ORIGINAL ARTICLE

Sociedad
de Ornitología
Neotropical

BREEDING AND MOLT PATTERNS OF THE COMMON GROUND-DOVE (*COLUMBINA PASSERINA*) IN XERIC, UNPREDICTABLE ENVIRONMENTS OF VENEZUELA

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Abstract · In non-migratory birds the annual cycle is composed of two critical events, breeding and molt, spaced by quiescent periods. Breeding in arid environments is frequently dependent on rainfall, but arid environments have unpredictable and irregular precipitation; therefore, birds of arid environments are thought to maintain their reproductive system in a partially or fully activated state to responding rapidly to favorable conditions. Molt most commonly follows the end of reproduction. We studied the annual cycle of the Common Ground-dove (*Columbina passerina*) for 15 months in arid scrub of Venezuela by determining gonadal sizes and maturation state, and by scoring wing, tail and body molt. As expected, both sexes underwent a brief period of gonadal regression of only about one month during the dry season, and maintained a partly or fully active reproductive system during the rest of the year. Breeding of Common Ground-doves was associated to rainfall, but not exclusively so; testicular recrudescence began in advance of the rains and gonadal cycles of both sexes followed more closely the year's precipitation rather than the long-term rainfall pattern. Although birds maintained an extended period of reproductive readiness, they bred during limited periods; yet, differences in reproductive activity between the same months of consecutive years showed their temporal flexibility and opportunistic breeding. Common Ground-doves molted throughout the year with no synchrony among individuals, replaced one primary per wing at a time, with no temporal overlap, and did not have a definite prebasic molt period of primary replacement. Lack of overlap in feather replacement would allow minimizing instantaneous energy and nutrient demands and lessening strain in birds that molt while breeding. Our results indicate that molt and breeding overlapped extensively at population and individual levels. Common Ground-doves in xeric environments further illustrate the diversity of life histories of tropical birds in relation to ecological conditions.

Resumen · El patrón de reproducción y muda de la Tortolita Grisácea (*Columbina passerina*) en ambientes xéricos e impredecibles de Venezuela

En aves no migratorias el ciclo anual se compone de dos eventos críticos, la reproducción y la muda, separados por períodos de quiescencia. La reproducción en ambientes áridos depende con frecuencia de las lluvias, pero los ambientes áridos tienen precipitación impredecible e irregular; por lo tanto, se considera que las aves de ambientes áridos mantienen su sistema reproductivo en un estado parcial o totalmente activado para responder rápidamente a condiciones favorables. La muda habitualmente ocurre al final de la reproducción. Estudiamos el ciclo anual de la Tortolita Grisácea (*Columbina passerina*) durante 15 meses en matorrales áridos de Venezuela mediante la determinación del tamaño y maduración de las gónadas, y el registro de la muda de alas, cola y cuerpo. De acuerdo a lo esperado, ambos sexos mostraron un breve período de regresión gonadal de alrededor de un mes durante la temporada seca, y mantuvieron parcial o totalmente activado su sistema reproductivo durante el resto del año. La reproducción de la Tortolita Grisácea estuvo asociada con la lluvia pero no exclusivamente con esta; la recrudescencia testicular comenzó antes de las lluvias y los ciclos gonadales de ambos sexos siguieron más fielmente la precipitación del año de estudio que el patrón de lluvias a largo plazo. Aunque las aves mantuvieron un período prolongado de disposición a la reproducción, se reprodujeron durante períodos limitados. Sin embargo, las diferencias en la actividad reproductiva entre los mismos meses de años consecutivos demostraron la flexibilidad temporal y reproducción oportunista. Las Tortolitas Grisáceas mudaron durante todo el año sin sincronía, reemplazando una primaria por ala a la vez, sin solapamiento temporal y sin mostrar un período de muda prebásica definido de reemplazo de las primarias. La ausencia de solapamiento les permitiría minimizar las demandas instantáneas de energía de nutrientes y reducir el

estrés en individuos que mudan mientras se reproducen. Nuestros resultados indicaron que la muda y la reproducción se superponen ampliamente tanto a nivel poblacional como individual. Las Tortolitas Grisáceas en ambientes xerófitos ilustran aún más la diversidad de historias de vida de las aves tropicales en relación con sus condiciones ecológicas.

Key words: Annual cycle · Columbidae · Molt-breeding overlap · Molt rate · Opportunistic breeding

INTRODUCTION

In non-migratory birds, the annual cycle is composed of two key events, breeding and molt, spaced by quiescent periods in specific yearly sequences (Echeverry-Galvis & Hau 2013). Since breeding and molt are energetically and nutritionally demanding (Murphy & King 1992, Murphy 1996, Williams 2012), they should occur at optimal times and in optimum sequence. In fact, in most small bird species these two events are often segregated in time to reduce their impacts on limiting resources (Dawson 2008, Rohwer & Wang 2010).

In birds, food abundance for the laying female, or for dependent young are considered the most important selective agents determining the optimum time to breed (Lack 1969, Perrins 1970), and birds living in seasonal environments adjust their life history events to changes in food availability (Tökölyi et al. 2012). Hence, birds inhabiting predictable environments have predictable breeding seasons and predictable periods when their reproductive system is shut down (Dawson 2008). In such environments, most species use photoperiod as the main environmental anticipatory cue for the initiation of physiological changes (Dawson 2008, Hau 2008). In contrast, arid environments frequently have unpredictable and irregular precipitation that brings about times of plenty when new vegetation and a flush of insects appear shortly after the rains. Breeding conditions in arid environments, are at their best during or shortly after wet periods (Immelmann 1973). Consequently, rainfall and its effects have been substituted for photoperiod as the most important extrinsic factor triggering bird breeding processes in arid regions (Hau et al. 2004, Dawson 2008, Hau 2008).

