REPRODUCTIVE BIOLOGY OF THE BAND-TAILED PIGEON IN COLORADO AND NEW MEXICO

R. J. GUTIÉRREZ, CLAIT E. BRAUN, AND THOMAS P. ZAPATKA

BAND-TAILED PIGEONS (*Columba fasciata*) occur in two major populations in western North America, a coastal population (*C. f. monilis*) and an interior population (*C. f. fasciata*) (A.O.U. 1957). The interior population inhabits portions of Colorado, New Mexico, Arizona, Utah, Texas, and the highlands of Mexico. This pigeon is one of several species of birds in western North America that show unseasonal and variable nesting periods (see Ligon 1971). Active nests have been found in some portion of the species' range in every month of the year (Swarth 1900, Thayer 1909, Stephens 1913, Lamb 1926, Abbott 1927, Vorhies 1928, Neff 1947, MacGregor and Smith 1955).

Although several studies of the breeding biology of the Band-tailed Pigeon have been made on the Pacific coast population (Glover 1953, MacGregor and Smith 1955, Houston 1963, March and Sadleir 1970, Zeigler 1971) few studies have been done of the interior population (Fitzhugh 1970). The breeding cycle of the interior population is poorly understood, although many observations of individual nests have been reported (Neff 1947, Fitzhugh 1970). The purpose of this study was to document the gonadal cycles of free-living Band-tailed Pigeons in Colorado and New Mexico and to study the species' photoperiod responses. From this information we have attempted to explain the normal breeding cycle of the pigeon and to explain its occasional unseasonal breeding.

MATERIALS AND METHODS

Gonadal studies.—Band-tailed Pigeons were obtained from banding trap mortalities, farmer kills (for crop depredations), hunter kills, and systematic collections. Gonadal materials were collected (May through September) from 121 birds in 1969, 107 in 1970, 115 in 1971, and 190 in 1972. Band-tailed Pigeons are present in Colorado and New Mexico from late April through early October. All data from 1969 through 1971 were from birds collected in Colorado. Pigeons from both Colorado and New Mexico were studied in 1972. Age was recorded as adult or juvenile by plumage characteristics (Silovsky et al. 1968). A few birds were classified as subadults (first breeding season) in 1970–72 (Braun MS).

Prior to 1972 all specimens collected were frozen in plastic bags; later each bird was thawed, weighed (nearest 0.1 g), and the gonads measured *in situ* with vernier calipers to the nearest 0.1 mm. Gonads were then excised and stored in either Bouin's fixative or 10% buffered formalin. During 1972 gonads were measured *in situ* and excised within 15 min of death and fixed in either Bouin's fixative or FAA.

Pigeons were collected from 17 areas within Colorado and New Mexico (Fig. 1).

The Auk 92: 665–677. October 1975

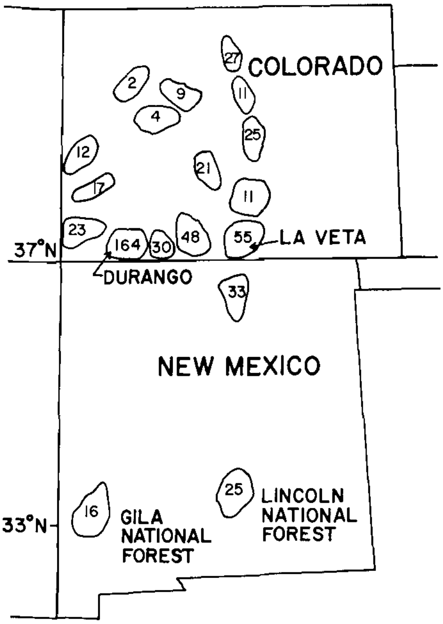

Fig. 1. Band-tailed Pigeon collection areas in Colorado and New Mexico, 1969–72. Sample size for each area is given within each area boundary.

As sampling effort was uneven through time and across area, locality was not considered in the statistical analysis.

