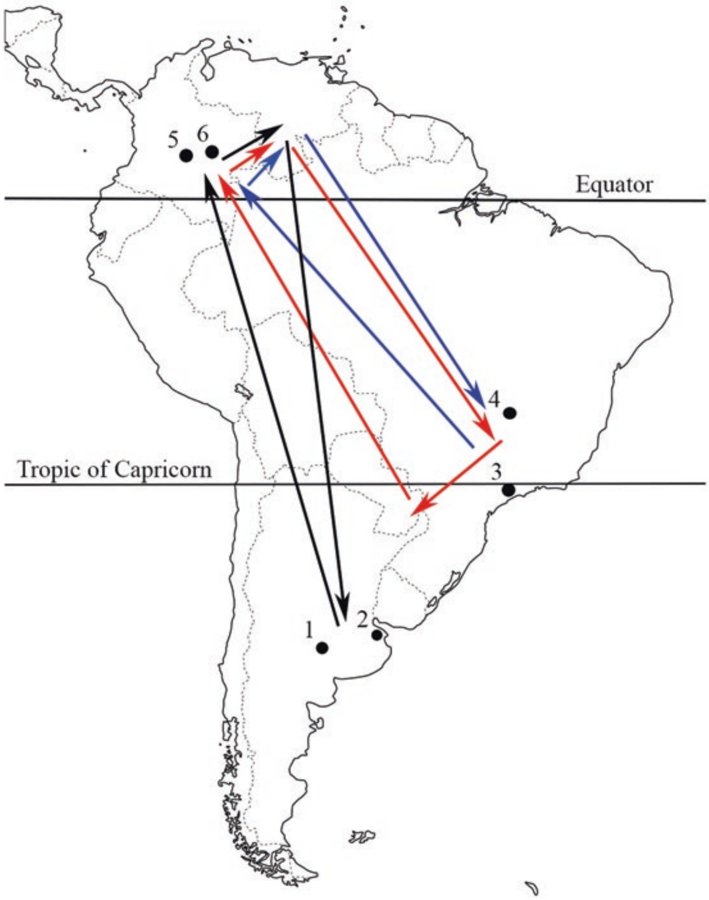

Fig. 7.4 Migratory pathway of *T. s. savana*, based on data collected at study sites in Argentina (1: El Destino and 2: Parque Luro), Brazil (3: Itirapina and 4: Brasília), and Colombia (5: Carimata and 6: Wakoyo). Black arrows: migratory route of temperate populations, red and blue arrows: migratory routes of breeding tropical populations. Data from Jahn et al. (2013a, b)

7.3 Breeding Period

Reproduction is one of the most costly events in the annual cycle of migratory birds, with constraints on individual condition, survival, timing and duration of feather molt, migration, and future reproduction (Romero 2002). For a migratory bird, the chances of successfully reproducing in any given year in large part depend on appropriately timing spring arrival to the breeding site, with an earlier arrival often increasing the probability of successfully raising a brood (e.g., Smith and Moore 2005). Because timing of spring migration is dependent on numerous factors, such as winter habitat quality (e.g., Studds and Marra 2005), which can ultimately affect breeding success (Marra et al. 1998; Inger et al. 2010; Harrison et al. 2011), understanding the underlying drivers of breeding success in a migratory bird requires information from across multiple seasons.

7.3.1 Reproduction of the Fork-tailed Flycatcher

Fork-tailed Flycatchers arrive at breeding sites from August–October, depending on the latitude of the breeding site. At tropical latitudes in Bolivia or Brazil, they arrive as early as late August (Jahn unpublished data), whereas individuals breeding at temperate latitudes in Argentina arrive on the breeding grounds in October (Jahn et al. 2014). Fall migration begins in January and February (Jahn et al. 2013a, 2016a), although tropical populations (e.g., in Brazil) begin fall migration earlier than do populations breeding at south-temperate latitudes (Jahn et al. 2013a, 2016b; MacPherson et al. 2018). Despite these differences in migration timing, the length of the breeding period of temperate- and tropical-breeding populations is about 3 months (Jahn et al. 2013a, 2017).

Reproductive effort in this species is also latitude-dependent. Populations breeding at south-temperate latitudes lay on average larger clutch sizes than tropical-breeding populations (3.5 ± 0.06 eggs, 2.9 ± 0.06 eggs, respectively; Jahn et al. 2014), as well as rear larger broods (Argentina: 3.3 ± 0.1 nestlings) than tropical-breeding populations (Bolivia: 2.3 ± 0.1 nestlings; Jahn et al. 2014). This pattern is maintained when sedentary populations are considered, and which have the lowest annual reproductive output (Colombia: 2.5 ± 0.5 eggs, Jahn et al. 2017; Belize: 2.6 ± 0.7 eggs, Teul et al. 2007). Therefore, Fork-tailed Flycatchers breeding at temperate latitudes, which migrate the longest distance, exhibit a higher annual reproductive investment than either intra-tropical migrants or residents.

7.3.2 Tradeoffs Between Reproduction and Molt

Birds must often face a tradeoff between breeding and molt, a relationship that has been experimentally documented (Nilsson and Svensson 1996). High reproductive investment can delay molt (Dawson et al. 2000) and the need to undergo post-breeding molt can have consequences on current reproductive output (Morales et al. 2007; Mumme 2018). High reproductive investment can also reduce individual condition (Done et al. 2011), in turn negatively affecting future reproduction and molt (Lessells 1986; Stearns 1992). A consequence of the energetic tradeoff between reproduction and molt is that, across bird species, these life-history stages typically do not overlap (Rohwer et al. 2011; Echeverry-Galvis and Hau 2013). Because the transition from reproduction to post-breeding molt and fall migration is often rapid, migratory birds must undergo fast hormonal changes (Ramenofsky 2010) and accumulate proper nutritional reserves (Lindström 1991; Rappole 2013). Thus, due to the need to migrate, as well as the energetic cost of breeding and molt, the amount of time and energy that migrants can allocate to both reproduction and molt is limited.

In migratory species, annual post-breeding molt is highly variable and may occur during the summer after breeding, in fall, or in winter. It can even begin in one area and be completed in another area (Newton 2008). Variation in timing of molt even occurs across a species' range (Hemborg et al. 2001) and can be dependent on age or sex (Siikamaki et al. 1994; Hemborg and Merilä 1998; Dietz et al. 2013). A potential compromise is a reduction in the amount of overlap between breeding, molt, and migration (Barta et al. 2008; Newton 2008). Temperate-breeding populations living in higher latitudes and experiencing a shorter summer often delay molt until after fall migration (Newton 2008). Alternatively, populations breeding at lower latitudes, including intra-tropical migrants, may not experience the same energetic constraints, due to more predictable resource availability in tropical systems (reviewed by Johnson et al. 2012), and therefore may more often molt while breeding. Nevertheless, due to a lack of information on the life-history strategies of the majority of intra-tropical migrants, such a pattern has yet to be widely evaluated.

Because South America's climate is buffered from the seasonality typical of Palearctic and Nearctic regions, the level of food resource availability on much of the continent is likely to also be relatively seasonally stable, thereby buffering food resource limitation between the end of breeding and the beginning of molt. However, given that laying larger clutches and migrating longer distances requires a greater energy expenditure, we would expect that long-distance migratory populations face a stronger tradeoff between molt, migration, and breeding than do short-distance migrants, or between molt and breeding relative to sedentary populations.

Here, we present evidence in support of an energetic constraint between reproduction, molt, and migration in the long-distance migratory Fork-tailed Flycatcher. Because annual reproductive investment in Fork-tailed Flycatchers increases with migratory distance (see above), a tradeoff between reproduction and molt should be highest in temperate-breeding populations. If the breeding period overlaps with the beginning of molt, it could be expected to overlap minimally in temperate breeders, moderately in tropical-breeding populations, and highest in sedentary populations. In lLong-distance migratory Fork-tailed Flycatchers breeding in Argentina (Buenos Aires and La Pampa), 30% of individuals showed trace body molt (i.e., a few molting feathers) during reproduction (Jahn et al. 2016a, b), but no individuals overlapped reproduction with flight feather molt (Jahn et al. 2017). However, following fall migration, the percentage of individuals (both young and adult flycatchers) undergoing body molt exceeded 85% (Jahn et al. 2016a, b). No individuals of either temperate or tropical populations molted flight feathers (wing or tail feathers) during reproduction (Jahn et al. 2017). Instead, the majority of migratory individuals molt both body and flight feathers while on the wintering grounds regardless of breeding latitude (Jahn et al. 2016a, b). Sedentary males, however, show a high overlap of body molt with reproduction (Jahn et al. 2017). These results support the pattern of an absence in overlap between the timing of reproduction and that of molt in migratory populations, but not in sedentary populations. Thus, at least for males, a stronger energetic tradeoff between reproduction, fall migration, and molt likely exists in migratory but not sedentary Fork-tailed Flycatchers.

7.3.3 *Tradeoffs Between Sexual Selection and Migration Impacting Secondary Sexual Traits in the Fork-tailed Flycatcher*

Fork-tailed Flycatchers may have traits that are molded by both sexual as well as natural selection. Fork-tailed Flycatchers show extreme sexual dimorphism in the tail length, with male tail length being 40% longer than in females (Tuero unpublished data). Sexual selection is likely the evolutionary mechanism driving the evolution of the extreme tail length in this species, as has been observed in other bird species with long tail (e.g., Andersson 1982; Møller 1988). In these cases, females (e.g., *Euplectes progne* and *Hirundo rustica*) show a preference for long-tailed males. Additionally, long-tailed male Forked-tailed Flycatchers mate with long-tailed females (Tuero unpublished data). Thus, a preference for a longer tails during mate choice is at odds with the value of shorter tails that reduce aerodynamic cost during migratory flight (Pennycuick 2008). As there is a genetic linkage between preference and secondary sexual traits, it is possible that elongate tail sizes can evolve to exceed the aerodynamic optimum size (Evans and Thomas 1997), resulting in significant energetic flight costs. Given the benefits to early arrival on the breeding grounds in spring (Bejarano and Jahn 2018), tail length of migratory males has the potential to act as a signal of fitness, if females prefer males that arrive to the breeding site early and also have a longer, less aerodynamically efficient tail. Nevertheless, residents should evolve longer tails than migrants, since residents do not have to pay the aerodynamic cost of migration.

Research supports such a scenario, since resident male Fork-tailed Flycatchers have on average longer tails than migratory males (sedentary: 25.7 ± 0.4 cm, $n = 28$; migratory: 23.5 ± 0.3 cm, $n = 210$; Tuero unpublished data). This result supports the potential of a tradeoff between sexual selection and migration in this species. To better understand this tradeoff, future research regarding sexual and natural selection in migratory birds should investigate whether tail morphology may affect the migratory routes used by the species, and what role tail morphology could play in adopting optimum migratory strategies (e.g., routes, timing, rate of migration) that minimize the energetic cost of migration.

7.4 Migratory Behavior

7.4.1 *Fall Migration*

After breeding, Fork-tailed Flycatchers prepare for their northward journey to their non-breeding grounds in northern South America. For those breeding in southeastern Brazil, fall migration begins in January (Jahn et al. 2016b), whereas those breeding in central Argentina begin fall migration primarily in February (Jahn et al. 2013a). This difference between populations in the initiation of fall migration may be related to differences in the phenology of available food resources or environmental factors in each region, although such a pattern has yet to be evaluated. A recent study of factors associated with migratory behavior showed evidence that seasonal increases in rainfall were positively correlated with the locations of Fork-tailed Flycatchers after the breeding season (MacPherson et al. 2018). Given that the timing of plant phenology (i.e., leafing, flowering, and fruiting, Patrícia et al. 2000; Gottsberger and Silberbauer-Gottsberger 2006; Myneni et al. 2007; Araujo et al. 2017) and arthropod abundance (Pinheiro et al. 2002; Amorim et al. 2009) is positively associated with rainfall, and because these are food resources consumed by Fork-tailed Flycatchers, the migration of this species likely tracks seasonal abundance of such food resources.

Whereas Fork-tailed Flycatchers breeding in Argentina migrate in fall directly to the non-breeding grounds (over a period of about 2–3 months; Jahn et al. 2013a; Jahn unpublished data; Fig. 7.4), individuals breeding in Brazil appear to employ one of the two fall migration strategies (Fig. 7.4). Some individuals first stopover in southwestern Brazil for approximately two weeks, before moving to the wintering grounds, while others migrate relatively directly (over about a 1-month period) to the northern South American wintering grounds (Jahn et al. 2016b). One possibility for why some flycatchers make a prolonged stopover in southwestern Brazil is to begin feather molt (Jahn and Guaraldo 2018). Such a behavior is known to occur in conspecific Western Kingbirds (*T. verticalis*), which employ a fall molt-migration (i.e., migration to a site specifically to molt feathers) to southwestern North America on their way to tropical wintering grounds (Barry et al. 2009; Jahn et al. 2013b). This also occurs in intra-tropical migratory Lesser Elaenias (*Elaenia chiriquensis*, Guaraldo et al. 2016). Fork-tailed Flycatchers undergo a post-migration flight feather molt (Pyle 1997; Jahn et al. 2016b); however, exactly when the flight feather molt begins is still unknown.

7.4.2 Molt During Fall Migration

Molting is not only an energetically costly process, but also one that produces a great impact on other biological functions. For instance, body molt can affect body thermoregulation (Dawson and Maloney 2004), which can in turn determine when and where the molt occurs. Flight feather molt can influence flight performance, as the replacement feathers reduce wing area (Hedenström 2003), which has been associated with a reduced escape capacity in some species (Williams and Swaddle 2003), potentially leading to survivorship costs during molt. The typical separation of migration and molt is expected to be a result of these factors, in addition to the potential energetic tradeoffs mentioned previously. In this section, we evaluate how the timing of fall migration and molt interacts in Fork-tailed Flycatchers and explain how generalizable these patterns are to other migratory birds in South America.

It appears that at least some migratory Fork-tailed Flycatchers actively molt remiges (i.e., flight feathers on the wings) while migrating in fall (Jahn et al. 2016a, b), as do some birds in other migration systems (Newton 2011). Molt-migration in the Fork-tailed Flycatcher was shown through capturing and measuring molt of 11 first-year and 22 adult Fork-tailed Flycatchers (7 females and 15 males) upon their arrival to their non-breeding grounds in eastern Colombia, at Reserva Natural y Productiva Tomo Grande, Vichada Department, Colombia (4.9°N, 70.2°W; Jahn et al. 2017). Three of these adults (two females and one male) were actively molting primaries (primary numbers three or four). However, none of the first-year flycatchers measured during late fall migration were undergoing flight feather molt, none of either age group sampled during late fall were undergoing tail feather molt, and most had no body molt. That two of the three flycatchers molting primary feathers during late fall migration had a clavicle half-filled with fat suggests that these flycatchers had not yet finished migrating, because no fat, trace fat, or a thin layer of fat is typical of flycatchers overwintering in Colombia (Jahn unpublished data).

Given that none of the first-year flycatchers sampled were actively molting remiges, it is possible that first-year flycatchers are too inexperienced at migrating and surviving to invest energy into both molt and migration simultaneously during their first migratory journey. Indeed, young birds often migrate more slowly than adults (Newton 2010), suggesting that the first migration is challenging enough without incurring further costs such as molt.

Molting prior to the wintering period, as observed in some flycatcher adults, may be possible in the population of Fork-tailed Flycatchers breeding at tropical latitudes, due to their lower reproductive investment (see above). Testing why some Fork-tailed Flycatchers overlap fall migration with molt—at least at the late stages of fall migration—may provide important insights into how the annual cycle of these birds is shaped. Other migratory species of this system belonging to the same family (i.e., Tyrannidae) have breeding populations at both tropical and temperate latitudes (e.g., *T. melancholicus, Pyrocephalus rubinus,* and *Elaenia parvirostris*), and also overwinter in northern South America. Therefore, the molt pattern described here would likely be observed in other migratory birds in South America. Comparative research across migratory systems could also show how common this behavior is in South America vs. other continents, and if so, why.

7.4.3 Spring Migration

Spring migration is much faster than fall migration and is assumed to be the result of a time-selected migration strategy in many migratory passerine birds (Alerstam and Lindström 1990; Alerstam 2011). Because spring migration marks the beginning of movements toward the breeding grounds, individuals that are among the earliest to arrive and those that arrive in good condition may have an advantage in acquiring high quality territories and mating opportunities. In Fork-tailed Flycatchers breeding at tropical latitudes, spring migration has been documented as lasting an average of 27 (±2.8) days at a rate of 129 km/day (±19.0, Jahn et al. 2016b), while fall migration has been shown to take an average of 59 (±13.2) days at just 69 km/

day (±13.7, Jahn et al. 2016b). Male Fork-tailed Flycatchers that arrived at a tropical breeding site earlier than other males had greater success in obtaining a mate, and nests that were laid earlier had a higher success of fledging than later nests (Bejarano and Jahn 2018). Although studies have yet to correlate breeding success with physiological condition of individuals (males or females) upon arrival in a Neotropical austral migrant, Bejarano and Jahn (2018) showed that seasonal reproductive output of females was driven in part by the arrival date of their male mate. These results provide support that spring migration in Fork-tailed Flycatchers is at least partially time-selected, as has been shown in other long-distance migratory passerines.

7.4.4 Physiological Preparation for Spring Migration

Preparations for spring migration include hyperphagic fueling that may require a diet-switch from primarily consuming arthropods to consuming fruit in migratory Fork-tailed Flycatchers. A diet-switch to more fruit may be important for the accumulation of specific pre-migratory fats to be used during migration. In a recent test of the hypothesis that migratory Fork-tailed Flycatchers switch their diet to fruits prior to spring migration (MacPherson unpublished data), results confirmed that austral migrant Fork-tailed Flycatchers physiologically prepare for spring migration in a similar way as do birds that migrate to North American and European breeding grounds (i.e., by fueling on C_{18} fatty acids from fruit, Bairlein 2002; McWilliams et al. 2002; Price 2010).