Close dependence of breeding on rainfall has been shown for a number of species of diverse taxonomic affiliations in communities of arid Neotropical environments: in the Santa Elena Peninsula of Ecuador (Marchant 1959, 1960), for Galapagos finches (*Geospiza*; Grant 1999, Hau et al. 2004), for wrens of northern Colombia (Ahumada 2001), in northeastern Venezuela (Poulin et al. 1992), and in dry Amazonian forest (Helder 2017). Likewise, in unpredictable arid regions of Australia and southern Africa, birds may breed any time of the year in an erratic pattern depending on rainfall (Keast & Marshall 1954, Maclean 1971, Immelman 1973, Lloyd 1999). Therefore, species of birds living in arid, unpredictable environments have unpredictable breeding seasons since they frequently rely on unpredictable ephemeral resources (Dawson 2008). When seasonal changes are not entirely predictable, birds

need to be flexible and reproduce opportunistically whenever environmental conditions permit (Astheimer & Buttemer 2002, Dawson 2008, Tökölyi et al. 2012). Thus, opportunistic breeders need to respond quickly to favorable changes in the environment. However, rapid initiation of breeding in response to rain spells requires several weeks of physiological preparations (Wingfield & Farner 1993, Williams 2012). As a result, birds living in highly variable environments are thought to maintain their reproductive system in a fully or partially activated state (Immelmann 1973, Hau et al. 2004). Although there is support for this prediction, not all birds respond in the same way. For instance, male Small Ground Finches (*Geospiza fuliginosa*) of the arid Galapagos Islands differ from other opportunistic breeders by having completely regressed gonads between breeding events (Hau et al. 2004).

The annual molt is also a critically important and physiologically demanding life-history stage within the annual cycle (Murphy & King 1987, 1992; Dietz et al. 1992), hence molt and breeding tend to be separate in time. In most species of birds, including Neotropical species, the primary molt is also seasonal and generally follows the termination of reproduction (Poulin et al. 1992, Piratelli et al. 2000, Verea et al. 2009, Sainz-Borgo & Lentino 2012, Helder et al. 2017). Nonetheless, among Neotropical species, temporal overlap of breeding and molt is widespread (Marini & Durães 2001, Echeverry-Galvis & Córdoba-Córdoba 2008, Johnson et al. 2012), even when overlapping may have negative fitness consequences (Svensson & Nilsson 1997, Echeverry-Galvis & Hau 2013).

A number of studies of Neotropical birds have focused on their annual cycle, but only a few have examined their gonadal pattern, these include passerines of forest and open habitat (Hau et al. 1998, 2004; Wikelski et al. 2000, 2003; Ahumada 2001), and non-passerines (Bosque et al. 2004). Other studies have used the presence of brood patches and cloacal protuberance as indicative of breeding, but observational techniques only track the outcome of the reproductive process (Wikelski et al. 2003). Examining gonadal patterns provides a more complete insight into the temporal outline of the breeding cycle. Likewise, with few exceptions, in studies of annual cycles of Neotropical birds (e.g., Johnson et al. 2012, Moreno-Palacios et al. 2013), molt periods have only been examined by recording molt occurrence (yes/no) of primary feathers, but with few exceptions (e.g., Stiles 1979, Rohwer et al. 2009, Guallar et al. 2016), little or no attention has been paid to the duration and intensity of molt.

We studied the breeding and molt periods of Common Ground-doves (*Columbina passerina*), a ground consumer of small seeds and a common inhabitant of the xeric northwestern coast of Venezuela, by examining their testes and follicle development and the extent of the molt during slightly over one year. We aimed to examine three questions of the annual cycle of Common Ground-doves: 1) Are they physiologically capable of reproducing year round by maintaining an active, or partially active, reproductive state?; 2) Do they reduce reproductive quiescence in order to respond to favorable environmental conditions rapidly?; 3) Do they show flexible molt cycles? We anticipated that Common Ground-doves would have brief or no gonadal quiescence in order to respond to favorable environmental conditions rapidly. We had no clear expectation on the timing, extension or intensity of the molt, because if breeding was flexible, it was possible that molt would also be flexible.

METHODS

Study area. Our fieldwork was carried out in northern Falcón State, in the north-western coast of Venezuela (Figure 1). Northern Falcón State is part of a dry belt extending along coastal margins of northern South America, bordering the southern Caribbean Sea. The center of this belt, from northern Falcón to the Goajira Peninsula, limiting Venezuela and Colombia, possesses a climate with limited and erratic rainfall (Lahey 1973). Long term annual precipitation in northern Falcón has a seasonal component; at the city of Coro (11°27'N, 69°34'W) annual rainfall averages 402 mm (Figure 2; World Weather Service 2014), a major portion of which (41.7%; 167.6 mm) falls between October and December. This rainy period is followed by a dryer period during the remaining eight or nine months. However, as it is frequent in arid environments, precipitation in northern Falcon is erratic and intense rainy spells can occur during the dry season; conversely, in very dry years there is virtually no rainy season (Bosque 1984). Rainfall during the major part of our study, 1995, did not follow the long-term pattern. Total precipitation in that year was 510 mm, most of which (441.8 mm; 86.6%) fell between June and Sept, while rainfall from October to December was only 15.9 mm (0.3%). Long-term average monthly temperature maxima range from 34.4°C to 31.4°C, and minima between 23.7°C and 25.9°C (World Weather Information Service 2014). At the latitude of Coro, the difference between the longest and shortest day is approximately 1.4 h. Northern Falcón is characterized by open thornscrub vegetation having a mixture of arborescent *Stenocereus* and *Opuntia* (Cactaceae), spinescent Fabaceae shrubs (*Prosopis*, *Cercidium*), deciduous and semideciduous Fabaceae (*Caesalpinia, Pithecellobium*), and a layer of ephemeral herbs and forbs. Fieldwork was carried out at two separate sites, one at approximately 6 km south of Coro, and

the other approximately 70 km northeast of it, in the vicinity of the town of El Vínculo (Figure 1). Both sites had similar vegetation structure and elevation (< 50 m a.s.l.). We did not intend comparisons between localities.

Gonadal cycles. We visited the study site for periods of three to four days at approximately monthly intervals between November 1994 and January 1996. Our protocol was as described in Bosque et al. (2004). We used six mist nets (6 m long, 3.8 cm mesh) throughout the day, and attempted to catch at least 10 adults of each sex during each monthly sampling. We determined the physiological state of reproduction by noting gonadal development of adult doves by unilateral laparotomies (Wingfield & Farner 1976) under light anesthesia with Halothant (2-Bromo-2-chloro-1,1,1-trifluoroethane), and recorded the length and width of each male's left testis or the diameter of the two largest ovarian follicle or ova of females to the nearest 0.1 mm. Testicular volume (mm^3) was calculated according to the formula for a prolate spheroid, $V = 4/3 \pi ab^2$, where "a" is half the testis length and "b" is half of the width. Undifferentiated, granular follicles smaller than 0.5 mm were given a diameter of 0.1 mm. Juveniles were distinguished by the presence of white-tipped upper wing coverts and white-tipped allulars (Passmore 1984), and by the degree of skull pneumatization when in doubt (Ralph et al. 1993). Overall, we captured 391 Common Ground-doves; of these, we laparotomized 337 adults, 199 males and 138 females. In addition, we captured 55 juveniles that we did not laparotomize.

