


Molting while breeding? Lessons from New World *Tyrannus* Flycatchers

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Abstract Songbirds must annually undergo two energetically demanding but important activities: breeding and feather molt. Due to the high energetic investment that each demands, these two events are generally not carried out simultaneously. However, substantial variation in the level of annual reproductive investment among populations may result in variation in molt-breeding overlap between them. With the goal of understanding whether different songbird populations overlap molt and breeding, and, if so, to determine directions for research on the potential tradeoffs involved, we describe the relationship between

clutch size, molt, and energetic condition within a genus of New World Flycatchers (*Tyrannus*). Of 219 Flycatchers sampled, only one individual molted flight feathers while breeding, suggesting that molting flight feathers and breeding simultaneously is too energetically expensive at any clutch size. However, some Flycatchers molted body feathers during the breeding season. When we tested for an effect of clutch size, sex and energetic condition on body molt intensity during the breeding season, only clutch size and sex had significant effects, with a negative effect of clutch size on body molt intensity in males but not in females. Based on these results, we develop a set of hypotheses to guide future studies on the potential tradeoffs between investment in reproduction and molt.

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Zusammenfassung

Mauser während der Brutzeit? Was machen die neuweltlichen *Tyrannus* Fliegenschnäpper?

Singvögel müssen zweimal im Jahr energetisch aufwändige, aber wichtige Prozesse durchlaufen: Brutzeit und Mauser. Da beide Aktivitäten hohe energetische Investitionen erfordern, laufen sie üblicherweise nicht gleichzeitig ab. Aber größere Unterschiede zwischen einzelnen Populationen in den jährlichen Fortpflanzungsinvestitionen haben möglicherweise Überlappungen von Mauser mit Brutzeit zur Folge. Ziel unserer Untersuchung war es, besser zu verstehen, ob und wie sehr sich Mauser und Brutzeit bei unterschiedlichen Singvogel-Populationen überschneiden, und festzuhalten, in welche Richtung zukünftige Untersuchungen der möglichen Vor- und Nachteile (tradeoffs) gehen sollten. Hierfür beschreiben wir für eine Gattung von Fliegenschnäppern (*Tyrannus*) aus der Neuen Welt die Zusammenhänge zwischen Gelegegröße, Mauser und energetischem Zustand. Von den 219 untersuchten Fliegenschnäppern zeigte nur ein einziges Tier während der Brutzeit auch Mauser an den Schwungfedern, was nahelegt, dass unabhängig von der Gelegegröße die Mauser der Schwungfedern und gleichzeitiges Brüten energetisch zu teuer ist. Dessen ungeachtet mauserten einige Fliegenschnäpper während der Brutzeit ihr Körpergefieder. Als wir untersuchten, ob es mögliche Auswirkungen der Gelegegröße, der sexuellen Aktivitäten und des energetischen Zustands der Vögel auf die Intensität ihrer Mauser während der Brutzeit gibt, zeigten nur die Gelegegröße und sexuellen Aktivitäten einen signifikanten Effekt; es gab einen negativen Effekt der Gelegegröße auf die Intensität der Mauser des Körpergefieders bei Männchen, nicht aber bei Weibchen. Auf der Basis dieser Befunde stellen wir eine Reihe von Hypothesen auf als Anregung für zukünftige Untersuchungen des potentiellen tradeoffs zwischen der Investition in Fortpflanzung und Mauser.

Introduction

Songbirds must accomplish several important activities on an annual cycle, such as breeding, migration, and feather molt. One way for birds to accomplish these activities in a timely fashion is to overlap two or more of them (Wingfield 2008). Two key events that overlap in numerous

songbird species are breeding and feather molt (e.g., Foster 1975; Johnson et al. 2012; de Araujo et al. 2017); however, breeding is costly for both sexes, since songbirds often share in defending their territory and feeding nestlings, and because incubation and egg production require a substantial input of calories and nutrients (Williams 2005; Reynolds 2015). Molting feathers is also energetically expensive (Lustick 1970; Murphy and King 1992; Lindström et al. 1993a; Murphy 1996) and its timing can be influenced by food availability (Danner et al. 2015); however, it is necessary because feather quality is key in several respects, such as in a bird's ability to fly efficiently (Swaddle and Witter 1997; Hedenström and Sunada 1999), reproduce successfully (Rohwer et al. 2011), and regulate body temperature (Dawson and Maloney 2004). Thus, although birds could potentially overlap molt and breeding to allow more time for molting and/or breeding, the energetic costs involved may translate to substantial behavioral and physiological trade-offs. For example, the hormonal stress response, which is key in promoting survival, is often suppressed in molting birds (Cornelius et al. 2011). Additionally, overlapping breeding and molting may result in a slower feather growth rate (Echeverry-Galvis and Hau 2012), lower feather quality (Nilsson and Svensson 1996; Rohwer et al. 2011; Echeverry-Galvis and Hau 2013), and even fitness costs (Svensson and Nilsson 1997; Hemborg and Lundberg 1998; Hemborg et al. 2001). Minimizing the overlap between molting and other costly life history activities such as breeding is therefore believed to be an adaptation to minimize fitness costs (Jenni and Winkler 1994; Murphy 1996; Pulido and Coppack 2004).