Fruit is likely an excellent energy source for fueling spring migration of flycatchers, as it has high concentrations of polyunsaturated fatty acids (PUFAs), which have lower boiling points than more saturated fatty acids and may thus be more easily mobilized during migratory flights. However, PUFAs contain less energy and produce harmful by-products during metabolism (Jones 2008; Price 2010). Unlike more saturated fatty acids, PUFA metabolism produces reactive oxygen species (ROSs), which can cause oxidative damage throughout the body (Wagner et al. 2004; Skrip and McWilliams 2016). Long-chain PUFAs are found at especially high concentrations in plants (Bairlein 1991; Brett and Muller-Navarra 1997; Wannes et al. 2010), and despite the potential negative impact of metabolizing PUFAs, families of passerine birds that migrate long distances all include species that are at least partially or seasonally frugivorous (Bairlein 2002; Chesser and Levey 1998). Although PUFA metabolism creates dangerous ROSs, these can be squelched by antioxidants, as documented by a growing body of literature exploring the role of dietary antioxidants (carotenoids) that could combat the harmful by-products of PUFA metabolism (Alan et al. 2013; Boyles 2011; McWilliams et al. 2004). To improve our understanding of the potential physiological consequences and solutions of a diet-switch to fruit in preparation for spring migration, future research should aim to link this pattern in fatty acid profiles from Fork-tailed

Flycatcher tissues more directly to their food choices, as has been done in some other species (see Boyles 2011).

7.4.5 *The Importance of Wet-Dry Cycles in Timing Migration*

During both spring and fall migration, Fork-tailed Flycatchers may be tracking with the dominant environmental factor driving seasonality in South America: rain. In a recent study, the locations of Fork-tailed Flycatchers positively correlated with high rainfall during both fall and spring migration (MacPherson et al. 2018). Although there is agreement among climate models for projected changes in temperature, it remains unclear how changes in the amplitude or distribution of precipitation will affect the availability of resources worldwide (Tulp and Schekkerman 2008). It is also unclear how changes in the timing, duration, amount, and location of South America's wet seasons could alter migratory patterns or stopover use for migratory birds in South America. While predictability in the timing and location of seasonal rainfall is likely important in driving increases in seasonal food resources (such as arthropods and fruit) upon which migrants such as Fork-tailed Flycatchers rely to prepare for spring migration, wet-dry cycles in South America are known to be highly variable (Wolda 1978; Jahn et al. 2010; Morán-Tejeda et al. 2016; Osman and Vera 2017). Long-term tracking studies of migratory birds in South America are needed to improve our understanding of how the timing of ephemerally abundant food resources affects time-selected migration strategies of Fork-tailed Flycatchers and other species, and how different populations across a species' range may respond to changing patterns in rainfall.

7.5 Conclusions

7.5.1 *Breeding*

We have shown here that migratory populations of Fork-tailed Flycatchers do not overlap major life-history events (i.e., reproduction and molt). Additionally, we have shown that temperate-breeding populations may experience a higher overall cost of reproduction due to a larger reproductive investment than tropical-breeding populations, whereas the sedentary population has a higher overlap between reproduction and molt. Therefore, the need to migrate may provide sufficient constraints so as to delay molt until winter. There remain gaps in our knowledge of whether the higher investment in breeding observed in temperate populations could constrain other aspects of their life history, including but not limited to the timing of migration, number of stopovers, or migration speed.

7.5.2 *Migration*

Fall migration patterns of Fork-tailed Flycatchers depend to a large extent on breeding latitude. We found that tropical populations followed two different migratory routes during fall migration. One is northward, more or less directly to the wintering grounds, similar to the migratory route of temperate populations. Another route taken by some tropical breeders involves an unexpected behavior never before described for a migratory bird in South America, in which fall migration first proceeds southwestwards. Those individuals move almost 1000 km to a stopover site prior to departing northward to the wintering grounds using the same route as that used by southern (temperate) populations. Our findings suggested that these individuals that made a stopover to the southwest of their breeding site do so to begin molt, which is later completed at winter sites in Colombia and Venezuela. These differences support the idea that temperate and tropical populations have different life-history strategies resulting in divergent migratory and molt schedules. This newly discovered migratory pathway in South America raises new questions about how this species uses fall stopover sites and why they move throughout winter. More importantly, to what extent is this fall migration pattern shared with other migratory birds on the continent? If shared widely, the annual cycle of migratory birds in South America may be substantially more complex than is currently appreciated.

Overall, much of the annual cycle of Fork-tailed Flycatchers may be for the most part explained by seasonal patterns in rainfall. This is not surprising, given that seasonality in most of South America is determined by wet-dry seasons, rather than hot and cold seasonality, as at north-temperate latitudes. However, it remains unclear whether flycatchers follow the rain because of precipitation-induced increases in food abundance (e.g., for migratory fattening or to fuel molt) or for other reasons. Recent studies showing migratory routes of this species across the Amazon Basin can also elucidate if and how this open habitat species uses stopover sites while crossing the planet's largest rainforest habitat.

7.6 Avenues for Future Research

Bird migration in South America comprises a highly diverse set of movements by a diverse set of species that move across a continent that harbors a wide variety ecosystems (e.g., temperate forest, Patagonian steppe, tropical forest, savannas, and arid woodland), such that gaining a more thorough understanding of the complex suite of drivers that shape this migratory system will require a long-term, imaginative research effort that spans a wide range of disciplines and employs the latest techniques and technologies. Yet, uncovering the proximate and ultimate drivers of bird migration in South America holds promise for addressing questions about the evolution of migration of birds that are part of various migratory systems, since intra-tropical bird migration may reflect the evolutionary origins of migration of species that breed at temperate latitudes (Chesser and Levey 1998; Boyle and Conway 2007; Stutchbury et al. 2016).

One major gap in information is a basic description of the annual cycle of most migratory birds in South America. Once a basic description of the annual cycle of a given migratory bird population is accomplished, research on the mechanisms driving its migratory patterns can be attempted. Such mechanisms are most likely to represent a complex set of genetically and environmentally molded interactions (e.g., Bell 2005) that are age- and sex-dependent. Thus, proximate drivers of bird migration in South America are likely highly population-specific and vary over time.

Given the available techniques and technologies, one area in which progress could be made is on the mechanisms that regulate the timing and pace of bird migration in South America, which could be accomplished by comparing gene expression prior to and during migration (e.g., Franchini et al. 2017). From an applied research perspective, understanding how vulnerable different migratory populations are to climate change can be aided by population genomics research (Bay et al. 2017).

Another open area of research in South America is about how events in one season of a migratory bird's annual cycle affect those in other seasons (i.e., carry-over effects; reviewed by Harrison et al. 2011). Understanding such processes can elucidate not only the drivers of a given migratory strategy (e.g., that some birds are able to migrate earlier than others in spring because of better winter conditions), but also the mechanisms that influence individual fitness and population level regulation, since carry-over effects have the potential to limit reproductive success (Harrison et al. 2011).

That bird migration on the continent that is home to the greatest diversity of birds in the world is still poorly understood represents a major obstacle toward the development of effective conservation actions to conserve South American migratory birds and the habitats they depend upon. To fill this gap, it is imperative that future research improves our understanding of the details of the annual cycle of these fascinating animals.

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Chapter 8
Visual and Acoustic Communication in Neotropical Birds: Diversity and Evolution of Signals

Ana S. Barreira and Natalia C. García

8.1 Avian Communication

Communication is the process through which a sender emits a signal that confers information to a receiver, who subsequently elaborates a response elicited by that information. True communication is an active action in which the objective of the sender is to confer the receiver with certain information that would provoke a desired answer while the receiver also obtains some sort of benefit by accessing this information (Bradbury and Vehrencamp 1998).

Birds communicate with each other for a great array of purposes including intraspecific interactions with the opposite sex for mating, to defend their territory from same sex individuals, to request food to parents, among others. Also, communication occurs interspecifically for species recognition, defense from predators, and interactions between host and nest parasite species. The information being passed in the process of communication may involve some indication of the characteristics of the sender (e.g., species, sex, health condition, and aggressiveness), and can also indicate the individual's current situation like reproductive state, fear, and willingness to fight. Birds also communicate with conspecifics as a defense strategy to advert others about the approaching of predators, to indicate members of a group where to find food and other resources, etc.

The most exploited signaling pathways among birds are the visual and acoustic ones. Visual signals include the coloration of plumage, gape, and bare skin patches as well as body posture displays. Acoustic signals used by birds involve mainly

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vocalizations, but also mechanical sounds produced with their wings (Bostwick and Prum 2005). Sound signals fulfill virtually the same functions in all bird species studied so far; yet they exhibit an extraordinary level of diversification. Other types of signaling, such as chemical signaling, are much less known in birds partially, perhaps, because these are much harder to study than visual and acoustic communication. Olfactory function in birds was frequently assumed to be limited, but some studies suggest that is not the case and that olfactory signals (i.e., body odor and other chemical substances) play a role in communication among birds. There is suggesting evidence that chemical signals intervene in a variety of interactions including nest location, mate recognition, detection of females' reproductive state that elicits sexual displays by males, and males' social status signaling (Hagelin and Jones 2007).

In this chapter we will focus on visual and acoustic communication of Neotropical birds, mostly of passerines, because research has been centered largely in these two signaling pathways in this avian order. Our aim is to explore some of the causes of the great diversity of visual and acoustic signals, with a particular interest in the findings from recent studies in Neotropical species. We will review recent research on the evolution of signals with special emphasis on the effect that factors such as the environment, morphology, and the receptor visual capacity have. We will go through the methods employed in the latest literature to study these signals in an objective and biologically meaningful way contemplating both the sender's production capacity and the receiver sensitivity (see Box 8.1). Among visual signals we will concentrate on plumage coloration and for the acoustic ones we'll focus on vocal sounds, but see Box 8.2 for a brief discussion on sonation (i.e., sounds produced intentionally with non-syringeal structures). Also, we include in this chapter a section about the relationship between these two communication channels and how and to what extent they counterbalance each other.

8.2 Acoustic Communication

Birds produce vocal sounds with the syrinx, a specialized structure localized where the trachea bifurcates into the bronchi. In this area, certain cartilaginous rings are incomplete, and the soft tissue that replaces them produces sounds when vibrating (Bradbury and Vehrencamp 1998). The number and location of such membranes as well as their roles in generating sound exhibit a remarkable variation among bird orders and families (Goller and Larsen 1997a, b; Bradbury and Vehrencamp 1998; Larsen and Goller 1999; Fee 2002; Mindlin and Laje 2005), and syringeal anatomy has been used for centuries to classify avian taxa (Ames 1971). For example, chickens have a tracheal syrinx (with a set of membranes in the base of the trachea), while penguins and cuckoos have a bronchial syrinx, with membranes on each bronchus at some distance of the tracheobronchial junction, and many species have a tracheobronchial syrinx, in which the syringeal membranes are located right below the tracheal bifurcation (common in the oscine passerines, Bradbury and Vehrencamp

1998; Mindlin and Laje 2005). Within the order Passeriformes, the suboscines show significant morphological diversity in their vocal organs, while syrinx anatomy is quite conserved across the oscine passerines (Ames 1971). The role that such anatomical diversity has in vocal diversification is just starting to be understood.

In the oscine syrinx the sound-producing vibrating tissues are located immediately below the trachea on each bronchus. The lateral labium is a thick tissue in the anterolateral part of the bronchial wall, connected to the third bronchial ring. The medial vibratory mass seals the medial side of the bronchi and it can be divided into two parts: a thicker one called medial labium, and a very thin one called medial tympaniform membrane (Mindlin and Laje 2005; Düring et al. 2013). The adduction of the labia closes the lumen of the bronchus and its vibration is responsible for the generation of sounds (Goller and Larsen 1997a, b; Larsen and Goller 1999). The fundamental frequencies of vocalizations are determined by the oscillation frequency of the labia, which in turn depends on the size, shape, and tension of the membranes (Mindlin and Laje 2005; Riede and Goller 2010, 2014).

The "tracheophones" is an interesting group of suboscines that includes the Neotropical families: Furnariidae (ovenbirds), Dendrocolaptidae (woodcreepers), Formicariidae (ground antbirds), Thamnophilidae (typical antbirds), Rhinocryptidae (tapaculos), and Conopophagidae (gnateaters). Only the members of this group have a set of membranes on the dorsal and ventral surfaces of the trachea, the membranae tracheales, immediately above the tracheal bifurcation and surrounded by a pair of skeletal elements known as processi vocales. The name "tracheophones" is derived from the assumption that the membranae tracheales were the primary sound source (Ames 1971), although these species also present membranes on each bronchus. A recent, detailed study of sound production in six species representing three of the tracheophone families showed that the bronchial labia are also involved in sound production and that they seem to be the main sound generators in tracheophones (García et al. 2017). This represents the largest number of sound sources described in syrinx and confirms Ames (1971) suggestion that the tracheophones actually have a "tracheobronchial" syrinx. But the results of this paper go beyond a mere description of syrinx function in a particular group of birds. Their results show how diversification of a same trait can be achieved through different adaptations. Vocal diversity in suboscines seems to be the result of the development of different morphological mechanisms, while oscines achieved diversity through a more sophisticated neuromuscular control of a conserved syringeal anatomy, which in turn required concurrent evolution of vocal learning. Both evolutionary trajectories may have played a significant role in the remarkable radiation in suboscines and oscines.

The supra-syringeal tract also plays an important role in the production of vocal signals in birds. Every non-sinusoidal periodic signal can be decomposed into a frequency spectrum formed by a fundamental frequency and a set of integral multiples of the fundamental frequency, called "harmonics." In 1987, Nowicki showed that the whistle-like sounds common in many bird songs are not pure tones, but have harmonics that are attenuated when passing through the vocal tract. This is because the vocal tract acts as a band-pass filter centered on the fundamental frequency of the song (which is determined by the syrinx). At equal cross-sectional area, the natural modes of vibration or formants of the column of air in the vocal tract depend on the length of the vocal tract (see Nowicki 1987 and references therein).

8.3 Visual Communication

Light bounces against objects differentially according to the object characteristics, and the transmission properties of the media in which it is located. Light reflected from an individual's body consists of a communication signal that is passively produced, but an individual can alter its visibility by moving to different backgrounds, blocking the vision by repositioning itself, selecting lighting scenarios, and also can produce body displays to increase its conspicuousness (Bradbury and Vehrencamp 1998). Birds have a highly developed visual system (see below) and visual signals involve a diverse set of colors produced through different mechanisms, coloration patterning within and between plumage patches, coloration of bare body parts as well as complex displays.

Colors differ in the intensity and wavelengths being reflected, emitted, or transmitted by a given surface, and can be broadly described by three properties: hue, chroma, and brightness (Montgomerie 2006). Hue refers to the range of wavelengths that are predominantly reflected, and is colloquially referred to as "color," such as blue, green, yellow, etc. Chroma defines the saturation or purity of the color as it refers to the proportion of light reflected within wavelengths similar to the hue in relation to the total range of wavelengths to which the animal is sensitive. Finally, brightness defines the non-chromatic component of colors, and represents the total amount of light reflected by a given surface. The definition of color cannot be separated from the receptor's visual capacity, since colors are defined by the visual system that perceives them (Cuthill et al. 2000). Therefore, colors are the result of light being reflected by an object and the perception and interpretation of this by the receptor's visual system. The term visible light is defined based on the human visual system, which can perceive wavelengths from 400 to 700 nanometers (nm), ranging from violet to red colors in the spectrum and this is achieved due to the presence of three types of photoreceptors in our retinas (i.e., trichromatic vision) that are sensitive to this range of wavelengths. In contrast, birds have tetrachromatic vision, with a fourth type of photoreceptor sensitive to near ultraviolet wavelengths (UV, i.e., wavelengths from 315 to 400 nm, Cuthill 2006, Fig. 8.1) and also a system of colored oil droplets located over the photoreceptors (Bowmaker et al. 1997). As a consequence of these differences the avian visual system is sensitive to both UV and visible colors, is capable of recognizing a much larger variety of colors, and has a higher color discrimination efficacy when compared to that of humans (Cuthill et al. 2000).