Reproductive readiness and breeding period. Columbids have no incubation patch (Baptista et al. 1997), consequently we inferred breeding seasonality in females by any of the following indicators: First, the presence of a thickened active crop; interpreted as evidence of feeding nestlings. Second, the presence of oviductal or shelled eggs and of an enlarged oviduct. Third, the presence of post-ovullatory follicles appearing as flaccid follicle membranes, and fourth, the presence of ovarian follicles ≥ 4 mm in diameter. Follicles ≥ 4 mm were considered to be enlarging prior to ovulation, based on the size of the quiescent stage in Common Ground-doves (< 4.0 mm; Passmore 1984). Above this size, egg-laying is possible within a few days. These criteria likely underestimate the length of the breeding period, as they are manifest for only a short slice of the nesting cycle. We also considered an average size of 1 mm for the largest follicle as indicator of reproductive readiness, because follicles of such size can deposit yolk for egg-laying within two to three weeks (Wingfield & Farner 1993, Wikelski et al. 2003).

Testes of birds that occasionally died during laparotomies (N = 8), were fixed in Bouin´s fluid, embedded in paraffin, sectioned at 5 μm, stained with haematoxylin-eosin, and examined for the presence of spermatids in the germinal epithelium, and sper-
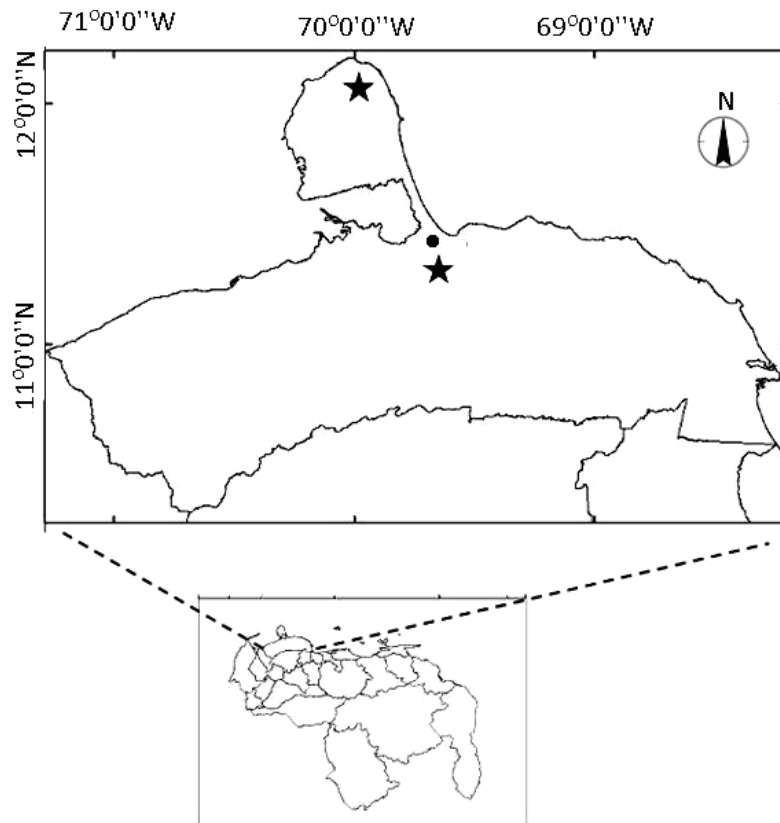
Figure 1. Map of the study site. Detail of Falcón State in relation to Venezuela. Locations of study sites are indicated by stars.

matozoa in the seminiferous tubules. In addition, we considered males in reproductive condition when average testes sizes reached half their average maximum value, because mature sperm can generally be found in testes of such sizes (Wingfield & Farner 1993, Wikelski et al. 2003).

Flight feathers and body molt. We assessed the state of the molt of the 10 left primaries -P(n)-, the first six left secondaries -S(n)-, rectrices, and body coverts of adult birds as described by Bosque et al. (2004). For wing and tail feathers we scored 0 for an old feather, 1 for a recently molted feather, and fractions of zero to one for the estimated fraction of the full length of feathers being molted (e.g., a feather that was half-grown received a score of 0.5). Thus a bird reading for primaries 1,1,1,1,1,0.5,0,0,0,0, would have a primary index of 5.5 indicating that P1–P5 were new, P6 was half grown and P7–P10 had not yet been replaced. Therefore, our molt scores for primaries, secondaries, and rectrices ranged from 0–10, 0–6 and, 0–12 respectively. We scored the extent of the body molt on a semi-quantitative scale from zero to four. A score of zero was given to a bird not molting, and scores of one to four to individuals that were molting an estimated >0–5%, >5–25%, >25–50%, and >50% of contour feathers in each of six body regions.

Fat deposits. We scored the extent of fat deposits on a scale of zero, no fat deposits visible, to a maximum

of four when large deposits of subcutaneous fat were visible around the clavicles, crop, abdomen, and flanks. Birds were normally fully alert about 10 min after the operation and were released shortly thereafter. Before release, we weighed each bird to the nearest 0.1 g with a spring balance, and fitted it with a numbered aluminum leg band.

Statistical analyses. We examined the yearly variation of mean testicular and ovarian follicle size through one-way ANOVAs. We examined molt duration and synchronicity by regressing individual molt scores on time (at monthly intervals), and molt-breeding overlap by regressing molt score on testis and follicle size, and by comparing the proportion of females molting while breeding and not breeding with a Fisher exact test. For statistical analysis, we excluded same month captures and recently fledged birds. Molt of juveniles was examined separately. Since we had only one recapture, a juvenile, we considered all captures as independent data points. Sample sizes are indicated in the figures and tables. Statistical analyses were performed on SYSTAT® 9.0.

