Breeding and multiple waves of primary molt in common ground doves of coastal Sinaloa

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Abstract: For adult Common Ground Doves from Sinaloa we demonstrate that the primaries are a single molt series, which sometimes feature two (in one case three) waves of feather replacement. Such stepwise primary replacement is found in many large birds but, at 40g, this dove is much the smallest species reported to have multiple waves of replacement proceeding through its primaries simultaneously. Pre-breeding juvenile Common Ground Doves never feature two waves of primary replacement. Juveniles usually have more than 2 adjacent feathers growing simultaneously and replace their primaries in about 100 days. In contrast adults, which show more or less complete overlap of molt and breeding, usually grow just a single primary growing at a time, and require at least 145 days to replace their primaries. Molt arrests are thought to drive the generation of new waves of primary replacement in a diversity of large birds. For adult Common Ground Doves, we found molt arrests to be strongly associated with active crop glands, suggesting that the demands of parental care cause arrests in primary replacement in this dove. For those adults with two primary molt waves, six feathers typically separate the outer growing primaries of each wave. Thus, unlike reports for large birds, Common Ground Doves usually suppress the initiation of a new wave of molt starting at P1 when the preceding wave arrests before reaching the distal primaries. This assures that relatively fresh inner primaries are not replaced redundantly, overcoming the single greatest flaw in stepwise molting known for large birds (Rohwer 1999).

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INTRODUCTION

In large birds that fly while molting the primaries are often replaced in multiple waves that proceed from the wrist outward or proximally to distally through the primary feathers.This is known as *Stafflemauser*, stepwise molt (Stresemann and Stresemann 1966), and has been documented in fairy tern *(Sternula nereis*) Ashmole,1968, Pelicaniformes (Dorward 1962), large herons (Shugart and Rohwer 1995), Accipitriformes (Edelstam 1984, Pyle 2005), and New World vultures (Snyder et al. 1987), among others. ~~simultaneously through these longest feathers of the wing. Two mechanisms can generate these waves. In several orders of large~~

~~birds, the primaries constitute a single molt series, but multiple waves are generated by arrests in the replacement of the primaries.~~ Multiple waves result from the arrest and re-initiation of waves while an additional wave arises from the proximal primary (Primary 1 or P1) ~~Following arrests, molt is re-initiated at the next feather to be replaced in molt waves that have not reached the distal-most primary and also at P1, the first feather of the primary molt series in most birds (~~Stresemann & Stresemann 1966, Rohwer 1999). Thus, depending on the history of arrests, ~~and~~ molt progression, and the number of primaries replaced in a bout of molt, ~~large species that fly while molting may have~~ from one to four descendant molt waves ~~of replacement~~ proceed~~ing~~ simultaneously through the primaries. ~~This is known as *stafflemauser*, or stepwise molt (Stresemann and Stresemann. 1966), and has been documented in pelicaniforms (Dorward 1962), large herons (Shugart and Rohwer 1995), Accipitriforms (Edelstam 1984, Pyle 2005), and New World vultures (Snyder et al. 1987), among other groups.~~ ~~The o~~Another way multiple waves of primary replacement are achieved is for the primaries to be divided into ~~two or more~~multiple molt series similar to secondary molt which starts from 2 to 3 nodes. Molt series differ from serial descendant stepwise molt in that ~~they~~ waves start ~~and stop~~ at predictable ~~feathers~~ primaries ~~within the wing~~ and usually proceed in opposite directions. ~~For large birds~~Permutations on this strategy has been ~~well~~ documented in albatrosses (Langston and Rohwer 1995, Rohwer et al. 2011) ~~and in~~, Falconiformes ~~and~~ ,Psittaciformes, Strigiformes (Pyle 2013) and some kingfishers (Alcidinedae) (Douthwaite 1971, Hamner 1980).

At least in large birds, multiple waves of feather replacement in the primaries have been interpreted as facilitating ~~more~~ less frequent or efficient replacement of the ~~outer flight feathers~~primaries. For large species this is intuitively sensible because the time required to replace the primaries increases with body size and many birds over 1kg do not replace all their primaries annually (Rohwer et al. 2009). In small birds ~~for which the rules of primary replacement have been established, the~~ primaries usually ~~constitute as a single replacement series that~~ are replaced in a single sequential descendant wave in a single bout of molting~~, without arrests~~. However, some ~~small~~ doves (Pyle et al. 2016; personal observation) and the

Commented [R1-2]: Throughout pick one, either serial descendant stepwise, an acronym SDS, or Stafflemauser

Commented [R1-3]: Only with replacement of all Ps,e.g. owls

Commented [R1-4]: Seems backward, Stafflemauser often interpreted as reducing replacement of outer and presumably more resiient Ps if incomplete molt or more efficient replacments in all Ps are replaced.

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Mustached Tree Swift (*Hemiprocne mystacea)* exhibit stepwise primary replacement (Rohwer and Wang 2010). Stepwise primary replacement is surprising in these species because they are small enough to easily be able to complete primary replacement in a single bout of molting (Rohwer et al. 2008). What seems ~~special~~ unique about them is their extensive overlap in molt and breeding (Rohwer and Wang 2010).

While arrests ~~are well documented to drive the generation of~~ and re-initiation can result in multiple waves of primary replacement in large birds (Rohwer 1999), ~~they~~arrest and re-initiation are only suggested for small species. In Mustached Tree Swifts of the New Guinea region, which breed and molt year-round, primary replacement is stepwise, and the generation of multiple molt waves have been suggested to be associated with arrests caused by the demands of feeding young; however, evidence for this interpretation is lacking (Rohwer and Wang 2010). Nonetheless, arrests associated with demanding periods of parental care could prove to be a general mechanism generating multiple waves of primary replacement in small birds that show extensive overlap in molt and breeding. Dividing the primaries into multiple molt series, which result in multiple molt waves, has recently been documented for three small birds, two cuckoos (Rohwer and Broms 2013) and a bell bird (Marini and Silveira 2012). Reorganizing the primaries into multiple molt series would seem to be a more improbable evolutionary transition than the development of stepwise molting, so multiple series in primaries probably will not characterize many groups of small birds.

We recently observed multiple waves of primary replacement in Common Ground Doves (*Columbina passerina*) from northwest Mexico. Here we quantitatively summarize their primary replacement to address two questions: 1) Do Common Ground Doves have stepwise primary molt or have they broken the primaries into multiple series? and 2) Is breeding activity associated with arrests in primary molt, thus making arrests a possible mechanism for generating multiple waves of feather replacement in this small dove?

Commented [R1-6]: If advantageous to do so, , they probably would, theoretically, so either they can't for energetic or aerodynamic reasons or something else is involve like extremely slow primary over an extremely long period of time allowing simultaneous molt and breeding

Commented [R1-7]: Seems the wood dove "model" Is more reasonable, simply an artifact of small, "more or less", proportion of birds not completing primary molt then picking up where they left off in the next bout of molt. Unclear why demands of feeding young would bave precendence over seasonality/non-breeding period especially there is evidence for this vs non for feeding young?

Commented [R1-8]: In contrast to secondaries

Commented [R1-9]: The dividing in to separate series hypothesis seems contrived given what is known about ground doves and dove molt in general. See BNA account and fortuitously " more research is needed" which is exactly what this ms provides. Maybe redo as is it fully fledged Stafflemauser or an artifact of a few birds not completing P replacement? The latter might be rejected given re-initiation at point of arrest and Ps (see Boddy woodpigeons)

~~Distinguishing between stepwise and multiple molt series can be non-intuitive from "snap-shot" data gathered from many individuals across the molting period (Rohwer 2008). Nonetheless, the distinction is key for understanding evolutionary transitions in feather replacement strategies across birds. If Common Ground Doves have stepwise primary replacement, then two predictions should refute the hypothesis multiple molt series in the primaries. First, non-breeding juveniles undergoing their first primary replacement should possess only a single wave of feather replacement beginning at P1, whereas adults that have re-initiated an arrested molt should have multiple waves of primary replacement (Rohwer 1999). In contrast, if their primaries are replaced in multiple series, then juveniles molting for the first time should initiate primary replacement at the same loci as adults. Second, in adults of species that are stepwise molters, nodal and terminal feathers, which mark the sites of initiation and cessation of bouts of primary replacement, should be scattered throughout the primaries. In contrast, if feathers are replaced in multiple series, then nodal and terminal feathers should be consistent across individuals because these feathers represent the beginning and end of replacement series, as has been established in cuckoos (Rohwer and Broms 2011).~~

Commented [R1-10]: Only true if all primaries are replaced

We use data from 175 common ground doves from coastal Sinaloa, Mexico to describe their primary replacement rules. We document strong differences in the intensity of molt between juveniles and adults, show that molt can be stepwise in breeding adults, and provide the first evidence that arrests associated with parental care are responsible for the generation of multiple waves of primary replacement in a small bird. Common Ground Doves, like other Columbiformes, regurgitate "crop milk", a liquid food consisting of protein, water and fat to their young, and the production of crop milk allowed us to assess how feeding young is associated with molt in breeding adults. Our results clearly show that this small dove, overlaps molt and breeding more or less completely, can replace its primaries completely during the breeding season, and has evolved a mechanism to suppress the initiation of new waves of primary replacement at P1 until the preceding wave has reached the distal primaries. As we discuss beyond, this discovery resolves an unexplained paradox in the primary replacement patterns for Mustached Tree Swifts (Rohwer and Wang 2010), which, very likely, also have a

Commented [R1-11]: 182 in supplemental table, AZ included there but not in ms?

mechanism for suppressing the immediate generation of new molt waves at P1 when the inner primaries are little worn.