The spectral location of the maximum absorbance value of the short wavelength sensitive photoreceptor varies across avian orders, and sometimes even within families, with some species being more sensitive to UV than others (Ödeen et al. 2009, 2011; Ödeen and Håstad 2010). Some species, such as parrots, most passerines,

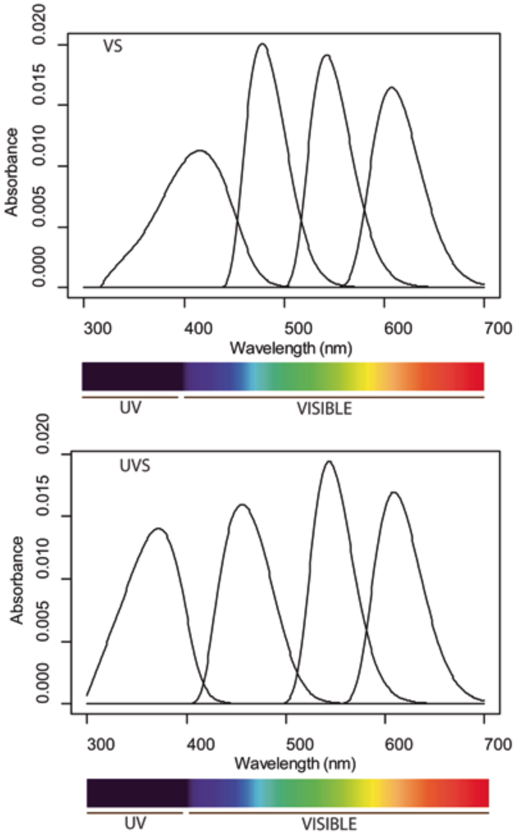

Fig. 8.1 Absorbance spectra of average UVS and VS avian vision types photopigments as a function of wavelengths from UV to red visible wavelengths. Graphs were constructed with the "sens data" function of pavo 1.3.0 package for R (Maia et al. 2013, see Box 8.1)

gulls, rheas, and one species of trogon, have a UV photoreceptor whose maximum sensitivity is located around 355–380 nm (UVS type of vision), while the ancestral avian version of the short wavelength photoreceptor has a maximum sensitivity wavelength located between 402 and 426 nm (VS type of vision, Osorio and Vorobyev 2008, Fig. 8.1). There were at least 14 switches from one type of short wavelength photoreceptor to the other across the avian phylogeny (Ödeen et al. 2011). This difference is given by the structure of the photosensitive pigment (opsin SWS1) present in the photoreceptor which can be determined by its DNA sequence codified by a single gene (Ödeen et al. 2009). Unfortunately, there are many species for which the specific sensitivity to short wavelengths is still unknown and, therefore, it needs to be approximated to the closest species for which it is known (many times very distant ones). This may be problematic for the employment of avian visual models to study color variation (see Box 8.1) given the existence of high divergence in this trait between species even at the family level (Ödeen et al. 2012). Such is the case of many Neotropical species, including all members of some very diverse families of passerines such as Furnariidae, Cardinalidae, Tyrannidae, etc., whose visual sensitivity has not been described yet.

Plumage coloration can be produced by the deposition of pigments (i.e., pigmentary colors), generated through the interaction of light with the feathers internal nanostructure (structural colors) or a combination of both. Pigments are organic molecules that absorb specific ranges of wavelengths and let others pass through, therefore acting as color filters. The most common pigments in the plumage are melanins which absorb most wavelengths in the visible range and produce dark and unsaturated colors such as gray, black, brown, rufous, and buff. Melanins are also involved in the production of iridescence (see below) and may appear forming patterns like stripes, spots, and bars among plumage patches in some species (McGraw 2006a). The second most common pigment found in bird's feathers are the carotenoids that absorb maximally medium wavelengths within the visible spectrum. These pigments produce colors in the range of orange, yellow, and red wavelengths (McGraw 2006b). Other less common pigments in birds' plumage include turacoverdin, which is responsible for the green coloration of turacos (family Musophagidae), and psittacofulvines that produce red, orange, and yellow coloration in parrots (McGraw 2006c). Yellow psittacofulvin has been found to fluoresce under UV light (Völker 1937; Boles 1990, 1991). This means that this pigment absorbs short wavelength light and re-emits it in the visible spectrum. This phenomenon is poorly known and has been studied with quantitative methods (spectrofluorometry) only in a few species, including the Australian budgerigar (*Melopsittacus undulatus*, Arnold et al. 2002; Pearn et al. 2003a) and the Neotropical blue-winged parrotlet (*Forpus xanthopterygius*, Barreira et al. 2012) where we also found sexual differences in the emission of fluorescence. It is still unknown if this property of psittacofulvines plays a signaling role or if it is only a by-product of the presence of this type of pigments (Arnold et al. 2002; Pearn et al. 2003a, b).

Structural non-iridescent colors in the plumage of birds include blue, violet, ultraviolet, and white colors which are the result of the physical interaction between light and the feathers' barbs internal structure that varies at a nanometer scale (nanostructure) in a tridimensional quasi-ordered manner. Structurally colored feathers' barbs possess an internal spongy layer composed of keratin with air vacuoles that can be spherical or rod-shaped (Prum 2006; Saranathan et al. 2012). Incident light is coherently scattered from the spongy layer and the resulting color depends on the size and spatial distribution of air vacuoles within it (Prum 2006). Some plumage colors such as green are produced by a combination of yellow pigments deposited in the cortex and the barb's internal nanostructure. Iridescence is also a structural phenomenon in which the perceived color depends on the angle of light incidence, the angle of observation, and the feather's orientation. Iridescent colors are produced at the feather's barbules through angle dependent coherent scattering of light reflected by melanosomes disposed in an array or crystal-like arrangement and can be typically observed in the plumage of hummingbirds, pigeons, and others (Prum 2006; Barreira et al. 2016 but see Igic et al. 2016).

Some structural "non-iridescent" plumage colors were shown to change in hue with changing viewing geometry (Osorio and Ham 2002; Barreira et al. 2016). Such is the case of male Swallow Tanagers (*Tersina viridis*), a Neotropical species, in which we documented a change in color from green/turquoise to deep blue as the angle between the light source and the direction of observation changes (Barreira et al. 2016). The observed change of coloration is consistent with the reflectance spectra that we registered, which changed from double-picked spectra, with a maximum reflectance peak at green wavelengths and a secondary peak in the UV region, into a unique reflectance peak in the UV-blue region as the angle between the light source and the observation direction increased (Barreira et al. 2008, 2016). This phenomenon is different from typical iridescence because it is not caused by the scattering of light by finely arranged melanosomes within feather barbules and the perceived color does not depend on the feather orientation but only exclusively on the angle conformed between the observation and illumination angles (Osorio and Ham 2002; Barreira et al. 2016). Male Swallow Tanager's plumage coloration has been shown to be produced by the coherent scattering of light from the barb's internal nanostructure (D'Ambrosio et al. 2017, 2018). As a result of this color change, sexual dichromatism and conspicuousness change considerably from an avian visual perspective with viewing geometry in male Swallow Tanagers, which could be taken advantage of by these birds in different situations (Barreira et al. 2016). This hypothesis needs to be tested in the field.

8.4 Some Hypothesis on Causes of Signal Diversification

Acoustic and visual signals evolution is influenced by some common factors that affect the efficacy with which these signals are transmitted and the likelihood of the intended receivers to detect them properly, such as environmental conditions. Also, as these signals mediate mate selection and intrasexual competition in many avian species, the interaction between closely related species also mediates song and plumage color evolution. Other factors like morphology and physical condition act as constraints to the elaboration and characteristics of these two kinds of signals. In the following paragraphs we review recent research studying the evolution of vocalizations and plumage coloration on Neotropical birds, and further detail some studies conducted by our own study group.

8.4.1 Acoustic Signals

Bird song can be considered as a set of multiple characters, each of them subject to different restrictions or "constraints" (Gil and Gahr 2002). Therefore, vocal traits may show different patterns of variation depending on which selection factors and/or morphological constraints have had a stronger influence on their evolution. Given the importance of bird song in mate choice and intrasexual competition, there is an extensive body of literature on the effect of sexual selection on bird song evolution (Catchpole and Slater 2008). Habitat can also act as a selective factor on song evolution, as several studies have shown that the characteristics of the habitat in which the organisms communicate could explain part of the design of the signals and their variations (Morton 1975; Ryan and Brenowitz 1985; Tubaro and Lijtmaer 2006). Additionally, since some of the structures involved in song production are fundamental to other vital functions such as breathing or feeding, song can evolve as a by-product of natural selection on non-vocal traits (Nowicki et al. 1992; Podos 1996; Podos et al. 2004a, b). We will focus on these last two factors, and the potential interaction with visual signals.

8.4.2 Singing in the Rain…Forest: Habitat as a Selective Factor on Song

The acoustic channel is one of the few that allows "long distance" communication (Bradbury and Vehrencamp 1998), but its reach is not unlimited, partly because the sound waves loss energy proportionally to the traveled distance. Additionally, the different environments in which the animals communicate impose other sources of sound attenuation and degradation, depending on their particular characteristics. In the case of bird song, it has been seen that in general the species of closed environments (rainforests and woods) produce signals of lower frequency, with notes more separated than those of open environments, like grasslands or savannahs (Morton 1975; Ryan and Brenowitz 1985; Wiley 1991; Tubaro and Lijtmaer 2006). These differences are usually interpreted as adaptations to minimize the degradation suffered by the signal when traveling through its native environment (Acoustic Adaptation Hypothesis or AAH, Morton 1975). The main source of acoustic degradation in closed environments are the reverberations (from trunks, leaves, and other elements of the vegetation) which can fill the spaces between the notes with echoes, modifying the original signal and potentially impairing its recognition by the receiver (Wiley and Richards 1978, 1982; Richards and Wiley 1980). Therefore, the AAH predicts that birds should produce songs with notes more separated in time than in open habitats. On the other hand, in open habitats it predominates the effect of "cells" or layers of air at different temperature or velocity, which impose irregular fluctuations in the amplitude of the sound wave. As a consequence, parts of the vocalization could be lost randomly (Wiley and Richards 1978, 1982; Richards and Wiley 1980), and birds in these environments would benefit from producing short notes at a high repetition rate, to generate a redundant signal to transmit the message effectively, even if part of the signal is lost randomly (Brown and Handford 1996).

As diverse environments would favor different temporal structures, the same would not be the case with the spectral variable (i.e., the frequencies used): whenever the bird is singing at least 1 m from the ground, lower frequencies would maximize the transmission of the sound in different types of environments (Wiley and Richards 1982). Therefore, the variation in the spectral aspects of the song would be related to other factors. Consistently with this, the evidence on the influence of the type of environment on the frequencies of vocalizations is contradictory. Several studies have found that closed-environment species have lower frequencies and smaller bandwidths than open habitats (Morton 1975; Shy 1983; Wiley 1991; Tubaro and Lijtmaer 2006), whereas in other species the opposite is true (Nottebohm 1975; Handford and Lougheed 1991; Tubaro and Segura 1994), and even contrasting patterns have been found within a species, as is the case of the Rufous-Collared Sparrow, a widely distributed species that occupies diverse environments (Handford and Lougheed 1991; Tubaro and Segura 1994).

8.4.3 Size Matters: Morphological Constraints

In 1980, Wallschläger (1980) compared the vocalizations of 90 species of passerines in Europe and found that the central frequency of their songs correlated negatively with their body weight. Similar results were obtained when comparing different species of birds, in passerines (Ryan and Brenowitz 1985; Seddon 2005; Price et al. 2006) and also in other groups such as pigeons (Tubaro and Mahler 1998) and tinamiformes (Bertelli and Tubaro 2002). As we mentioned previously, the fundamental frequencies of vocalizations in passerines are determined by the frequency of oscillation of the syrinx labia (Goller and Larsen 1997a, b; Larsen and Goller 1999). If the size of the structures of the syrinx covariates with body size the theory predicts that birds of larger body size will produce vocalizations of lower frequency (Bradbury and Vehrencamp 1998). In fact, the absolute size of the labia was shown to correlate directly with body size, and inversely with the fundamental frequencies of song when comparing 8 species of oscines (Riede and Goller 2014).

Though the negative correlation between body size and song frequencies is well established at a macro-evolutionary level, it is still unclear if, within a population, larger individuals produce significantly lower frequencies. Appleby and Redpath (1997) found that larger individuals in a species of owl (*Strix aluco*) produced lower frequencies, as described above. The same was found in other non-Passeriformes such as *Gavia immer* (Mager et al. 2007) and also in Passeriformes such as *Hirundo rustica* (Galeotti et al. 1997), *Luscinia svecica* (Turčocová et al. 2010), and *Malurus coronatus* (Hall et al. 2013). However, no relationship between frequency and body size was found in males of two other species (*Serinus serinus* and *Junco hyemalis*, Cardoso et al. 2008). Therefore it remains unclear if song could convey information about the emitter such as its body size.

As we also explained before, the resonance properties of the supra-syringeal structures also play a key role in sound production. If the vocal tract is modeled as a tube, longer vocal tracts will have lower fundamental resonance frequency and vice versa. This could explain why species with longer beaks produce songs with lower emphasized frequencies (Palacios and Tubaro 2000) and also the changes in beak gape observed in singing birds (Westneat et al. 1993). Changing the vocal tract length by changing the beak gape would allow a bird to track the different fundamental frequencies that are normally present in a song. Consistently, measurements in singing birds showed that beak gape is wider when higher frequencies are being emitted (Westneat et al. 1993; Hoese et al. 2000).

Beak morphology also affects the temporal parameters of song, particularly the pace at which song notes are produced. For example, in several species of birds that produce trills (rapid succession of similar or equal notes in all or part of the song), it has been seen that species or individuals with larger beaks produce trills with lower note rates (Podos 2001; Podos et al. 2004b; Huber and Podos 2006). The reason for this would be that larger beaks are associated with a more robust jaw musculature which allows greater bite forces (van der Meij and Bout 2004) but in turn may limit the speed at which the beak can be opened or closed to emphasize the different fundamental frequencies of the song (Herrel et al. 2005).

8.5 Two Study Cases in the Neotropics

8.5.1 Inter-Specific Variation: Unraveling the Roles of Body Size, Beak Size, and Habitat in the Evolution of Song in the "Blue" Cardinalids

Given the allometric relationship between body size and beak dimensions, it is not always easy to identify the different effects they may have on song evolution/diversification. And, as both song frequencies and temporal structure can also be strongly influenced by the characteristics of the habitat in which the birds communicate, it is fundamental to take into account habitat type when analyzing the effect of other factors.

We analyzed vocal variation in relation to different morphological traits in a group of closely related passerines, the "blue" clade of Cardinalidae family (sensu Klicka et al. 2007; hereafter referred to as the blue cardinalids). The blue cardinalids are a widespread group of New World songbirds, comprising species of the genera *Amaurospiza*, *Cyanocompsa*, *Cyanoloxia*, and *Passerina*. Like most cardinalids, they produce rich and complex vocalizations (Ridgely and Tudor 1989; Orenstein and Brewer 2011). We had previously shown that differences in body size were related to song variation among three species of the clade (García et al. 2014). Our objective was to test if body size and beak morphology have had an effect in shaping bird song within this group, and to determine which of the different aspects of vocal phenotype were affected by them.

To do so, we assembled three datasets: song recordings, body weight data, and beak dimensions. Our main data source were biological collections: most recordings came from sound libraries, body weight data came from information of museum specimens tags that had been digitized, and beak dimensions were taken on museum skins from four ornithological collections (García and Tubaro 2018). We analyzed one song per individual of 13 out of the 14 species in the clade, covering most of the species ranges and their subspecies (mean ± SD of individuals per species: 14.56 ± 9.96; range: 6–43). We used a software (Raven v1.4, Bioacoustics Research Program 2011) to generate spectrograms and measure on them four spectral variables: minimum, maximum, and emphasized frequencies (i.e., the highest and lowest frequencies, and the frequency produced at the highest amplitude) and bandwidth (the difference between the maximum and minimum frequencies). We also measured five temporal parameters (song duration, mean note and inter-note interval duration, number of notes, and note rate). We used body mass as a proxy of body size, and took three linear measurements to estimate beak size (depth, width, and length). As these data were obtained from different specimens, we used the mean values per species to calculate the phylogenetic residuals (Revell 2009) of beak length, width, and depth on body mass, based on the tree topology and branch lengths of the Bayesian multilocus estimation of Bryson Jr et al. (2014).

We used phylogenetic generalized least squares (PGLS, see Martins and Hansen 1997) to evaluate the correlation of each of the nine acoustic parameters with body mass and the phylogenetic residuals of each of the three beak measurements. The acoustic variables were also natural log-transformed prior to the analyses. We used the tree topology and branch lengths of the species tree reconstructed by Bryson Jr et al. (2014) from a multilocus dataset and calculated the PGLS models using the "gls" function of the "nlme" package (Pinheiro et al. 2018) for R (R Core Development Team 2017). We considered a Brownian motion model of character evolution and fit the model by the maximum likelihood method. To control for a possible effect of habitat characteristics we assigned each species to one of the three habitat types (open, semi-open, or closed) according to the primary environment designated for each of them according to Stotz et al. (1996). Then, each of the 36 base linear models (acoustic variable ~ morphological trait) was compared to other two models where habitat type was included as an additive or interactive factor. We identified the best-fit model based on the second order bias corrected AIC value (AICc) for each one.

We found that variation in spectral parameters is correlated to body size, while the pace of notes production is related to beak length (see Fig. 8.2). But, notably, song evolution within this group has apparently been independent of the habitat type, similar to what some previous studies had found in other Neotropical groups like the tanagers (Mason and Burns 2015). Maximum, minimum, and emphasize frequencies of song decrease as body size increases, which is congruent with previous results in both passerines and non-passerines (Ryan and Brenowitz 1985; Galeotti et al. 1997; Tubaro and Mahler 1998; Bertelli and Tubaro 2002; Seddon 2005; Price et al. 2006; Mager et al. 2007; Hall et al. 2013; Mason and Burns 2015). Our results are particularly interesting considering that size variation is not extreme in this group of species, and that it has been argued elsewhere that song learning could "mask" the constraint imposed by morphology (see, for example, Cardoso et al. 2008).