RESULTS

Gonadal cycles. Common Ground-doves showed a seasonal pattern in testis recrudescence and full testis regression (Figure 3), as revealed by the effect of month on testis volume (ANOVA F_{12-174} = 24.8, P <
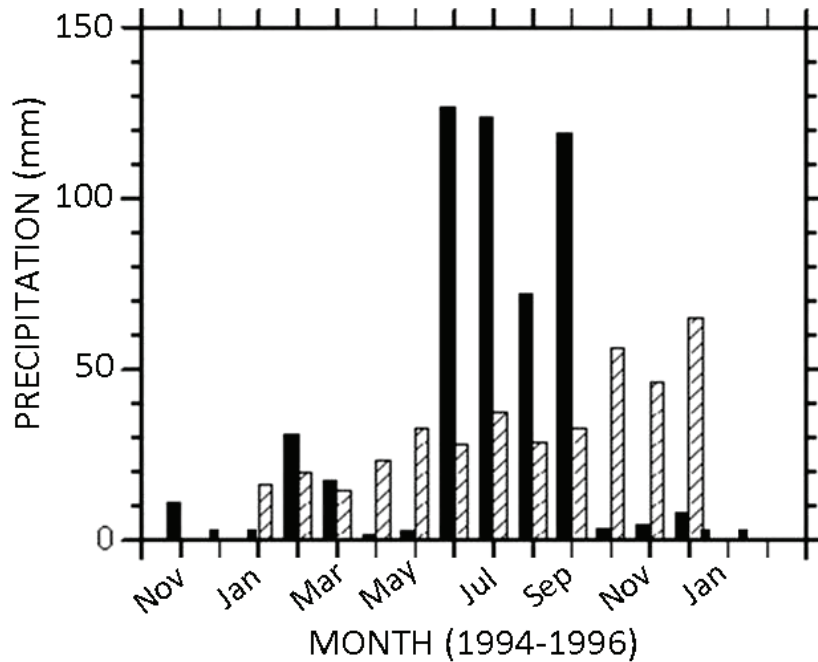
Figure 2. Average monthly precipitation at the city of Coro (north-western Venezuela) for the 30-year period 1971–2000 (hatched bars; data from World Weather Information Service), and monthly precipitation during the study period (1994–1996) at Coro (filled bars, data from Cesma-USB 2012).

0.001). During 1995, testes were briefly but fully regressed in February; thereafter, testes started to enlarge during the dry months (March–April) way in advance of the June-September rains, and reached their peak in September, coinciding with the late part of the rainy season of that year (Figure 2). After full recrudescence, testis size declined progressively from October until becoming fully regressed again in January 1996, coinciding with a severe four-month dry period of only 15.9 mm precipitation. Except for the brief periods of complete recrudescence, testis volume remained above the minimum size that displayed spermatogenic activity throughout the year (Figure 3). There was a striking difference in testis development between November 1994–January 1995 and November 1995–January 1996. During the first period, testis were fully recrudesced, and reached the maximum average of 118.3 mm³ (SD = 31, N = 15) in January. In contrast, in January of the following year (1996), testis volume reached an absolute minimum of 15.6 mm³ (SD = 5.6, N = 6); a 7.5-fold variation in testis volume between both periods. Tukey's HSD posthoc test showed that, in general, testes sizes of November 1994, January, July, September, and October 1995 did not differ significantly (*P* > 0.05). While minima of February, March, and December 1995, and January 1996, were also statistically similar to each other (*P* > 0.05).

Likewise, there was a clear seasonal variation in the diameter of the largest follicle (Figure 3), as shown by the effect of month (ANOVA $F_{12\text{-}111}$ = 11.13, *P* < 0.001). The seasonal follicle development paralleled the gonadal cycle of males but peaked one or two months earlier. During 1995, average follicle size was minimum in February before increasing progressively until July–October. Thereafter, it declined sharply until ovaries became fully regressed from November 1995 through January 1996. As for male testes, there was a contrasting difference between the largest average follicle size of November 1994–January 1995, and that of November 1995–January 1996 when ovaries were fully regressed. However, this result should be taken with caution since we only sampled two birds in November 1994. Standard deviations of follicle diameter were small when gonads were partly or fully regressed, but exhibited considerable variation depending on their stage of the nesting cycle when follicles were developing. Tukey's HSD posthoc test showed that, in general, average follicle diameter did not differ significantly (*P* > 0.05) among most of the drier months of the study period (January, February, March, May, November, and December 1995, and January 1996).

Reproductive readiness and breeding period. Since we did not monitor nesting activity, we do not know precisely when breeding occurred; however, the following evidence permits to infer the breeding of Common Ground-doves during the study period. In 1995, we performed laparotomies of 11 females that had follicles ≥ 4 mm: three in April, June, and July each, and one in September and October each. In addition, we found four females having oviductal eggs: one in July, two in September, and one in October. Four females had a thickened crop wall: one in April and three in July. One female was captured with an ovulated follicle in June, and two females having a thickening of the uterus lining,
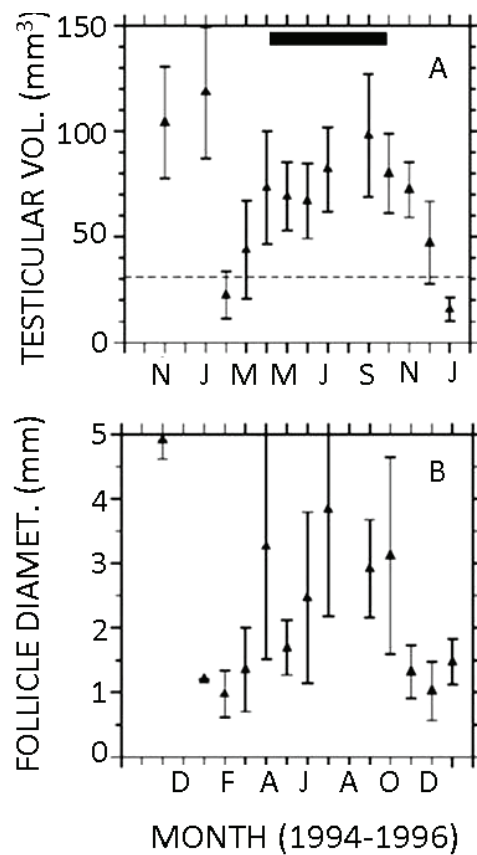
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Figure 3. Seasonal changes (means ± SD) in monthly testicular volume (A; N = 188) and diameter of the largest follicle (B; N = 124) of Common Ground-doves (*Columbina passerina*) captured in north-western Venezuela. The broken horizontal line in (A) indicates the minimum testicular volume above which testes showed spermatogenic development. The black bar on top of the figure indicates the inferred breeding period (see text). Sample sizes for (A) were: Nov. = 16 (1994), Jan. = 15, Feb. = 19, Mar. = 19, Apr. = 23, May = 20, Jun. = 13, Jul. = 7, Sep. = 20, Oct. = 12, Nov. = 10, Dec. = 9 (1995), and Jan. = 6 (1996). Sample sizes for (B) were: Nov. = 2 (1994), Jan. = 1, Feb. = 15, Mar. = 14, Apr. = 12, May = 20, Jun. = 11, Jul. = 6, Sep. = 13, Oct. = 6, Nov. = 10, Dec. = 10 (1995), and Jan. = 4 (1996).