Commented [R1-12]: A little premature. Maybe just say "provide additional data on patterns of replacement and speculate on significance and controlling mechanism

METHODS

Common Ground Doves are largely resident birds, with a range extending from the southern United States through Central America, across northern South America, and throughout the West Indies (Bowman 2002). They are among the smallest doves, with a mass of about 40 grams (UWBM specimens from Sinaloa). Breeding in juveniles can occur when they are about 6 months old (Johnston 1962; Passmore 1984), and we also confirmed breeding by three birds in partial juvenile plumage that were likely less than 6 months old. They do not defend territories and exhibit little aggression (Nicholson 1937), which may explain why they are slow to resorb the bursa of Fabricius and why both males and females in breeding condition often retain glandular bursas (Mase and Oishi 1991).

Molt scoring and the analysis of the rules of primary replacement followed Rohwer (2008). Growing primaries were given fractional scores representing, to the nearest tenth, their length as fully-grown feathers. New feathers were scored as 1 and old feathers as 0, but it is important to note that these age assignments are unlikely to be year classes in this data set; instead they represent activation classes of molt separated by unknown intervals that were likely on the order of a few months. Where blocks of adjacent feathers represented different replacement classes, they were distinguished as newer or older than adjacent blocks. Sometimes adjacent groups of primaries were extremely worn and faded and assigned a score of ragged; these were likely feathers approaching a year of use that had been retained through the non-breeding season. The total molt score for a bird was the sum of the values for its new and growing feathers.

We assessed breeding activity of doves that we netted and released by the presences or absence of crop-milk; for doves that were prepared as specimens, we noted the condition of the glands inside the crop, where vascularized crops with thickened walls indicated active milk production. We also recorded dates for a number of nests with eggs or young.

We have restricted all of our analyses to observations we made in coastal Sinaloa from 2005 through 2011, during the months of May through September. Most of our field work in Sinaloa was designed to study molt migrants (e. g. V. Rohwer et al. 2009, S. Rohwer et al. 2007, 2015, S. Rohwer 2013); consequently, we have scored molt for only 15 birds for the months of May and June, but many for the months of July through September. When work on other projects was slow, some doves were collected and many more were scored for primary replacement before being released. Time constraints, and not the condition of the bird, dictated whether birds were either collected or scored and released; thus, our data should be an unbiased representation of the birds that we caught. The number of birds scored for molt offers a good index of the relative amount of time we spent in the field in these months.

Our field work in Sinaloa was conducted on various communes in the Rio Fuerte flood plain between Los Mochis on the coast and El Fuerte near the foothills of the Sierra Madre Occidental. Many birds were scored for molt in the field and then released, but approximately 40 additional birds that were collected are also included in our analyses. These specimens were particularly important because they had associated extended wings that were used to measure the lengths of the primaries and primary growth rates. Growth bands could not be seen in juvenile primaries and they were faint and difficult to see in most primaries and in most adults and could not have been measured on specimens with folded wings. As part of our other studies of molt-migrants, we also collected or scored for molt a smaller sample of Common Ground Doves in Arizona, but these birds were excluded from this study so possible geographic variation in the phenology of molting and breeding of this resident bird would not confound our results. Our Arizona observations were important, however, in demonstrating breeding by juveniles and multiple waves of primary replacement in adults.

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Field work for this project was approved by the University of Washington Institutional Animal Care and Use Committee (protocol 4309-01).

RESULTS

Primary replacement patterns~~rules~~ for juveniles.

Most of the 50 juveniles that we captured and scored for molt were replacing primaries, suggesting that they likely begin this molt shortly after fledging (Table 1). Of the 50 juveniles we scored, just two had not yet commenced flight feather replacement, and had all juvenile primaries and secondaries. We spent little time in the field in May and June, so the low numbers of juveniles scored in these months does not imply the production of few young during that time.

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Without exception, juveniles replaced their primaries distally, starting at P1 (Table 2). P1 is strongly nodal and no other primary in our sample of 50 juveniles received a score of nodal, suggesting that arrests in the replacement of the juvenile primaries do not occur. Our sample includes many more juveniles replacing inner than outer primaries, but good samples of growing primaries were available for all primaries except P8 and P9 for juvenile ground doves (Table 2). Having samples for these distal most feathers requires recognizing remnants of juvenile feathers in other parts of the body, which we likely failed to do in some cases; this means that our sample of adults likely contains some older juveniles that were not recognized as such in the field. This problem suggests that the percentage of adults with multiple waves of primary replacement is somewhat underestimated.

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Commented [R1-16]: Explain in methods

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Primary replacement ~~rules~~ patterns for adults.

Primary replacement in adult Common Ground Doves is considerably more complex than it is in juveniles. Of the 138 adults we scored for molt, 78 percent were replacing primaries; most of the 31 remaining adults had adjacent blocks of newer and more worn primaries in their wings, suggesting that they had arrested primary replacement. Just 17% of the adults that were growing primaries had two separate waves of molt. However, multiple waves of primary replacement are more common in adults than this figure suggests. Many adults with arrested molt had two groups of newer primaries that were separated by one to several older primaries. These non-molting adults clearly had had two waves of primary replacement; when they are added to those with two active waves of molt, 31% of adults can be inferred to have been replacing their primaries in two waves (Table 3).

Commented [R1-18]: In a single descendant wave?

Commented [R1-19]: 28 excluding UWBM 90871 in one not molting that was growing P1

Commented [R1-20]: Methods question: Do you really think that a pause for breeding would create sufficient differential wear to allow scoring. Depends on how long the pause is, which isn't considered. If a few weeks for crop milk production/feeding young, there would be no difference. Similar probably for a month or two and several to 12 months are needed to create obvous wear categories. No rationale is presented for the suggestion that there is an arrest for raising young while the possibility that the breaks result from prolonged period of no molt imposed by seasonality.
Related in scoring non-molting birds. The molt is so slow what is the likelihood that a bird without a growing primary feather has finished one and there is a lag in dropping the next? Secconaries might provide some clue here. More than likely molt is continuous and slow creating so little energy drain that all adults are molting.

As in juveniles, the direction of primary replacement is strongly distal in adults (Table 4). However, the generation of multiple waves after molt arrests in adults complicates scoring of directionality. Thus, directionality scores between P1 and P2 were distal in 6 adults, but proximal in 4. These 4 proximal scores are almost certainly scoring artifacts caused by P1 being too short to be compared for wear and fading with its adjacent inner primaries. Thus, if P1 was scored as growing, and its distal neighbors were scored as new, the inferred direction of replacement between P1 and P2 is proximal. However, if we had been able to determine that P1 was newer than P2, directionality between this feather pair would have been scored as distal. In three of these four anomalous cases, P1 was a pin feather, which could not be scored for wear or fading; in the other the tip of P1 was just emerging from its sheath. A similar problem arises with arrests at P9, which, apparently, are relatively common. When molt is reinitiated at P10 and the feather(s) immediately proximal to it are scored as old, then, by definition, the inferred direction of replacement between P9 and P10 is proximal, readily accounting for the 6 proximal directionality scores between P9 and P10 as artifacts of arrests (Table 4). In contrast, the 14 distal directionality scores between P9 and P10 are unambiguous, To summarize, all of the proximal directionality scores between primary pairs P1/P2 and P9/P10 can be interpreted as scoring artifacts of the frequent arrests that characterize primary replacement in adult Common Ground Doves.

Commented [R1-21]: Redo this section excluding P1 &P10 as these do not have two adjacent Ps and use only growing feather in P2-P9 for clarity.