A negative relation between beak size and rate of note production has been found in the trilled songs (i.e., with series of notes or groups of notes repeated at a constant rate) of oscines (Podos 2001) and suboscines (Derryberry et al. 2012). Our results are the first, to the best of our knowledge, to show a similar relationship in species with vocalizations where the notes are not equal nor occur at regular intervals as in a trill (but see Badyaev et al. 2008 for an example at the intra-specific level in partially trilled songs). Previous studies had also found that body mass correlated with certain temporal parameters of song, such as the duration of the notes, the pauses

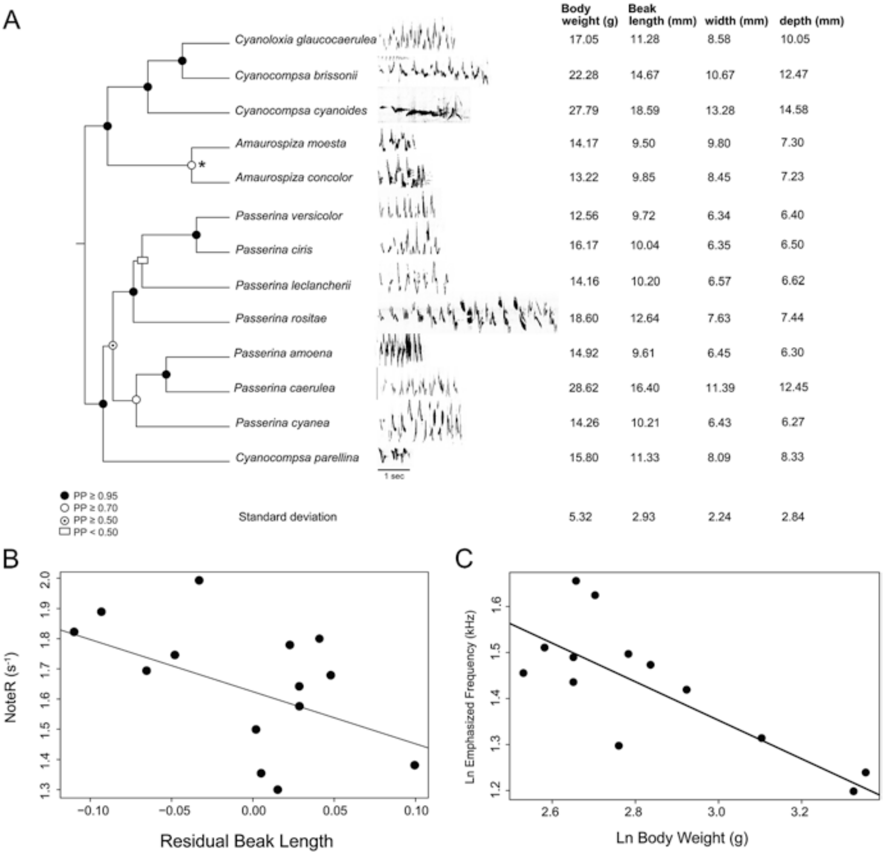

Fig. 8.2 (**a**) Tree topology depicting the relationships between the "blue" cardinalids used for PGLS regressions and based on the species tree reconstructed by Bryson Jr et al. (2014). Mean values per species and standard deviation of the morphological predictors are shown, along with a representative song for each species. Spectrograms are based on recordings from the Cornell University Macaulay Library (CUML): *Amaurospiza concolor* (CUML 130404); *A. moesta* (CUML 20247); *Cyanocompsa brissonii* (CUML 171724); *C. cyanoides* (CUML 55262); *Cyanoloxia glaucocaerulea* (CUML 67599); *Cyanocompsa parellina* (CUML 184333); *Passerina amoena* (CUML 106549); *P. caerulea* (CUML 105519); *P. ciris* (CUML 105233); *P. cyanea* (CUML 26418); *P. leclancherii* (CUML 16952); *P. rositae* (CUML 55473); and *P. versicolor* (CUML 16954). *Note: Bryson Jr et al. (2014) found that *A. concolor* was paraphyletic and that *A. c. aequatorialis* was more closely related to *A. moesta*. Because all the analyzed recordings of *A. concolor* but one are *A. c. aequatorialis*, we used the corresponding branch length. (**b**, **c**) Examples of two acoustic variables that showed significant relationships with morphology: note rate vs. beak length (**b**) and emphasized frequency vs. body mass (**c**). (Modified from García and Tubaro 2018)

between notes, or the note rate (García et al. 2014; Mason and Burns 2015). Given the allometric relationship between beak and body size, such results may actually be due to differences in beak morphology (not considered in those studies) being reflected by the differences in body size.

8.5.2 Intra-Specific Variation: Song Dialects in Zonotrichia Sparrows

Many bird species studied to date show some level of intra-specific geographical variation in their songs. “Dialects” are a particular form of variation where discrete song variants with sharp geographic boundaries can be recognized (Podos and Warren 2007). Dialects have now been described in several species, showing that dialect systems vary significantly in terms of the acoustic features that define them, their geographical range, and their temporal stability (Podos and Warren 2007).

Marler and Tamura (1962, 1964) first described the highly localized song types of different populations of White-Crowned Sparrow (*Zonotrichia leucophrys nuttalli*) within the San Francisco Bay area, each of them with very small geographical ranges. After that, studies at different geographical and time scales, and comparing resident and migratory populations have revealed that, for example, subspecies that migrate farther have larger dialect ranges (Chilton et al. 2002) and dialects with larger ranges are more stable through time. What seems to be constant across the dialect systems of different subspecies of the White-Crowned Sparrow and other North-American *Zonotrichia spp*. is that song variants are apparently “neutral” in terms of advantages for long-range communication (Ramsay and Otter 2015). Their distribution is more likely a consequence of population changes, such as local extinctions and colonization of empty patches of habitat (Baker 1975). Taken together, this has led to the notion that song dialects originate mainly due to limited dispersal and cultural drift (Toews 2017). However, the Neotropical cousin of the *Zonotrichia* “family” has a different story to tell.

The Rufous-Collared Sparrow (*Zonotrichia capensis*) is the only species in the *Zonotrichia* genus with a Neotropical distribution, from Chiapas, Mexico, to Tierra del Fuego, Argentina. Its song has two parts: an introductory theme and a final trill (Nottebohm 1969). Significant geographical variation has been found in the duration of the interval between consecutive notes of the trill, the trill interval, defining dialects in this species (Nottebohm 1969, 1975; Handford and Lougheed 1991). However, contrary to what happens in the other *Zonotrichia spp*., there is a strong relationship between the trill dialects of the Rufous-Collared Sparrow and the vegetation types in which they are found: trill intervals are longer in closed (forested) habitats than in open habitats (Nottebohm 1969, 1975; Handford 1981, 1988). Therefore, the dialects in this species are parsimoniously explained by the AAH, with juvenile males more likely to learn songs that have been less degraded by the environment (Hansen 1979; Lynch 1996).

Dialects in this species also occur at a micro-geographical scale. In 1993, Tubaro and Segura described two distinct trill dialects within Estancia El Destino, a private reserve of approximately 18 km^2 adjacent to the river coast on the northeast of Buenos Aires province, Argentina. If an imaginary transect perpendicular to the river coast is followed 7 km inland, one encounters three different habitats: marshland (from the river banks to ~0.4 km inland), talar woodland (0.4–2.5 km inland from the river), and steppe grassland (2.5–7 km inland). Detailed descriptions of these communities can be found elsewhere (Parodi 1940; Cabrera 1949, 1976), but the main difference among them is that the marsh and the steppe can be described as “open” habitats in terms of vegetation coverage, while the talar woodland is a “closed” habitat. Tubaro and Segura (1994) found that the sparrows singing in the steppe had songs with a trill interval significantly shorter than that of the individuals singing in the woodland, and distinguished a “talar” dialect versus a “steppe” dialect. The sparrows from the marsh produced trills with short interval as well, though due to small sample sizes they were not considered in statistical analyses.

Kopuchian et al. (2004) returned to the same study site 13 years later and compared their recordings to those made in 1987 (Tubaro and Segura 1994). Kopuchian et al. (2004) studied both the geographical stability of dialects (whether there had been changes in the geographical boundaries of dialects) and the stability of acoustic properties within each dialect. They found that the geographical boundaries of the dialects remained stable, as expected due to the lack of gross changes in the habitat characteristics they examined. However, within each dialect there had been some changes, for which they suggested three alternative explanations: that there had been subtle, undetected changes in habitat between 1987 and 2000 that acted as a selection pressure on song evolution; that the observed variation was a response to changes in the environment that occurred before the first time point sampled (1987) but there had been a delay in the adaptation of dialects to changes in the acoustical characteristics of the environment; or that the changes were the result of neutral change as a result of copying errors over time.

To try to better understand dialect evolution in this species, we returned to the same transect in north-eastern coastal Buenos Aires province in 2010 and 2011 and recorded and analyzed the songs of 184 Rufous-Collared Sparrows (García et al. 2014). We generated a spectrogram for each recording and then selected a song to analyze. On each song (one per individual) we measured a series of time-frequency and frequency-related variables. We measured the duration of the entire song, the introductory theme and the final trill, the number of trill notes, and the duration of trill interval (TI, in ms, calculated as the trill duration divided the number of trill notes -1). Trill duration was measured from the middle of the first note of the trill to the middle of the last note. For both the theme and the trill we measured the maximum, minimum, and emphasized frequencies and calculated the bandwidth.

The first question we wanted to answer was if the differences between dialects (and their boundaries) have remained similar after 24 years. To do so, we looked for differences in all the measured song parameters between the dialects of open and closed habitats for the 2010–2011 seasons, and compared those results to those obtained previously (Tubaro and Segura 1994; Kopuchian et al. 2004). Adding a third time point also allowed us to examine if the differences within dialects detected by Kopuchian et al. (2004) had increased, remained stable, or reverted. The first two options (increase or stable) would be possible under any of the scenarios proposed by Kopuchian et al. (2004): undetected changes in the environment (actual or past) acting as pressures to change song, or neutral change. However, reversions in changes detected between 1987 and 2000 characters would go against the hypothesis of variation in song being adaptive and only the null hypothesis of neutral change would stand.

We found that the dialect boundaries remained stable: songs from closed habitat (talar woodland) had longer trill intervals than those from the open habitats (marshland and steppe grassland). These results are consistent with the fact that our study site is included in a natural reserve, where no significant changes in habitat structure or distribution were detected, since trill temporal structure is associated with habitat. Additionally, previous studies have shown that there are no genetic discontinuities within Argentinean populations of Rufous-Collared Sparrows; therefore, phylogeographic structure could not explain patterns of variation in vocal structure (Lougheed et al. 2013; Campagna et al. 2014). Taken altogether, this supports that the maintenance of dialects is not a genetic phenomenon but is most likely the consequence of processes of cultural selection (i.e., a process analogous to natural selection acting on traits that are inherited through learning, Crozier 2010), where habitat structure has acted as a selective factor to maintain dialect boundaries.

Trills in the closed habitat have lower frequencies than those in the open habitat, in concordance with previous findings. However, this pattern of association is not easily predicted in terms of sound transmission (see previous section). Trills from the closed habitat also had higher maximum frequencies, and therefore a wider bandwidth. The trade-off between note rate (inversely related to trill interval) and frequency bandwidth could explain the spectral differences between habitats we found. Thus, this difference between habitats may not represent an adaptive advantage but may just be a by-product of the temporal characteristics of the trill that were selected in each habitat. This is an interesting example of how a constraint imposed by a vocal mechanism, which is often associated with the idea of stasis in song evolution (Podos et al. 2004a), might actually be partly responsible for intra-specific variation in songs among close populations.

We also found that some of the changes detected by Kopuchian et al. (2004) intensified, while others reverted, and some acoustic parameters did not change from 2000 to 2010. We could not find any association of the changes that intensified with any selective factor (which of course does not mean there are not), but the reversal in some changes that had been detected in earlier studies in the absence of factors following the same patterns indicates neutral variation as the most probable explanation for those changes. As non-deleterious mutations can be fixed by genetic drift, song differences arising from learning errors can also be transmitted in a population and become fixed if they are neutral in relation to the long-range communication properties of the song, in an analogous process known as cultural drift.

8.6 Evolution of Visual Signals

Many avian species show sexual dichromatism (i.e., differences in coloration between sexes), usually being the males the most conspicuously colored sex. Darwin (1871) suggested that this secondary sexual character evolved mainly through sexual selection pressures acting on males, favoring bright and elaborate coloration through mate selection and intrasexual competition. In turn, other authors (Wallace 1889; Martin and Badyaev 1996; Burns 1998; Hofmann et al. 2008) advocated for a higher role of natural selection in the evolution of sexual dichromatism, through an increased predation risk for the females, especially during the incubation period, which favors cryptic coloration in them. These two theories are not mutually exclusive since both forces are likely to be acting on each sex with opposite directions and varying intensities (Dakle et al. 2015; Shultz and Burns 2017). Also, the evolution of preferences for specific traits in potential sexual mates has been subject to discussion. Some authors believe that sexually selected signals are preferred by females because they confer honest information about male's quality, while others argue that mate selection could be based on purely esthetic preferences (Zahavi and Zahavi 1997; Prum 2010, 2012; Weaver et al. 2017).

The role of natural and sexual selection on the evolution of sexual dichromatism was tested by some family scale studies of Neotropical birds and their results suggest that several factors affect sexual dichromatism with varying degrees of intensity on both sexes. For instance, Drury and Burroughs (2015) studied the evolution of sexual dichromatism among New World blackbirds (Icteridae) in relation to nest shape and exposure level during incubation. They found that transitions from monochromatism and exposed nests to either sexual dichromatism or concealed nests were frequent, suggesting an important role of natural selection on females on the evolution of sexual dichromatism in this family; but they also found evidence of positive selection for female ornamentation leading to sexual monochromatism, possibly due to positive social selection (Drury and Burroughs 2015). Shultz and Burns (2017) studied the evolution of sexual dichromatism in tanagers, the largest family of Neotropical songbirds, including 334 species in which a great array of plumage coloration patterns are found, from some of the most colorful to drab plumages, including both sexually dichromatic and monochromatic species. Their results indicate that throughout the evolution of plumage coloration in this family decreases in the levels of sexual dichromatism are more frequently related to changes in male plumage, while increases in this parameter are not specifically related to changes on either sex. The levels of sexual dichromatism in tanagers are positively correlated with the complexity of coloration patterns found in the plumage of males. The evolution of sexual dichromatism within tanagers seems to be the result of both sexual and natural selection acting on both sexes (Shultz and Burns 2017). In contrast, Doucet et al. (2007) studied the evolution of sexual dichromatism patterns among 50 species of manakins (family Pipridae) and found that increases in sexual dichromatism are associated with increases in male coloration conspicuousness (i.e., contrast to a typical green vegetated background). The authors therefore concluded that sexual dichromatism in manakins is likely the result of sexual selection pressures acting on males (Doucet et al. 2007).

It is worth mentioning that the degree of sexual dichromatism is very frequently interpreted as a measure of the intensity of sexual selection pressures but this relationship is not usually tested. For instance, we studied the evolution of sexual dichromatism among blue cardinalids with a comparative approach and found that sexual dichromatism levels were not related to plumage color complexity of either sex. Instead, we found that sexual dichromatism level was associated with the color production mechanism involved, being differences between sexes in plumage coloration consistently larger when structurally based coloration was involved (García unpublished data). Therefore, it is likely that the evolution of sexual dichromatism is influenced not only by the intensity of sexual and natural selection forces acting on each sex, but also constrained by the evolution of particular mechanisms of color production.

Another factor commonly thought to influence the evolution of plumage coloration is the environment. Habitat conditions can alter the efficacy with which signals are transmitted, and therefore, signals are presumed to be somehow adapted to the specific environmental conditions where each species displays in order to increase their visibility. At the same time, non-signaling plumage patches are expected to show reduced contrast against the background and higher crypsis. The light environment hypothesis establishes that plumage coloration characteristics (such as hue and brightness) should match those of the ambient light and differ from those common in the reflectance spectra of the background to increase conspicuousness, and *vice versa* (Endler 1993, 2000; Zahavi and Zahavi 1997; Théry 2006). Gomez and Théry (2004, 2007) evaluated this hypothesis in an avian community of the Neotropical rainforest employing avian visual models and a comparative approach and found that canopy and understory function as different selective regimes for color patterns; plumage brightness and hue seem to have evolved for increased crypsis in each light environment, while the proportion of UV in the color signal is probably selected to increase conspicuousness in canopy birds. Concordantly, the evolution of plumage coloration in a clade of tanagers and a group of 33 Amazonian species of furnariids was found to be influenced by ambient type and foraging strata as plumage coloration correlated significantly with light environment (Shultz and Burns 2013; Hernández-Palma 2016). The patterns observed on different plumage patches suggest that small patches are more frequently used in signaling (i.e., higher conspicuousness), while large and dorsal patches are mostly cryptic and likely subject to more intense natural selection pressures (Gomez and Théry 2007).

Finally, another important factor in the evolution and diversification of plumage coloration is the role of this character in species recognition and reproductive isolation, with closely related species living in sympatry being more divergent in plumage coloration than allopatric ones (Martin et al. 2015). An extreme example of this factor within Neotropical birds is the southern capuchino seedeaters clade (*Sporophila spp.*, family Thraupidae). This group consists of nine mostly sympatric species distributed in South America in which adult males show clear differences of plumage coloration, which is melanin-based, and vocalizations, while females and juveniles cannot be classified to species level at least by the human eye (but see Benites et al. 2010; Campagna et al. 2012). Capuchino seedeaters constitute a recent continental radiation and show extremely low levels of genetic differentiation despite very clear phenotypic differentiation (Campagna et al. 2010, 2015). A comprehensive study of this group of species through whole genome sequencing showed that there are very few areas of divergence consistent with species classifications and many of these involve regulatory regions of the melanogenesis pathways suggesting an important role of sexual selection in their diversification (Campagna et al. 2017).

8.7 Sing, Shine, or Both?

When Darwin (1871) formulated the theory of sexual selection, he proposed that secondary sexual traits (i.e., characters differing between sexes that are not directly associated with the production and fertilization of gametes) evolved as a consequence of competition between males or because they were selected for the attraction of females. In this way, there are secondary sexual characteristics that work as "weapons" to repel competing males, a result of intrasexual selection, and others that function as "ornaments" as a result of intersexual selection (Andersson 1994). Up to this point we have considered song and plumage coloration separately, but both can act as "ornaments" or "weapons" (Catchpole and Slater 2008; Hill 2006). Could their evolution be related? Darwin (1871) noted that many species of birds with complex songs had dull plumages, as if they were "compensating" the lack of attractive plumage with complex songs. If both characters are expensive to produce, an inverse correlation in the complexity of the characters could be expected due to a "trade-off" or compromise between the resources that can be allocated to each of them (Shutler 2011).