one in April and one in September. Consequently, the evidence indicates that in 1995 most breeding occurred from April until October, during the dryer months (Figure 2) through the rains of June–September, at the beginning of the following dry season. No evidence of breeding was collected before April or after October of 1995. Interestingly, in November 1994, we laparotomized two females having follicles ≥ 4 mm, and one with an ovulated follicle. Hence, doves bred in November 1994 but not in November 1995.

The breeding period inferred from females in 1995 coincided well with the estimated period of reproductive condition of males, from April to November, when testes averaged over 60 mm³, above half-maximum size. During the period of reproductive condition, average testicular volume was 78.3 mm³ (SD = 25.4, N = 95). In addition, we made histological sections of the testes of eight individuals, whose volumes ranged from 21.2 to 100.7 mm³; only testes smaller than circa 31 mm³ did not contain spermatids or spermatozoa in the tubules. Therefore, testes remained in an activated or semi-activated state during most of the year (Figure 3).

Flight feathers and body molt. We examined 334 adults for molt, of these, 138 (41.3%) were molting primaries. Adult Common Ground-doves replaced their primary feathers in a centrifugal sequence from P1. Since molting sequence was regular across most individuals (N = 135, 97.8%), there was little uncertainty in discerning the direction of replacement and the assignment of P1 as the node of molt initiation. Only three birds that were molting one feather different from P1, were not molting, or had molted P1; this was most likely the result of an accidental feather replacement that we inadvertently scored. We found that primaries were a single molt series not containing two runs of new primaries separated by older primaries, as pointed out by Rohwer & Wang (2010) that often occurs in tropical *Columbina*. We found no evidence that molt was arrested in any of the adults examined.

The primary molt was not synchronous among individuals, as indicated by the considerable proportion of adults in various molt stages in any one month (Tables 1, 2), and by the lack of a monotonic positive correlation between primary molt score and month (Figure 4; Spearman rank correlation, rs = -0.15; N =

Table 1. Monthly medians of molt scores of adult Common Ground-doves (*Columbina passerina*) molting remiges or rectrices (N = 204) in north-western Venezuela (1994–1996); 128 non-molting individuals have been excluded. In parenthesis the percentage of individuals from the monthly sample (N) in molt. *Medians of tail molt scores are not depicted; see text.

Year	Month	N	Median of molt score (percentage of birds)		
			Primaries	Secondaries	Rectrices*
1994	Nov.	19	7.2 (5.3)	- (0.0)	(5.3)
1995	Jan.	16	3.0 (50.0)	0.9 (18.8)	(62.5)
	Feb.	40	7.2 (50.0)	2.3 (20.0)	(47.5)
	Mar.	37	6.9 (24.3)	0.8 (8.1)	(16.2)
	Apr.	39	7.6 (25.6)	1.7 (2.6)	(41.0)
	May	40	6.0 (20.0)	2.7 (12.5)	(40.0)
	June	26	5.9 (57.7)	3.0 (15.4)	(57.7)
	July	13	6.3 (38.5)	1.6 (7.7)	(69.2)
	Sep.	34	3.4 (47.1)	2.6 (29.4)	(61.8)
	Oct.	18	5.1 (66.7)	2.2 (22.2)	(44.4)
	Nov.	20	7.4 (70.0)	4.1 (30.0)	(60.0)
	Dec.	20	2.7 (60.0)	1.6 (10.0)	(55.0)
1996	Jan.	11	6.6 (45.5)	0.8 (27.3)	(54.5)
	Total	332			

Table 2. Progress of the primary molt in adult Common Ground-doves (*Columbina passerina*) in north-western Venezuela (1994–1996), with monthly number of individuals molting the indicated primary feather P(n). The primary molt progresses centrifugally starting at P1; a hypothetical bird molting P8 already replaced P1 to P7.

Year	Month	Primary feather										Total
		P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	
1994	Nov.	0	0	0	0	0	0	0	1	0	0	1
1995	Jan.	2	1	1	1	0	0	1	0	2	0	8
	Feb.	2	0	0	0	0	5	3	1	3	6	20
	Mar.	0	0	0	0	0	2	3	3	1	0	9
	Apr.	0	0	0	0	0	0	4	2	4	0	10
	May	1	1	1	0	1	0	0	1	3	0	8
	June	0	1	3	2	1	0	1	2	3	2	15
	July	1	0	0	0	0	0	3	0	0	1	5
	Sep.	2	0	4	2	0	2	0	4	1	1	16
	Oct.	3	0	1	1	0	2	1	1	1	2	12
	Nov.	1	0	1	0	1	0	3	4	3	1	14
	Dec.	2	0	0	0	2	2	1	1	3	1	12
1996	Jan.	0	0	0	0	0	1	2	0	2	0	5
	Total	14	3	11	6	5	14	22	20	26	14	135

138), as would be expected if the molt was synchronous (Pimm 1976, Haas & Amend 1979). Consequently, there was no discrete primary molt period. Only between March and May the fraction of adults that were replacing primaries was lower. These results indicate that birds were following their own individual molt cycle. Given the lack of relationship between primary molt score and time, it was not possible to estimate the rate or duration of the molt (see Primm 1976). We did not have enough recaptures to estimate primary molt duration (e.g., from raggedness; Bensch & Grahn 1993).