The scattering of nodal and terminal feathers from P6 to P9 again reflects multiple waves (Table 4). Nodal feathers ~~appropriately~~ mark the beginning of waves of replacement in ~~the outer~~ primaries. However, they can only be recognized as nodal when an arrest has been long enough that the feathers replaced in the preceding bout of molt have accumulated noticeable wear or fading. Then, the primary at which a molt wave is re-activated will be newer than its proximal neighbor and thus be scored as nodal. That the recognition of nodes in the ~~distal~~ primaries requires arrests of sufficient duration to recognize older feathers surely means that our data underestimates the number of adults inferred to have ~~two or more~~multiple replacement waves in their primaries. The same scoring problem a~~r~~rises when a proximal wave of replacement meets a more distal wave. In these cases the distal-most feather in the proximal wave will be scored as terminal because both of its neighboring feathers will be older than it is. To reiterate, the scattering of feathers scored as nodal or terminal in the distal primaries confirms, but likely under-represents the frequency of multiple waves of primary replacement in Sinaloan ground doves.

Commented [R1-22]: Same for proximal

Commented [R1-23]: But proximal feather assuming descendant movement will be the same wear category so not seeing the point here.

Commented [R1-24]: not true for proximal?

Data linking breeding attempts with arrests in primary molt in adults is shown in Table 5 where we compare crop gland activity with primary replacement. Many adults that were replacing primaries had active crop glands, so molt is not always arrested when young are being fed (Table 5). Nonetheless, arrested primary replacement was strongly associated with having an active crop gland, suggesting that adults that are tending large or newly fledged young may arrest their molt to conserve energy. It is these arrests, we postulate, that generate multiple waves of primary replacement in adults. Apparently, molt is reinitiated where it arrested in the distal primaries and also starts anew at P1, thus generating two, or in one case (Table 6), three waves of primary replacement.

Commented [R1-25]: 8/14, since about half of the active crop gland birds were molting and half were not, there is no trend other than they can molt when crop gland is active.

Commented [R1-26]: Why not having?

Commented [R1-27]: Refer to BNA and dove literature, crop milk is fed to small nestlings but there is or maybe a shift to food as they grow. This doesn't preclude energetic constraints from breeding as a cause for arrest but the few that do arrest suggest it is rare..

Finally, the generation of new waves of replacement at P1 following arrests seems mostly to be restricted to cases where primary replacement had proceeded into the distal primaries before the arrest. In Figure 1 we plot the number of feathers separating distal and proximal growing primaries for the 17 adults that had two active waves of replacement. There is a strong peak in this distribution at 6 primaries between these waves, indicating that arrests that take place when less than 6 inner primaries have been replaced usually do not result in the generation of a new replacement wave starting at P1. When fewer than 6 inner primaries have been replaced before the arrest, molt usually resumes with the next feather to be replaced, without also initiating a new wave of replacement at P1. Two birds directly support this contention. Feather wear showed that both had arrests at P5 and later reinitiated primary replacement at P6, without starting a new wave at P1.

Molt breeding overlap and molt duration.

Our records suggest that primary molt and breeding overlap extensively in Common Ground Doves in Sinaloa (Table 6). We found nests and birds with active crop glands from May through September and more than 50% of adults examined were molting in all of these months except May (Table 6). The long breeding season and the extensive overlap of molt and breeding in adult ground doves suggests that there should be little relation between day of year and primary molt score for adults (Figure 2). While this relationship is significantly positive, the distribution of points strongly suggests that the data ~~is largely~~ are a composite of two flat lines representing the months of July and September. This is indeed the theoretical expectation when some birds are completing molt as others are just beginning (Rohwer and Broms 2012, Rohwer 2013). Thus, the presence of two "flat" regression lines in Figure 2 is evidence that, as in other species, where molt is little synchronized among individuals in a population, neither regression nor maximum likelihood estimates of molt duration are reliable. "Flat" lines in Pimm regression plots suggest extremely rapid molts, something that ground doves do not do. Such regression lines likely ~~to~~ characterize many species that show extensive overlap in molt and breeding, as in these ground doves~~, and also characterize species where some individuals have completed primary replacement before others have started, as in Painted Buntings, *Passerina ciris*, (Rohwer 2013).~~

Commented [R1-28]: 18 but only quantified for 16, clarify

Commented [R1-29]: See general comment regarding growing P1s and P10, except for 2 wings, the distal wave is being generated long after proximal wave unless one assumes abutting waves in the proximal and medial Ps.

Commented [R1-30]: With multiple broods, how long to raise a single brood? If 30 days, a pair could get many broods in and perhaps suggest that the energetic constraints for molt and breeding come into play nearing the end of the breeding window leading to arrested molts in the last brood.

Commented [R1-31]: statistical expectation.

Commented [R1-32]: Agreed, but the two flat lines result from large samples in the two periods leaving the middle June with few data. If filled the data cloud would be an ovoid tilted to the right. Try binning by 10 or 15 day intervals and use averages to plot a line to eliminate the two flat line appearance.

Commented [R1-33]: Flat horizontal line from a regression would indicate no correlation, i.e., no relation between molt score vs day of year (or other time).

Following Rohwer and Broms (2012), we estimated the time required to replace the 10 primaries in adult Common Ground Doves from the summed length of the primaries, primary growth rate, and the number of primaries growing simultaneously. Our measurements for primary lengths and growth rates are summarized in Table 7. For birds in active molt, the mean number of primaries growing was 1.37 for adults and 2.02 for juveniles (weighted averages computed from data in Table 3). Assuming no interruptions in the molt, which of course is not true in adults, but is true in juveniles, the number of days (D) required to replace all the primaries is

$$D = L/(G \times N),$$

where L is the summed length of the 10 primaries, G is primary growth rate measured in mm/d, and N is the mean number of primaries growing simultaneously. Using this equation, adult males are estimated to require 149 days to replace their primaries, adult females 145 days, and juveniles 101 days. Because birds were breeding during the extent of our field work from May through September, we do not know how much time they have to spend in molt. Nonetheless, these figures suggest that adults could replace all their primaries in less than 5 months, so most adults should be able to complete their molt while they are breeding, even with arrests during intense periods of parental care. Juveniles take considerably less time to molt but, if foraging is difficult during the dry months of winter, late fledged juveniles may not be able replace all their primaries before their first breeding season.

Commented [R1-34]: Reword legend, 1 primary could not grow simultaneously

Commented [R1-35]: Incorrect based on result and supplemental data unless juveniles are mis-aged, probably many should SYs?

Commented [R1-36]: Or how long the breeding window is or conversely how long the non-molting or non-breeding period are if they exist. So the rest is just speculation.

Commented [R1-37]: Suggest that there will be a progression of arrested molt in juvys from complete molt in first to fledge to only a few molted in late fledged. This creates a nightmare for interpretation as SYs because presumably body plumage of juvy is gone or does body plumage also arrest? And given productivity from multiple brood, the preponderance of birds are probably SYs?

DISCUSSION

We show that the primaries of Common Ground Doves constitute a single molt series and are replaced distally from P1 to P10. In contrast to juveniles, adults often have two simultaneously active waves of primary replacement but they usually have just one feather growing per wave. Molt arrests are thought to be the mechanism by which multiple waves of primary replacement develop (Rohwer 1999). We document that molt arrests in adult Common Ground Doves are

Commented [R1-38]: Quantify this and include in results

Commented [R1-39]: This is a prerequisite for Stafflemaouse, but arrests in non-Stafflemauser patterns also result in multiple waves.

strongly associated with active crop glands, indicative of adults feeding young. Thus, arrests associated with periods of intense parental care are likely the mechanism by which new waves of primary replacement are generated at P1 before distal waves of molt have reached P10 in adults. Juveniles replace their primaries in a single wave that starts at P1 and no juvenile had two waves of primary replacement, unless they were breeding precociously, as rarely occurs in this species (Johnston 1962, Passmore 1984). Stepwise primary replacement is common in large birds, but this represents only the second well documented case of stepwise molting in a small bird, the other being the Mustached Tree Swift (Rohwer and Wang 2010). At 40 grams, Common Ground Doves are the smallest species for which stepwise molting has been documented.

Commented [R1-40]: Not strongly. Also consider that if molt is so slow and only one P growing per wave, what is the likelihood of sampling a bird that is molt but has finished growing a feather and not yet dropped the distal neighbor. Molt is likely continuous during the breeding window and the arrest occur during the non-breeding/non-molting periods. Really no evidence that molt arrests during the breeding period other than a few birds were not molting Ps.

Commented [R1-41]: Maybe, but more likely simply a result of non-molting period due to environmental constraints.

Commented [R1-42]: No evidence to support breeding as a cause for arrest in juvys

Commented [R1-43]: Agreed on documented but assuming scoring and assumptions are correct, only 30% of adults have the pattern. What about the other 70% that do not. Focusing on exceptions missing the more common pattern.