Gilliard (1956) observed that, among birds of the Ptilonorhynchidae family (in which males build structures and adorn them with different elements to attract females) species with more elaborate or striking plumages build simpler structures and vice versa. According to the author, the sexual selection pressure had been "transferred" to the constructions of the males, thus relaxing the sexual selection pressure on plumage coloration. A similar relationship could be expected between plumage coloration and song, but previous works on the subject are few and very heterogeneous in the variables used to measure complexity (Shutler and Weatherhead 1990; Read and Weary 1992; Badyaev et al. 2002; Ornelas et al. 2009; De Repentigny et al. 2000; Gonzalez-Voyer et al. 2013; Mason et al. 2014). Also, the results of these studies are mixed, so it is not yet clear how singing and coloration are related. If both characters are under strong sexual selection, one would not expect a compromise between the complexity of each character (Ornelas et al. 2009), or could even expect them to be positively related (Shutler and Weatherhead 1990). Choosing a variable as indicator of complexity or elaboration is not trivial, especially if its biological relevance has not been explicitly tested (e.g., does a complexity estimator really reflects higher production costs?). This is not to say it is useless to explore correlations among variables that are assumed to reflect character complexity, but that the "leap of faith" it implies should be kept in mind when interpreting the results obtained.

The blue cardinalids (family Cardinalidae) are an excellent model to analyze if the evolution of the song and the coloration of the plumage are related in some way for several reasons. On the one hand, all the species present sexual dichromatism, and the song would be produced only by the males (Orenstein and Brewer 2011), which would indicate that both characters are, to some degree, under the influence of sexual selection. On the other hand, they have a high degree of diversity in their acoustic and visual signals. To determine if there is a relationship, and of what kind, between song and plumage coloration elaboration or complexity among the blue cardinalids we considered three acoustic variables: bandwidth, since it represents the ability to produce songs with a wider range of frequencies; the length of the song, as an estimate of the ability to include a higher variety of notes; and the mean duration of the notes, as an estimate of the complexity of notes structure. These variables were selected mainly because they were used in previous studies as indicators of the complexity of vocalizations (Shutler and Weatherhead 1990; Gonzalez-Voyer et al. 2013; Mason and Burns 2015) and thus facilitate comparison with previous results. Also, they showed no correlation with body weight, beak size, or habitat type.

We evaluated the complexity of the coloration through two variables that quantify the heterogeneity of the complete plumage of a species: the color space volume and the average color span (Stoddard and Prum 2008) only using the values corresponding to the males. In addition, the relationship with the acoustic variables of the plumage color perceptual distance between males and females (ΔS, see Box 8.1) was also analyzed as an indicator of the level of sexual dichromatism. These indicators take into account the UV component of the coloration, and are not based on human visual perception, and neither showed a correlation with body weight nor habitat type. We tested the existence of a relationship between the colorimetric and acoustic variables using a phylogenetic generalized minimum squares (PGLS) regression, comparing each of the three acoustic variables with each of the three colorimetric variables. None of the variables considered as representative of the plumage color complexity showed a significant correlation with the acoustic variables considered. The correlation of ΔS with the bandwidth was the only one with a negative sign and close to being significant.

These results suggest that there is no relationship (neither positive nor negative) between the complexity of the song and the coloration among the blue cardinalids. Similar results were obtained by Ornelas et al. (2009), and Mason et al. (2014) in Trogonidae (Trogoniformes) and Thraupidae (Passeriformes), respectively. In contrast, Badyaev et al. (2002) found an inverse correlation between the brightness of the plumage of the males and the complexity of the song in passerines of the family Carduelinae, while Shutler and Weatherhead (1990) and Gonzalez-Voyer et al. (2013) found a positive association between the indicators of elaboration of the vocalizations and plumage in the Parulidae (Passeriformes) and Megalaimidae (Piciformes) families, respectively. It should be noted that, from previous studies on the subject, the majority is based on the analysis of illustrations or photos of field guides (Shutler and Weatherhead 1990; Read and Weary 1992; De Repentigny et al. 2000; Badyaev et al. 2002; Ornelas et al. 2009; Gonzalez-Voyer et al. 2013).

These inconsistencies could be due to several reasons. First, the relationship between the two characters may depend on the type of coloration involved: Badyaev et al. (2002) found a negative relationship between song and plumage coloration complexity only when considering plumage patches with carotenoid pigmentation, but found no relationship with melanin-based plumage coloration. Second, the effect of each type of sexual selection (intra- and intersexual) on each character (song and coloration) could differ among the groups studied. As an alternative to the "transfer" hypothesis, it has been proposed that the elaboration of two sexual characteristics will not be correlated, if each of them is subject to different types of sexual selection (Shutler and Weatherhead 1990). This might be the case in the blue cardinalids, but the evidence is still scarce. For example, *Passerina caerulea* males adjust their level of "mate-guarding" depending on the brightness of neighboring males' plumage, but females of this species show no preference for the intensity of blue in the plumage of males (Ballentine and Hill 2003). Song, on the other hand, would be important both for mate attraction and aggressive interactions between males (Ballentine et al. 2003; Lattin and Ritchison 2009). If song and color are subject to different types of sexual selection, their evolution does not necessarily has to be correlated, which coincides with our results obtained for blue cardinals. Finally, it is important to consider that the "trade-off" may exist but the analysis fails to detect it, but not only because the variables chosen may not be biologically relevant (see above). When a trade-off imposes a restriction on the production mechanism of a character, it establishes a range of potential states of that character which cannot be exceeded (potential phenotype). But within that range, the character can evolve freely (effective phenotype, see Slabbekoorn and Smith 2002; Podos et al. 2004a). In this case, if the amount of resources invested in one of the characters limits how much is invested on the other, the negative correlation would be detectable only if the effective phenotype approaches the potential in all or most of the cases under study.

Box 8.1: Methods for the Study of Bird Coloration

As a consequence of the large differences between the human and avian visual systems and the need to make quantitative, and not only qualitative comparisons, the study of color signals in birds requires the employment of objective methods of measurement and biologically meaningful means of interpretation. To do this it is convenient to use a spectrometer, which allows measuring light reflectance from a given surface within the range of wavelengths of interest (i.e., 300–700 nm, the range to which birds are sensitive) in relation to a white standard (Andersson and Prager 2006). The collected reflectance data can be characterized with typical parameters descriptive of coloration,

(continued)

Box 8.1 (continued)

such as brightness, hue, and chroma (a measure of color saturation). There are several formulas that have been used by different studies to estimate each of these parameters, each with certain advantages and disadvantages, in relation to the shape of the reflectance spectra of the colors measured (Montgomerie 2006). These parameters are useful to describe the light being reflected by a given surface, allowing to compare colors produced by different individuals or populations and to study color production mechanisms (Butler et al. 2011), but they do not provide information about how the measured colors are perceived by intended (and unintended) receivers.

In order to describe color visual signals as perceived by birds it is necessary to employ avian visual models (Vorobyev and Osorio 1998; Endler and Mielke Jr 2005; Stoddard and Prum 2008). These models contemplate the chromatic component of the measured reflectance spectra (i.e., do not consider brightness but only hue and chroma), but also the spectral sensitivity to different wavelengths, the irradiance spectra of the ambient light, the reflectance spectra of the background where the signal would be typically emitted, and physiological properties of the neural and visual system of the receiver. Any given color stimuli can be described as a point within the tetrahedral color space that represents the avian visual system according to the stimulation of each photoreceptor and where each vertex represents each of the four photoreceptors in the avian retina. Moreover, the avian visual model developed by Vorobyev and Osorio (1998) allows the estimation of the perceptual distance between two given color points (as the Euclidean distance between two color points in the tetrahedral color space, ΔS), and sets a theoretical threshold for this value above which two colors are likely to be distinguishable by the viewer.

Unfortunately, the results obtained through the application of avian visual models are sensitive to the parameters selected, particularly regarding the spectral sensitivity of the photoreceptors and their relative abundance in the retina (Bitton et al. 2017; Olsson et al. 2017). These parameters are approximated most of the times to the closest described species available, usually not a very phylogenetically close one. This is the case of many Neotropical bird species. Despite this consideration that requires some caution for the interpretation of results (Bitton et al. 2017), the use of avian visual models is currently highly extended and useful to answer questions regarding the use of color signals in avian communications and there are several analysis tools that make the implementation straightforward. Such is the case of the *pavo* package for R (R Core Development Team 2017) by Maia et al. (2013) that allows the analysis, visualization, and implementation of visual models to reflectance spectra data and the TETRACOLORSPACE program for MATLAB software (MathWorks, MA) and for R (rtetracolorspace at https://github.com/ajshultz/rtetracolorspace) developed by Stoddard and Prum (2008). There are also some statistical analyses suggested to evaluate variation in the perceptual distance values among and within groups as well as to obtain mean and confidence intervals for these data (Endler and Mielke Jr 2005; Delhey et al. 2015; Maia and White 2018).

Box 8.2: Non-vocal Sounds

Birds have been known to use non-vocal sounds to communicate for centuries. However, the production mechanisms of these signals were unknown until relatively recently. Bostwick and Prum (2005) proposed the term sonation to designate these sounds (as opposed to vocalizations), which are produced intentionally with structures other than the syrinx such as the bill, wings, tail, feet, and/or body feathers. These signals are used by several species in different contexts, such as territory defense or courtship displays (reviewed in Bostwick and Prum 2005). They are believed to have originated as passive by-products of movements or locomotion that eventually became salient to the receiver, and evolved into communication signals through a modification of behavior or morphology that produced variation in acoustic properties that could be subject to selection (Clark and Prum 2015).

Sonation is widespread among the manakins (Passeriformes: Pipridae). Manakins are Neotropical, lek-breeder species where the males perform elaborate courtship displays. Half of the species sonate during these displays, and sonation was shown to have originated independently several times within the family (Prum 1998).

Extreme modifications of wing morphology have been known in several piprid species for decades (especially among the *Manacus* genus), but the connection between such modifications and the several classes of sonations they produce using their wings have started to be understood only recently. The use of high-speed video recordings was key to describe the different mechanisms used to produce wing sonations such as wing-to-wing claps or wing flicks in the air (Bostwick and Prum 2005).

A particularly interesting case is that of the club-winged manakin (*Machaeropterus deliciosus*), where the male's fifth, sixth, and seventh secondary feathers (inward from the wrist) are noticeably modified, the tip of the fifth in the shape of a blade and the sixth and seventh tips are swollen forming twisted knobs. Male Club-winged Manakins flip their wings rapidly above their backs, but the frequency of the sound produced is approximately 15 times faster than the frequency of the feather oscillations (Prum 2017). A careful inspection of high-speed video recordings showed that with each oscillation the fifth secondary feather tip rubs the swollen tip of the sixth secondary feather, inducing the sixth and seventh secondary feathers to resonate loudly at the frequency of the sound produced (Bostwick and Prum 2005). This mechanism, known as stridulation, is the same used by insects like crickets and cicadas to produce their sounds.

In addition to the secondary feather modifications, male Club-winged Manakins are the only birds known to have solid ulnas, which are also wider and larger than those of other manakins, and present grooves and peaks for ligamentous attachments (Prum 2017). Apparently, in the field "it is easy to see that male Club-wings fly awkwardly" (Prum 2017, p. 151). However, there is still no data on how these modifications affect flight biomechanics. Thus, a question remains unanswered: Have the Club-winged Manakins sacrificed efficiency in their flight ability to produce a love song?

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Chapter 9
A Reappraisal of the Fruit-Taking and Fruit-Handling Behaviors of Neotropical Birds

Marco A. Pizo, Eliza C. Batista, and Erison C. Monteiro

9.1 Introduction

The techniques used by frugivorous birds to take and handle fruits is a research topic that, though superficially known, does not get the attention of researchers interested in the behavioral ecology of frugivorous birds. Notwithstanding, empirical observations and experimental studies conducted mostly in the 1980s revealed that the fruit-taking and fruit-handling behaviors of birds affect their feeding and digestion rates (Levey 1987), the profitability of fruits (Avery et al. 1993; Foster 1987), and, ultimately, which fruits they eat and which seeds they disperse (Denslow and Moermond 1982; Levey et al. 1984; Moermond and Denslow 1983, 1985; Pratt and Stiles 1985).

As factors in the equation of fruit choice by birds, fruit-taking and fruit-handling behaviors are influenced by the interaction between the structure of plants and their fruits and the bird's anatomy. The placement of the fruit on the plant (e.g., terminal, axillary, or cauliflorous), for instance, influences fruit accessibility or the "ease with which a given bird can reach and take fruits presented in different ways" (Moermond and Denslow 1983). Although, as Moermond et al. (1986) noted, most small frugivorous birds are agile enough to render any fruit accessible, this is not so for large birds with more limited maneuverability, and even small birds have to balance the energy cost of taking a fruit against its energy and nutrient rewards (Moermond

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and Denslow 1983). Energetic costs are influenced by the fruit-taking technique used, with aerial maneuvers in general costlier than perched maneuvers. As a consequence, birds taking fruits on flight tend to be more selective in relation to fruit traits that bear on the fruit energetic profitability (e.g., ripeness; Moermond et al. 1986). Fruit and seed sizes, on the other hand, are traits that interact with bill dimensions to influence the fruit-handling behavior of birds (Moermond and Denslow 1985). It is expected that the larger the bird and its bill, the greater the chance of swallowing the fruit whole, while small birds are mechanically constrained by correspondingly small bills, being only able to eat large fruits piecemeal. However, bird size and bill dimensions alone are not sufficient to predict the way a bird handle fruits since certain bird clades are constrained to certain handling techniques (Foster 1987). For instance, manakins (Pipridae) are characteristically "gulpers" (i.e., swallow fruits whole), while tanagers (Thraupidae) are "mashers" (i.e., crush the fruits in the bill prior to ingestion; Levey 1987). The extent to which evolutionary history determines the fruit-taking or fruit-handling behaviors of frugivorous birds in a broad phylogenetic perspective is, however, unknown.

The fruit-taking and fruit-handling behaviors of birds have implications for seed dispersal, either by influencing fruit selection or the fate of seeds (Moermond and Denslow 1985; Levey 1987). In a Mediterranean network involving frugivorous birds and fruits, Jordano et al. (2003) found that 6.1% of the interactions did not occur due to structural constraints of the plants (i.e., branch architecture or fruit display limiting accessibility to the fruits). In a concrete example, Greenberg (1981) suggested that the capsulated fruits of *Lindackeria laurina* (Achariaceae), that generally open downward from the end of a long branch, restrict access to birds able to fly to grab the fruits. Therefore, fruit accessibility is an additional, poorly known factor contributing to the so-called forbidden interactions, i.e., interactions that for some biological reason do not occur but shape the topology of networks involving plants and frugivores, often forming a non-trivial part of them (Olesen et al. 2011). On the other hand, the way the birds handle fruits influences their feeding rate and where the seeds are deposited, thus affecting the quantity and quality components of seed dispersal effectiveness (Levey 1987; Jordano and Schupp 2000; Palacio et al. 2017; Loayza and Knight 2010).

Experimental studies were decisive to reveal the behavioral subtleties and costs associated with the interaction with fruits, but, as expected, have dealt with a few bird species: (Denslow and Moermond 1982; Moermond and Denslow 1983; Levey et al. 1984; Levey 1987). Observational studies involved a greater number of species, but the information they provide are scattered in the literature, some of which hard to access. Here we compile such information from the literature to reveal broad patterns of fruit-taking and fruit-handling behaviors observed in the wild for a variety of bird species representing a wide spectrum of the bird phylogeny. With this dataset, we tested the influence of phylogeny on fruit-taking and fruit-handling behaviors, and also investigate the previously unexplored relationship between the flexibility in fruit-taking and fruit-handling behaviors with body size and degree of frugivory (i.e., a measure of the importance of fruits in the diet). Embedded in the concept of frugivory specialization is the notion that highly frugivorous birds consume a variety of fruits with diverse morphologies and presentation modes that necessarily require a variety of feeding techniques to be exploited. Therefore, positive relationships between the degree of frugivory and the flexibility of fruit-taking and fruit-handling behaviors are expected. As with many other biological aspects (Bonner 2011), body size plays an important role in frugivory and the demise of large frugivorous birds has been of conservation concern for its consequence on seed dispersal and plant recruitment (Galetti et al. 2018). Therefore, instead of exploring the many morphological traits that in a complex way may influence fruit-taking and fruit-handling behaviors (e.g., several wing and bill dimensions), some of them hard to obtain (e.g., the development of leg musculature that affects the fruit-taking behavior of birds; Moermond and Denslow 1985), we focused on body mass. Body mass is expected to be negatively correlated to behavioral flexibility in fruit-taking since large body sizes should restrict the ability to perform certain foraging maneuvers (e.g., aerial maneuvers) to take fruits. Similarly, the positive correlation between body mass and gape width (Wheelwright 1985) should make large birds able to swallow whole the majority of fruits they interact with, thus reducing the array of handling techniques they use and their flexibility of fruit-handling behavior. We are ultimately interested in stimulating further studies that incorporate the often neglected behaviors used by birds to take and handle fruits to investigate the reciprocal ecological and evolutionary consequences between birds and plants (Palacio et al. 2017; Loayza and Knight 2010).

