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

Sievert Rohwer [Corresp., 1], **Vanya G Rohwer** [2]

[1] Burke Museum of Natural History and Culture and Department of Biology, University of Washington, Seattle, Washington, United States of America

[2] Museum of Vertebrates, Cornell University, Ithaca, New York, United States of America

Corresponding Author: Sievert Rohwer
Email address: rohwer@uw.edu

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 extensively overlap molt and breeding, usually grow just a single primary 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, initiation of an inner wave was most frequently observed once the outer wave had reached P10. 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 a serious flaw in stepwise molting in large birds (Rohwer 1999).

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

3 Sievert Rohwer[1] and Vanya G. Rohwer[2]

4 [1]Department of Biology and Burke Museum of Natural History and Culture, University of
5 Washington, Seattle, Washington, 98195, USA

6 [2]Cornell University Museum of Vertebrates, 159 Sapsucker Woods Road, Ithaca, New York,
7 14850, USA

8 Corresponding author:

9 Sievert Rohwer

10 Email address: rohwer@uw.edu

11   *Abstract*: For adult Common Ground Doves from Sinaloa we demonstrate that the primaries are

12   a single molt series, which sometimes feature two (in one case three) waves of feather

13   replacement. Such stepwise primary replacement is found in many large birds but, at 40g, this

14   dove is much the smallest species reported to have multiple waves of replacement proceeding

15   through its primaries simultaneously. Pre-breeding juvenile Common Ground Doves never

16   feature two waves of primary replacement. Juveniles usually have more than 2 adjacent

17   feathers growing simultaneously and replace their primaries in about 100 days. In contrast

18   adults, which extensively overlap molt and breeding, usually grow just a single primary at a time,

19   and require at least 145 days to replace their primaries. Molt arrests are thought to drive the

20   generation of new waves of primary replacement in a diversity of large birds. For adult Common

21   Ground Doves, we found molt arrests to be strongly associated with active crop glands,

22   suggesting that the demands of parental care cause arrests in primary replacement in this dove.

23   For those adults with two primary molt waves, initiation of an inner wave was most frequently

24   observed once the outer wave had reached P10. Thus, unlike reports for large birds, Common

25   Ground Doves usually suppress the initiation of a new wave of molt starting at P1 when the

26   preceding wave arrests before reaching the distal primaries. This assures that relatively fresh

27   inner primaries are not replaced redundantly, overcoming a serious flaw in stepwise molting in

28   large birds (Rohwer 1999).

29   INTRODUCTION

30   In large birds that fly while molting the primaries are often replaced in multiple waves that

31   proceed simultaneously through these longest feathers of the wing. Two mechanisms can

32   generate these waves. In several orders of large birds, the primaries constitute a single molt

33   series, but multiple waves of primary replacement are generated by molt arrests. Following

34   arrests, molt is re-initiated at the next feather to be replaced in molt waves that have not

35   reached the distal-most primary and also at P1, the first feather of the primary molt series in

36   most birds. Thus, depending on the history of arrests and molt progression, large species that

37   fly while molting may have from one to four waves of replacement proceeding simultaneously

38   through the primaries (Rohwer 1999). This is known as *stafflemauser*, or stepwise molt

39   (Stresemann and Stresemann. 1966), and has been documented in pelicaniforms (Dorward

40   1962, Rasmussen 1988), large herons (Shugart and Rohwer 1995), accipitriforms (Edelstam

41   1984, Pyle 2005), and New World vultures (Snyder et al. 1987), among other groups. Multiple

42   waves of primary replacement are also achieved by dividing the primaries into two or more molt

43   series. Multiple replacement series differ from stepwise molt in that they start and, with

44   complete replacement, also stop, at predictable feathers within the wing. For large birds

45   multiple molt series in the primaries has been well documented in albatrosses (Langston and

46   Rohwer 1995, Rohwer et al. 2011) and in Falconiforms and Psittaciformes (Pyle 2013); multiple

47   molt series are also found in some kingfishers (Douthwaite 1971, Hamner 1980), cuckoos

48   (Rohwer and Broms 2013), and a bell bird (Marini and Silveira 2012).

49   At least in large birds, multiple waves of feather replacement in the primaries seem to facilitate

50   more frequent replacement of the primaries because primaries may be growing at several loci

51   that are separated by fully grown feathers. Some adaptation to increase the number of feathers

52   grown simultaneously without creating large molt gaps in the wing is intuitively sensible because

53   the time required to replace the primaries increases exponentially with body size and many

54   birds over 1kg do not replace all their primaries annually (Rohwer et al. 2009). In small birds for

55   which the rules of primary replacement have been established, the primaries usually constitute

56   as a single replacement series that are replaced in a single wave in a single bout of molting,

57   without arrests. However, at least some small doves (Pyle et al. 2016; personal observation) and

58   the Mustached Tree Swift (*Hemiprocne mystacea*) exhibit stepwise primary replacement

59   (Rohwer and Wang 2010). Stepwise primary replacement is surprising in these species because

60   they seem small enough to be able to complete primary replacement in a single bout of molting

61   (Rohwer et al. 2008). What seems special about them is their extensive overlap in molt and

62   breeding (Rohwer and Wang 2010).

63   While arrests and the re-initiation of molt are documented to drive the generation of multiple

64   waves of primary replacement in large birds (Rohwer 1999), they are only suggested for small

65   species. In Mustached Tree Swifts of the New Guinea region, which breed and molt year-round,

66   primary replacement is stepwise, and the generation of multiple molt waves have been

67   suggested to be associated with arrests caused by the demands of feeding young; however,

68   evidence for this interpretation is lacking (Rohwer and Wang 2010). Nonetheless, arrests

69   associated with demanding periods of parental care could prove to be a general mechanism for

70   generating multiple waves of primary replacement in small birds that show extensive overlap in

71   molt and breeding. In contrast, reorganizing the primaries into multiple molt series would seem

72   to be a more improbable evolutionary transition than the development of stepwise molting, so

73   multiple series in the primaries may not characterize many groups of small birds.

74   We recently observed multiple waves of primary replacement in Common Ground Doves

75   (*Columbina passerina*) from northwest Mexico. Here we quantitatively summarize their primary

76   replacement to address two questions: 1) Do Common Ground Doves have stepwise primary

77   molt or have they broken the primaries into multiple series? and 2) Is breeding activity

78   associated with arrests in primary molt, thus making arrests a possible mechanism for

79   generating multiple waves of feather replacement in this small dove?