Although overlap between molt and other energetically costly activities such as reproduction or migration should be minimal (Barta et al. 2008), substantial geographic (Hemborg et al. 2001) and demographic variation (Siikamäki et al. 1994; Hemborg 1998; Dietz et al. 2013) exists. In particular, birds may vary the duration and/or intensity (i.e., number of feathers molting simultaneously) of molt while undertaking such energetically costly activities. Faster, higher intensity molts are characteristic of migratory species that molt in late summer at high latitudes, since they have a limited window during which to molt before initiating fall migration (e.g., Butler 2013). In contrast, a slower molt may be more characteristic of temperate breeding species that molt in winter or which do not migrate (de la Hera et al. 2011).

In terms of geographic variation in molt rates, many tropical breeding bird species are characterized by slower or more protracted molts than their temperate counterparts (Helm and Gwinner 1999; Collar 2005; Ryder and Wolfe 2009). Explanations for this pattern include higher parasite pressure on tropical breeding birds, resulting in a need to

maintain a high level of immune responsiveness. This would in turn lead to a conflict between investment in molt and in immune responses, such that tropical birds would have to slow down their rate of molt to maintain immune preparedness (Moreno 2004). Other reasons proposed for the slower, more protracted molts of tropical breeding birds include decreased seasonality and more predictable resource availability in tropical systems (reviewed by Johnson et al. 2012). Such protracted molts would in turn lead to the relatively high incidence of molt-breeding overlap observed in tropical birds (e.g., Foster 1975; Johnson et al. 2012; but see Marini and Durães 2001; Silveira and Marini 2012). Additionally, because tropical birds are characterized by an overall slower pace of life compared to temperate breeding birds (Wingfield 2005; Wiersma et al. 2007; Johnson et al. 2012), laying fewer eggs per clutch compared to birds breeding at temperate latitudes (e.g., Young 1994; Martin et al. 2000; Jetz et al. 2008), they may have sufficient energy savings to overlap feather molt and reproduction (Foster 1974; Moreno 2004; Johnson et al. 2012).

With the aim of developing specific predictions on potential tradeoffs in investing in molt while breeding, we explore the relationship between the incidence of molt during the breeding season and reproductive investment in New World Flycatchers of the genus *Tyrannus* (Tyrannidae). This group is an ideal system with which to investigate the timing of molt and reproduction because the populations of the genus breed across a wide geographic range (Fitzpatrick et al. 2004), and are characterized by different levels of annual investment in reproduction. Those breeding at north-temperate latitudes, such as Western Kingbirds (*Tyrannus verticalis*) and Scissor-tailed Flycatchers (*Tyrannus forficatus*) lay the largest clutches, whereas those breeding at tropical latitudes (Fork-Tailed Flycatchers, *Tyrannus savana*) lay the smallest clutches (Table 1), as seen across birds globally (Jetz et al. 2008). Substantial variation in molt timing also exists across the genus, with Western Kingbirds initiating molt in late summer and fall (Barry et al. 2009), whereas Scissor-tailed Flycatchers begin molting prior to leaving the breeding grounds (Pyle 1997; Jahn et al. 2013a). In contrast, Fork-Tailed Flycatchers of the nominate subspecies (*Tyrannus savana savana*) molt during the non-breeding season (Zimmer 1937; Pyle 1997; Jahn et al. 2016).

Here, we evaluate the relationship between molt intensity, clutch size and energetic condition in *Tyrannus* Flycatchers (hereafter, “Flycatchers”) during the breeding season. Based on these results, we offer directions for future research on the potential tradeoffs that Flycatchers and other birds face when overlapping molt and breeding.

Methods

Study sites

Fork-tailed Flycatchers of the subspecies *T. savana monachus* were studied at Reserva Natural y Productiva Tomo Grande (RTG), Vichada Department, Colombia (4.9°N, 70.2°W). We monitored nests and banded Flycatchers here during two breeding seasons (2014 and 2015; Table 1). This site is primarily composed of grasslands (llanos) with low scattered trees (*Curatella* sp.), as well as gallery forest along the Tomo River.

Fork-tailed Flycatchers of the subspecies *T. savana savana* were studied at the following sites:

1. Distrito Federal (DF), Brazil (15.8°S, 47.8°W). We banded Flycatchers and monitored their nests during two breeding seasons (2013 and 2014; Table 1) within the city limits of Brasilia (Parque da Alvorada and the campus of the Universidade de Brasilia). The habitat here is primarily short, mowed grass and scattered trees.
2. Estação Ecológica de Itirapina, São Paulo State, Brazil (22.3°S, 47.9°W). We banded Flycatchers and monitored nests here during two breeding seasons (2013 and 2014; Table 1). This reserve is primarily composed of low campo and cerrado grassland.
3. Reserva Natural El Destino, Buenos Aires Province, Argentina (35.1°S, 57.4°W). We banded Flycatchers and monitored nests here during four breeding seasons (2011–2014; Table 1). This reserve is primarily composed of temperate grasslands and marshes grazed by cattle, intersected by woodland tracts dominated by *Celtis ehrenbergiana* and *Scutia buxifolia*.
4. Reserva Provincial Parque Luro and surrounding properties, La Pampa Province, Argentina (36.8°S, 64.3°W). We banded Flycatchers and monitored nests here during two breeding seasons (2013 and 2014; Table 1) along a right-of-way road (Ruta 35) and in the reserve, which is composed primarily of tracts of *Prosopis caldenia* trees and grasslands with scattered bushes.