In large birds stepwise molting results in the inner primaries being replaced two or more times before the distal-most juvenile primaries are replaced for the first time (see diagrams in Rohwer 1999). This seems remarkably maladaptive because the outer primaries wear considerably more than inner primaries, yet are the last to be replaced in young birds. Prior to this study, the only mechanism identified for overcoming this problem was “omissive” molts (Rasmussen 1988; Schugart and Rohwer 1995). In omissive molts P8, P9 or P10 is lost out of sequence in some, but not all, juveniles of a species, thus setting up replacement of the outer primaries before the first wave of molt replacing the juvenile primaries has progressed that far. Omissive molts have remained perplexing because only some individuals show such replacement, and because the primary that is replaced varies. These complications may be resolved by the recent discovery that some birds have the ability to preferentially replace broken primaries or rectrices (Ellis et al. 2016). If omissive molts are generated by the preferential replacement of extremely worn primaries, then the fact that not all juveniles show this pattern of replacement in their outer primaries and that the replaced primary can be any of three different feathers is resolved: very worn outer primaries could be replaced out of their normal sequence.

Commented [R1-44]: Seems to indicate a misinterpretation of Stafflemauser, see general comments

Our results for Common Ground Doves have revealed another, previously unknown, mechanism for avoiding unnecessarily frequent replacement of the inner primaries in birds with stepwise primary replacement. Somehow, ground doves largely suppress initiation of new replacement waves at P1 until the distal wave has proceeded to about P6. Because inner primaries wear more slowly than distal primaries, this suppression of new waves starting at P1 largely eliminates unnecessarily frequent replacement of the inner primaries, something that has not, to our knowledge, been reported for large birds (Rohwer 1999). Common Ground Doves were serendipitously well suited for this discovery because the number of primaries between the distal growing feather in birds with two molt waves is little affected by differences between feather lengths and growth rates, which vary little across their primaries (Table 7). Thus, data from individuals with two waves of molt could be used for this test, without differences in the time it takes to grow different feathers strongly biasing results. In Wood Pigeons (*Columba palumbus*), most late-hatched first year birds or adults that had two waves of replacement in their primaries had 5-6 newly replaced feathers between waves (Boddy 1981), consistent with a mechanism of suppressing additional waves of feather replacement until the outer molt series has reached a certain point in the wing.

Commented [R1-45]: Delete, not supported by the supplemental data

Delaying the development of new waves of feather replacement starting at P1 also explains the surprisingly greater frequency of growing feathers in the outer than in the inner primaries (Table 4), which, initially, seemed anomalous to us. If new waves that follow too closely on the heels of a previous wave are suppressed, then molt summary tables, which aggregate molt scores across many individuals, should show more growing primaries in the distal part of the wing. This is partly because outer primaries are longer and take more time to grow, but that likely has little effect in Common Ground Doves because the longest primaries (P7 or P8) are only 12mm longer than P1 (Table 7). Instead, this higher frequency of growing feathers in the distal primaries probably results from new waves of replacement being suppressed in the inner primaries following arrests until molt in the outer primaries has reached at least P6. This pattern of more active molt in the distal primaries was also discovered in Mustached Tree Swifts, but was perplexing to Rohwer and Wang (2010). Now it seems likely that the suppression of new waves starting at P1 until the next distal wave is well out into the primaries could be a general solution to the problem of excess replacement of inner primaries in small birds with stepwise primary replacement. In Mustached Tree Swifts the outer primaries are progressively much longer than the inner primaries, but the strong break in the frequency of replacement occurred between P5 and P6, with P6-10 showing about twice as many growing feathers as P1-5. Because this was a more or less dichotomous break in frequencies, despite progressive length differences in the primaries, we suggest that Mustached Tree Swifts may also suppress the commencement of new replacement waves at P1 until molt in the outer wave has reached at least P6. Studies of marked and recaptured birds with known breeding histories will be essential to support our suggestions that arrests are responsible for generating multiple waves of primary replacement, and that new waves are suppressed when an arrest occurs before the initial molt wave has progressed, on average, to the replacement of P6.

Commented [R1-46]: Change to suggest there is latency to molt after renewal

Pigeons and doves exhibit remarkable flexibility in their molts. Mourning Doves (*Zenaida macroura*) and White-wing Doves (*Zenaida asiatica*) replace their primaries distally from P1 to P10, in a single series with apparently few arrests (Otis et al. 2008). By contrast, we have seen multiple waves of replacement in small *Ptilinopus* doves collected in the Solomon Islands, and Pyle et al. (2016) report two waves of feather replacement in two *Ptilinopus poryphyraceus* from American Samoa, suggestive of stepwise molting. Stepwise molts, ~~presumably generated by arrests for breeding,~~ are also reported from some Band-tailed Pigeons, *Patagioenas fasciata*, (Silovsky et al. 1968) and Wood Pigeons (Boddy 1981). These observations suggest flexibility in the scheduling of annual molts relative to breeding opportunities. When breeding conditions are favorable, some individuals in active molt arrest then resume their molts at multiple feather loci, while other individuals simply continue their annual molts without arrests. Stopping and starting molt likely increases the potential for creating asymmetries between wings, but any costs of asymmetric molts appear outweighed by the benefits of additional breeding attempts. Pigeons and doves, with their specialized crop glands for feeding young, may be especially prone to arrested molts when the food demands of large young are high.

Commented [R1-47]: See Stresemann and Stresemann 1966 or Ashmole 1968 for similar suggestion

Many of the regions in coastal Sinaloa where we worked has been converted to irrigated agriculture (Rohwer et al. 2015), which provides extensive habitat and more predictable mesic areas around fields that are excellent for breeding by Common Ground Doves. This also means that breeding opportunities for ground doves may extend for longer periods of time and be less confined to the annual late-summer monsoon (Comrie and Glenn 1998) than would have been the case prior to the 1970s, when reservoirs and extensive systems of cement-lined canals began to be developed in coastal west Mexico (Rohwer et al. 2015). The possibility that landscape-level changes has affected the phenology of molt and breeding or the extent of molt-breeding overlap could be assessed by comparing ground doves in parts of Sonora where monsoon rains continue to drive the annual vegetation cycle in the absence of irrigation.

As more tropical species are examined that exhibit extensive molt breeding overlap, many more small species will likely be discovered to replace their primaries in multiple waves, either in a stepwise fashion, or by dividing the primaries into multiple series. Distinguishing between these two strategies requires data on substantial numbers of actively molting birds summarized in tables similar to those presented here. As more such studies accumulate, the comparative studies they will support should help illuminate both the evolutionary history and lability of primary replacement patterns across birds and how primary replacement strategies are integrated into other major life-history features of birds.

Commented [R1-48]: Fixing the data table is a first step

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Primary 10 molting independently

Series	Date	Day of Year	Sex	Age A	# active waves	# infered waves	Inferred arrests, no new wave	Any ragged Ps ®	Burke Specimen # (r= released)	P Molt?	Ps in prox/distal waves	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P molt score	Notes	breeding flag colum
13	2-Aug-06	214	m	a	2	2		yes	82497	yes	*3/3	1	1	1	0.1	r	r	r	1	1	0.6	5.7	L 10x5	
60	18-Jul-06	199		a	2	2			r	yes							growing				growing		no additional data	
99	5-Sep-06	248	f	a	2	2			r	yes	*8/1	1	1	1	1	1	1	1	0.3	0	0.8	8.1	same bird, Right wing	
101	6-Sep-06	249	m	a	1	1			r	yes		1	1	1	1	1	1	1	1	0.3	0.01	8.31		P7 is post arrest
109	6-Sep-06	249	m	a	2	2			r	yes	*5/1	1	1	1	1	0.8	0	0	0	0	0.2	5		
110	6-Jul-07	187	m	a	2	2			r	yes	*3/1	1	1	0.7	0	0	0	0	0	0	0.3	3		
111	6-Jul-07	187	f	a	2	2			r	yes	*4/1	1	1	1	0.6	0	0	0	0	0	0.3	3.9		
122	14-Jul-07	195	m	a	2	2			r	yes	*4/2	1	1	0.9	0.5	0	0	0	0	1	0.6	5	CROP inactive; S molt recorded	
124	15-Jul-07	196	m	a	2	2			r	yes	*4/1	1	0.99	0.9	0.1	0	0	0	0	0	0.01	3	CROP inactive; S molt recorded	
160	9-Sep-07	252	f	a	1	1			r	yes		1	1	1	1	1	1	1	1	0.99	0.3	9.29	Marco	
186	14-Sep-07	257	m	a	2	2			r	yes	*7/1	1	1	1	1	1	1	0.01	0	0	0.9	6.91	CROP not active	
187	15-Sep-07	258	m	a	2	2		yes	r	yes	*7/1	1	1	1	1	1	1	0.8	r	0	0.9	7.7	CROP not active; P1-6 newish, suggesting P7 is nodal	
	12-Sep-10	255		a	2	2			CSW 9167	yes	*1/1	0.4	1	1	1	1	1	1	1	1	0.9	9.3		

P1 indendpent of waves?