80   Distinguishing between stepwise primary replacement and having the primaries divided into

81   multiple molt series can be non-intuitive from "snap-shot" data gathered from many individuals

82   across the molting period (Rohwer 2008). Yet, the distinction is essential for understanding

83   evolutionary transitions in primary replacement strategies across birds. The key is to understand

84   that stepwise replacement is characterized by incomplete primary molts of unpredictable

85   extent, with the result that, in the next episode of molting where molt reinitiates in the

86   primaries distal to P1 varies across individuals. In contrast, the evolution of multiple molt series

87   in the primaries seems designed to generate complete primary replacement by dividing the

88   primaries into two or more short blocks of feathers, each of which is fully replaced in the same

89   short period of time during a single bout of molting (Rohwer and Broms 2011).

90   If Common Ground Doves have stepwise primary replacement, then three predictions should

91   refute the hypothesis that the primaries are organized into multiple molt series. First, in

92   stepwise molters, primary replacement should often be incomplete in a single bout of molting

93   but rarely or never so in species with multiple molt series in the primaries. Second, in stepwise

94   molters, juveniles undergoing their first bout of primary molt should possess only a single wave

95   of feather replacement beginning at P1 while in species with multiple molt series in the

96   primaries, juveniles molting for the first time should, like adults, initiate primary replacement at

97   two or more fixed loci. Third, in adults of species that are stepwise molters, P1 will dominate as

98   a site of molt initiation, but other sites of initiation will be scattered throughout the primaries,

99   marking places where molt was reinitiated following an arrest. In contrast, when the primaries

100   are organized into multiple series, molt will be initiated at a few consistent sites in the primaries,

101   all with about equal frequency in composite summaries of "snap-shot" data (Rohwer and Broms

102   2011).

103   We use data from 180 common ground doves from coastal Sinaloa, Mexico to describe their

104   primary replacement rules. We document strong differences in the intensity of molt between

105   juveniles and adults, show that molt can be stepwise in breeding adults, and provide the first

106   evidence that arrests associated with parental care may be responsible for the generation of

107   multiple waves of primary replacement in a small bird. Common Ground Doves, like other

108   Columbiformes, regurgitate "crop milk", a liquid food consisting of protein, water and fat to their

109   young, and the production of crop milk allowed us to assess how feeding young is associated

110   with molt in breeding adults. Our results clearly show that this small dove overlaps molt and

111   breeding more or less completely, can replace its primaries completely during the breeding

112   season, and has evolved a mechanism to suppress the initiation of new waves of primary

113   replacement at P1 until the preceding wave has reached the distal primaries. This discovery

114   resolves an unexplained paradox in the Mustached Tree Swift (Rohwer and Wang 2010), which,

115   very likely, also has a mechanism for suppressing the immediate generation of new molt waves

116   at P1 when the inner primaries are little worn.

117   METHODS

118   Common Ground Doves are largely resident birds, with a range extending from the southern

119   United States through Central America, across northern South America, and throughout the

120   West Indies (Bowman 2002). They are among the smallest doves, with a mass of about 40

121   grams (UWBM specimens from Sinaloa). Breeding in juveniles can occur when they are about 6

122   months old (Johnston 1962; Passmore 1984); we also confirmed breeding by three birds in

123   partial juvenile plumage that were likely less than 6 months old. They do not defend territories

124   and exhibit little aggression (Nicholson 1937). Because the bursa of Fabricus is resorbed under

125   the influence of sex steroids (Mase and Oishi 1991), and because sex steroids are associated

126   with aggressive behavior, the very limited aggression reported for Common Ground Doves may

127   explain why they are slow to resorb the bursa and, thus, why both males and females in

128   breeding condition often retain glandular bursas.

129   We studied Common Ground Doves on various communes in the Rio Fuerte flood plain between

130   Los Mochis on the coast and El Fuerte near the foothills of the Sierra Madre Occidental in

131   Sinaloa, Mexico. Prior to the development of massive irrigation, this region of coastal northwest

132   Mexico was largely deciduous thorn scrub that leafed out in late summer with the arrival of the

133   monsoon rains, but lost its leaves in November after the monsoons had ceased by the end of

134   September. Even with massive conversion to irrigated agriculture (Rohwer et al. 2015), ground

135   doves nesting here are exposed to intense solar radiation while foraging and often while on their

136   nests; thus, their feathers are subject to rapid fading from sunlight, as well as wear from the

137   hard and thorny vegetation they use for nesting.   This rapid fading and wear of new feathers

138   enabled us to recognize blocks of newer and older feathers that were undoubtedly less than a

139   year's difference in age.

140   Molt scoring and the analysis of the rules of primary replacement followed Rohwer (2008).

141   Growing primaries were given fractional scores representing, to the nearest tenth, their length

142   as fully-grown feathers. New feathers were scored as 1 and old feathers as 0, but it is important

143   to note that these age assignments are unlikely to be year classes in this data set; instead they

144   represent activation classes of molt separated by unknown time intervals that likely were on the

145   order of a few months. Where blocks of adjacent feathers represented different replacement

146   classes, they were distinguished as newer or older than adjacent blocks. Rarely, adjacent groups

147   of primaries were extremely worn and faded and assigned a score of ragged; these were likely

148   feathers approaching a year of use that had been retained through the non-breeding season.

149   The total molt score for a bird was the sum of the values for its growing and new or newer

150   primaries. When molt scores from many individuals are summarized in tables, nodal feathers

151   mark loci in the primaries where molt is initiated, either with the commencement of the annual

152   molt or following arrests. In species with stepwise primary replacement and in species with the

153   primaries organized into multiple molt series, stable nodes predominate in summary tables

154   based on snap-shots of the molt status of many individuals; however, in stepwise molters,

155   transient nodes, which mark sites where molt was reinitiated following an arrest, will be

156   recorded at lower frequencies at unpredictable sites distal to P1 where molt restarted after an

157   arrest.

158   We assessed breeding activity of doves that were captured and released by the presences or

159   absence of crop-milk; for doves that were prepared as specimens, we noted the condition of the

160   glands inside the crop, where vascularized crops with thickened walls indicated active milk

161   production. We also recorded dates for a number of nests with eggs or young.

162   We have restricted all of our analyses to observations we made in coastal Sinaloa from 2005

163   through 2011, during the months of May through September. Most of our field work in Sinaloa

164   was designed to study molt migrants (e. g. V. Rohwer et al. 2009, S. Rohwer et al. 2007, 2015, S.

165   Rohwer 2013); consequently, we have scored molt for only 15 birds for the months of May and

166   June, but many for the months of July through September. Some doves were collected and

167   many more were scored for primary replacement before being released when work on other

168   projects was slow. Time constraints, and not the condition of the bird, dictated whether birds

169   were either collected or scored for molt and released; thus, our data should be an unbiased

170   representation of the birds that we caught, even though our samples were obviously not

171   collected systematically throughout the season. The number of birds scored for molt offers a

172   good index of the relative amount of time we spent in the field in these months.