Western Kingbirds (*T. verticalis*) and Scissor-tailed Flycatchers (*T. forficatus*) were studied in Lawton, Oklahoma (LOK), USA. We banded Flycatchers and monitored nests here during three breeding seasons (2011–2013; Table 1) on the campus of Cameron University, Elmer Thomas Park, and the Lawton Country Club, all in the town of Lawton (34.38°N, 98.24°W). These sites are primarily characterized by mowed grass and scattered trees (*Quercus* spp.).

Table 1 Life history table of *Tyrannus* Flycatcher populations studied

Population	North-temperate breeders		South-temperate breeders	Tropical breeders	
	Scissor-tailed Flycatcher (<i>Tyrannus forficatus</i>)	Western Kingbird (<i>Tyrannus verticalis</i>)	Fork-tailed Flycatcher (<i>Tyrannus savana savana</i>)	Fork-tailed Flycatcher (<i>Tyrannus savana savana</i>)	Fork-tailed Flycatcher (<i>Tyrannus savana monachus</i>)
Mean clutch size, this study	LOK, 4.5 (0.68); $n = 21$	LOK, 4.5 (0.51); $n = 21$	BA, 3.4 (0.63), $n = 124^f$; LP, 3.8 (0.46), $n = 8^g$	DF, 2.9 (0.32), $n = 18^j$; SP, 2.8 (0.55), $n = 13^k$	RTG, 2.5 (0.52), $n = 11^n$
Mean clutch size, previous studies	4.7 (0.52) ^a ; 4.7 (0.12) ^b ; 4.6 (0.65) ^c ; 4.5 (0.5) ^d	4.1 (0.7) ^e ; 4.4 (0.21 SE) ^b ; 4.2 (0.72) ^c	3.3 (0.03) ^h ; 3.8 (0.63) ⁱ	2.5 (0.3 SE) ^l ; 2.9 (0.06) ^m	2.5 ^o ; 2.6 (0.71) ^p
Breeding season length (days)	LOK, 2 May–18 July (77)	LOK, 9 May–19 July (71)	BA, 15 November–25 January (71); LP, 12 November–19 January (68)	DF, 25 September–25 November (61); EEI, 30 October–26 December (57)	RTG, 9 March–9 April (31) ^q

Numbers in parentheses following mean clutch size values represent \pm SD, except as noted. For data from previous studies reporting multiple years of research on clutch size, the highest yearly value was consistently used

Breeding season length Number of days between the earliest date that eggs were observed and the last date on which nestlings fledged, across years of study at each site [the breeding season at Reserva Natural y Productiva Tomo Grande (RTG) Vichada, Colombia and Distrito Federal (DF), Brazil is likely longer, since we ended nest monitoring there before all nestlings fledged]

LOK Lawton, Oklahoma, USA; BA Reserva Natural El Destino, Buenos Aires, Argentina; LP Reserva Provincial Parque Luro, La Pampa, Argentina; SP Estação Ecológica de Itirapina, São Paulo, Brazil

^a Regosin and Pruett-Jones (1995), data from USA

^b Murphy (1988), data from USA

^c Murphy (1989), data from USA

^d Nolte and Fulbright (1996), data from USA

^e Gamble (1985), data from USA

^f Present study, from 2011 to 2014

^g Present study, from 2013 and 2014

^h Mezquida (2002), data from Argentina

ⁱ Salvador (2013), data from Argentina

^j Present study, from 2013 and 2014

^k Present study, from 2013 and 2014

^l Marini et al. (2009), data from Brazil

^m Jahn et al. (2014), data from Bolivia

ⁿ Present study, from 2014 and 2015

^o Cruz and Andrews (1989), data from Venezuela

^p Teul et al. (2007), data from Belize

^q Breeding season is likely longer, as some nests were still active when monitoring ended

Capture and banding

We captured Flycatchers by either placing a predator model (e.g., Southern Crested Caracara, *Caracara plancus*; American Crow, *Corvus brachyrhynchos*) or a speaker emitting a conspecific call, within 2 m of one or two 3 × 12-m or 3 × 18-m polyester or nylon mist nets (38-mm mesh size). Nets were placed 2–4 m from an active Flycatcher nest (i.e., containing eggs or nestlings). At all sites, captured birds were first held in a cotton bag, then

banded with an individually numbered metal band and up to three Darvic color bands, and processed before being released.

We aged captured Flycatchers based on the presence of a primary feather notch, which is only present in Flycatchers more than 1 year old [hereafter, “adults” (Pyle 1997)] and sexed Flycatchers using the shape of the primary notch (Pyle 1997). We also used the shape of the 8th primary notch, as well as the coloration of the back and neck, to identify subspecies of Fork-Tailed Flycatcher

(Pyle 1997). We identified females in breeding condition by the presence of an active brood patch [i.e., only female *Tyrannus* Flycatchers incubate eggs (Pyle 1997; Ergosine 1998; Gamble and Bergin 2012)] and scored the level of brood patch development on a five-point scale [0 = no patch, 1 = smooth, 2 = vascularized, 3 = wrinkled, 4 = molting (Ralph et al. 1993)]. We scored development of the cloacal protuberance in males on a four-point scale [0 = none, 1 = small, 2 = medium, 3 = large (Ralph et al. 1993)]. We estimated subcutaneous fat content of the furculum and abdomen on an eight-point scale (0 = no fat, 1 = trace fat, 2 = thin layer, 3 = half filled, 4 = more than 2/3 filled, 5 = slightly bulging; 6 = bulging greatly, 7 = very large fat pads (Ralph et al. 1993)]. We scored body molt intensity on a five-point scale, from none to heavy [none = no feathers molting, trace = few molting feathers, light = involving more than one feather tract, medium = half of body feathers molting, heavy = most/all body feathers molting (Ralph et al. 1993)]. We scored remiges molt by noting which primary feather [ten/wing in Flycatchers (Pyle 1997)] and secondary feather (six/wing) was molting on each wing, and scored tail feather molt (12 rectrices) by noting which rectrix was molting (Ralph et al. 1993). We measured unfastened wing chord to the nearest millimeter using a wing ruler, tarsus and bill length (from the front of the nares to bill tip) using plastic dial calipers (to the nearest 0.1 mm), and body mass (to the nearest 0.1 g) using an Oahu ABS hand-held portable electronic scale. In order to minimize measurement error, A. E. J. worked at all study sites to ensure that measurements were standardized among banders within and between study sites.