Series	Date	Day of Year	Sex	Age A	# active waves	# infered waves	Inferred arrests, no new wave	Any ragged Ps ®	Burke Specimen # (r= released)	P Molt?	P1 independent ?	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P molt score	Notes
37	17-Jun-11	168	f	a	1	2	2	yes	90871	no	yes?	0.01	1	1	r	r	r	r	0	0	0	2.01	2 small rupt follicles; crop glands inactive
119	14-Jul-07	195	m	a	2	2			r	yes	yes	0.01	1	1	1	0.8	0.01	0	0	0	0	3.82	CROP inactive; S molt recorded
125	15-Jul-07	196	m	a	2	2			r	yes	no, synchronized	0.6	0	0	0	0	0	0.2	0	0	0	0.8	CROP inactive; S molt recorded; inners that are old may be newer
133	17-Jul-07	198	m	a	2	2			r	yes	yes	0.3	1	0.7	0	0	0	0	0	0	0	2	Crop thick, but no water out of mouth; S molt noted
61	18-Jul-06	199		a	1				r	yes		0.3											
151	20-Jul-07	201	m	a	2	2			r	yes	yes	0.1	1	1	0.9	0.2	0	0	0	0	0	3.2	Crop inactive; S molt recorded
192	27-Jul-09	208		a	2	2			r	yes	yes	0.1	1	1	1	1	0.6	0.1	0	0	0	4.8	
103	6-Sep-06	249	m	a	1	2	1		r	yes	yes	0.01	1	1	1	1	1	1	newer	newer	f/w	6.01	f/w = faded and worn
	12-Sep-10	255		a	2	2			CSW 9167	yes	no, synchronized	0.4	1	1	1	1	1	1	1	1	0.9	9.3	

column L added by reviewer

Series	Date	Day of Year	Sex	Age A	# active waves	# infered waves	Inferred arrests, no new wave	Any ragged Ps ®	Burke Specimen # (r= released)	P Molt?	reviewer comments on scoring	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P molt score	Notes	breeding flag colum
32	########	150	m	a	0	0	1		90694	no		0	0	0	0	0	0	0	newer	newer	newer	0	crop glands large; no bursa; T11x6; first wing of 2	
33	##########	150	m	a	0	2		yes	90695	no		0	0	0	0	0	r	r	0	0	0	0	crop glands large; no bursa; T10x6; first wing of 2	
34	##########	150	m	a	0	2		yes	90696	no		0	0	0	0	0	r	r	0	0	0	0	crop glands tiny; no bursa; R11x5; first wing of 2	
29	##########	150	f	a	0	2			90691	no		1	1	1	1	0	0	0	0	1	1	6	oviduct slightly thickened, no collapsed follicles; crop glandular; no bursa; both wings saved, so just first scored used	
30	##########	150	m	a	1	2		yes	90692	yes		1	1	1	1	0.95	0.5	r	0	0	0	5.45	10x 5; no bursa; crop glandular; first scored of 2 wings	
209	1-Jun-11	152	m	a	0	0			r	no molt													P ages nor recorded	
212	8-Jun-11	159	f	a	0	0			r	no molt													P ages nor recorded	
37	17-Jun-11	168	f	a	1	2	2	yes	90871	no		0.01	1	1	r	r	r	r	0	0	0	2.01	2 small rupt follicles; crop glands inactive	Red marks birds known to be breeding other than by crop: f with rupt follicles; bird from a nest
38	17-Jun-11	168	f	a	1	2	1		90873	yes		1	1	1	1	1	1	0.5	0	1	1	8.5	crop inactive	
36	20-Jun-11	171	m	a	2	2			90784	yes	1 or 2 & 10	P10 and 0ne of 2 inners growing; both wings too dammaged to determine what feather, but two active waves												
110	6-Jul-07	187	m	a	2	2			r	yes	1 & 10	1	1	0.7	0	0	0	0	0	0	0.3	3		
111	6-Jul-07	187	f	a	2	2			r	yes	1 & 10	1	1	1	0.6	0	0	0	0	0	0.3	3.9		
114	7-Jul-07	188	f	a	1	1			r	yes		1	1	1	1	0.7	0.1	0	0	0	0	4.8	INACTIVE crop	
112	7-Jul-07	188	f	a	1	1			r	yes		1	1	1	1	1	1	0.3	0	0	0	6.3	same in both wings	
113	7-Jul-07	188	m	a	1	1			r	yes		1	1	1	1	1	1	0.5	0	0	0	6.5	INACTIVE crop	
115	7-Jul-07	188	xx	a	0	2		yes	r	No		1	1	1	1	r	r	r	0	0	0		CROP active	
117	10-Jul-07	191	m	a	1	1			r	yes		1	1	1	1	1	1	0.4	0	0	0	6.4	CROP inactive; S molt recorded	
116	10-Jul-07	191	f	a	1	1			r	yes		1	1	1	1	1	1	1	0.6	0	0	7.6	CROP inactive; S molt recorded	
10	12-Jul-06	193	m	a	1	1		yes	82397	yes		1	1	1	1	0.95	r	r	0	0	0	4.95	L9x4; no bursa	
118	13-Jul-07	194	m	a	1	2		yes	r	yes		1	1	1	0.8	r	r	r	0	0	0	3.8	No S molt	
11	14-Jul-06	195	f	a	1	1		yes	82407	yes		1	1	1	1	0.99	0.5	r	r	0	0	5.49	ova to 5mm	
119	14-Jul-07	195	m	a	2	2			r	yes	1 & 2	0.01	1	1	1	0.8	0.01	0	0	0	0	3.82	CROP inactive; S molt recorded	
121	14-Jul-07	195	f	a	1	2			r	yes		1	1	0.8	0	0	0	0	0	1	0	3.8	CROP inactive; S molt recorded	
122	14-Jul-07	195	m	a	2	2			r	yes	1 & 9	1	1	0.9	0.5	0	0	0	0	1	0.6	5	CROP inactive; S molt recorded	
120	14-Jul-07	195	f	a	1	1			r	yes		1	1	1	1	0.7	0	0	0	0	0	4.7	CROP inactive; S molt recorded	
125	15-Jul-07	196	m	a	2	2			r	yes	1 & 7	0.6	0	0	0	0	0	0.2	0	0	0	0.8	CROP inactive; S molt recorded; inners that are old may be newer	
129	15-Jul-07	196	m	a	1	1			r	yes		1	0.7	0.01	0	0	0	0	0	0	0	1.71	Crop inactive; all old of same generation; S molt recorded	
124	15-Jul-07	196	m	a	2	2			r	yes	1 &10	1	0.99	0.9	0.1	0	0	0	0	0	0.01	3	CROP inactive; S molt recorded	
123	15-Jul-07	196	m	a	1	2		yes	r	yes		1	1	1	0.01	r	r	r	0	0	0	3.01	CROP inactive; S molt recorded	
127	15-Jul-07	196	f	a	0	1	1	yes	r	no		1	1	1	1	1	1	r	r	r	r		r = more faded; in net with next baby	
7	16-Jul-05	197	m	a	1	1			81208	yes		1	1	1	1	1	1	1	0.8	0	0	7.8	Sinaloa; small bursa; breeding male L 10x5; 9&10 NOT J	
59	17-Jul-06	198		a	1	1			r	yes		1	1	1	1	0.9	0	0	0	0	0	4.9		
133	17-Jul-07	198	m	a	2	2			r	yes	1 & 2 or a single wave from P2 then P3 & P1	0.3	1	0.7	0	0	0	0	0	0	0	2	Crop thick, but no water out of mouth; S molt noted	
135	17-Jul-07	198	m	a	1	1			r	yes		1	0.9	0.01	0	0	0	0	0	0	0	1.91	Crop inactive; S molt recorded	
131	17-Jul-07	198	m	a	1	1			r	yes		1	1	1	1	0.5	0	0	0	0	0	4.5	Crop inactive; S molt recorded	
134	17-Jul-07	198	f	a	1	1			r	yes		1	1	1	1	1	1	1	0.95	0	0	7.95	CROP inactive	
132	17-Jul-07	198	m	a	1	1			r	yes		1	1	1	1	1	1	1	1	0.9	0	8.9	Crop thick, no juice; S molt recorded	
61	18-Jul-06	199		a	1	1			r	yes		0.3											both wings; no further data	
60	18-Jul-06	199		a	2	2			r	yes	6 & 10						growing				growing		no additional data	
139	18-Jul-07	199	f	a	1	2			r	yes		1	1	1	0.9	0	0	1	1	1	0	6.9	Crop inactive; S molt recorded	
138	18-Jul-07	199	m	a	1	1			r	yes		1	1	1	1	1	1	0.7	0	0	0	6.7	Crop thick, no drip; S molt noted	
63	19-Jul-06	200	f	a	1	1			r	yes		1	1	1	0.9	0	0	0	0	0	0	3.9		
143	19-Jul-07	200	f	a	0	1			r	no		1	1	1	0	0	0	0	0	0	0		S molt recorded	
144	19-Jul-07	200	m	a	1	1			r	yes		1	1	1	1	0.3	0	0	0	0	0	4.3	S molt recorded	
140	19-Jul-07	200	m	a	1	1			r	yes		1	1	1	1	0.9	0.2	0	0	0	0	5.1	Crop inactive; S molt recorded; bp bare dry	
142	19-Jul-07	200	m	a	1	2			r	yes		1	1	1	1	0.95	0.25	0	0	0	1	6.2	Crop inactive; S molt recorded	
141	19-Jul-07	200	m	a	1	1			r	yes		1	1	1	1	1	0.01	0	0	0	0	5.01	Crop thick, no drip; S molt noted	
145	19-Jul-07	200	m	a	1	1			r	yes		1	1	1	1	1	1	0.8	0	0	0	6.8	Crop inactive; S molt recorded r = released or r = ragged under the Ps	
65	20-Jul-06	201	f	a	1	1			r	yes		1	1	1	0.95	0	0	0	0	0	0	3.95		
64	20-Jul-06	201		a	1	1			r	yes		1	1	1	1	1	0.4	0	0	0	0	5.4	Crop glands active xx = no notes on molt	
151	20-Jul-07	201	m	a	2	2			r	yes	1 & 2	0.1	1	1	0.9	0.2	0	0	0	0	0	3.2	Crop inactive; S molt recorded	
152	20-Jul-07	201	m	a	1	2			r	yes		1	1	1	0.1	0	0	0	0	0	1	4.1	S molt recorded; crop likely inactive, no drip from bill	
149	20-Jul-07	201	m	a	1	1			r	yes		1	1	1	1	0.2	0.1	0	0	0	0	4.3		
153	20-Jul-07	201	m	a	1	2			r	yes		1	1	1	1	1	0.8	0	0	0	1	6.8	Crop inactive; S molt recorded	
154	20-Jul-07	201	m	a	1	1			r	yes		1	1	1	1	1	1	0.3	0	0	0	6.3	Crop thick, bill not drippig; S molt recorded	
150	20-Jul-07	201	f	a	1	1			r	yes		1	1	1	1	1	1	1	1	0.1	0	8.1	Crop inactive; S molt recorded	
66	21-Jul-06	202		a	1	1			r	yes		1	1	1	1	1	0.8	0	0	0	0	5.8		
24	26-Jul-09	207	f	a	1	2			88901	yes		1	1	1	0.1	0	0	0	newer	newer	newer	3.1	s collapsed follicles5,3mm;newer are old but less worn than the 0s; no S molt: S1-6 =1; S7 =0; 8,9=1	
192	27-Jul-09	208		a	2	2			r	yes	1 & 2	0.1	1	1	1	1	0.6	0.1	0	0	0	4.8		
1	28-Jul-05	209	m	a	0	0			r	none														
2	29-Jul-05	210	?	a	0	0			r	none														
3	29-Jul-05	210	?	a	0	0			r	none														
28	30-Jul-09	211	m	a	1	2			89045	yes		1	1	0.2	0	0	0	0	newer	newer	newer	2.2	testes 13x7; field molt score wrong	
194	30-Jul-09	211	m	a	1	2			r	yes		1	1	1	0.8	older	older	older	0	0	0	3.8	S molt noted	
13	2-Aug-06	214	m	a	2	2		yes	82497	yes	1 & 8	1	1	1	0.1	r	r	r	1	1	0.6	5.7	L 10x5	
195	2-Aug-09	214	m	a	1	1			r	yes		1	1	1	1	1	0.3	0	0	0	0	5.3		
26	2-Aug-09	214	m	a	1	1			88934	yes		1	1	1	1	1	1	0.5	0	0	0	6.5	testes 7x4; bursa 6x4; in the field we would have called this an ad: no fringing on feathers	
69	3-Aug-06	215	m	a	0	0			r	no molt														
196	10-Aug-09	222		a	1	1			r	yes		1	1	1	1	1	1	0.8	0.01	0	0	6.81		Green marks bursa birds with enlarged testes
203	13-Aug-09	225	m	a	2	2			r	yes	1 & 3	1	0.2	1	1	1	1	1	0.7	0	0	6.9	S molt recorded	
198	13-Aug-09	225	f	a	1	1			r	yes		1	1	1	1	0.1	0	0	0	0	0	4.1	S molt recorded	
199	13-Aug-09	225	f	a	1	1			r	yes		1	1	1	1	0.7	0.1	0	0	0	0	4.8	S molt recorded	
200	13-Aug-09	225	m	a	1	1			r	yes		1	1	1	1	0.8	0	0	0	0	0	4.8	S molt recorded	
202	13-Aug-09	225		a	0	1			r	No		1	1	1	1	1	1	1	0	0	0		S molt wear recorded; none growing	
205	16-Aug-09	228	f	a	1	1			r	yes		1	1	1	1	1	1	0.8	0	0	0	6.8	S molt recorded	
204	16-Aug-09	228	m	a	0	1			r	No		1	1	1	1	1	1	1	0	0	0		S molt recorded	
206	17-Aug-09	229	m	a	0	1			r	No		1	1	1	1	1	1	1	0	0	0		S molt recorded	
70	21-Aug-06	233		a	0	0			r	no molt													no b.p.	
71	21-Aug-06	233		a	0	0			r	no molt													not aged	
72	21-Aug-06	233		a	0	0			r	no molt													not aged	
17	23-Aug-06	235	f	a	1	1			82673	yes		1	1	1	1	1	1	1	0.7	0	0	7.7		
9	28-Aug-06	240	m	a	1	1			82340	yes		1	1	1	0.95	0.5	0.01	0	0	0	0	4.46	L12x6; no bursa	
16	30-Aug-06	242	f	a	0	2			82594	no		1	1	1	1	1	1	0	0	1	0		both wings with 2 waves, but not quite the same	
79	4-Sep-06	247	f	a	1	1			r	yes		1	1	1	1	1	0.8	0	0	0	0	5.8		
83	4-Sep-06	247	m	a	1	1			r	yes		1	1	1	1	1	1	0.95	0	0	0	6.95		
78	4-Sep-06	247	f	a	1	1			r	yes		1	1	1	1	1	1	1	0.8	0.01	0	7.81		