173   The approximately 40 ground doves that were collected were particularly important because

174   they had associated extended wings that were used to measure both primary length and

175   primary growth rates. Growth bands could not be seen in juvenile primaries; further, they were

176   faint and difficult to see in most primaries of most adults and could not have been measured on

177   specimens with folded wings. As part of our other studies of molt-migrants, we also collected or

178   scored for molt a smaller sample of Common Ground Doves in Arizona; however, these birds

179   were excluded from this study so possible geographic variation in the phenology of molting and

180   breeding of this resident bird would not confound our results. Our Arizona observations were

181   important, however, in demonstrating breeding by juveniles and multiple waves of primary

182   replacement in adults.

183 Field work for this project was approved by the University of Washington Institutional Animal

184 Care and Use Committee (protocol 4309-01). Collecting for this project was conducted under

185 scientific collection permits issued by the Secretaría de Medio Ambiente y Recursos Naturales

186 (SEMARNAT) to the Facultad de Ciencias (B. Hernández-Baños FAUT 0169) of UNAM.

187   RESULTS

188 **Primary replacement rules for juveniles.**

189 Most of the 44 juveniles that we captured and scored for molt were replacing primaries,

190 suggesting that they likely begin this molt shortly after fledging (Table 1). Of the 44 juveniles we

191 scored, just one had not yet commenced flight feather replacement and retained all juvenile

192 primaries and secondaries, and one other had either arrested molt at P4, or was replacing

193 primaries so slowly that active molt was scored as an arrest. Four juveniles were omitted from

194 our count of 42 that were molting because they had two waves of molt; at least two of these

195 were precocious breeders and the other two were uninterpretable. We spent little time in the

196 field in May and June, so the low numbers of juveniles scored in these months does not imply

197 the production of few young during that time.

198 Without exception, juveniles replaced their primaries distally, starting at P1 (Table 2). P1 was

199 strongly nodal and no other primary in our sample of 42 molting juveniles received a score of

200 nodal, suggesting that arrests in the replacement of the juvenile primaries did not occur during

201 the months of our field work. However, some late-fledged juveniles may be unable to complete

202 their first primary molt, and these birds could be adding to the numbers of adults recorded as

203 having multiple waves of primary replacement if we captured them in their second year. Our

204 sample includes many more juveniles replacing inner than outer primaries, but good samples of

205 juvenile ground doves growing primaries were available for all primaries except P8 and P9 (Table

206 2). Having samples for these distal most feathers requires recognizing remnants of juvenile

207 feathers in other parts of the body, which we likely failed to do in some cases; this means that

208 our sample of adults likely contains some older juveniles that were not recognized as such in the

209 field. This problem suggests that the percentage of adults with multiple waves of primary

210 replacement was underestimated.

211 **Primary replacement rules for adults.**

212 Primary replacement in adult Common Ground Doves is considerably more complex than it is in

213 juveniles (Table 3). Of the 126 adults we scored for molt, 108 (86 percent) were replacing

214 primaries; 5 of the 18 remaining adults had adjacent blocks of newer and more worn primaries

215 in their wings, suggesting that they had arrested primary replacement. Just 17% of the adults

216 that were growing primaries had two separate waves of molt. However, multiple waves of

217 primary replacement are more common in adults than this figure suggests because some adults

218 with arrested molt had two groups of newer primaries that were separated by one to several

219 older primaries. These non-molting adults clearly had had two waves of primary replacement;

220 when they are added to those with two active waves of molt, at least 21% of adults can be

221 inferred to have been replacing their primaries in two waves.

222 Reviewers of this paper observed that the relatively limited numbers of adult Common Ground

223 Doves with multiple molt waves suggests that adults showing two active molt waves could be

224 late-fledged juveniles from the preceding year that were unable to complete replacement of

225 their juvenile primaries. If this were the case, adults with multiple waves should be more

226 frequent early than late in the breeding season, but there was no evidence of a seasonal decline

227 in the frequency of adults showing two active waves of primary replacement (X^2 = 2.37; p =

228 0.498; Table 4, May and June poled).

229 As in juveniles, the direction of primary replacement is strongly distal in adults, with no cases of

230 proximal replacement between any of the interior primary pairs (Table 5). However, molt arrests

231 in adults complicate scoring of directionality. Thus, directionality scores between P1 and P2

232 were distal in 6 adults, but proximal in 4. These 4 proximal scores are almost certainly scoring

233 artifacts caused by P1 being too short to be compared for wear and fading with its adjacent

234 inner primaries. Recall that feathers scored as new are relatively fresh, and thought to have

235 been grown in that season and, further, that most cases of adjacent newer and older primaries

236 probably do not represent year-class differences in feather age because molt arrests are

237 common (see below). Thus, if P1 was growing, but too short to compare with P2 in its color and

238 freshness, then, the inferred direction of replacement between P1 and P2 will be proximal when

239   P2 is also scored as fresh. However, if we had been able to determine that P1 was newer than

240   P2, directionality between this feather pair would have been scored as distal. All four of the

241   anomalous directional scores between P1 and P2 were cases where P1 was a pin feather or a

242   short brush just emerging from its sheath; thus, none of these 4 cases legitimately imply

243   proximal replacement between P2 and P1 because the age of P1 could not be assessed by

244   feather color. Further, we saw no evidence of P1 and the outer series of secondaries being part

245   of a single molt series (unpublished data).

246   A similar problem arises with arrests at P9. When molt is reinitiated at P10 and the feather(s)

247   immediately proximal to it are scored as old, then, by definition, the inferred direction of

248   replacement between P9 and P10 is proximal, readily accounting for the 6 proximal

249   directionality scores between P9 and P10 as artifacts of arrests (Table 5). In contrast, the 14

250   distal directionality scores between P9 and P10 are unambiguous. Summarizing, all of the

251   proximal directionality scores between primary pairs P1/P2 and P9/P10 can be interpreted as

252   scoring artifacts of the frequent arrests that characterize primary replacement in adult Common

253   Ground Doves; directionality between interior primary pairs was exclusively distal.

254   Unlike the situation in large birds, scattering of nodal and terminal feathers from P6 to P9 does

255   not only reflect the generation of multiple waves, but also the locations of arrested molts (Table

256   5). Nodal feathers mark the beginning of waves of replacement in the outer primaries.

257   However, they can only be recognized as nodal when an arrest has been long enough that the

258   feathers replaced in the preceding bout of molt have accumulated noticeable wear or fading.

259   Then, the primary at which a molt wave is re-activated will be newer than its proximal neighbor

260   and thus be scored as nodal. That the recognition of nodes in the distal primaries requires

261   arrests of sufficient duration to recognize older feathers surely means that our data

262   underestimates the number of adults inferred to have arrested primary replacement. The same

263   scoring problem arises when a proximal wave of replacement extends into older feathers from a

264   previous arrest. In these cases the distal-most growing feather in the proximal wave of active

265   molt will be scored as terminal because both of its neighboring feathers will be older than it is.