Adult Common Ground-doves that were growing primaries, had the lowest molt intensity possible, replacing only one feather per wing at a time (mean = 1.05 ± 0.2 SD, N = 134). Only seven birds were molting two feathers simultaneously, but in five of them feather growth of the feather next in sequence
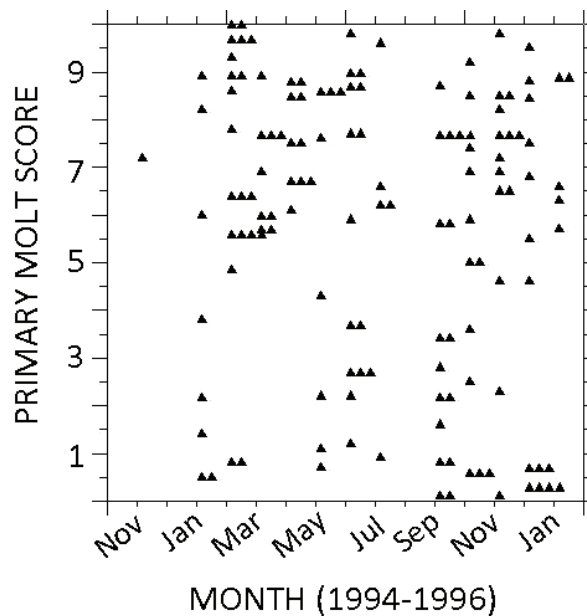
Figure 4. Primary molt score of adult Common Ground-doves (*Columbina passerina*) in active molt (N = 138) in northwestern Venezuela, (1994–1996). There is no synchrony in the molt of primaries in the population. Points have been jittered on the horizontal axis to avoid overplotting. See Table 1 for monthly percentages of individuals molting.

started when replacement of the inner primary was 80–90% complete. Therefore, even in these few cases, the gap in the wing caused by feather replacement was minimal.

Only 44 doves (13.2% of 334 adults examined) were growing the first six secondary feathers, and 31 (70.5%) of these were also replacing primaries; therefore, in most cases doves molted secondaries concurrently with the replacement of primaries. However, in most cases, 77.5% (107 out of 138) birds growing primaries were not replacing secondaries. Adult Common Ground-doves replaced their inner six secondaries proximately starting at S1, seemingly as a single molt series. Again, since the molting sequence was very regular across most (N = 36) individuals, there was no uncertainty in discerning the direction of replacement and the assignment of S1 as the nodal feather. Like for primaries, there was neither synchrony among individuals nor a tendency to molt secondaries in a definite period of the year (Table 1).

We could not discern the node of molt initiation or the direction of replacement of tail feathers because we could not distinguish unambiguously between old and newly replaced feathers. Therefore, we are not giving rectrix molt scores in Table 1. Again, no definite period of tail molt was apparent since in most months more than half of individuals were molting tail feathers (Table 1). Consequently, like for remiges, there was no synchrony in the timing of tail feather replacement; doves followed their own individual cycles. We had 150 (45.3% of 331) adults molting tail feathers, 90 (60%) of these were also molting primaries. The body molt did not show a marked seasonal pattern either; in any one month a large fraction of the population was in active body molt (Table 3).

We examined 54 juveniles for molt, of these, 42 (77.8%) were undergoing the post-juvenal (= preformative) molt; a complete molt. Although for some months the sample was very small, it was clear that juveniles were not replacing primaries in synchrony or that there was a defined molt period (not shown). Lack of synchrony and of a well-defined primary molt period, indicates that juveniles followed their own individual cycle, likely determined by the moment when they fledged. Juveniles were captured in all months except March 1995.

Body mass and fat deposits. There was a distinct temporal variation in the body mass of both, adult males (Figure 5; ANOVA $F_{12,182}$ = 6.99, $P < 0.001$), and females (ANOVA $F_{12,117}$ = 6.55, $P < 0.001$); even though the seasonal pattern of females could be obscured by egg production. The pattern of male and female mass fluctuation closely matched each other, reaching a minimum in February and March, during the dryer months, and a maximum in September, at the end of the wetter months of 1995 (Figure 5). This pattern also roughly matched fluctuations in gonadal sizes, which were at a minimum in February–March and peaked during the later rains (Figure 3). Overall mass of adult males 35.5 g (SD = 3.1, N = 195) and females 35.8 g (SD = 3.5, N = 130) did not differ significantly (t_{323} = 1.23, $P > 0.05$). Average body mass of juveniles was 32.5 g (SD = 3.6, N = 55). Median fat index of adults remained on the lower half of the score range throughout the year (Table 3).

Molt-breeding overlap. Since doves replaced primaries in every month, including the inferred breeding period from April to October, it is clear that there was extensive molt-breeding overlap at the population

Table 3. Monthly percentages of adult Common Ground Doves (*Columbina passerina*) in body molt, and median fat indexes in north-western Venezuela from 1994 to 1996. N is the monthly sample size.

Year	Month	N	Percentage of individuals						Median fat index
			Head	Back and rump	Uppertail coverts	Undertail coverts	Belly and breast	Wing coverts	
1994	Nov.	19	0.0	78.9	26.3	10.5	78.9	10.5	2
1995	Jan.	16	68.8	75.0	62.5	62.5	75.0	68.8	1
	Feb.	40	30.0	90.0	50.0	55.0	90.0	45.0	2
	Mar.	37	32.4	73.0	40.5	27.0	73.0	13.5	1
	Apr.	39	51.3	79.5	64.1	66.7	82.1	38.5	1
	May	40	17.5	42.5	37.5	30.0	45.0	15.0	1
	June	26	76.9	73.1	61.5	73.1	84.6	50.0	1
	July	13	38.5	69.2	53.8	46.2	69.2	23.1	2
	Sep.	33	48.5	63.6	60.6	63.6	66.7	45.5	2
	Oct.	18	50.0	83.3	61.1	66.7	72.2	44.4	0
	Nov.	20	65.0	85.0	45.0	75.0	75.0	50.0	2
	Dec.	20	55.0	55.0	45.0	65.0	65.0	20.0	1
1996	Jan.	11	45.5	81.8	45.5	36.4	81.8	45.5	2
	Total	332							

level. Furthermore, there was no apparent relationship between testicular volume (Figure 6; Pearson r = -0.14, P = 0.06, N = 187), or diameter of the largest follicle (r = -0.13, P = 0.19, N = 109; not shown) and primary molt score. Therefore, primary feather replacement occurred independently of gonadal development. Since we recorded no bird suspending the primary molt, molt, and breeding must have overlapped temporarily at individual level also. Likewise, there was no relationship between testicular volume (r = -0.01, P = 0.89, N = 187) or diameter of the largest follicle (r = -0.06, P = 0.52, N = 109) and secondary molt. To scrutinize more closely molt breeding-overlap at the individual level, we examined the molt stage of the 23 females for which we had breeding certainty (see above); 13 of these (56.5%) were in various stages of primary and/or rectrix replacement. Additionally, the proportion of females molting while breeding was not different from that of females not breeding (two-tailed Fisher exact test, P = 0.48). Therefore, we conclude that there is firm and direct statistical support of molt-breeding overlap in Common Ground-doves, at both population and individual level.