9.2 Methods

We searched the literature (i.e., papers in peer-reviewed indexed journals as well as dissertations and theses) for studies that reported quantitative data on the fruit-taking and fruit-handling behavior of birds (i.e., the frequency of each behavior adopted to take and handle each fruit species). We found 29 studies conducted in different biomes (Atlantic Forest, Cerrado, and Amazonian Forest). To this dataset we added our own unpublished observations (Appendix). Data came invariably from plant-oriented studies that focused on fruiting plants to record the visiting bird species and their behaviors. The nomenclature adopted to designate fruit-taking behaviors was based on Moermond and Denslow (1985), as follows: (1) *stalling*—the bird takes the fruits in a single uninterrupted flight, losing the movement briefly in front of it, (2) *hovering*—the bird invests in the direction of the fruit hovering briefly in front of it, (3) *picking*—the bird picks the fruit from a perch without stretching its body or taking special positions for it, (4) *reaching*—the bird extends the body above or below the perch to take the fruit, and (5) *hanging*—the bird uses the legs and fingers to hang below the level of the feet to reach the fruit. Stalling and hovering are aerial maneuvers, while picking, reaching, and hanging are perched maneuvers. Two other maneuvers described by Moermond and Denslow (1985), swooping and snatching, were never reported, likely because they are easily confounded with each other, are rare and inconspicuous. Moermond and Denslow (1985) mentioned they saw cotingids and *Tytira* spp. swooping and snatching. For fruit-handling behavior, we adopted the terms (1) *swallowing*—when the bird eats the fruit whole with minimal, if any, previous mandibulation, (2) *mashing*—when the fruit is mandibulated to become flattened or crushed prior to ingestion, and (3) *pecking*—when the bird eats the fruit piecemeal by biting and tearing out chunks of pulp. Categories 1 and 2 correspond, respectively, to *gulpers* and *mashers* of Levey (1987), while categories 1 and 3 correspond, respectively, to *seed dispersers* and *pulp consumers* of Jordano and Schupp (2000).

The data often includes sequential maneuvers of a given foraging bird. As such records cannot be considered independent from each other for statistical purposes (Hejl et al. 1990), and we did not adopt any procedure to trim the data, the statistical tests should be interpreted with this caveat in mind.

To test for a phylogenetic signal in the fruit-taking and fruit-handling behaviors at the family level, we submitted the bird family list to "Bird tree" (birdtree.org) getting an output of 1000 random phylogenetic trees based in 10,000 Ericsson set of sequenced species in a multiphylo data. We then used the TreeAnnotator v1.8.4 to condense the multiphylo archive in a single phylogenetic tree by a parsimonious method (Bouckaert et al. 2014). Using the *vegan*, *FD*, and *ape* packages in R we performed the EM.Mantel function of Debastiani and Duarte (2017) to calculate the phylogenetic signal based on a Mantel test. This function generates an r.Mantel value expressing the power of the association between the proportion of each behavior adopted to take and handle fruits and the phylogeny. As aerial and perched maneuvers form two clearly distinct functional categories, they were used instead of the five fruit-taking behaviors listed above.

We used the Levins' index to characterize the foraging versatility of birds with ≥10 records (Levins 1968). This index varies from 0 to 1, with values closest to 0 indicating the most conservative birds in relation to the behaviors used to take and handle fruits, and 1 being related to the most flexible birds. Levins' indexes were correlated with body masses (log-transformed) and degree of frugivory, both metrics extracted from Wilman et al. (2014). We, however, modified the frugivory degree values for some species based on our field experience. We also correlated Levins' indexes with sample size (log-transformed) to explore the possibility that the greater the number of observations on a given bird species, the greater the chance of recording unusual behaviors that would increase the foraging flexibility. Psitacids were excluded from correlations because of their distinct morphology (bill shape and strong legs used to climb the branches to reach fruits) and foraging abilities (use of the feet to handle fruits). Bird nomenclature follows Remsen Jr. et al. (2018).

9.3 Results

9.3.1 Fruit-Taking

We got data for 188 bird species (115 genera, 26 families) that performed 42,159 maneuvers to eat 156 plant species (105 genera, 48 families) (Table 9.1). Perched predominated over aerial maneuvers, with picking (51.8%) and reaching (31.9%) being the most common maneuvers, followed by stalling (8.1%), hovering (7.2%),

Table 9.1 Number of bird genera and species included in the fruit-taking dataset for each bird family, the number of plant families, genera, and species with which they interacted, the proportions of aerial and perched maneuvers performed by each bird family, and their indexes of flexibility in fruit-taking given by the Levins' index

						Aerial maneuvers			Perched maneuvers			
Bird families	Bird genera	Bird species	Plant families	Plant genera	Plant species	Stalling	Hovering	Picking	Reaching	Hanging	*N*	Levins' index
Cardinalidae	2	2	7	7	8	0.21	0.05	0.40	0.35	0.00	35	0.53
Columbidae	4	7	13	14	15	0.00	0.00	0.68	0.32	0.00	220	0.19
Corvidae	1	4	21	24	24	0.01	0.00	0.38	0.61	0.00	354	0.23
Cotingidae	4	5	9	11	12	0.37	0.00	0.52	0.06	0.05	57	0.35
Cracidae	2	2	13	15	16	0.00	0.01	0.96	0.03	0.01	63	0.02
Cuculidae	2	2	2	2	2	0.00	0.00	1.00	0.00	0.00	2	0.00
Emberizidae	2	2	8	9	9	0.02	0.00	0.81	0.16	0.00	28	0.11
Fringillidae	1	5	14	17	19	0.00	0.00	0.07	0.92	0.00	684	0.04
Furnariidae	1	1	1	1	1	0.00	0.00	0.57	0.43	0.00	4	0.24
Icteridae	3	5	12	14	15	0.02	0.01	0.82	0.12	0.03	50	0.11
Mimidae	1	2	16	18	18	0.00	0.01	0.81	0.17	0.00	285	0.11
Momotidae	1	1	5	5	5	0.49	0.09	0.03	0.40	0.00	39	0.37
Oxyruncidae	1	1	3	3	3	0.08	0.00	0.42	0.25	0.25	9	0.57
Parulidae	2	2	3	3	3	0.00	0.00	0.36	0.43	0.21	12	0.45
Passeridae	1	1	2	2	2	0.00	0.00	1.00	0.00	0.00	2	0.00
Picidae	7	10	10	10	11	0.00	0.00	0.81	0.18	0.00	556	0.11
Pipridae	5	5	23	32	41	0.39	0.19	0.15	0.27	0.01	1140	0.64
Psittacidae	8	10	13	14	15	0.04	0.02	0.52	0.41	0.01	233	0.32
Ramphastidae	3	8	9	9	9	0.00	0.01	0.81	0.16	0.02	182	0.11
Thamnophilidae	1	3	4	5	5	0.09	0.00	0.27	0.64	0.00	13	0.26
Thraupidae	26	46	44	82	115	0.03	0.03	0.37	0.55	0.02	8468	0.31
Tityridae	3	7	20	23	25	0.51	0.07	0.34	0.08	0.01	231	0.40
Trogonidae	1	4	11	14	15	0.95	0.05	0.00	0.00	0.00	78	0.03
Turdidae	2	8	39	68	89	0.04	0.02	0.74	0.19	0.00	2715	0.17
Tyrannidae	28	41	39	56	76	0.21	0.26	0.34	0.17	0.01	5656	0.70
Vireonidae	3	4	20	27	30	0.11	0.06	0.33	0.45	0.05	652	0.51

Definitions of the aerial and perched maneuvers are in the text. Bird families are arranged in alphabetical order

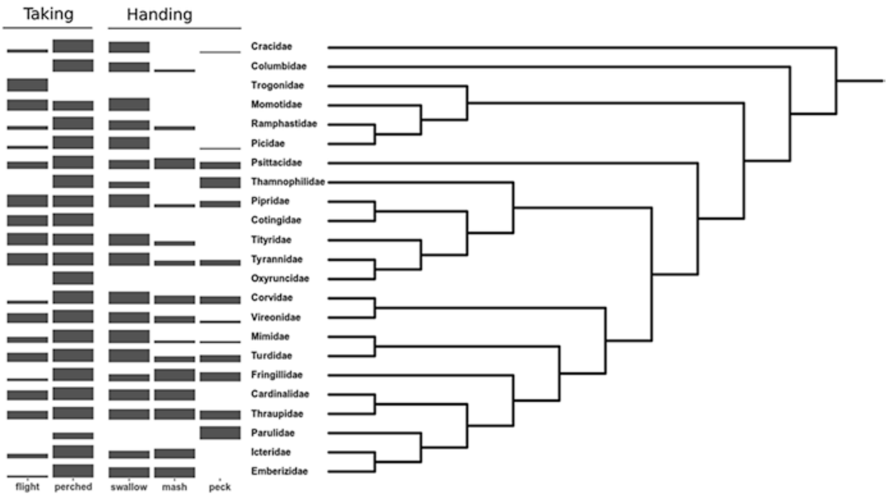

Fig. 9.1 The proportions of each of the fruit-taking and fruit-handling behavior performed by the different families of frugivorous birds arranged according to a bird phylogeny based on birdtree.org (Jetz et al. 2012). Behavioral categories are explained in the text. Numerical values and sample sizes for each family are in Tables 9.1 and 9.2. No handling data are available for Trogonidae, Cotingidae, and Oxyruncidae. Only families with >10 records are represented

and hanging (1.0%). The ability to take fruits on flight is well developed in few passerine and non-passerine clades. In the former, especially in the Tyrannida parvorder formed by families Pipridae, Tityridae, Cotingidae, and Tyrannidae, while among non-passerines the families Trogonidae and Momotidae take fruits exclusively or predominantly on flight (Fig. 9.1). Accordingly, we detected a significant though weak phylogenetic signal in the proportions of flight and perched maneuvers performed by bird families (r.Mantel = 0.2464, $p = 0.05$).

Tyrant flycatchers (Tyrannidae) were the most flexible family, while other families show low flexibility, taking fruits exclusively on flight (e.g., Trogonidae) or from perches (e.g., Cracidae, Columbidae) (Table 9.1, Fig. 9.1). Flexibility in fruit-taking behavior was not related to sample size ($r = 0.15$, $n = 126$, $P = 0.09$) or the degree of frugivory ($r = -0.06$, $n = 126$, $P = 0.47$), but body mass was negatively correlated to flexibility ($r = -0.26$, $n = 126$, $P = 0.003$) indicating that the pool of maneuvers used to take fruits diminishes as birds get larger (see the sharp decrease in flexibility index for birds heavier than 140 g in Fig. 9.2a). More specifically, the larger the bird, the greater its reliance on perched maneuvers (Fig. 9.2a).

9.3.2 *Fruit-Handling*

We got data for 122 bird species (85 genera, 22 families) handling 29,526 fruits from 72 plant species (54 genera, 38 families) (Table 9.2). Fruits were more frequently swallowed whole (79.7%) than mashed (15.4%) or pecked (4.9%)

Table 9.2 Number of bird genera and species included in the fruit-handling dataset for each bird family, the number of plant families, genera, and species with which they interacted, the proportions of each handling behavior performed by each bird family, and their indexes of flexibility in fruit-handling given by the Levins' index

						Handling behavior				
Bird families	Bird genera	Bird species	Plant families	Plant genera	Plant species	Swallowing	Mashing	Pecking	*N*	Levins' index
Cardinalidae	2	2	4	4	4	0.51	0.49	0.00	67	0.50
Columbidae	2	3	7	7	7	0.97	0.03	0.00	133	0.03
Corvidae	1	2	16	17	18	0.75	0.15	0.10	468	0.33
Cracidae	1	1	11	12	13	1.00	0.00	0.00	461	0.01
Emberizidae	2	2	6	6	6	0.49	0.51	0.00	77	0.50
Fringillidae	1	3	5	5	6	0.07	0.79	0.14	643	0.27
Icteridae	3	3	3	3	3	0.30	0.70	0.00	69	0.37
Mimidae	1	1	14	15	16	0.99	0.00	0.00	1258	0.01
Momotidae	1	1	4	4	4	1.00	0.00	0.00	34	0.00
Parulidae	1	1	1	1	1	0.00	0.00	1.00	221	0.01
Picidae	5	7	7	7	7	1.00	0.00	0.00	2595	<0.01
Pipridae	4	4	13	16	19	0.97	0.01	0.03	982	0.04
Psittacidae	4	6	5	5	5	0.28	0.61	0.10	229	0.57
Ramphastidae	1	3	7	7	7	0.95	0.05	0.00	165	0.06
Thamnophilidae	1	3	4	4	4	0.30	0.00	0.70	10	0.36
Thraupidae	22	30	35	50	64	0.34	0.55	0.11	7118	0.67
Tityridae	3	4	16	18	20	0.95	0.05	0.00	137	0.05
Trogonidae	1	1	1	2	2	1.00	0.00	0.00	5	0.00
Turdidae	2	7	27	39	50	0.98	0.01	0.02	8784	0.03
Tyrannidae	24	33	33	44	61	0.99	0.01	0.01	5643	0.01
Vireonidae	3	4	11	17	18	0.88	0.11	0.01	427	0.14

Definitions of the handling behavior are in the text. Bird families are arranged in alphabetical order

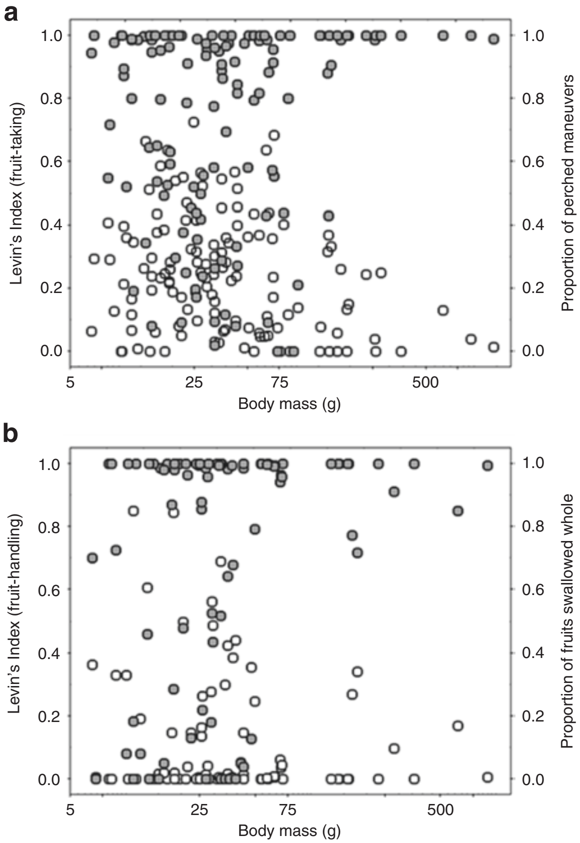

Fig. 9.2 The relationship between body masses of frugivorous birds and their flexibility in (**a**) fruit-taking and (**b**) fruit-handling behavior, as measured by Levins' index represented by white dots. Gray dots illustrate the relationship between body masses and the proportions of perched maneuvers performed by birds to take fruits (**a**), and the proportions of fruits swallowed whole (**b**). Note the logarithmic scale in the body mass axis

(Table 9.2). Contrary to fruit-taking, no phylogenetic signal was detected for any of the fruit-handling behaviors at the family level (all $p > 0.75$).

Tanagers (Thraupidae) form the most flexible family in what concerns fruit-handling. While swallowing whole or mashing fruits predominate for several birds families, Parulidae was the only family for which pecking predominates (Table 9.2). Flexibility in fruit-handling behavior was not correlated to sample size ($r = 0.18$, $n = 87$, $P = 0.10$), to degree of frugivory ($r = 0.17$, $n = 87$, $P = 0.11$), or body mass ($r = -0.14$, $n = 87$, $P = 0.19$), although a tendency for birds larger than 50 g to swallow fruits whole is clear in Fig. 9.2b.

9.4 Discussion

We have provided details on the foraging abilities that expanded and complemented the information available for Neotropical birds, even for well-known and frequent frugivores as tanagers (Thraupidae). Moermond and Denslow (1985) provided so far the most comprehensive dataset of fruit-taking behaviors of Neotropical birds. From their data and subsequent information from others (Moermond and Denslow 1983; Naoki 2007), we are informed that tanagers use almost exclusively perched maneuvers to take fruits. We have shown, however, that they are able to take fruits also on flight, doing so in 8.4% of their foraging attempts, which potentially permit them to exploit a greater variety of fruit morphologies and presentation modes than previously thought.

Body size was negatively correlated with fruit-taking flexibility, indicating that large birds are restricted in the ways they take fruits, using mostly perched maneuvers. Therefore, although such birds are able to eat a greater range of fruit sizes than small birds (Moermond and Denslow 1985), they are likely constrained by certain fruit presentation modes, such as fruits in long and thin stalks requiring flight maneuvers to be taken (Greenberg 1981). From a conservation perspective, large frugivorous birds are of much concern since they are able to disperse large seeds which remain undispersed when they are absent (Galetti et al. 2018). Fruit accessibility, however, can make small birds that are able to take fruits on flight equally essential for the dispersal of plant species with fruits in long and thin stalks.

Different from fruit-taking, body size did not correlate with flexibility in fruit-handling, though a tendency for smaller flexibility among larger birds was apparent. Indeed, Foster (1987) has already noted that handling method and body size are not necessarily correlated, and that although bill dimensions do reflect body size, increases in each are not necessarily proportional. Such imperfect correlation, together with the importance of fruit attributes other than fruit size to influence fruit-handling by birds (e.g., exocarp hardness), makes bird body size a weaker predictor of the fruit-handling behavior adopted by birds. This result could also stem from the influence of phylogeny on fruit-handling behavior, with certain families adopting stereotyped modes of handling fruits irrespective of body size as is clearly the case for fruit-taking behaviors. But we have found no phylogenetic signal in fruit-handling behavior at the family level, with several families frequently employing the three fruit-handling behaviors considered. In this aspect, once again tanagers should be highlighted. Likely from the work of Levey (1987), which studied a few species in captivity, tanagers are sometimes taken as mashers and, as such, poor seed dispersers for dropping the seeds below parent plants while mashing fruits. We have shown, however, that tanagers may employ a variety of fruit-handling behaviors, which is not surprising for such a diverse bird family. Tanagers thus constitute an alert of how one can erroneously assign a functional category to birds without knowing their actual behavior towards fruits in the field.