266   To reiterate, the scattering of feathers scored as nodal or terminal in the distal primaries

267   confirms, but likely under-represents the frequency of arrested waves of primary replacement in

268   ground doves from Sinaloa.

269   Data linking breeding attempts with arrests in primary molt in adults is shown in Table 6 where

270   we compare crop gland activity with primary replacement. Many adults that were replacing

271   primaries had active crop glands, so molt is not always arrested when young are being fed (Table

272   6). Nonetheless, arrested primary replacement was strongly associated with having an active

273   crop gland (2-tailed Fisher's exact p = 0.002), suggesting that adults providing crop milk to young

274   may arrest their molt to conserve energy. In large birds with stepwise primary replacement,

275   these arrests are thought to generate multiple waves of primary molt. When primary

276   replacement reinitiates, it picks up where it left off in the distal primaries and also starts anew at

277   P1, thus generating two or more waves of primary replacement.

278   Common Ground Doves stand in striking contrast to this understanding of stepwise primary

279   replacement in large birds. As we show in Figure 1, most arrests do not result in the generation

280   of a new wave of primary replacement at P1 when molt is resumed. Instead, new waves of molt

281   are not initiated in the inner primaries until the prior replacement wave has reached P10, or

282   sometimes P9 (Figure 1).

283   To show this we have used three common patterns of primary scores. First are birds showing

284   blocks of new feathers in the inner primaries (the outermost of which may be growing), and old

285   feathers in the outer primaries, characteristic of a single wave of primary molt. For these cases,

286   the outermost new or growing primary was plotted, giving the blue line in Figure 1. This line

287   shows that new waves are seldom initiated until molt has reached distal primaries P9 and P10.

288   All lines in this figure start with P3 because primary replacement had to have progressed far

289   enough into the wing for a block of new inner primaries to be discernable. In contrast, multiple

290   waves are represented by blocks of new or growing feathers in the inner and outer primaries,

291   separated by a block of old feathers in the middle primaries; in this case we plotted the

292   outermost new or growing primary (Figure 1, black line). This black line clearly shows that

293   blocks of new inner primaries are rarely seen until molt in the distal block of new primaries has

294   reached P9 (just 3 cases) or P10 (19 cases). Together, the contrasts between the blue and black

295   lines strongly suggest that inner waves are suppressed, even if there are arrests, until primary

296   replacement has reached the outermost primary. Finally, the orange line confirms this

297   conclusion because it represents cases where molt could be seen to have been arrested in the

298   inner primaries (a block of new feathers) and restarted (a block of *newer* middle primaries),

299   while the outer primaries were scored as old. In this case, we plot the location of the arrests,

300   which we scored as the break between the inner new and outer *newer* feathers, and not the

301   outer most growing primary. This line is important because, while surely underestimating the

302   frequency of arrests (because new and *newer* blocks of feathers were not always distinguished),

303   it clearly illustrates primary replacement can arrests and restart from P5 to P7 without a new

304   molt wave initiating at P1. The take-home message of Figure 1 is that arrests in primary

305   replacement do not initiate new waves of replacement at inner primaries unless molt has

306   proceeded to the distal-most primaries.

307   **Molt breeding overlap and molt duration.**

308   Our records suggest that primary molt and breeding overlap extensively in Common Ground

309   Doves in Sinaloa (Table 4). We found nests and birds with active crop glands from May through

310   September and more than 50% of adults examined were molting in all of these months except

311   May (Table 4). The long breeding season and the extensive overlap of molt and breeding in

312   adult ground doves suggests that there should be little relation between day of year and primary

313   molt score for adults. When all the data are plotted (Figure 2), there is a significantly positive

314   trend (slope = 8.06, p < 0.0001; r^2 = 0.27), with replacement of the primaries being closer to

315   completion in September, which is likely near the end of the breeding season. This does suggest

316   that molt is scheduled to replace all primaries during the breeding season. It is critical to note,

317   however, that the distribution of points strongly suggests that the data is largely a composite of

318   two lines that are almost flat, representing the months of July and September when many adults

319   were scored for molt. This is indeed the theoretical expectation when some birds are

320   completing molt as others are just beginning (Rohwer and Broms 2012, Rohwer 2013). Thus, the

321   presence of two "flat" regression lines in Figure 2 is evidence that, as in other species, where

322   molt is little synchronized among individuals in a population, neither regression nor maximum

323   likelihood estimates of molt duration are reliable. Almost "flat" lines in Pimm regression plots

324   suggest extremely rapid molts, something that ground doves do not do. Such "flat" regression

325   lines likely characterize many species that show extensive overlap in molt and breeding, and

326   they also occur when some individuals have completed primary replacement before others have

327   started, as is true in Painted Buntings, *Passerina ciris* (Rohwer 2013).

328   Following Rohwer and Broms (2012), we estimated the time required to replace the 10 primaries

329   in adult Common Ground Doves from the summed length of the primaries, primary growth rate,

330   and the number of primaries growing simultaneously. Our measurements for primary lengths

331   and growth rates are summarized in Table 7. For birds in active molt, the mean number of

332   primaries growing was 1.62 for adults and 2.52 for juveniles (weighted averages computed from

333   data in Table 3). Assuming no interruptions in the molt, which of course is not true in adults, but

334   the rule for juveniles, the number of days (D) required to replace all the primaries is

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

336   where L is the summed length of the 10 primaries, G is primary growth rate measured in mm/d,

337   and N is the mean number of primaries growing simultaneously. Using this equation, adult

338   males are estimated to require 149 days to replace their primaries, adult females 145 days, and

339   juveniles 101 days. Because birds were breeding during the extent of our field work from May

340   through September, we do not know how much time they have to spend in molt. Nonetheless,

341   these figures suggest that adults could replace all their primaries in less than the 5 months when

342   we know they are breeding, so most adults should be able to complete their molt while they

343   breeding, even with arrests during intense periods of parental care. Juveniles take considerably

344   less time to molt but, if foraging is difficult during the dry months of winter, late-fledged

345   juveniles may not be able to replace all their primaries before their first breeding season.

346   DISCUSSION

347   We show that the primaries of Common Ground Doves constitute a single molt series and are

348   replaced distally from P1 to P10. In contrast to juveniles, adults often had two active waves of

349   primary replacement and they usually had just one feather growing per wave. Molt arrests are

350   thought to be the mechanism by which multiple waves of primary replacement develop in large

351   birds (Rohwer 1999). Although, we document that molt arrests in adult Common Ground Doves

352   are strongly associated with active crop glands, indicative of adults feeding young, arrests in

353   primary replacement seem not to result in a new wave of molt starting at P1 unless earlier bouts

354   of primary replacement have reached P9 or P10. Juveniles replace their primaries in a single

355   wave that starts at P1 and no juvenile had two waves of primary replacement, unless they were

356   breeding precociously, as rarely occurs in this species (Johnston 1962, Passmore 1984). Stepwise

357   primary replacement is common in large birds, but this represents only the second well

358   documented case of stepwise molting in a small bird, the other being the Mustached Tree Swift

359   (Rohwer and Wang 2010). At 40 grams, Common Ground Doves are the smallest species for

360   which stepwise molting has been documented.