DISCUSSION

This study documents the seasonal changes in gonadal development and the progress of the molt of the Common Ground-dove in a xeric habitat with erratic precipitation. First, we found that Common Ground-doves displayed a synchronous fluctuation in gonadal development, undergoing gonadal regression through a brief, one month, period and displaying reproductive readiness throughout most of the year. Second, the molt was unusually prolonged, not synchronous among individuals, and there was no definite prebasic molt of wing feathers. We will discuss these findings in relation to ecological properties of a xeric and erratic environment.

Flexible breeding. The flexible timing of reproduction in male and female Common Ground-doves was evidenced by the difference in their gonadal maturation and reproductive activity between November and January of consecutive years. In 1994–1995 males had fully recrudesced testes, yet they were fully regressed, or were in the process of regression, during the same months in 1995–1996. Likewise, females had minimum size follicles in November 1995–January 1996 but showed firm evidence of breeding in November 1994. These differences indicate that breeding schedule may vary among years, and suggests that breeding strategy of Common Ground-doves in our study site may be partly opportunistic. Additional support for this conclusion is provided by the data in Bosque (1984) who recorded 49 of 52 nests of Common Ground-doves in November and December of 1980 at a site close to our northern study site.

Nearly permanent reproductive readiness. Male and female Common Ground-doves showed a similar temporal pattern of gonadal maturation, and underwent brief (one month) periods of complete regression in February 1995 and January 1996. Apart from these brief regressions, average testis volume of Common Ground-doves remained above the minimum testis size that had spermatozoa in the tubules. The fluctuation of testes volume of Common Ground-
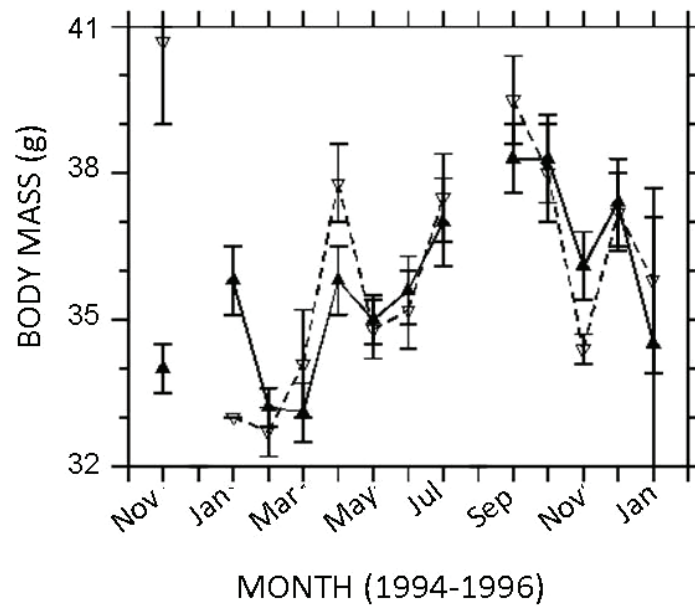
Figure 5. Seasonal changes in body mass (means ± SD) of adult males (filled triangles, solid line; N = 195) and females (open triangles, broken line; N = 130) Common Ground-doves (*Columbina passerina*) in northwestern Venezuela (1994–1996). Monthly sample sizes were (males first): Nov. = 16, 3 (1994); Jan.= 14, 1; Feb.= 20, 19; Mar. = 23, 14; Apr. = 24, 13; May = 20, 19; Jun. = 14, 12; Jul. = 7, 6; Sep. = 21, 13; Oct. = 12, 5; Nov. = 10, 10; Dec. = 8, 10 (1995); Jan. = 6, 5 (1996).

doves between the highest and lowest monthly averages was relatively small, less than eight-fold. Testes of Wood Pigeons (*Columba palumbus*) exhibit a 42-fold mass increase over the regressed condition (Murton et al. 1974), and 400–500-fold variations are typical of temperate birds (Lofts and Murton 1973). The small difference in testicular volume could mean that Common Ground-doves may become fully active sexually without the lengthy preparatory period typical of temperate birds. Similarly, females had an extended period of reproductive readiness as indicated by the presence throughout most of the year of follicles > 1 mm. These results support that Common Ground-doves in arid regions maintained a fully active, or partly active, reproductive system throughout the year.

Relationship of breeding and rainfall. Like in other arid zones (Hau 2008), breeding of Common Ground-doves was associated to rainfall, but not exclusively so. Common Ground-doves feed on the seeds of grasses, herbs, and shrubs taken from the ground. Therefore, food availability should be related to the size of the seed bank in the upper layer of soil, which, in arid zones of northwestern Venezuela, is larger during rainy periods (Weiss 2015). Nonetheless, we found birds breeding in April and May, two of the driest months during the study period. Similarly, the main breeding period of congeneric Scale Doves (*Columbina squammata*) occurs in the dry season in seasonal savannas of Venezuela (Bosque et al. 2004), and Common Ground-doves throughout their range have breeding periods which include dry seasons (summary in Baptista et al. 1997). Columbids feed

crop milk to their young, which presumably allows them to buffer adverse conditions and consequently may have extended breeding seasons (Murton & Westwood 1977, Murton et al. 1974), including species of *Columbina* (Cintra 1998, Bowman & Woolfenden 1997).