Volumes of the left testis were calculated using the formula for an ellipsoid, $V = 4/3\pi W^2 L$ where $L = \frac{1}{2}$ length and $W = \frac{1}{2}$ diameter at widest point (Lofts et al. 1966). Samples of testes of different volumes were processed using standard histological techniques and sectioned at 10 μm to determine the relationship between volume and spermatogenic state. Sections were stained with Harris' hematoxylin and counterstained with eosin. Spermatogenic stages were classified according to Lofts et al. (1966).

The diameter of the largest ovarian follicle was measured and in most cases the number of follicles greater than 5.5 mm was recorded. All ovaries with no follicles more than 2.0 mm were classified as granular (not in breeding condition). Each ovary was also examined macroscopically for ruptured follicles (Meyer et al. 1947).

Photoperiod studies.—Adult pigeons caught with cannon nets near La Veta, Colorado, in late August 1972 were taken to the University of New Mexico, placed in outdoor aviaries (2.51 m × 2.51 m × 2.51 m), and sexed by laparotomy.

Five experiments designed to illustrate the relationship between testis growth and photoperiod are discussed in a later section.

All birds in outdoor aviaries were fed a mixture of 50% cracked corn and 50% wheat; grit and water were provided *ad libitum*. Perch space sufficient to prevent excessive aggressive behavior was provided. Roofing covering half of each enclosure provided shade and weather protection.

TABLE 1

OVARIAN CONDITION AS INDICATED BY FOLLICLE SIZE OF FEMALE BAND-TAILED PIGEONS FROM COLORADO AND NEW MEXICO 1969–1972

	Diameter of largest follicle			
	Granular to 2.0 mm	2.1 to 5.4 mm	5.5 mm and larger	Number of birds with oviductal egg and/or ovulated follicles
	Number of birds in size class			
1–15 May	0	2	2	0
16–31 May	2	6	9	0
1–15 June	1	9	6	2
16–30 June	9	17	10	4
1–15 July	4	35	28	10
16–31 July	0	5	7	3
1–15 Aug.	1	9	2	2
16–31 Aug.	3	5	0	0
1–15 Sept.	21	4 (5)[1]	(3)	(2)
16–30 Sept.	16	0	0	0
TOTALS	57	97	67	23

[1] (N) indicates birds which were taken in the Gila National Forest, New Mexico, 1972.

Birds in the laboratory were housed in cages (1.22 m × 0.92 m × 0.61 m), with either one or two birds per cage at 25° C. Each experimental group received the light intensity provided by four 150-watt light bulbs. These birds also were fed wheat and cracked corn. Water and granite grit were always available.

Gonadal activity was determined by laparotomy. The birds were anesthetized with an intramuscular injection of ketamine hydrochloride. Dosage varied from 30 mg/kg in early fall to 100 mg/kg in winter. The 30 mg/kg dosage will not produce anesthesia during winter—the reason for this change in sensitivity to the drug is not fully understood, but may be related to seasonal change in the birds' physiological state (i.e., fat deposition). Each bird was weighed and the operation begun within 7–10 min of injection. The left testis was measured in each case, as was done with collected birds. The largest follicle of each female's ovary was measured in the same manner.

Statistical analyses.—No analysis of inter-area variation was done, as the randomness of obtaining dead birds resulted in uneven distribution of samples. Therefore standard measurements of dispersion were calculated for male testis volumes by year and plotted for 15-day time periods of the breeding season. It became apparent from these measurements that some year-to-year difference might be occurring in the gonadal cycle of males. A Kruskal-Wallis test was used to determine if differences occurred between the testis cycle of different years. As testis size varied greatly throughout the summer, we were interested in the extent of the breeding season. Therefore the period of earliest testis decline was subjected to the Kruskal-Wallis test to determine if differences during this critical time period occurred between years.

As an enlarged follicle in a given female is a temporary, short-term physiological condition, the data for females were listed descriptively (Table 1) according to size and time period. No statistical tests were justified because of the nature of the data. The gonadal state of the female is a more important indicator of the breeding status of a population; it is used here as documentation of the breeding season.