Nest monitoring

At each site, we searched for and monitored Flycatcher nests from construction until failure or fledging of nestlings, noting the number of eggs and/or nestlings on each visit to nests, following Ralph et al. (1993). We attempted to search for and monitor nests at each site until no active nests were found, although this was not always possible (i.e., at RTG, Colombia and DF, Brazil; Table 1). Nevertheless, we are confident we monitored nests during the period of maximum breeding effort at each site, since clutch sizes remained similar throughout the monitoring period at all sites (Table 2).

Statistical analysis

We only analyzed molt data collected from actively breeding adults upon initial capture (i.e., data from recaptures were excluded). Actively breeding Flycatchers were identified by the presence of a smooth or vascularized

brood patch in females or of a small, medium or large cloacal protuberance in males. In classifying flight feather molt, we excluded birds with adventitious molt, following Wolfe et al. (2010), who consider symmetrical molt of the first primary feathers to indicate the start of a molt cycle. Thus, we classified Flycatchers as being in remiges molt when they were molting at least one primary feather on each wing or in rectrix molt when molting at least one rectrix on each side of the tail.

We classified individual reproductive investment using the mean clutch size of each species at each study site for each breeding season. We did so because, although we captured individual Flycatchers near active nests, we cannot be sure that captured individuals were the owners of a given nest because we suspect that congeners from neighboring territories or individuals without territories were often captured.

Bias in comparing investment in molt and reproduction between populations could arise from temporal variation in measuring molt and in monitoring nests during the breeding season, since *Tyrannus* Flycatcher clutches often decrease in size as the breeding season progresses (e.g., Blancher and Robertson 1987; Murphy 1988). To ensure that capture effort was constant across the breeding season, we calculated the date of each capture as a fraction of the length of the breeding season for each species at each site (i.e., between the date first eggs were observed and the date the last nestlings were observed/nest monitoring ended, combining years of study). We then calculated cumulative captures of each species as a function of the fraction of the breeding season at each site. To ensure that our nest monitoring effort was constant across the season at each site, we partitioned the breeding season into quarters and quantified the mean clutch size and number of nests monitored within each quarter (Table 2). Further bias could arise if some populations re-nest more often than others; however, to the best of our knowledge, the Flycatcher populations we studied lay only one clutch per season unless a clutch is depredated early in the season (A. E. J., personal observation).

Although we minimized measurement error by comparing measurements among banders (see above), body molt and subcutaneous fat measurements are qualitative measurements that can be difficult to standardize among banders (A. E. J., personal observation). We therefore combined “trace” and “light” body molt categories into one “trace/light” category, and combined the “medium” and “heavy” body molt categories into one “medium/heavy” category. For subcutaneous fat, we combined “thin layer” and “half filled” into one “medium” category.

We estimated energetic condition using the scaled mass index (SEMI), which accounts for the scaling relationship between body length and mass at different body sizes

Table 2 Mean clutch size by quarter of the breeding season at each study site

	DF Fork-tailed Flycatcher (<i>T. savana savana</i>)		SP Fork-tailed Flycatcher (<i>T. savana savana</i>)		BA Fork-tailed Flycatcher (<i>T. savana savana</i>)		LP Fork-tailed Flycatcher (<i>T. savana savana</i>)		RTG Fork-tailed Flycatcher (<i>T. savana monachus</i>)		LOK Western Kingbird (<i>T. verticalis</i>)		LOK Scissor-tailed Flycatcher (<i>T. forficatus</i>)	
	Mean	<i>n</i>	Mean	<i>n</i>	Mean	<i>n</i>	Mean	<i>n</i>	Mean	<i>n</i>	Mean	<i>n</i>	Mean	<i>n</i>
First quarter	3	1	2.8 (0.84)	5	3.6 (0.55)	35	3 (0)	2	NA	NA	5 (0)	2	5	1
Second quarter	2.5 (0.71)	2	2.8 (0.45)	5	3.4 (0.73)	44	4 (0)	2	2.7 (0.52)	6	5	1	4.8 (0.44)	13
Third quarter	3 (0)	10	3 (0)	2	3.3 (0.57)	33	4 (0)	3	2.3 (0.58)	3	4.5 (0.52)	11	4.3 (0.96)	4
Fourth quarter	2.8 (0.45)	5	3	1	3.3 (0.45)	12	4	1	2 (0)	2	4.1 (0.38)	7	3.7 (0.58)	3

n Number of nests monitored

For study site abbreviations, refer to Table 1

(Peing and Green 2009, 2010). To calculate SEMI, we first estimated the scaling exponent between body mass and size by performing a standardized major axis regression on the natural log of body mass by the natural log of wing chord (Peing and Green 2009). We found a significant difference in SEMI values among subcutaneous fat scores (Kruskal–Wallis test: $\chi^2_2 = 7.63$, $P = 0.022$; Fig. 1), and a post hoc Dunn's test showed that birds with no subcutaneous fat have significantly lower SEMI values than those with the highest SEMI values, suggesting that SEMI is a reliable measure of energetic condition in Flycatchers. We therefore use SEMI as an estimate of energetic condition.