361   Stepwise primary replacement seems adaptive in large birds because it facilitates the generation

362   of multiple waves of primary replacement in species with too little time to replace all their

363   primaries annually (Stresemann and Stresemann 1966, Rohwer et al. 2009) or between breeding

364   attempts in species that breed year-round (Ashmole 1968). The key feature of stepwise primary

365   replacement is that molt recommences where it was arrested and also at P1 (Rasmussen 1988,

366   Shugart and Rohwer 1996, Rohwer 1999). Recommencing at P1 generates considerable within-

367   species flexibility in primary replacement, both across individuals and populations. Where the

368   time available to replace primaries is limited, the generation of multiple waves eventually results

369   in more primaries being renewed in each bout of molting, while more time for primary molt

370   should generate fewer waves of replacement, resulting in fewer molt gaps in the airfoil.

371   The discovery of stepwise primary replacement in small species that likely could replace all their

372   primaries annually begs the question of whether stepwise primary replacement is adaptive in

373   small species. We suspect it is because we see no reason that arrests must always be followed

374   by the generation of a new molt wave starting at P1. Although this is a key feature of stepwise

375   molting in large birds, reinitiating molt at P1 seems not to occur in Common Ground Doves until

376   replacement of the primaries has progressed at least to P9 or P10. Further, at least in some

377   shorebirds, arrests are frequent, but molt picks up where it was arrested, without starting over

378   at P1 (Pienkowski et al. 1976, Summers et al. 1989, Remsiewick et al. 2009). These shorebirds

379   are also small species that usually can replace all their primaries during the nonbreeding season.

380   The tendency for Common Ground Doves to suppress replacing P1 following arrests unless the

381   preceding molt wave has progressed into the distal primaries further suggests adaptation to

382   stepwise molting in this small bird. We note, however, that satisfactorily addressing the

383   adaptive significance of stepwise molting in small species will surely require far more

384   descriptions of molt in small to mid-sized species that are not closely related.

385   In large birds, stepwise molting often results in the inner primaries being replaced two or more

386   times before the distal-most juvenile primaries are replaced for the first time (see diagram in

387   Rohwer 1999). This seems remarkably maladaptive because the outer primaries wear

388   considerably more than inner primaries, yet are the last to be replaced in young birds. Prior to

389   this study, the only mechanism identified for overcoming this problem was "omissive" molts,

390   reported for shags and large herons (Rasmussen 1988; Schugart and Rohwer 1995). In omissive

391   molts either P8, P9 or P10 is lost out of sequence in some (but not all) juveniles, thus setting up

392   replacement of outer primaries before the first wave of molt replacing juvenile primaries has

393   progressed into the distal primaries. Omissive molts have remained perplexing because only

394   some individuals show such replacement, and because the primary that is replaced varies.

395   These conundrums may be resolved by the recent discovery that some birds have the ability to

396   preferentially replace broken primaries or rectrices (Ellis et al. 2016). If omissive molts are

397   generated by the preferential replacement of extremely worn primaries, then the fact that not

398   all juveniles show this pattern of replacement in their outer primaries and that the replaced

399   primary can be any of three different feathers is resolved: very worn outer primaries could be

400   replaced out of their normal sequence; further, if the replaced feather is not the terminal

401   primary, its replacement could also start a distal wave of primary molt.

402   Our results for Common Ground Doves have revealed another, previously unknown mechanism

403   for avoiding unneeded frequent replacement of the inner primaries in birds with stepwise

404   primary replacement. Somehow, ground doves largely suppress initiation of new replacement

405   waves at P1 until the distal wave has proceeded to P9 or P10. Because inner primaries wear

406   more slowly than distal primaries, this suppression of new waves starting at P1 largely eliminates

407   frequent replacement of the inner primaries, something that has not, to our knowledge, been

408   reported for large birds (Rohwer 1999). This difference in when and how inner replacement

409   waves are generated in Common Ground Doves compared to large birds, suggests that this

410   stepwise-like molt may be better thought of as "stepwise with suppression". Clearly, some other

411   mechanism regulating the activation of molt waves frees doves from initiating inner

412   replacement waves with the re-initiation of arrested outer waves. Common Ground Doves were

413   serendipitously well suited for this discovery because the number of primaries between the

414   distal growing feather in birds with two molt waves is little affected by differences between

415   feather lengths and growth rates, which vary little across their primaries (Table 7). Thus, data

416   from individuals with two waves of molt could be used for this test, without differences in the

417   time it takes to grow different feathers strongly biasing results.

418   Delaying the development of new waves of feather replacement starting at P1 also explains the

419   surprisingly greater frequency of growing feathers in the outer than in the inner primaries (Table

420   4), which, initially, seemed anomalous to us. If new waves that follow too closely on the heels of

421   a previous wave are suppressed, then molt summary tables (which aggregate molt scores across

422   many individuals) should show more growing primaries in the distal primaries. This is partly

423   because outer primaries are longer and take more time to grow, but that likely has little effect in

424   Common Ground Doves because the longest primaries (P7 or P8) are only 12mm longer than P1

425   (Table 7). Instead, this higher frequency of growing feathers in the distal primaries probably

426   results from new waves of replacement being suppressed in the inner primaries following

427   arrests until molt in the outer primaries has reached at least P9 or P10.

428   This pattern of more active molt in the distal primaries was also discovered in Mustached Tree

429   Swifts, but was perplexing to Rohwer and Wang (2010). Now it seems likely that the

430   suppression of new waves starting at P1 until the next distal wave has progressed into the distal

431   primaries could be a general solution to the problem of excess replacement of inner primaries in

432   small birds with stepwise-like primary replacement. In Mustached Tree Swifts the outer

433   primaries are progressively much longer than the inner primaries, but the strong break in the

434   frequency of replacement occurred between P5 and P6, with P6-10 showing about twice as

435   many growing feathers as P1-5. Because this was a more or less dichotomous break in

436   frequencies, despite progressive length differences in the primaries, we suggest that Mustached

437   Tree Swifts may also suppress the commencement of new replacement waves at P1 until molt in

438   the outer wave has progressed at least to P6. Another species with data consistent with

439   "stepwise with suppression" molts are Wood Pigeons (*Columba palumbus*), where late-hatched

440   first year birds, as well as adults that had two waves of replacement in their primaries, had 5-6

441   newly replaced feathers between waves (Boddy 1981), suggesting suppression of an inner wave

442   until the outer wave has reached the distal primaries. Studies of marked and recaptured birds

443   with known breeding histories will be essential to support our suggestions that arrests are

444   responsible for generating multiple waves of primary replacement, and that new waves are

445   suppressed when an arrest occurs before the initial molt wave has progressed to P6 or beyond.