86	4-Sep-06	247	f	a	1	1			r	yes		1	1	1	1	1	1	1	1	0.3	0	8.3	all new the same
85	4-Sep-06	247	m	a	0	1	1		r	no		1	1	1	1	1	1	newer	newer	0	0	6	
81	4-Sep-06	247	f	a	1	1	1		r	yes		1	1	1	1	1	newer	0.1	?	0	0	5.1	
80	4-Sep-06	247	f	a	1	1	1		r	yes		1	1	1	1	1	newer	newer	0.2	0	0	5.2	
95	5-Sep-06	248	f	a	1	1			r	yes		1	1	1	1	1	0.4	0	0	0	0	5.4	no break in new and growing
91	5-Sep-06	248	f	a	1	1			r	yes		1	1	1	1	1	0.6	0	0	0	0	5.6	
94	5-Sep-06	248	m	a	1	1			r	yes		1	1	1	1	1	0.8	0	0	0	0	5.8	no break in new and growing
99	5-Sep-06	248	f	a	2	2			r	yes	1 & 10	1	1	1	1	1	1	1	0.3	0	0.8	8.1	same bird, Right wing
92	5-Sep-06	248	m	a	1	1			r	yes		1	1	1	1	1	1	1	0.8	0	0	7.8	
96	5-Sep-06	248	m	a	0	1			r	no		1	1	1	1	1	1	1	1	0	0		
90	5-Sep-06	248	m	a	0	1	1		r	yes		1	1	1	1	1	1	newer	0	0	0	6	
89	5-Sep-06	248	m	a	0	1	1		r	yes		1	1	1	1	1	1	newer	0.3	0	0	6.3	
93	5-Sep-06	248	m	a	1	1	1		r	yes		1	1	1	1	1	1	newer	0.95	0	0	6.95	
88	5-Sep-06	248	m	a	0	1	1		r	no		1	1	1	1	1	newer	0	0	0	0		
20	5-Sep-06	248	m	a	1	1	1		82696	yes		1	1	1	1	1	newer	0.1	0	0	0	5.1	molt symmetrical; the 5/6 arrest is clear; R10x5 no bursa; two wings.
98	5-Sep-06	248	f	a	1	3			r	yes		1	1	older	older	older	1	0.4	0	0	1	4.4	same bird, Left wing
103	6-Sep-06	249	m	a	1	2	1		r	yes		0.01	1	1	1	1	1	1	newer	newer	f/w	6.01	f/w = faded and worn
109	6-Sep-06	249	m	a	2	2			r	yes	1 & 10	1	1	1	1	0.8	0	0	0	0	0.2	5	
102	6-Sep-06	249	m	a	1	1			r	yes		1	1	1	1	1	1	0.1	0	0	0	6.1	P1-6 fresh, not new; olds are very P7 is post arrest
101	6-Sep-06	249	m	a	1	1			r	yes		1	1	1	1	1	1	1	1	0.3	0.01	8.31	P7 is post arrest
105	6-Sep-06	249	m	a	1	2	1		r	yes		1	1	1	1	1	1	newer	0.1	f/w	f/w	6.1	
107	6-Sep-06	249	m	a	0	2	1		r	no		1	1	1	1	1	newer	newer	0	0	0		
108	6-Sep-06	249	m	a	1	2	1		r	yes		1	1	1	1	1	newer	newer	0.6	0	0	5.6	
155	9-Sep-07	252	m	a	1	1			r	yes		1	1	1	0.99	0.8	0.3	0	0	0	0	5.09	Marco record: age?
159	9-Sep-07	252	m	a	1	1			r	yes		1	1	1	1	1	1	0.99	0.9	0	0	7.89	Marco
156	9-Sep-07	252	m	a	1	1			r	yes		1	1	1	1	1	1	1	0.99	0.01	0	8	Marco: crop inactive
160	9-Sep-07	252	f	a	1	1			r	yes		1	1	1	1	1	1	1	1	0.99	0.3	9.29	Marco
162	10-Sep-07	253	m	a	1	1			r	yes		1	1	1	1	1	1	1	1	0.6	0	8.6	Marco
161	10-Sep-07	253	f?	a	1	1			r	yes		1	1	1	1	1	1	1	1	0.7	0	8.7	Marco
42	10-Sep-10	253	m	a	1	2	1		116921	yes		0	0	0	0	0	1	1	0.9	1		3.9	bursa 5x3; no fringing; odd bird
	10-Sep-10	253		a	1	1			CSW 9164	yes		1	1	1	1	1	0.9	0.05	0	0	0	5.95	
40	10-Sep-10	253	m	a	1	1			116914	yes		1	1	1	1	1	1	0.3	0	0	0	6.3	L9x6
41	10-Sep-10	253	f	a	0	1			116920	no		1	1	1	1	1	1	1	1	1	1	10	bursa 5x3; no fringing; odd bird
172	11-Sep-07	254	m	a	1	1			r	yes		1	1	1	1	1	1	1	0.8	0	0	7.8	
176	11-Sep-07	254	m	a	1	1			r	yes		1	1	1	1	1	1	1	1	0.9	0	8.9	Marco
171	11-Sep-07	254	f	a	0	0			r	no													
	11-Sep-10	254		a	1	1			CSW 9193	yes		1	1	1	1	1	1	0.9	0.3	0	0	7.2	
183	12-Sep-07	255	m	a	1	2			r	yes		1	1	1	1	1	1	0.8	older	older	older	6.8	P1-6 faded, so P7 is nodal
182	12-Sep-07	255	m	a	1	1			r	yes		1	1	1	1	1	1	1	0.95	0.5	0	8.45	
181	12-Sep-07	255	m	a	1	1			r	yes		1	1	1	1	1	1	1	1	0.9	0	8.9	
	12-Sep-10	255		a	2	2			CSW 9167	yes	1 & 10	0.4	1	1	1	1	1	1	1	1	0.9	9.3	
186	14-Sep-07	257	m	a	2	2			r	yes	1 & 10	1	1	1	1	1	1	0.01	0	0	0.9	6.91	CROP not active
185	14-Sep-07	257	f	a	0	1			r	no		1	1	1	1	1	1	1	1	0	0	8	CROP active; P molt arrested, urt molting Ss
184	14-Sep-07	257	m	a	0	1		yes	r	no		1	1	1	1	1	1	1	1	r	r		CROP active; molt arrested; Likely bird on near nest
188	15-Sep-07	258	m	a	1	2		yes	r	yes		1	1	1	1	1	0.6	0.2	r	r	r	5.8	CROP not active
187	15-Sep-07	258	m	a	2	2		yes	r	yes	1 & 10	1	1	1	1	1	1	0.8	r	0	0.9	7.7	CROP not active; P1-6 newish, suggesting P7 is nodal
	15-Sep-10	258		a	1	1			CSW 8883	yes		1	1	1	1	1	1	1	0.3	0	0	7.3	
	15-Sep-10	258		a	1	1			CSW 8882	yes		1	1	1	1	1	1	1	0.7	0	0	7.7	Data for these 6 are in Ads w P molt
	17-Sep-10	260		a	1	1			CSW 9493	yes		1	1	1	1	1	1	1	1	0.5	0	8.5	
191	22-Sep-07	265	m	a	1	1			r	yes		1	1	1	1	1	1	1	0.7	0	0	7.7	
190	23-Sep-07	266	m	a	1	1			r	yes		1	1	1	1	1	1	0.7	0	0	0	6.7	CROP not active
189	23-Sep-07	266	m	a	1	1			r	yes		1	1	1	1	1	1	0.8	0	0	0	6.8	
31	########	150	m	j	1	1			90693	yes		0.7	0.1	J	J	J	J	J	J	J	J	0.8	bursa 6x5l T 3x2; crop inactive; first wing of 2
208	1-Jun-11	152		j	1	1			r	yes		1	1	0.7	0.15	J	J	J	J	J	J	2.85	S molt recorded
210	6-Jun-11	157		j	1	1			r	yes		0.5	0.1	J	J	J	J	J	J	J	J	0.6	No note on S molt
211	7-Jun-11	158		j	1	1			r	yes		0.9	0.1	J	J	J	J	J	J	J	J	1	No note on S molt
39	11-Jun-11	162	f	j	2	2			91231	yes		1	0.95	0.2	J	J	J	0.6	1	1	1	5.75	smooth ovary; bursa6x5; molt asymmetrical, but 2 waves in both wings
35	20-Jun-11	171	m	j	1	1			90783	yes		1	0.8	0.4	0.1	J	J	J	J	J	J	2.3	3x1.5; bursa 6x6; first wing of 2
21	12-Jul-06	193	m	j	0	1			82702	no	arrested?	1	1	1	1	r	r	r	r	r	r		Crop not thickened or producing milk; shape, extreme wear and fainl partial fringing suggest outters are J
23	15-Jul-07	196	?	j	1	1			84027	yes		0.1	J	J	J	J	J	J	J	J	J	0.1	bursa 8x4; no S molt
126	15-Jul-07	196		j	1	1			r	yes		0.8	0.6	J	J	J	J	J	J	J	J	1.4	No S molt
128	15-Jul-07	196		j	1	1			r	yes		0.99	0.4	0.3	J	J	J	J	J	J	J	1.69	in with female
130	15-Jul-07	196		j	1	1			r	yes		1	0.95	0.8	0.6	0.2	J	J	J	J	J	3.55	
62	18-Jul-06	199		j	1	1			r	yes		0.4	0.01	J	J	J	J	J	J	J	J	0.41	Note on this record that we need to start looking at them carefully!
146	19-Jul-07	200		j	1	1			r	yes		1	1	0.7	0.1	J	J	J	J	J	J	2.8	S1-11 = J
147	19-Jul-07	200	f	j	1	1			r	yes		1	1	1	1	1	1	0.5	0	0	0	6.5	Old juv with a couple of fringed S coverets; S molt recorded; crop inactive
148	19-Jul-07	200	f	j	1	1			r	yes	P9-10 0 or J	1	1	1	1	1	1	1	0.9	0	0	7.9	Old juv, fringed S cvts; S molt recorded; crop inactive
8	29-Jul-05	210	m	j	1	1			81473	yes		1	1	1	1	0.9	0.5	J	J	J	J	5.4	L8x3; bursa6x6
12	1-Aug-06	213	?	j	1	1			82405	yes		0.2	J	J	J	J	J	J	J	J	J	0.2	busa 7x5
14	1-Aug-06	213	f	j	2	1			82606	yes		1	1	1	1	0.1	1	0.3	rJ	0J	0J	5.4	P5 lost accidentally? oviduct convuleted; crop gland active; apparently a juv breeding in its summer of hatch
15	2-Aug-06	214	f	j	2	2			82608	yes	contradicts P1 initiation until in distal part of wing, adult?	0.4	0.1	1	1	0.8	0.1	J	J	J	J	3.4	B 6x5; crop vascularized, but not producing milk; ODD distal Ps with J fringing
25	2-Aug-09	214	f	j	1	1			88931	yes	0 or J	1	1	1	1	1	1	0.8	0.01	0	0J	6.81	bursa 7x4; many S growing simultaneously likely some catostrophy; crop not active
197	11-Aug-09	223	m	j	1	1			r	yes	0 or J	1	1	1	1	0.95	0.5	0	0	0	0	5.45	S molt recorded S2-7 fringed = juv?
27	13-Aug-09	225	f	j	3	2			89025	yes	P3-P5 0 or J, arrested as early breeding, probably adult	0.6	0.1	0	0	0	0.2	1	0.8	0.1	0J	2.8	ODD bird; molting S; very fat; field molt score wrong
201	13-Aug-09	225		j	0	0			r	None in wi	all Ps should be J												
87	4-Sep-06	247		j	1	1			r	yes	P5-10 0 or J, should be adult?	0.9	0.6	0.4	0.1	0	0	0	0	0	0	2	
19	4-Sep-06	247	f	j	1	1			82693	yes		0.99	0.6	0.4	0.1	J	J	J	J	J	J	2.09	B 5x4
82	4-Sep-06	247	?	j	1	1			r	yes		0.99	0.6	0.5	0.3	J	J	J	J	J	J	2.39	
84	4-Sep-06	247	?	j	1	1			r	yes		0.99	0.99	0.8	0.7	0.4	0.01	J	J	J	J	3.89	
18	4-Sep-06	247	m	j	1	1			82692	yes		1	0.99	0.8	0.7	0.3	0.2	J	J	J	J	3.99	L 4x2; B 5x4; SV 4x3 tubules visible
100	5-Sep-06	248		j	1	1			r	yes		0.8	0.3	J	J	J	J	J	J	J	J	1.1	20mm scored as .3
97	5-Sep-06	248	?	j	1	1			yes	yes	P10 0 or J	1	1	1	1	1	1	0.95	0.7	0.05	0	7.7	
104	6-Sep-06	249		j	1	1			r	yes		0.6	0.2	0.01	J	J	J	J	J	J	J	0.81	
106	6-Sep-06	249		j	1	1			r	yes		1	0.8	0.3	0.01	J	J	J	J	J	J	2.11	
158	9-Sep-07	252	f?	j	1	1			r	yes		1	1	0.6	0.3	J	J	J	J	J	J	2.9	Marco
157	9-Sep-07	252	f	j	1	1			r	yes	P9-10 0 or J	1	1	1	1	1	1	0.9	0.2	0	0	7.1	Marco