We used non-parametric tests in INFO STAT (2009) to describe differences in clutch size and intensity of molt between populations. We also used cumulative link mixed models using the lme4, ordinal and bbmle packages in program R (R Core Team 2016), which allow for an ordinal response variable (i.e., molt intensity), to evaluate the additive effect of the log of clutch size, the log of energetic condition, and sex on intensity of molt. We included study

site and species as random factors. We first tested this full model, then used backward elimination to remove effects that contributed the least to the model. We compared the goodness of fit of each model using likelihood ratio tests in program R (R Core Team 2016).

Results

We sampled a total of 219 breeding Flycatchers (57 females and 162 males) and monitored 216 nests (Tables 1, 2). Cumulative capture rates at each site were similar, occurring through at least the mid-point of the breeding season at all sites (the site at which captures ended earliest was at DF, Brazil on date 0.58; Fig. 2). Our nest monitoring effort (i.e., number of nests monitored) usually peaked in the second or third quarter of the breeding season at all study sites (Table 2).

Clutch size between populations

Mean clutch size was significantly different between populations (Kruskal–Wallis test, $\chi^2 = 87.3$, $P < 0.0001$). A post hoc Dunn's test showed no significant difference between clutch sizes among tropical populations; however, clutch sizes of populations at tropical latitudes were significantly smaller than those at south- and north-temperate latitudes (Table 1). Additionally, clutch sizes at south-temperate latitudes were significantly smaller than those at north-temperate latitudes (Table 1).

Molt intensity by clutch size, sex and energetic condition

Only one Flycatcher that we sampled throughout the study molted flight feathers (a male Western Kingbird that was symmetrically molting the first three primary feathers).

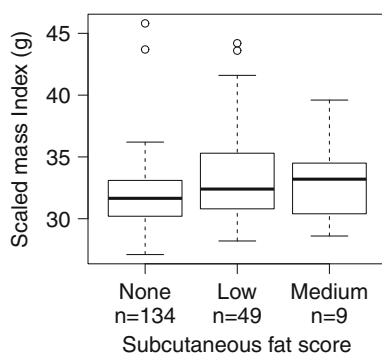


Fig. 1 Energetic condition (as measured by the scaled mass index) as a function of level of subcutaneous fat among the *Tyrannus* Flycatchers studied. Line inside each box represents the median; top and bottom of each box represent upper and lower quartiles, respectively; whiskers represent maximum and minimum values; circles represent outliers

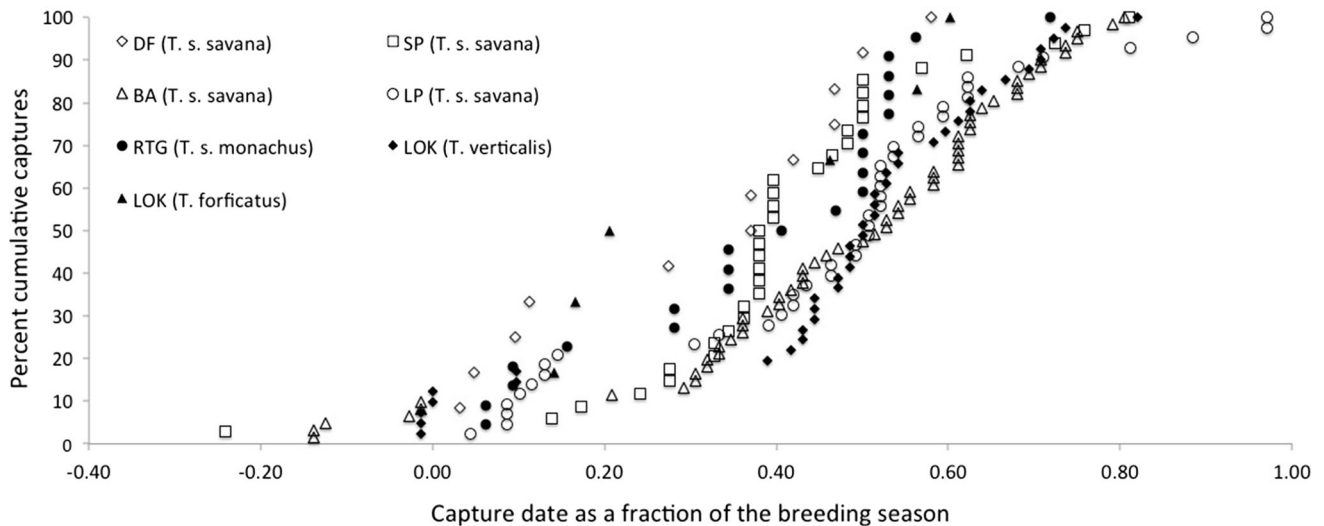


Fig. 2 Cumulative captures of *Tyrannus* Flycatchers at each study site, expressed as the percentage of total Flycatchers captured at each study site as a function of the fraction of breeding season length of each species at each site (0 = date first eggs were observed, 1 = date last nestlings were observed when site/nest monitoring ended,

combining years of study); some captures occurred during a negative fraction of the breeding season because the breeding Flycatchers were identified by the presence of incubation patches (in females) or cloacal protuberances (in males), which may develop before eggs appear in nests; refer to Table 1 for study site abbreviations

However, some Flycatchers molted body feathers during the breeding season.

was a higher than expected proportion of males with trace/light body molt and a lower than expected proportion with no body molt.