446   More broadly, pigeons and doves exhibit remarkable flexibility in their molts. Mourning Doves

447   (*Zenaida macroura*) and White-wing Doves (*Zenaida asiatica*) replace their primaries distally

448   from P1 to P10, in a single series with apparently few arrests (Otis et al. 2008). By contrast, we

449   have seen multiple waves of replacement in small *Ptilinopus* doves collected in the Solomon

450   Islands, and Pyle et al. (2016) report two waves of feather replacement in two *Ptilinopus*

451   *poryphyraceus* from American Samoa, suggestive of stepwise molting. Stepwise molts,

452   presumably generated by arrests for breeding, are also reported from some Band-tailed Pigeons,

453   *Patagioenas fasciata*, (Silovsky et al. 1968) and Wood Pigeons (Boddy 1981). These observations

454   suggest flexibility in the scheduling of annual molts relative to breeding opportunities. When

455   breeding conditions are favorable, some individuals in active molt arrest and then resume their

456   molts at multiple feather loci, while other individuals simply continue their annual molts without

457   arrests. Stopping and starting molt likely increases the potential for creating asymmetries

458   between wings, but any costs of asymmetric molts appear outweighed by the benefits of

459   additional breeding attempts. Pigeons and doves, with their specialized crop glands for feeding

460   young, may be especially prone to arrested molts when the food demands of young are high.

461   Many of the regions in coastal Sinaloa where we worked have been converted to irrigated

462   agriculture (Rohwer et al. 2015), which provides extensive habitat and more predictable mesic

463   areas around fields that are excellent for breeding by Common Ground Doves. This also means

464   that breeding opportunities for ground doves may extend for longer periods of time and be less

465   confined to the annual late-summer monsoon (Comrie and Glenn 1998) than would have been

466   the case prior to the 1970s, when reservoirs and extensive systems of cement-lined canals began

467   to be developed in coastal west Mexico (Rohwer et al. 2015). The possibility that landscape-

468   level changes has affected the phenology of molt and breeding or the extent of molt-breeding

469   overlap could be assessed by comparing ground doves in parts of Sonora where monsoon rains

470   continue to drive the annual vegetation cycle in the absence of irrigation.

471   As more tropical species are examined that exhibit extensive molt breeding overlap, many more

472   small species will likely be discovered to replace their primaries in multiple waves, either in a

473   stepwise fashion, or by dividing the primaries into multiple series. Distinguishing between these

474   two strategies requires data on substantial numbers of actively molting birds summarized in

475   tables similar to those presented here. As more such studies accumulate, the comparative

476   studies they will support should help illuminate both the evolutionary history and lability of

477   primary replacement patterns across birds and how primary replacement strategies are

478   integrated into other major life-history features of birds.

479   REFERENCES

480   Ashmole, N. P. 1968. Breeding and molt in the White Tern (*Gygis alba*) on Christmas Island,

481   Pacific Ocean. Condor 70:33-55.

482   Bowman, Reed. 2002. Common Ground-Dove (*Columbina passerina*), The Birds of North

483   America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of

484   North America: https://birdsna.org/Species-Account/bna/species/cogdov

485   DOI: 10.2173/bna.645.

486   Boddy, M. 1981. Primary moult in juvenile and adult woodpigeons. Ringing & Migration 3:113-

487   122.

488   Comrie, A. C., and E. C. Glenn. 1998. Principal components based regionalization of

489   precipitation regimes across the southwest United States and northern Mexico, with an

490   application to monsoon precipitation variability. Climate Research 10:201-215.

491   Dorward, D. F. 1962. Comparative biology of the White Booby and the Brown Booby at

492   Ascension. Ibis 103b: 174-220.

493   Douthwaite, R. J. 1971. Wing moult of the Pied Kingfisher Ceryle rudis (Linn.). Bulletin of the

494   British Ornithologists' Club 91:147-149.

495   Edelstam, C. 1984. Patterns of moult in large birds of prey. Ann. Zool. Fennici 21:271-276.

496 Ellis, D. H., V. G. Rohwer, and S Rohwer. 2016. Experimental evidence that a large raptor can
497 detect and replace heavily damaged flight feathers long before their scheduled moult dates.
498 Ibis 159:217-220.

499 Hamner, D. B. 1980. Mensural and moult data for eight species of kingfisher from Mozambique
500 and Malawi. Ostrich 51:129-150.

501 Johnston, R. F. 1962. Precocious sexual competence in the Ground Dove. Auk 79:269-270.

502 Passmore, M. F. 1984. Reproduction by juvenile Common Ground Doves in south Texas. Wilson
503 Bulletin 96:241-248.

504 Langston, N. E., and S. Rohwer. 1995. Unusual patterns of incomplete primary molt in Layson
505 and Black-footed Albatrosses. Condor 97:1-19.

506 Mase, Y., and T. Oishi. 1991. Effects of castration and testosterone treatment on the
507 development and involution of the bursa of Fabricus and the thymus in the Japanese Quail.
508 General and Comparative Endocrinology 84:426-433.

509 Nicholson, D. J. 1937. Notes on the breeding of the ground dove in Florida. Wilson Bulletin
510 49:101-114.

511 Otis, David L., John H. Schulz, David Miller, R. E. Mirarchi and T. S. Baskett. 2008. Mourning Dove
512 (*Zenaida macroura*), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of
513 Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-
514 Account/bna/species/moudov. DOI: 10.2173/bna.117

515 Pimm, S. 1976. Estimation of duration of bird molt. Condor 78:550–550.

516 Pyle, P. 2005. Remigial molt patterns in North American Falconiformes as related to age, sex,
517 breeding Status, and life-history strategies. Condon 107:823-834.

518 Pyle, P. 2013. Evolutionary implications of synapomorphic wing-molt sequences among falcons
519 (Falconiformes) and parrots (Psittaciformes). Condor 115:593-602.

520 Pyle, P., K. Tranquillo, K. Kayano, and N. Arcilla. 2016. Molt patterns, age criteria, and molt-
521 breeding dynamics in American Samoan landbirds. Wilson Journal of Ornithology 128:56-69.

522 Rasmussen, P. C. 1988. Stepwise molt of remiges in Blue-eyed and King Shags. Condor 94:297-
523 300.

524 ROHWER, S. 1999. TIME CONSTRAINTS AND MOULT-BREEDING TRADEOFFS IN LARGE BIRDS. PROC. 22 INT.
525 ORNITHOL. CONGR., DURBAN: 568-581. JOHANNESBURG: BIRDLIFE SOUTH AFRICA.

526 ROHWER, S. 2008. A primer on summarizing molt data for flight feathers. Condor 110:799–806.

527 Rohwer, S. 2013. Molt intensity and conservation of a molt migrant (*Passerina ciris*) in
528   Northwestern Mexico. Condor 115:421-433.