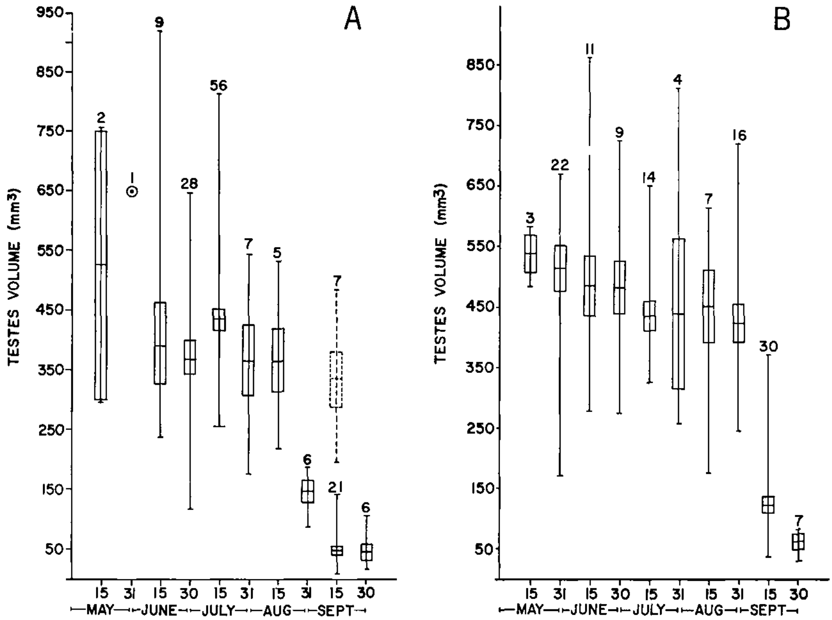

Fig. 2. A, testis variation in Colorado and New Mexico Band-tailed Pigeons during the breeding seasons of 1969 and 1972. Vertical lines indicate ranges, horizontal lines indicate means, rectangles indicate twice the SE of the mean. Sample size is given above each vertical line. The dashed line, bar, and rectangle indicate data collected from the Gila National Forest, New Mexico. B, testis variation in Colorado Band-tailed Pigeons during the breeding seasons of 1970 and 1971.

In all photoperiod experiments, gonads were measured by laparotomy at the beginning and end of each treatment. The results were analyzed using the student's *t* test for paired observations. The level of significance in all the photoperiod experiments was $P < 0.05$. In the one experiment (10 hours light:14 hours dark) where no statistically significant increase was observed, the birds were sacrificed and the testes examined histologically. Birds held in outdoor aviaries were measured near the first of each month, and month-to-month changes in gonad size (at $P < 0.05$) were tested using Student's *t*-distribution.

RESULTS

Testis cycles.—Testis volumes of males are shown in Figs. 2A and 2B. Male pigeons were in breeding condition when collections began in May and remained so until August. Differences in the length of the breeding seasons between years were noted. In one area late breeding occurred.

There was a significant difference ($\chi^2 = 2.366$, df $= 3$, $P < 0.05$) in the location of the data each year. The data for this time period were then treated by testing six combinations of years by the use of a two

TABLE 2

STAGES OF SPERMATOGENESIS ASSOCIATED WITH TESTIS VOLUME OF 46 ADULT MALE BAND-TAILED PIGEONS

Volume (mm^3) range	N	Stage[1]
8.9– 22.3	6	Stage 1, completely regressed
66.5–126.5	3	Stage 2, a few primary spermatocytes
74.0–181.0	3	Stage 3, secondary spermatocytes seen
102.4	1	Stage 4, first spermatids seen
57.0–814.9	33	Stage 5, spermatozoa present

[1] Stages described completely by Lofts et al. 1966.

sample Wilcoxon W test. By setting the level of significance at $P < 0.01$ we assume significant differences at this level will compensate for getting a significant difference due to chance alone.