When we ran the full model on the effects of clutch size, energetic condition and sex on body molt intensity, with study site and species as random factors, energetic condition showed no significant effect ($\chi^2_1 = 0.95, P = 0.329$). When we excluded energetic condition, the resulting model showed significant effects of both clutch size ($\chi^2_1 = 17.7, P < 0.0001$) and sex ($\chi^2_1 = 6.23, P = 0.013$), such that our best-fitting model included only the additive effects of sex and clutch size on body molt intensity. When we evaluated the effect of the random factors, we found no significant effect of species ($\chi^2_1 = 0.00, P = 0.956$) or study site ($\chi^2_1 = 1.03, P = 0.311$). Because there was a significant effect of sex, we ran a cumulative link model for the effect of clutch size on body molt intensity separately for each sex and found that there was a significantly negative effect of clutch size on body molt intensity in males ($z = -4.10, P < 0.0001$), but not in females ($z = -1.73, P = 0.084$; Fig. 3). Male Flycatchers with no molt have larger clutch sizes than those with either ‘trace/light’ or ‘medium/heavy’ molt scores (Fig. 3b).

Notably, females had higher energetic condition values than males across all clutch sizes (Fig. 4). Females also had higher energetic condition values than males across all levels of body molt intensity (Fig. 5).

Discussion

Although study site had no significant effect within the model, when we evaluated body molt intensity as a function of study site within males, we found that body molt intensity is significantly site dependent (χ^2 test for independence: $\chi^2_{10} = 32.10, P = 0.0004$). There was a higher than expected proportion of males with no body molt and a lower than expected proportion of males with trace/light body molt at LOK (Oklahoma, USA). The opposite pattern was apparent for males at RTG (Colombia), where there

Flight feather molt during breeding has been found in other New World Flycatchers (Repenning and Fontana 2011), but only one Flycatcher showed this in the present study. For the Flycatchers we studied, molting flight feathers may be too energetically costly an activity to be undertaken while breeding, regardless of clutch size. Indeed, rectrices, primaries and secondaries of *Tyrannus* Flycatchers are much larger than body feathers and likely require much more energy to molt. However, some Flycatchers do molt body feathers while breeding, and we found a strong, negative effect of clutch size on intensity of body molt in male but not female Flycatchers. This pattern was largely latitude dependent: male Flycatchers breeding at north-temperate latitudes (Oklahoma), where clutch sizes are the largest, were more likely to exhibit no body molt during the breeding season, whereas the opposite was true for those breeding at the study site located at the lowest latitude, in Colombia, where clutch sizes are the smallest.

Previous research has suggested that a tradeoff exists between investment in reproduction and molt (e.g., Rohwer

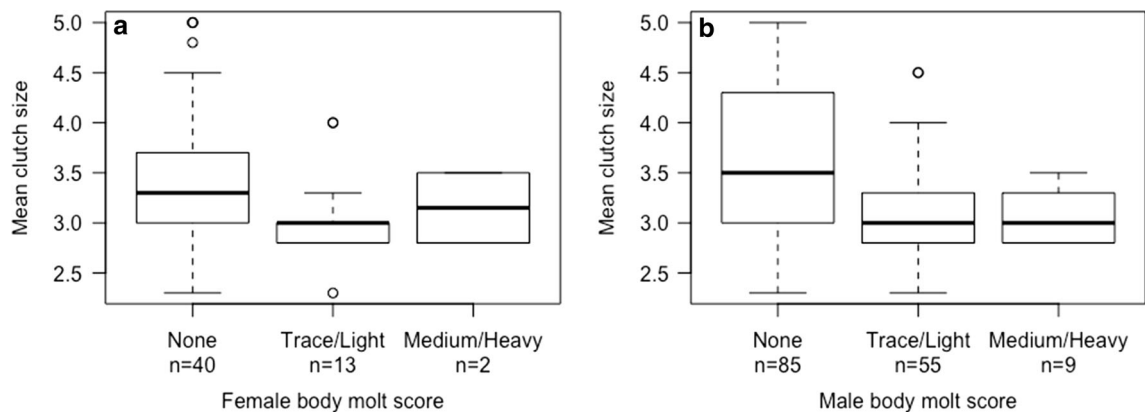


Fig. 3 Clutch size as a function of body molt intensity in **a** female and **b** male *Tyrannus* Flycatchers. Line inside each box represents the median; top and bottom of each box represent upper and lower

quartiles, respectively; whiskers represent maximum and minimum values; circles represent outliers