529 Rohwer, S., and K. Broms. 2013. Replacement rules for the flight feathers of Yellow-billed
530   Cuckoos (*Coccyzus americanus*) and Common Cuckoos (*Cuculus canorus*). Auk 130:599-608.

531 Rohwer, S., and L.-K. Wang. 2010. A quantitative analysis of flight feather replacement in the
532   Moustached Tree Swift *Hemiprocne mystacea*, a tropical aerial forager. PLoS One 5:e11586.

533 Rohwer, S., E. Grason, and A. G. Navarro- Siguenza. 2015. Irrigation and avifaunal change in
534   coastal Northwest Mexico: has irrigated habit attracted threatened migratory species? PeerJ
535   3:e1187; DOI 10.7717/peerj.

536 Rohwer, S., A. G. Navarro, and G. Voelker. 2007. Rates versus counts: Fall molts of Lucy's
537   Warblers (Vermivora luciae). Auk 124:806-814.

538 Rohwer, S., A. Viggiano, and J. M. Marzluff. 2011. Reciprocal tradeoffs between molt and
539   breeding in albatrosses. Condor 113:61–70.

540 Rohwer, V. G., S. Rohwer, and M. F. Ortiz-Ramirez. 2009. Molt biology of resident and migrant
541   birds of the monsoon region of west Mexico. Ornitología Neotropical 20:565-584.

542 Shugart, G. W., and S. Rohwer. 1995. Serial descendant primary molt or *Staffelmauser* in Black-
543   crowned Nightherons. Condor 98:222-233.

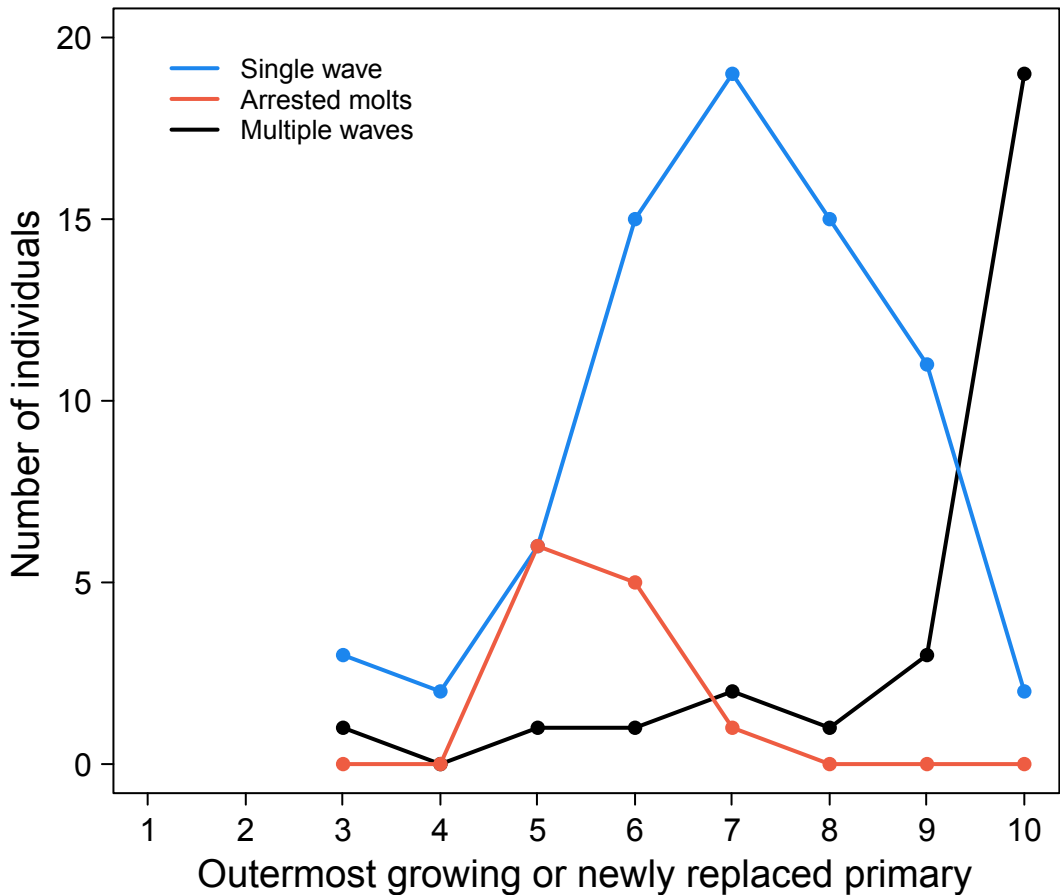
544 Silovsky, G. D., H. W. Wight, L. H. Sisson, T. L. Fox, and S. W. Harris. 1968. Methods for
545   determining age of Band-tailed Pigeons. Journal of Wildlife Management 32:421-424.

546 Silveira, M. B., and M. A., Marini. 2012. Timing, duration and intensity of molt in birds from a
547   Neotropical savanna in Brazil. Condor 114:435–448.

548 Snyder, N. F. R., E. V. Johnson, and D. A. Clendenen. 1987. Primary molt of California Condors.
549   Condor 89:468–485.

550 Stresemann, E., and V. Stresemann. 1966. Die Mauser der Vogel. Journal fur Ornithologie 107:1-
551   448.

The progression of molt in outer molt waves corresponds to the initiation of inner molt waves in adult Common Ground Doves.

Individuals with a single molt wave (blue line) are commonly observed until molt has progressed to P9 and P10. By contrast, the frequency of individuals with two molt waves (black line) dramatically increases once the outer molt wave has reached P10. Individuals that arrested and re-initiated molt without starting a new series at P1 (orange line) show that arrests do not activate a molt series at P1, as occurs in large birds. All lines start at P3 because our scoring scheme required groups of feathers for determining feather ages. See text for more information.

Progression of molt in adults.