Contrary to expected, the degree of frugivory was not related to feeding flexibility. One of the most frugivorous taxa analyzed, euphonias (Fringillidae) have a low fruit-taking flexibility (0.04), indicating that even if they eat a variety of fruit species they use a few stereotyped ways to take them (in the case of euphonias, mainly reaching; Fig. 9.1, Table 9.1). Do some fruits are uneaten by euphonias due to accessibility constraints? A positive answer to this question is somehow counterintuitive to the general concept of a highly frugivorous bird as a bird capable of exploiting a great variety of fruits adopting whatever maneuver is necessary to take them.

Interestingly, among the most flexible bird families are families that are predominantly insectivorous (e.g., Tyrannidae: average frugivory degree 24.1 ± 20.6, $N = 32$; Vireonidae: 15.0 ± 7.1, $N = 2$). It is possible that the maneuverability required to prey on arthropods, food sources that conceal themselves and are much harder to catch than fruits, have provided these birds with the behavioral flexibility to take fruits on different ways. Predominantly insectivorous birds that use frequently flight maneuvers to catch fruits are expected to be particularly selective in relation to the fruits they eat. First, as previously noted, compared to perched maneuvers flight maneuvers are particularly costly, making fruit energetic reward a greater issue for birds that take them on flight (Moermond et al. 1986). Second, compared to frugivorous birds, predominantly insectivorous birds have a longer seed retention time, thus a greater commitment to fruit processing (Milton 1981; Levey and Martinez del Rio 2001). They are then expected to select high quality fruits (either in terms of nutrition and/or energy rewarding) to compensate for their comparatively costly foraging and gut processing of fruits. Does this lead to a smaller variety of fruits eaten by such particularly selective birds, as previously suggested for the quetzal (*Pharomachrus mocinno*, an aerial feeder) in comparison with a toucanet (*Aulacorhynchus prasinus*, a perched feeder) (Santana and Milligan 1984), is a question still open to investigation.

The interplay between fruit accessibility or fruit morphology and the feeding abilities of frugivorous birds is not the only or even the chief factor influencing the complex issue of fruit choice by birds, seed fate, or the structure of bird–plant interaction networks, but it is certainly an important one. As such, the fruit-taking and fruit-handling behaviors of frugivorous birds are functional traits to be considered in empirical studies and theoretical models to improve our understanding of the process operating at the community level. Recent studies, for instance, explored the match of bird and plant functional traits revealing that birds appear to consume fruits of plant species that closely match their traits (González-Castro et al. 2015; Donoso et al. 2017). The focus of these studies has been on bird morphological traits (e.g., gape width), but the behaviors explored here, not easily predicted by bird morphology, are additional functional traits to consider due to its potential to influence fruit choice and the fate of seeds. We expect our compilation and analyses of literature data encompassing a broad range of bird families provoke a renewed interest on the fruit-taking and fruit-handling behaviors for a thorough understanding of the ecological and evolutionary relationships between frugivorous birds and plants.

Appendix

Sources of Data Used in the Analyses for Fruit-Taking (T) and Fruit-Handling (H) Behaviors with Information on the Number and Identity of Plant Species Studied

Source	Plant species (Families)
Argel de Oliveira (1999) (T)	21 species (13 families)
Athiê (2009) (T)	13 species (10 families)
Basler (2005) (T)	*Myrsine coriacea* (Primulaceae)
Batista EC (unpubl. data) (T, H)	*Cinnamomum zeylanicum* (Lauraceae)
Colussi and Prestes (2011) (T)	3 species (2 families)
Correia (1997) (T)	13 species (10 families)
Faustino and Machado (2006) (H)	10 species (9 families)
Francisco and Galetti (2001) (T)	*Myrsine lancifolia* (Primulaceae)
Francisco and Galetti (2002a) (H)	*Ocotea pulchella* (Lauraceae)
Francisco and Galetti (2002b) (T)	*Davilla rugosa* (Dilleniaceae)
Francisco et al. (2007) (T, H)	*Pera glabrata* (Peraceae)
Gondim (1995) (T, H)	4 species of Trichilia (Meliaceae)
Gondim (2002) (T, H)	40 species (27 families)
Gridi-Papp et al. (2004) (H)	2 species (Melastomataceae)
Guimarães (2003) (T, H)	*Tapirira guianensis* (Anacardiaceae)
Jacomassa (2016) (T)	*Solanum granulosoleprosum* (Solanaceae)
Lamberti et al. (2012) (T, H)	*Eugenia uniflora* (Myrtaceae)
Lopes (2000)	4 species (4 families)
Marcondes-Machado (2002)	*Miconia rubiginosa* (Melastomataceae)
Masteguin and Figueiredo (1995) (H)	*Prunus reflexa* (Rosaceae)
Melo and Oliveira (2009) (H)	*Lacistema hasslerianum* (Lacistemataceae)
Motta (1991) (T, H)	19 species (14 families)
Muller (2006) (T)	4 species (4 families)
Oliveira AP et al. (2013a) (T)	*Matayba guianensis* (Sapindaceae)
Oliveira DSF et al. (2013b) (H)	*Michelia champaca* (Magnoliaceae)
Pascotto (2006) (T, H)	*Alchornea glandulosa* (Euphorbiaceae)
Pascotto (2007) (T, H)	*Myrsine coriacea* (Primulaceae)
Pascotto et al. (2012) (T)	*Curatella americana* (Dilleniaceae)
Pizo MA (unpubl. data) (T)	62 species (35 families)
Purificação et al. (2015) (T)	*Schefflera morototoni* (Araliaceae)
Robinson (2015) (T)	6 species (6 families)
Silva (2010) (H)	*Ficus organensis* (Moraceae)
Silva et al. (2013) (T, H)	*Psidium guajava* (Myrtaceae)
Valente (2001) (H)	*Alchornea glandulosa* (Euphorbiaceae)

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Chapter 10
Perspectives on the Study of Field Hummingbird Cognition in the Neotropics

Paulina L. González-Gómez and Marcelo Araya-Salas

10.1 Introduction

Cognitive abilities such as learning and memory are critical for the performance of behavioral traits strongly linked to fitness (Balda et al. 1998). In fact, many species depend on learning and memory abilities to perform mating displays which involve ritualized movements and songs, where the quality of this copy is directly related to the number of offspring (Araya-Salas and Wright 2013; Boogert et al. 2011). Furthermore, cognitive abilities could act as a buffer against environmental unpredictability, facilitating resource exploitation, and exploration of new resources (Pravosudov et al. 2015). For example, animals inhabiting harsh environments use their cognitive abilities seasonally to survive energetically demanding life cycles (Krebs et al. 1989). Every winter when the food is not abundantly available and also unpredictable, scatter-hoarding avian species rely on their memory abilities to retrieve as many as 100,000–500,000 individual items per year per individual which have been stored months ago (Sherry et al. 1989). Seasonal cognitive challenges, such as caching behavior, have been linked to seasonal reversible changes in brain structures associated with spatial memory, such as the avian hippocampal formation (hippocampus and parahippocampal area).

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Despite the relative success explaining the neural and proximate mechanisms associated with cognitive performance (Bolhuis and Gahr 2006; Sherry 2006), the selective regimes shaping the evolution of cognition have been less studied (Morand-Ferron et al. 2015). Comparative studies among taxa and populations have shed light on the forces driving the differences in cognition (Lefebvre et al. 2004; Dunbar and Shultz 2007; Dechmann and Safi 2009; Roth et al. 2010). It has been shown that environmental heterogeneity linked to abiotic factors such as social complexity (Domjan et al. 2002; Hansen and Slagsvold 2004), predation risk (Lönnstedt et al. 2012), or foraging success (Healy and Hurly 2003), as well as to abiotic variables, as seasonality or the frequency and duration of unpredictable events (González-Gómez et al. 2015), can enhance cognitive abilities. These patterns have emerged as the study of free-living animals became more popular (Pravosudov and Clayton 2002; Pritchard et al. 2016). Although there are studies assessing the heritability of cognitive traits (Dukas 2004, 2008), our understanding of differences in individual cognitive performance is more limited, although extremely necessary to fully understand the evolutionary trajectory of cognitive abilities (Morand-Ferron et al. 2015). In this context, the environmental heterogeneity and biodiversity in the Neotropics present a compelling scenario where to study the functional and mechanistic links in the evolution of cognition.

10.2 Field Cognition in the Neotropics

For long time cognitive abilities were studied in laboratory animals, mainly rats and pigeons, through traditional approaches in experimental psychology (Brodin and Ekman 1994; Balda and Kamil 2006); however, in recent years many studies have focused on the adaptive role of cognition, and therefore taking the experimental study of cognitive abilities to the field (Pravosudov et al. 2015; Pritchard et al. 2016). Working in the free-living animals provides an insight of what animals actually do in their environment, and what kind of environmental challenges they face, including predators, competitors, mating opportunities, spatial and temporal variations of foraging resources. In summary, a number of variables, which are virtually impossible to reproduce in laboratory studies, which, as mentioned before, could have shaped the evolution of cognition.

Cognitive abilities in free-living birds have been relatively well described for North American species (Ten Cate and Healy 2017), but it has rarely been addressed in Central and South America despite the high biodiversity of birds in the Neotropics. The evolution of its highly endemic biota could be explained by the isolation of South America until the uplift of Central America, 3 million years ago, unlike North America, which was geographically connected to eastern Asia during the Pleistocene (50–60 MYA) (Simpson 1980; Ricklefs 2002). Thus, cognitive abilities, and their relation with resource availability, and environmental heterogeneity in the Northern and Southern hemispheres could have evolved in a completely different scenario of selective pressures; however, they are frequently treated as similar, and the findings are usually extended to the other as generalizations among taxonomic groups. In our opinion, these findings should be viewed with some caution considering the evolutionary history of both regions. More efforts should be allocated to the development of long-term research programs in Neotropical birds where comparisons could explore historical divergence in patterns, and thus the selective landscape experienced by species in both regions, which possibly shaped cognitive abilities.

10.3 Studying Cognition in the Field: Cognitive Ecology in Hummingbirds

Hummingbirds are a particularly interesting group in which to examine cognitive performance, their energetic balance is the result of a complex interplay among foraging behaviors, cognitive performance, physiological constraints, and environmental conditions (Suarez and Gass 2002). Hummingbirds have the highest basal metabolic rate per gram in vertebrates, and the most expensive flight style known (Suarez and Gass 2002). In addition, during daily life, these birds do not storage large amounts of energy-constraining their ability to face long periods without food. However, in migratory hummingbirds, the accumulation of large amounts of fat has been observed prior to departure (Suarez 2013). On the other hand, hummingbirds inhabit a variety of regions encompassing a gradient of environmental heterogeneity, which includes tropical and temperate environments (McGuire et al. 2014). This variability includes daily and seasonal variations which impact their thermoregulatory requirements, and food abundance, as their diet is mainly composed by nectar of flowers, which is temporally and spatially variable, as different plant species have different blooming schedules across the year (Suarez 2013). Furthermore, within the flowering season, nectar is dispersed among hundreds of flowers and varies in concentration, composition, and rate of renewal (Chalcoff et al. 2006). In addition, most of flowers pollinated by hummingbirds present flowers with long corollas, where nectar is enclosed inside of a nectar chamber, which makes nectar not visually detectable (Irwin 2000). Thus, and considering relatively poor olfactory capability of hummingbirds (Ioale and Papi 1989), they rely on cognitive abilities to keep track of, and harvest, the best sources of nectar (Healy and Hurly 2003).

10.4 Spatial Memory in Hummingbirds

Field studies in Neotropical hummingbirds have shown that they are able to recall the spatial location of the highest rewarding feeder among several poorer feeders (Healy and Hurly 1995; Hurly 1996; Henderson et al. 2001). The simplest protocol was initially carried out with territorial males of green-backed firecrown (*Sephanoides sephaniodes*, 5.5 g), a migratory species that inhabits highly seasonal environments both at wintering and breeding grounds (González-Gómez and

Vasquez 2006). These hummingbirds were exposed to one nectar feeder among several feeders containing water. In the first phase of the experiment (i.e., search phase) the individual was allowed to explore the experimental grid and locate the nectar feeder. In the second phase (i.e., return phase), the hummingbird was allowed to return, and the number of feeders visited until finding the nectar source was recorded. If individuals are able to recall the location of the rewarding feeder, during the return phase of the experiment, they should visit the most rewarding feeder, ignoring the non-rewarding ones. As shown in Fig. 10.1a, most of green-backed firecrowns were able to return to the nectar feeder with no mistakes. In the second part of the experiment, and considering flowers vary in nectar quality, individuals were presented to a grid with one high-quality feeder and three low-quality feeders. Similarly to the first experiment, males recalled the best nectar source (Fig. 10.1b), although less accurately than in the first experiment (Fig. 10.1c).

In order to test the spatial memory in male of long-billed hermits (*Phaetornis longirostris*, 6 g), a tropical trapliner resident species, the protocol used with ter-

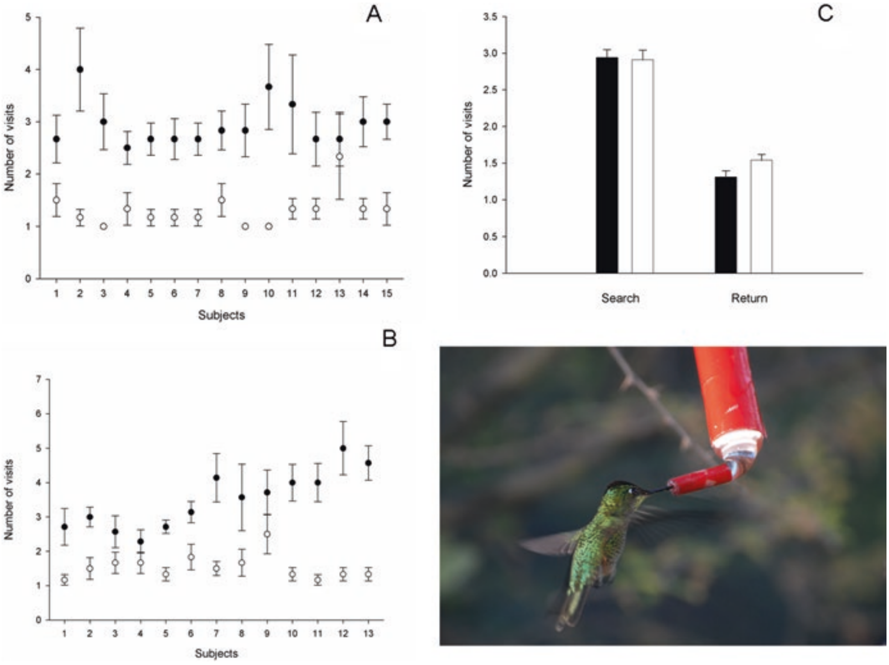

Fig. 10.1 Number of feeders visited by green-backed firecrown hummingbirds during the search (black dots) and return phases (white dots) during: (**a**) An experiment assessing the ability to recall the position of one rewarding feeder among non-rewarding feeders. (**b**) One high-rewarding feeder among several low-rewarding feeders (mean ± SE, $n = 6$ trials for each subject). (**c**) Comparison of both experiments. During the search phase individuals visited the same number of feeders in both experiments (black bars); however, they visited significantly less feeders during the return phase of the first experiment, suggesting that it is easier to recall the location of a resource than the quality. Modified from González-Gómez and Vasquez (2006)

ritorial hummingbirds in temperate environments was modified (Araya-Salas et al. 2018). Considering that long-billed hermits do not defend feeding territories, we observed many individuals visiting the feeders in a short period of time, thus several individuals were tested simultaneously (i.e., with the same feeder setup during the same days). Similarly to the experiment with temperate hummingbirds, we carried out an experiment with two phases (search and return), where we registered the number of feeders visited in both phases. As many individuals were tested simultaneously, the feeder positions were not shuffled after each individual male has completed a trial, instead the position of the rewarding feeder was changed after most visiting individuals have completed the return phase and the experiment was run until most visiting marked individuals had completed at least 10 trials. Different from the study on *S. sephanoides*, spatial memory in long-billed hermits was compared with other traits related to territory ownership such as body size, bill tip length (used as weapon in agonistic interactions), load lifting, and singing. Spatial memory was also compared between "territorial" and "floater" males. In general, hummingbirds showed they were able to remember the most rewarding feeder. In comparison with other elements, although spatial memory and body size both positively affected the probability of lek territory ownership, the results suggest a stronger effect of spatial memory (Fig. 10.2). Bill tip length also showed a positive but smaller effect. Load lifting during vertical flight, a measure of physical performance relevant to agonistic interactions, had no effect on territory ownership. Finally, both body size and spatial memory were indicated in the structure of male song: body size negatively correlated with song lowest frequency, while spatial memory positively predicted song consistency. These findings lend support for cognition as a sexual selection target.