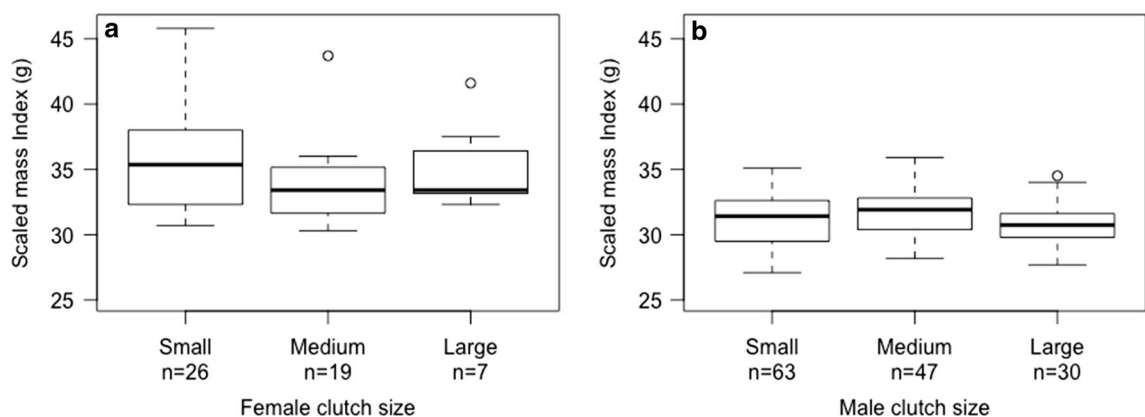


Fig. 4 Energetic condition, as measured by the scaled mass index, as a function of clutch size in **a** female and **b** male *Tyrannus* Flycatchers. Clutch sizes: ≤ 3 eggs/clutch (small), 3.1–4.0 eggs/clutch (medium), > 4 eggs/clutch (large). Line inside each box represents the median; top and bottom of each box represent upper and lower

quartiles, respectively; whiskers represent maximum and minimum values; circles represent outliers

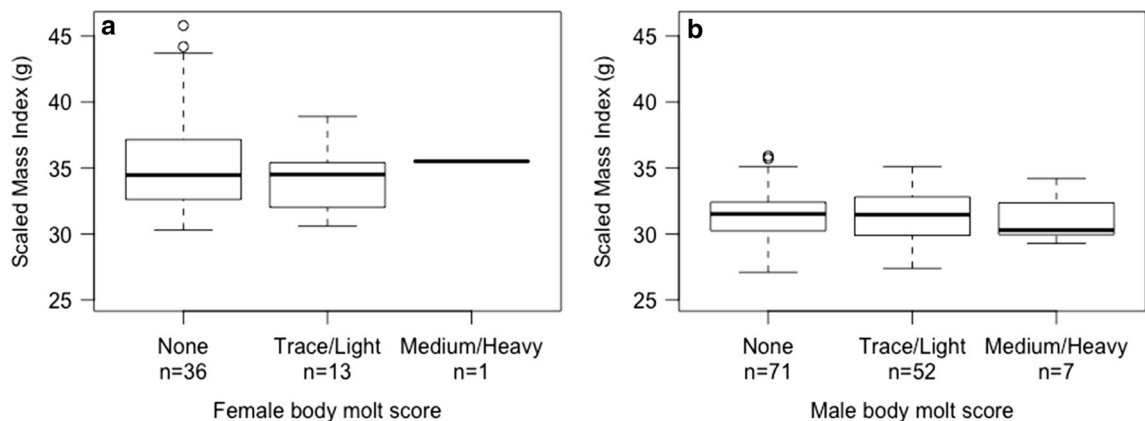


Fig. 5 Energetic condition (as measured by the scaled mass index) as a function of body molt intensity in **a** female and **b** male *Tyrannus* Flycatchers. Line inside each box represents the median; top and

bottom of each box represent upper and lower quartiles, respectively; whiskers represent maximum and minimum values; circles represent outliers

et al. 2011; Echeverry-Galvis and Hau 2013), and that larger clutches are more energetically costly (e.g., Coleman and Whittall 1988; Moreno and Carlson 1989). Although we did not find a significant relationship between energetic condition and body molt intensity, future studies using other measures of energetic condition may provide further insights. Furthermore, understanding the underlying mechanisms driving a given life history strategy, as well as the tradeoffs incurred in adopting a given strategy, requires knowledge of individual variation in quality (van Noordwijk and de Jong 1986; Stearns 1989), quantified through experimental studies (reviewed by Verhulst and Nilsson 2008). Such experimental studies should also take into account ecological and physiological aspects, as well as year-to-year environmental variability (McNamara and Houston 2008). Our results point to several promising avenues of research on the tradeoffs involved in overlapping molt and reproduction. We offer two research questions that, if addressed, promise key insights into potential tradeoffs:

What are the sex-specific tradeoffs involved in overlapping molt and breeding, and how do they vary across populations?

Because life history strategies of songbirds are often sex specific [e.g., only female Flycatchers incubate eggs (Jahn and Tuero 2013)], the tradeoffs involved when life history stages, such as molt and reproduction, overlap need to be understood for each sex Barta et al. (2008). We found that male Flycatchers generally had a lower energetic condition than females. Male *Tyrannus* Flycatchers often arrive on breeding territories before females to secure breeding territories in spring (Cooper et al. 2009), aggressively defending the breeding territory (e.g., Ergosine and Pruett-Jones 1995) and guarding the female as she incubates (Jahn and Tuero 2013). Males also participate in feeding nestlings (e.g., Ergosine and Pruett-Jones 1995), and because larger broods result in a greater investment in time spent caring for nestlings (e.g. Rosa and Murphy 1994) the energetic investment by males during the breeding season is likely to be high. *Tyrannus* Flycatcher males are also often larger than females [e.g., Fork-Tailed Flycatchers (A. E. J. unpublished data); Scissor-tailed Flycatchers (D. V. R., unpublished data)] and could therefore have higher overall energetic costs than females. Indeed, clutch size in Eastern Kingbird females is independent of body condition (Murphy 1986, 2004), females carry more fat than males, and males have proportionally more muscle mass than females, such that males may expend more energy than females (Murphy 2007).