165	10-Sep-07	253	f	j	1	1		r	yes		1	1	1	1	1	0.7	J	J	J	J	5.7	Marco
168	10-Sep-07	253	f	j	1	1		r	yes		1	1	1	1	1	0.95	0.2	J	J	J	6.15	Marco
167	10-Sep-07	253	m	j	1	1		r	yes		1	1	1	1	1	1	0.3	J	J	J	6.3	Marco: age contradiction
163	10-Sep-07	253	f	j	1	1		r	yes		1	1	1	1	1	1	0.6	J	J	J	6.6	Marco
169	10-Sep-07	253	f	j	1	1		r	yes		1	1	1	1	1	1	1	0.3	J	J	7.3	
164	10-Sep-07	253	m	j	1	1		r	yes		1	1	1	1	1	1	1	0.8	J	J	7.8	Marco
170	10-Sep-07	253	m	j	1	1		r	yes		1	1	1	1	1	1	1	1	1	0.85	9.85	
166	10-Sep-07	253	f	j	1	1		r	yes		1	1	1	1	1	1	1	1	1	0.9	9.9	Marco
173	11-Sep-07	254		j	1	1		r	yes		1	1	1	1	1	0.9	0.1	J	J	J	6	
175	11-Sep-07	254	f	j	1	1		r	yes	P10 0 or J	1	1	1	1	1	1	1	1	0.4	0	8.4	Marco
						*numbers in red added by reviewer for numbers check																