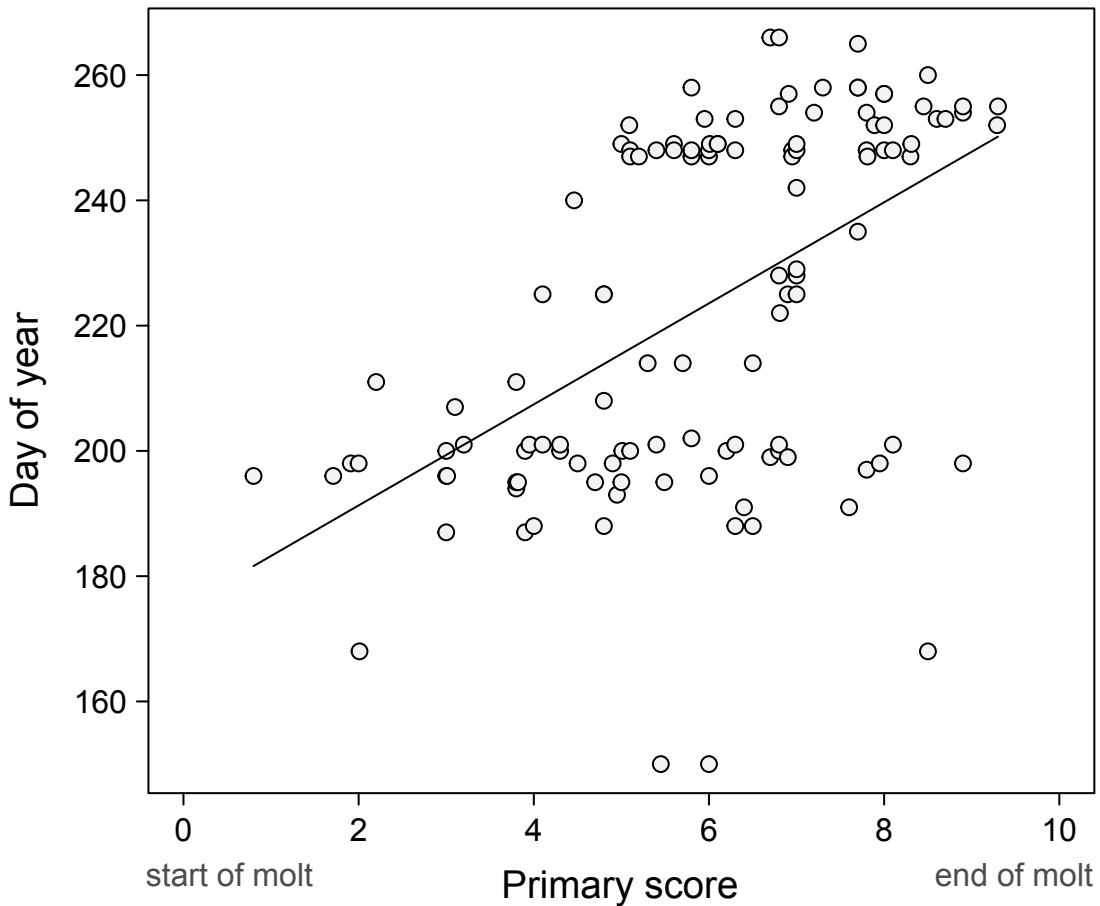
Pimm (1976) regressions fail to correctly estimate the duration of primary replacement when start and finish dates overlap broadly in the studied population, as is the case for these doves. Thus of the progression of molt in adults largely reflects birds in various stages of molt in the months of July and September when most of our birds were scored.

Summary of primary molt in juvenile Common Ground Doves by month.

Table 1. Summary of primary molt in juvenile Common Ground Doves by month.

Month	# juvs sampled	# replacing Ps	% replacing Ps
May	1	1	100
Jun	5	5	100
Jul	10	9	90
Aug	7	6	86
Sep	21	21	100
Totals	44	42	95

Summary table for 40 juvenile Common Ground Doves that were growing primaries.

Note that the primaries are a single molt series with P1 nodal and P10 terminal and directionality always distal. Excluded are 4 juveniles with multiple waves of primary replacement, possibly associated with late fledging or precocious breeding.

Table 2. Summary table for 40 juvenile Common Ground Doves that were growing primaries. Excluded are 2 juveniles with multiple waves of primary replacement, presumably associated with precocious breeding.

	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10
# nodal	16	0	0	0	0	0	0	0	0	0
# distal	17	19	13	13	8	13	11	7	4	
# proximal	0	0	0	0	0	0	0	0	0	
# terminal	0	0	0	0	0	0	0	0	0	2
# growing	14	16	13	11	5	7	8	6	2	2

Number of primaries growing for two classes of adults and for juveniles.

Table 3. Number of primaries growing for two classes of adults and for juveniles.

	Number of growing primaries			
	1	2	3	4
Adults, 1 wave	102	15	1	0
Adults, 2 waves	--	14	4	0
Juveniles, 1 wave	12	16	6	4

Summary of primary molt in adult Common Ground Doves by month.

Table 4. Summary of primary molt in adult Common Ground Doves by month.

Month	# ads sampled	# replacing Ps	% replacing Ps	# replacing Ps in 2 waves	# with 2 active or inferred waves
May	5	1	20	0	4
Jun	5	3	60	1	3 of 3[1]
Jul	54	48	89	10	6 of 50[1]
Aug	19	11	58	2	3 of 15[1]
Sep	49	39	80	5	12 of 48[1]
Totals	132	102	77	18	31

[1]Primaries were not assigned ages in some birds, precluding inferring additional waves.

Summary table for 108 adult Common Ground Doves that were growing primaries.

Table 5. Summary table for 108 adult Common Ground Doves that were growing primaries.

	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10
# nodal	12	0	0	0	0	2	3	0	2	1
# distal	6	8	16	29	29	40	38	26	12	
# proximal	4[1]	0	0	0	0	0	0	0	6	
# terminal	0	0	0	0	0	0	3	1	1	9
# growing	8	4	8	15	19	21	25	19	12	11

[1]These 4 exceptions to distal replacement are likely unavoidable scoring problems caused by P1 being a pin or short feather. P1 was presumable initiating a new wave in each case, but was too short to be compared with its neighboring inner primaries, which were little worn.

Association between primary replacement and active crop glands in adults.

Table 6. Association between primary replacement and active crop glands in adults.

	Molting Ps	Not molting Ps	% molting
Crop gland active	8	6	57
Crop gland not active	30	1	97

Mean primary lengths (standard deviations in parentheses) and growth rates for Common Ground Doves.

Primary growth rates were measured from growth bands in 2 or 3 feathers; standard deviations are given when there were 3 measurements.

Table 7. Mean primary lengths (standard deviations in parentheses) and growth rates for Common Ground Doves. Primary growth rates were measured from growth bands in 2 or 3 feathers; standard deviations are given when there were 3 measurements.

	Primary length		Primary growth rate (mm/d)
	Females (n=8)	Males (n=6)	(Sexes combined)
P1	51.8 (0.75)	54.1 (1.69)	2.88
P2	52.9 (1.10)	54.8 (1.47)	2.72
P3	53.7 (0.76)	55.5 (1.38)	2.68 (0.63)
P4	55.1 (1.28)	56.9 (0.67)	2.90 (0.18)
P5	56.9 (1.02)	59.1 (0.92)	2.78
P6	61.0 (1.29)	63.0 (1.27)	2.44
P7	63.5 (0.58)	64.7 (1.48)	3.61
P8	63.6 (0.89)	65.2 (1.17)	3.03
P9	62.5 (0.84)	63.8 (0.75)	3.15 (0.38)
P10	59.4 (0.67)	60.3 (0.82)	3.01 (0.29)