Sex-specific differences are likely to vary by population. For example, the negative relationship between clutch size

and the intensity of body molt in males is in large part latitude dependent, since clutch size was significantly higher at north-temperate latitudes than at tropical latitudes. Thus, males breeding at tropical latitudes may be better able to spread out investment in body molt throughout the year. In contrast, those breeding at north-temperate latitudes may have to invest more heavily in both flight and body molt outside of the breeding season. Additionally, we found that females at tropical latitudes were difficult to capture (i.e., explaining our low sample sizes of females at tropical sites), potentially due to a greater aversion to risk when defending their nests relative to temperate populations. Controlling for such variation will be imperative to understanding the drivers of molt-breeding overlap.

What are the selective advantages to overlapping molt and breeding within the context of the annual cycle?

As outlined by Wingfield (2008), as the number of life history stages (e.g., molt, reproduction, migration) increases, the less flexibility an individual will have in timing those stages. Thus, expressing fewer life history stages translates to an increase in flexibility in timing each stage but potentially less tolerance to variation in environmental conditions, since a greater number of stages allows for flexibility in the face of environmental variation. One way around this problem is to overlap some life history stages (Wingfield 2008). Depending on where an organism is located along the spectrum of life history stage flexibility may in large part determine its ability to tolerate current and future rapid climate change. For example, migratory birds have more life history stages than non-migrants (i.e., because migratory birds must migrate twice per year), such that migratory birds potentially have a lower flexibility in the timing of life history events than non-migrants (Wingfield 2005). Nevertheless, some migratory birds may be able to molt during migration. In Red Knots (*Calidris canutus*), the overlap between molt and migration is positively related to migration distance, likely because as migration distance increases, the longer the migration stage lasts and is therefore more likely to encompass other life history events, such as molting (Buehler and Piersma 2008). However, overlapping migration and molt can be costly, since molting birds can experience reduced flight efficiency (Swaddle and Witter 1997; Echeverry-Galvis and Hau 2013) and overlapping molt and migration may lower feather signal quality (Norris et al. 2004). In North America and Europe, migration and molt generally do not overlap, with most short-distance migrants undergoing a pre-basic molt (i.e., molting all body and flight feathers) before initiating fall migration, and long-distance migrants

generally molt before fall migration or at a staging area along the fall migratory route, or on the wintering grounds (e.g., Lindström et al. 1993b; Svensson and Hedenström 1999; Rohwer et al. 2005; Newton 2011).

The population we studied with a lower than expected proportion of males with no body molt are non-migratory (i.e., RTG in Colombia), whereas all other study populations are migratory. Fork-tailed Flycatchers that breed in Brazil are intra-tropical migrants (Jahn and Tuero 2013), and those that breed in Argentina migrate >2800 km in fall (Jahn et al. 2013b). Both Scissor-tailed Flycatchers and Western Kingbirds migrate >1200 km in fall to their Neotropical wintering grounds (Jahn et al. 2013a). Thus, given their investment in migration, migratory male Flycatchers may need to invest energetic reserves gained during the breeding season in preparation for fall migration rather than in molting. In contrast, non-migratory males may be better able to molt while breeding, since they do not have to also invest in migration after breeding.

Conclusion

In summary, understanding tradeoffs involved in overlapping molt with breeding and/or migration should involve comparisons among males and females of migratory vs. resident, partially migratory and non-migratory populations that migrate different distances, while controlling for morphological, energetic, and other measures of individual quality. Such comparisons should potentially focus on vital rates [e.g., addressing whether tropical breeders have greater flexibility between their breeding and molt stages, thereby permitting more re-nesting attempts (Foster 1974)]. Additionally, a full appreciation of the mechanisms determining flexibility in the timing of molt throughout the annual cycle will depend on a basic understanding of the extent to which molt is under genetic control (Helm and Gwinner 1999). Rohwer and Rohwer (2013) have suggested that molt intensity, in particular, is a labile trait, and that flexibility in molt intensity may be how birds fit molting into the annual cycle, while also maximizing productivity and meeting constraints related to living in seasonal environments. Indeed, research on some well-studied taxa has shown that flexibility in molt timing is widespread in both resident and migratory birds (Hall and Tullberg 2004). Information on both intrinsic (e.g., physiology) and extrinsic (e.g., availability and quality of food resources) factors will be necessary to acquire a comprehensive understanding of the mechanistic underpinnings of the timing and intensity of molting Barta et al. (2008).

Research on the full annual cycle of birds is key to understanding seasonal interactions and developing effective conservation and management plans, and we echo previous calls to include molt dynamics in the evaluation of avian life histories (e.g., Leu and Thompson 2002). Full annual cycle

research across vertebrates is still rare, due to a bias towards research during the reproductive period (Marra et al. 2015) and temperate-zone breeders (Jahn and Cueto 2012). Although comparative research on avian life history strategies has been ongoing for decades (reviewed by Robinson et al. 2010), very rarely is molt explicitly included in such studies (but see Wikelski et al. 2003). Understanding the timing and overlap of events such as molt and reproduction, as well as the consequences of such overlap in songbirds across the planet, offers valuable insights into how they cope with numerous conflicting demands on an annual basis, and therefore a more comprehensive evaluation of their vulnerability to such potential threats as climate change.

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