The results of this testing procedure showed that the testes of birds collected in 1969 and 1972 were not significantly different with respect to size ($W = 9$, $P > 0.01$). Similarly, size of testes of birds collected in 1970 and 1971 was not significantly different ($W = 23$, $P > 0.01$). The following combinations showed a significant difference ($P < 0.01$) in size at this time of year: 1969 and 1970 ($W = 6$); 1969 and 1971 ($W = 6$); 1972 and 1970 ($W = 6$); 1972 and 1971 ($W = 6$).

Subadult testes were generally smaller than those of adults. They may develop more slowly as in the Woodpigeon (*Columba palumbus*) (Lofts et al. 1966). Subadults were included with adults in the analyses because even though testes were smaller, histological examination showed a capability to breed as early as adults. Also subadults bred as early as April in captivity (Braun MS).

Results of the histological examination of testes are shown in Table 2. All testes examined above 181 mm^3 volume were in stage 5 (producing sperm). On the basis of this examination and April breeding of captive subadults, most subadults were thought to be in breeding condition. Juvenile males were not considered in the testis analysis because testis size alone indicated they are not capable of breeding ($\overline{X} = 11.0\ mm^3$; range $= 4.5–30.4\ mm^3$; $n = 23$).

Testis regression occurs between 15 August and 15 September (Figs. 2A, 2B), but in 1969 and 1972 regression began approximately 2 weeks earlier (see above analysis and Fig. 2A) than it did in 1970 and 1971 (Fig. 2B).

Collection areas were expanded during the 1972 September hunting season to include parts of southern New Mexico. Males collected from the Gila National Forest in southwest New Mexico (latitude 33° N) were in full breeding condition, whereas pigeons collected from Durango, Colorado (latitude 37° N), and all other sampled areas of Colorado and New Mexico were not. Fig. 2A illustrates that the ranges of testis volume do not overlap. Unfortunately only one male from the Lincoln National Forest, an area at the same latitude as the Gila, was collected (testis volume = 66.5 mm^3).

In 1972 we checked many areas in New Mexico for acorns (*Quercus* spp.), one of the primary foods of Band-tailed Pigeons (Neff 1947, Fitzhugh 1970), but we found large numbers of them only in the Gila National Forest. In Colorado the acorn crop in 1972 in most places was only fair, with few sites checked producing large numbers. We suspect that the stimulus for this late breeding attempt may have been the large acorn crop in the Gila Forest.

Ovarian cycles.—Conditions of ovaries from females collected in Colorado and New Mexico are listed in Table 1. Most females taken (88%) were in breeding condition (follicle diameter 2.1–5.5 mm+) from May through August. Altogether 19 birds (8.6%) had two or more follicles greater than 5.5 mm, 7 birds contained either an egg and large follicle, or two ovulated follicles.

Data from eight females from the Gila National Forest in September 1972 showed they were breeding when collected (Table 1). All other females collected at the same time from Colorado and the Lincoln National Forest had granular ovaries (undifferentiated-regressed). None of the birds from the Gila had granular ovaries. One pigeon collected on 2 September 1972 had two large ruptured follicles (15.5 and 10.7 mm, after fixation and storage). Another bird had one large ruptured follicle of 10.1 mm. This indicates that eggs had been laid a few days prior to collection. Ovaries from all juvenile females examined were granular.

Photoperiod studies.—Results of the photoperiod experiments are shown in Figs. 3A and 3B.

Experiment 1.—Five males with regressed or regressing testes were subjected to 14L:10D photoperiod from 23 September to 23 October 1972. These birds showed a highly significant testicular volume increase ($t = 4.9215$, df. = 8, $P < 0.01$) (see Fig. 3A). This experiment was designed to determine the presence or absence of a refractory period in late summer. The responses obtained suggest that these pigeons may be continuously photoresponsive, but more experiments are needed to determine this conclusively.