It was not evident if, or how, the activation of the reproductive systems was related to rainfall. Doves had fully mature gonads ahead of the long-term rainfall pattern; their gonads were regressing during October to December when most rain occurs in the long term. Therefore, gonadal cycles of males and females did not match the long-term precipitation pattern of the area. Although breeding was partly associated with the year's rainfall, the initiation of gonadal recrudescence did not occur in response to precipitation, since it began in April, well in anticipation of the year's major rains. It is however possible that the 31 and 17 mm of rain that fell in February and March stimulated the initiation of gonadal recrudescence in the population. Hence, it is not clear if rainfall cues could modulate intrinsic mechanisms controlled by annually recurring stimuli such as photoperiodic information or the long-term precipitation pattern.

Protracted wing molt. Common Ground-doves molted one primary per wing at a time, with no temporal overlap in feather growth; each feather was dropped only after its adjacent inner feather was fully grown. Absence of primary growth overlap may permit an instantaneous, or daily, reduction in demands of energy and nutrients involved in feather growth, and reduces aerodynamic and other costs
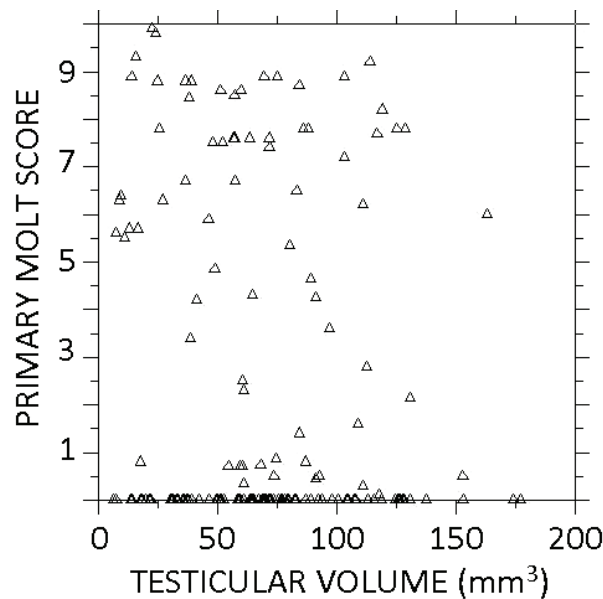
Figure 6. Primary molt index in relation to testicular volume (N = 187) in adult Common Ground-doves (*Columbina passerina*) in arid scrub of northwestern Venezuela (1994–1996). Molt and complete testicular recrudescence were not separated in time.

related to missing feathers (e.g., Slagsvold & Dale 1996, Echeverry & Hau 2013). Yet, no overlapping makes the period of primary replacement longer than it would if temporal overlap existed. Duration of feather replacement in species with simple molts (those with a simple wave of primary replacement) mainly depends on the number of primaries growing on each wing simultaneously, and not on the rate (mm·day^{-1}) at which feathers can grow (Rohwer et al. 2009). This is because the rate at which flight feathers grow is constrained by allometric considerations, seemingly related to the architecture of feather follicles (Rohwer et al. 2009).

We could not estimate the rate of feather growth from individual birds recaptured while progressing through a complete wing molt, but for a 35.5 g bird that flies while molting and grows one feather at a time, it would take about 214 days, or slightly over 7 months, to replace all primaries (calculated from Rohwer et al. 2009). In contrast, most smaller birds (i.e., generally < 1 kg), usually grow simultaneously two to three primaries on each wing, and non-aerial foragers grow three to four primaries simultaneously, hence reducing considerably the time to replace all primaries (Rohwer et al. 2009, Rohwer & Wang 2010). Replacement of contour feathers is also likely to be slow given the high proportion of birds molting every month. The prolonged molt of Common Ground-doves can be appreciated by the fact that only 20 of 327 (6.1%) of our captures were not molting. Prolonged molt of Neotropical birds has been previously reported for a number of species (Bosque et al. 2004, Johnson et al. 2012, Stouffer et al. 2013).

Timing of molt and lack of population synchrony. Our results differed from reports of a number of studies showing that tropical birds (e.g., Miller 1961, Wolf 1969) and columbids in general (Baptista et al. 1997) most frequently undergo prebasic molt after breeding. Common Ground-doves molted asynchronously throughout the year. Although little is known about the environmental or physiological control of molt (Dawson 2008), it is clear that environmental factors, such as photoperiod (Dawson 2008), or pattern of precipitations (Miller 1962) did not induce molt in doves of our study area, because doves did not show a uniform reaction to such stimuli at population level. The lack of flight feather molt synchrony among adult and juvenile Common Ground-doves suggests that individuals followed their own cycle, possibly determined by their hatching date, rather than by environmental cues or physiological condition.

Molt-breeding overlap. Although it is commonly assumed that breeding and molt periods seldom overlap in temperate regions (Williams 2012), their overlap is particularly widespread in tropical Africa and America (Payne 1969, Foster 1975). Our data clearly showed that molt and breeding overlap extensively in Common Ground-doves at the population level, and provided solid evidence that it also occurs at the individual level. Although it is widely assumed that limiting resources, such as energy and nutrients are the currency involved in a trade-off between breeding and molt, breeding and molt might involve a trade-off between feather renewal and parental care (Williams 2012: section 7.3). Supporting evidence comes from studies demonstrating fitness costs through negative effects on nestling or fledglings of parents that molted while raising chicks (e.g., Svensson & Nilsson 1977). If this is the case, it should

be relevant that in columbids possible negative effects of a conflict between nestling care and molt may be ameliorated by raising chicks on "crop milk."

Common Ground Doves in erratic xeric environments. Results supported our expectation that Common Ground-doves maintain a partly (see Farner & Serventy 1960) or fully active reproductive system throughout the year, and that they behave as opportunistic breeders. When there is uncertainty about the onset of the favorable season, because of environmental unpredictability, birds of arid environments face a trade-off between incurring the cost of maintaining active gonads during unfavorable periods, and delaying reactivation but risking missing possible breeding opportunities (see Tökölyi et al. 2012). This strategy allows Common Ground-doves in Venezuela to respond quickly to favorable conditions for breeding. The duration, timing, and lack of molt synchrony of Common Ground-doves revealed an uncommon molt pattern. The lengthy duration of wing feather replacement seems adaptive in harsh environments since it minimizes daily energy and nutrient needs, and lessens strain in individuals that molt while breeding. In turn, the absence of a definite prebasic molt period poses interesting problems on the relationship between the end of breeding and the start of molt. Common Ground-doves in xeric environments further illustrate variations of life-history of tropical birds in relation to ecological conditions.

ACKNOWLEDGMENTS

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