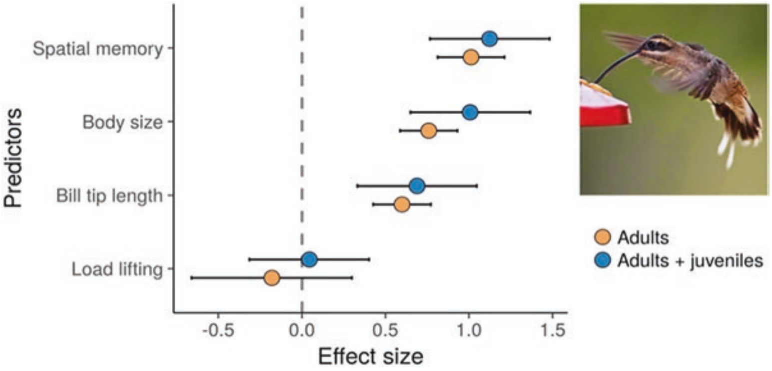

Fig. 10.2 Standardized effect sizes and 95 confidence interval traits related to territory acquisition in lekking long-billed hermit males. Effect sizes are shown for models on the complete data set, including juveniles ($n = 30$, blue markers) and the one on the subset of adult males ($n = 20$, orange markers). Effect sizes with confidence intervals that do not overlap with zero (highlighted by the vertical dashed line) were considered to have an effect on lek territory ownership. Photo (by David McDonald) shows a long-billed hermit visiting a feeder like those used in the spatial memory test. Figure from Araya-Salas et al. (2018)

10.5 Memory for Time and Location

In addition to variability in nectar quantity, quality, and location, plants replenish nectar several times a day, thus imposing the challenge to nectar renewal rate. As previously shown, hummingbirds can match their visits to renewal nectar rates, remembering when the nectar is available (Gass and Sutherland 1985; Sutherland and Gass 1995; Henderson et al. 2006). For example, Gill (1988) studied flower pattern visitation by long-tailed hermit hummingbirds (*Phaethornis superciliosus*), a species that exhibits traplining foraging strategies (i.e., regular foraging circuits). Hummingbirds visiting feeders that were refilled at fixed intervals established patterns matching nectar availability, often visiting before a scheduled refill. The ability to match visits to nectar renewal rate has also been observed in territorial hummingbirds inhabiting temperate environments, with similar results (Fig. 10.3).

In a more complex setting, Neotropical hummingbirds have been tested for their ability to recall time, location, and nectar quality at the same time. Free-living male green-backed firecrown hummingbirds (*Sephanoides sephaniodes*) were trained to defend feeders with different nectar quality and nectar renewal rates (González-Gómez et al. 2011a, b). After this training, individuals were presented with a similar grid than used for the spatial memory experiments, saving that the feeders contained a small amount of nectar, which was renewed every 10 min (high nectar quality) or 5 min (low nectar quality). The experiment was designed so if the individuals matched their visits with the low-rewarding feeders (and therefore visiting more often), they would gain the same energy amount than matching the high-rewarding feeders. Hummingbirds were successfully able to match their visits with the nectar schedules, although they preferred the high-quality reward, showing they can integrate time, location, and nectar renewal rates (Fig. 10.4).

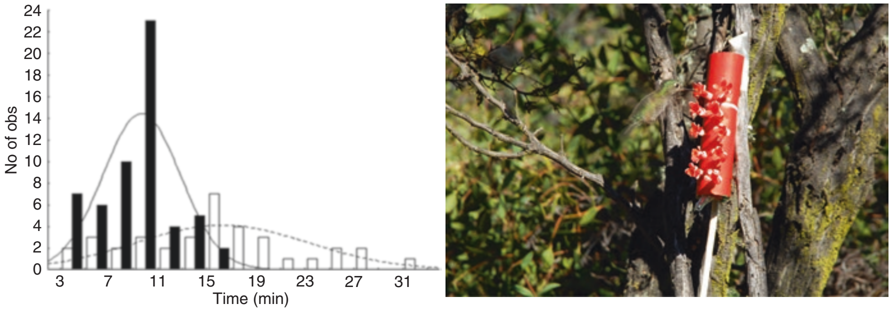

Fig. 10.3 (**a**) In order to measure the ability to recall nectar renewal schedules, free-living male green-backed firecrown hummingbirds were presented with two experimental groups of flowers with short (i.e., 10 min) and long (20 min) replenishment intervals. (**b**) The frequency distribution of visits to both, long (white bars, dashed line) and short interval (i.e., black bars, solid line), suggests that hummingbirds are able to recall nectar renewal times, and match their visits accordingly. Lines represent normal distribution adjustment. Modified from González-Gómez et al. (2011)

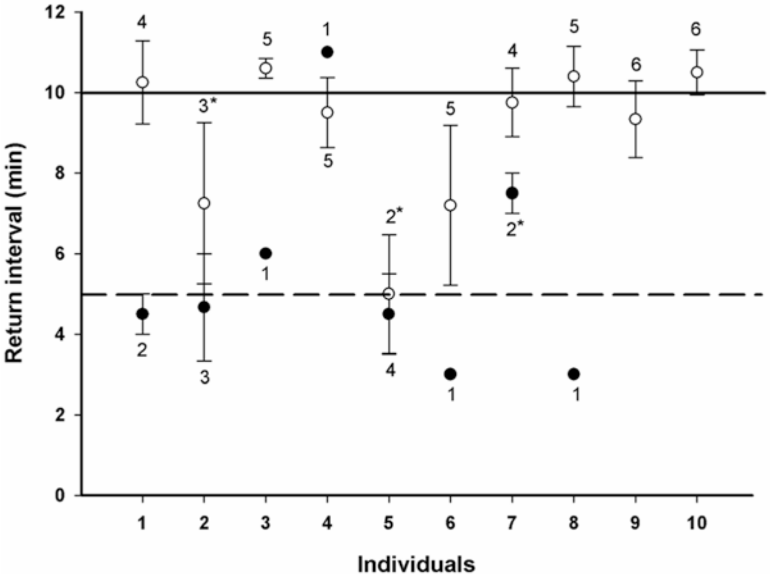

Fig. 10.4 Return intervals performed by individuals of green-backed firecrown hummingbirds to high-quality feeders (white dots, mean ± SE) and low-quality feeders (black dots) between the search and return phase of the experiment. Number of visits to both nectar qualities is shown. Solid line shows the nectar renewal interval of high quality nectar feeders. Dashed line shows the renewal interval of low-quality nectar feeders. *Significantly different from the nectar renewal interval, 1000 bootstrap sampling (95% CI: 8.94–10.22 min). Birds 3, 4, 6, 8, 9, and 10 did not perform enough visits to low-quality feeders to analyze statistical differences from nectar renewal interval. In fact, individuals 9 and 10 did not visit the low-quality feeders in the return phase of the experiment. Modified from González-Gómez et al. (2011)

10.6 Role of Visual Cues, Observational Learning, and Competition in Cognitive Performance

Plant species which are pollinated by hummingbirds normally offer nectar enclosed in a nectar chamber, which is accessed through a long corolla (Fenster et al. 2004). This morphology implies that nectar is not visually detected. Thus, hummingbirds rely on cognitive abilities to recall several nectar characteristics such as nectar quantity, quality, and temporal availability within a plant species (Healy and Hurly 2003). However, among plant species, several visual cues are also relevant to maximize nectar harvesting. Plants vary their nectar composition (i.e., proportion of glucose, fructose, and sucrose), concentration, and production (Hornung-Leoni et al. 2013).

In this context, *visual cues* could be an important component of the foraging ecology of hummingbirds, facilitating information retrieval through association between visual and non-visual cues. Several experiments have tested the effect of visual cues on cognitive performance in Neotropical hummingbirds. For example, Perez et al. (2012) carried out a field experiment with white-eared hummingbirds.

Hylocharis leucotis, to assess their use of locations or visual cues when foraging on natural flowers *Penstemon roseus*. Their findings suggest that white-eared hummingbirds use both, visual cues and location, to visit unvisited rewarded flowers. Ornelas and Lara (2015) compared the role of color visual cues comparing four migratory (*Colibri thalassinus, Amazilia beryllina, Eugenes fulgens,* and *Selasphorus rufus*) and two non-migratory species (*Hylocharis leucotis* and *Lampornis amethystinus*), hypothesizing that migratory species would be more likely than resident to adjust their behavior to environmental change. As expected, migratory species visited more flowers and display more exploratory behaviors than resident species. Visual color cues were relevant for both, resident and migratory species, showing higher performance when red colors were used, which is coincident with the mainly red colors of hummingbird pollinated species (Chittka et al. 2001) and eye adaptations in hummingbirds (Herrera et al. 2008).

In a more complex setting, González-Gómez et al. (unpublished data) compared the performance of green-backed firecrown hummingbirds recalling time and location with and without visual cues. Using an experimental setting combining nectar availability schedule, location, and nectar quality, hummingbirds were presented with a grid in which all feeders were red (i.e., no visual cues) or a grid in that the high-rewarding feeder had black dots. Remarkably, the ability to recall location, which was related to nectar quality, significantly increased when using visual cues, unlike memory for time, which was the same using visual cues or not.

In addition to visual cues provided by plants, individuals also could obtain foraging information from conspecifics or heterospecifics exploiting the same resources. Lara et al. (2009) carried out a study to assess the role of *social learning* in hummingbirds with and without a knowledgeable tutor. Tutored hummingbirds were more successful in visiting the rewarding feeders than individuals without tutor. Furthermore, all tutored individuals only visited flowers of the color that had been previously visited by their tutors.

Although other individuals could provide valuable information about resources, they also could be an obstacle to exploitation. In fact, many hummingbird species defend foraging or reproductive territories by performing chases, vocalizations, direct attacks (Powers and McKee 1994; Camfield 2006; González-Gómez et al. 2011), and even escalated physical encounter that include stabbing opponents with a dagger-like structures at the tip of the bill (Rico-Guevara and Araya-Salas 2014). *Territorial status* may also be linked to cognitive performance. In both, tropical and temperate hummingbirds it has been observed that territorial individuals present higher cognitive performance than non-territorials (Rico-Guevara and Araya-Salas 2014), suggesting a competitive advantage of males related to more efficient foraging.

10.7 Energetics, Foraging, and Cognitive Performance

Environmental heterogeneity, and thus the frequency of unpredictable perturbation, is most likely a powerful variable in the development of cognitive traits (Roth et al. 2010; Sayol et al. 2016). During predictable events such as day/night, seasons, or tides, animals carry out life cycles, such as breeding or migration which vary in energy cost (McEwen and Wingfield 2003). The initiation and duration of life cycles is mainly linked to the variation in local environmental cues, such as changes in environmental temperature or rainfall, and orchestrated by a series of changes in molecular and endocrine levels (Wingfield 2005). In contrast, during unpredictable perturbations of the environment, rapid changes in physiology and behavior, mediated by elevated levels of glucocorticoids, allow individuals to cope (Wingfield et al. 1998; Wingfield 2006). Thus, rapid mobilization of energy reserves via gluconeogenesis, increase of foraging behavior and immune response, among many other traits, to prioritize immediate survival (Wingfield et al. 1998; Landys et al. 2006), even interrupting the current life state (e.g., abandon breeding, interrupting molt), which detrimental effects on future fitness (Cornelius et al. 2011; Walker et al. 2015). Cognitive abilities can act as a buffer against environmental variation, helping individuals to explore new resources, and decreasing the uncertainty linked to environmental perturbations (Allman et al. 1993; Deaner et al. 2003; Sol 2009). In fact, González-Gómez et al. (2015) observed that avian species inhabiting highly variable environments showed better cognitive performance than species occurring in more stable habitats. Hummingbirds in particular showed more exploratory behaviors in more variable environments (González-Gómez et al. 2015).

10.8 Sexual Dimorphism in Cognitive Abilities

Many hummingbird species show sexual dimorphism in morphological and behavioral traits such as resource exploitation strategies (Temeles et al. 2005; González-Gómez and Estades 2009). In species where males are territorial and females are not, usually dominant males secure access to dense patches of nectar-rich flowers while subordinate females perform rapid intrusions into male territories to raid the good resources, or they are forced to forage in nectar-poor, scattered flowers (Kodric-Brown and Brown 1978). Thus, González-Gómez et al. (2014) hypothesized that territorial males should have higher demands on spatial abilities as a result of tracking nectar quality and availability in their territories. In contrast, females could be opportunistic foragers, guided mainly by visual cues about the presence/absence of flowers but without information about nectar quantity, quality, or availability (González-Gómez et al. 2014). Comparisons of cognitive performance between males and females of green-backed firecrown hummingbirds support this idea. González-Gómez et al. (2014) assessed the ability of males and females to recall position, quality, and nectar renewal schedule, where females show poorer cognitive performance than males (Fig. 10.5a).

According to the adaptive specialization hypothesis, natural selection may change behavior and its underlying neural mechanisms if such modifications enhance fitness (Krebs et al. 1989; Sherry et al. 1989; Sherry et al. 1992). Evidence supporting this hypothesis has been observed in several species in foraging and breeding contexts, where the group that performs behaviors which involve more developed cognitive abilities shows larger hippocampal areas (Roth and Pravosudov 2009; Pravosudov et al. 2015). Hummingbirds have larger HF than other avian groups (Ward et al. 2012) (Fig. 10.5b). Nevertheless, González-Gómez et al. (2014) observed that despite females of greenbacked firecrown had lower cognitive performance than males, their HF was larger (Fig. 10.5c), which contradicts the adaptive specialization hypothesis. Possible explanations could be that females recall nectar characteristics at larger spatial scales, and therefore the experimental setup did not assessed their cognitive abilities. On the other hand, it could be that females remember social interactions; such males that display lower aggression levels. Nevertheless,

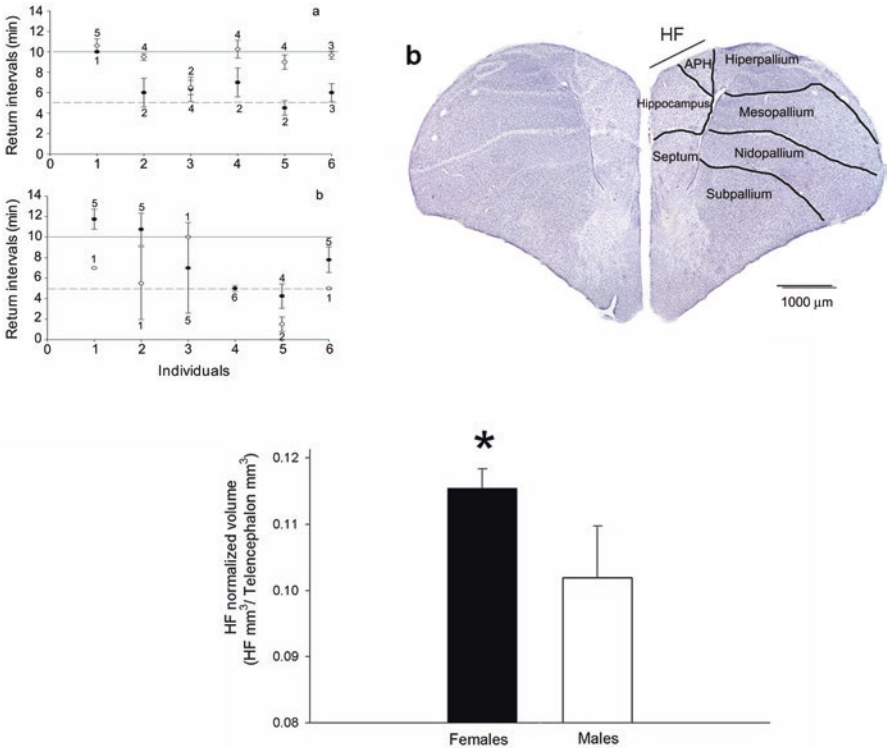

Fig. 10.5 (**a**) Return intervals of males (upper panel) and females (lower panel) to high-quality (white dots) and low-quality (black dots) feeders between the search and return phase of the experiment. Number of visits (mean ± SE) to both nectar qualities is shown. Solid line: renewal interval of high-quality nectar feeders; dashed line: renewal interval of low-quality nectar feeders. *Return interval differed significantly from the nectar renewal interval, 1000 bootstrap sampling (high-quality nectar, 95% CI: 11.1–9.75 min, low-quality nectar, 95% CI: 6.15, 4.75 min). (**b**) Coronal section through the telencephalon of the green-backed firecrown hummingbird showing the hippocampal formation (i.e., hippocampus and area parahippocampalis (APH)) in the medial-dorsal aspect. Scale bar: 1000 µm. (**c**) The HF is significantly larger in females (13.96 ± 0.81 mm^3, mean ± SE) than males (12.04 ± 0.8) respect to the telencephalon volume (121.31 ± 8.30, 117.81 ± 5.36, respectively). Please note the statistical analysis was performed using telencephalon volume as a covariable. Data are presented as mean ± SE. *$p < 0.05$. Modified from González-Gómez et al. (2014)

the study exemplifies the link between cognitive challenges of the environment and the structure of the underlying neural mechanisms.

10.9 Concluding Remarks

The Neotropics present extremely high habitat diversity with at least 10 bioregions, each of them with several ecoregions. Most likely, this environmental diversity promoted the high number of species occurring in this region, with a total of ~4750 species (Jenkins et al. 2013; Pimm et al. 2014). This contrasts with the number of species found in North America (1321) and Europe (552), where most of the studies in animal behavior, and in particular in animal cognition, are carried out. Overall, data in our revision showed that hummingbird species in the Neotropics present similar cognitive abilities than species at the Nearctic region. However, the diversity of environments in the Neotropical region allowed us to assess the role of environmental heterogeneity and resource exploitation strategies on learning and memory, although the lack of information in relation to the species richness is striking. Thus, our conclusions are limited by the few studies that have been carried out. Among different habitats, environmental heterogeneity seems to drive the development of cognitive abilities, however mediated by individual traits such as sex and social status. This could explain why, across all the studies, we observed important individual differences in cognitive performance, although more data are needed. Furthermore, inhabiting variable environments requires flexible adjustments in physiology and behavior to increase the chances of survival and reproduction. For example, in seasonal environments, animals are restricted in the initiation and duration of the different life history stages across the annual cycle. Thus, avoiding the overlap of expensive processes such as breeding and molt, and matching their cycles to resource availability. In this context, long-term integrative studies could be key to understand variations in cognitive performance, and how cognition acts to buffer environmental variability. In our opinion, the role of these variables should be further assessed integrating physiological traits, such as endocrine levels and energy balance. Thus, integrative and comparative studies in hummingbirds in the Neotropics could shed light on the different selective pressures that might have shaped the evolutionary trajectory of avian cognition.

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