Series is the sequence of data entry, matching the date ssequence in the field notes, except for the collected specimens run spell check on data table, complete field notes so the are meaningful to a non-bird person

87 wrong age? if all Ps are 0, should be J

typo - ssequence in end note

typo - dammaged type P10 and 0ne of 2 inners growing; both wings too dammaged to determine what feather, but two active waves

Clarify - 71, 72 were not aged or primaries were not aged? looking at comment on 209, 212 were not aged, note typo "nor" for "not"

71	21-Aug-06	233		a	0				r	no molt													not aged
72	21-Aug-06	233		a	0				r	no molt													not aged
209	1-Jun-11	152	m	a	0				r	no molt													P ages nor recorded
212	8-Jun-11	159	f	a	0				r	no molt													P ages nor recorded

bursa 6x5l should be 6x5 mm??

31	30-May-11	150	m	j	1	1			90693	yes	0.7	0.1	J	J	J	J	J	J	J	J	1		bursa 6x5l T 3x2; crop inactive; first wing of 2

typo convoluted

14	1-Aug-06	213	f	j	2	1			82606	yes	1	1	1	1	0	1	0.3	rJ	0J	0J	5		P5 lost accidentally? oviduct convuleted; crop gland active; apparently a juv breeding in its summer of hatch

no score for #201 but has to be J for all Ps if newly fledged?

201	13-Aug-09	225		j	0				r	None in wing must be newly fledged													

type - Col G heading typo, should be inferred

in scoring juvenile primaries, all primaries would be J unless replaced then a 1 (=new), r presumably is "ragged", unclear why some are scored as 0 (=old). Juvy primaries are held such a short time these would have to be SY birds or mis-aged adults

147	19-Jul-07	200	f	j	1	1			r	yes		1	1	1	1	1	1	0.5	0	0	0	6.5	Old juv with a couple of fringed S coverets; S molt recorded; crop inactive
148	19-Jul-07	200	f	j	1	1			r	yes	P9-10 0 or J	1	1	1	1	1	1	1	0.9	0	0	7.9	Old juv, fringed S cvts; S molt recorded; crop inactive
197	11-Aug-09	223	m	j	1	1			r	yes	0 or J	1	1	1	1	1	0.5	0	0	0	0	5.45	S molt recorded S2-7 fringed = juv?
87	4-Sep-06	247		j	1	1			r	yes	P5-10 0 or J, should be adult ?	0.9	1	0	0	0	0	0	0	0	0	2	
97	5-Sep-06	248	?	j	1	1			yes	yes	P10 0 or J	1	1	1	1	1	1	0.95	0.7	0	0	7.7	
157	9-Sep-07	252	f	j	1	1			r	yes	P9-10 0 or J	1	1	1	1	1	1	0.9	0.2	0	0	7.1	Marco
175	11-Sep-07	254	f	j	1	1			r	yes	P10 0 or J	1	1	1	1	1	1	1	1	0	0	8.4	Marco
37	17-Jun-11	168	f	a	1	2	2	yes	90871	no	ated, b	0.01	1	1	r	r	r	r	0	0	0	2.01	2 small rupt follicles; crop glands inactive Red marks birds known to be breeding other than by crop: f with rupt follicles; bird from a nest

newer than new (=1), explain scoring

85	4-Sep-06	247	m	a	0	1	1		r	no	than n	1	1	1	1	1	1	newer	newer	0	0	6	
96	5-Sep-06	248	m	a	0	1			r	no		1	1	1	1	1	1	1	1	0	0		
88	5-Sep-06	248	m	a	0	1	1		r	no	than n	1	1	1	1	1	newer	0	0	0	0		
107	6-Sep-06	249	m	a	0	2	1		r	no	than n	1	1	1	1	1	newer	newer	0	0	0		

standardize column K "P Molt?, for no molt now has no molt, no, none, & none in wing must be newly fledged

comment seems questionable. P1-5 are 1 (=new) and older than P8-10 (=0 or old) then if an arrest P1-5 would be 0, P6 must be a 1 but newer than P5

20	5-Sep-06	248	m	a	1	1	1		82696	yes		1	1	1	1	1	newer	0.1	0	0	0	5.1	molt symmetrical; the 5/6 arrest is clear; R10x5 no bursa; two wings.

both wings included? Older is older than 0 (old)

98	5-Sep-06	248	f	a	1	3			r	yes		1	1	olde	olde	olde	1	0.4	0	0	1	4.4	same bird, Left wing
99	5-Sep-06	248	f	a	2	2			r	yes		1	1	1	1	1	1	1	0.3	0	1	8.1	same bird, Right wing