Experiment 2.—Five males with regressed testes were subjected to 12.5L:11.5D photoperiod from 30 November 1972 to 3 January 1973. Exposure of this second group of birds to a 12.5 h light regime would provide information on the light stimulation of an April photoperiod (we had no April collections from Colorado or New Mexico). Ad-

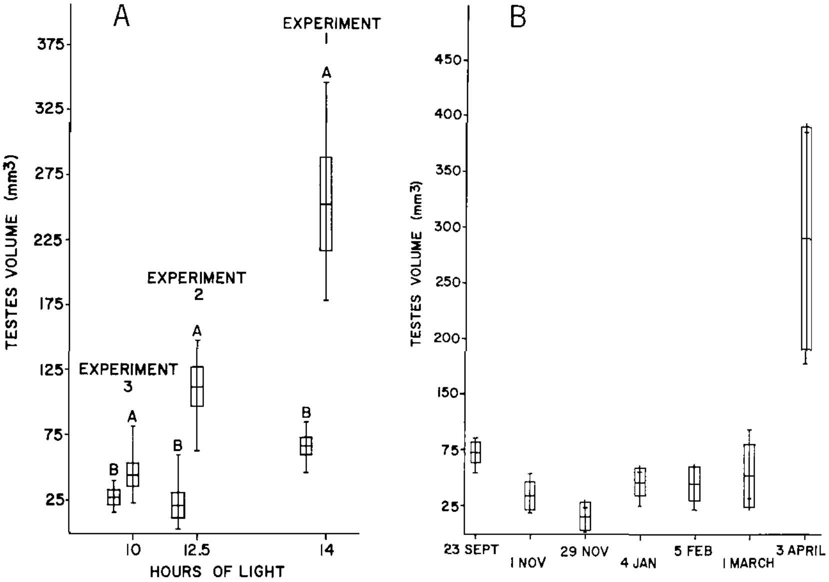

Fig. 3. A, changes in testis volume of Band-tailed Pigeons in three experimental groups. B indicates the initial testes volumes, and A indicates the testes volumes at the end of light treatment. Sample size is 4 in experiment 1 and 5 in experiments 2 and 3. See text for explanation of experiments. B, testis variation in four Band-tailed Pigeons outside the breeding season.

ditionally this experiment should demonstrate a refractory period if Band-tailed Pigeons become refractory later than September. Testis growth was significant during this photoperiod treatment ($t = 5.948$, df. = 8, $P < 0.01$).

Experiment 3.—Four males with regressed testes were subjected to 10L:14D photoperiod from 15 January to 15 February 1973. Ten hours of light caused some increase in testes size (Fig. 3A), but the increase was not significant ($t = 2.0445$, df. = 6, $P > 0.05$). However histological examination of the testes showed spermatogenesis had begun (stages 2 or 3, see Lofts et al. 1966) in all but one bird This is what would be expected of increasing testes of this volume (Table 2).

Experiment 4.—Eight males and four females were housed in outdoor aviaries from 23 September to 1 November 1973. Five of the males and one female were lost on 28 October 1972 and subsequently were replaced by a single male and female on 1 November 1972. These eight birds (two pairs in each aviary) were maintained from 1 November 1972 to 3 April 1973. As Band-tailed Pigeons normally overwinter in Mexico, specimens available for gonadal analyses are rare (three adult males and two adult females were collected in Durango, Mexico, during April and December 1973, all in breeding condition) (Braun MS). Accordingly this experiment was designed to monitor gonadal change throughout the fall, winter, and spring in relation to naturally decreasing and increasing photoperiod.

Males continued a slight testicular regression until December (Fig. 3B). The decrease was significant between 23 September and 1 November 1972 ($t = 2.677$, df. $= 6$, $P < 0.05$). The increase noted between 30 November and 4 January was also significant ($t = 6.316$, df. $= 6$, $P < 0.01$). Testes size did not increase significantly ($t = 0.5907$, df. $= 6$, $P > 0.05$) between 4 January and 1 March 1973, but they again increased significantly ($t = 4.442$, df. $= 6$, $P < 0.05$) during the period 1 March to 3 April 1973. Ovaries of female pigeons showed no change between 23 September 1972 and 1 March 1973. Follicles grew significantly between 1 March and 3 April 1973 ($t = 3.63$, df. $= 6$, $P < 0.05$).

Experiment 5.—Two females were held in outdoor aviaries from September 1971 to August 1972 under natural photoperiod to observe ovarian change in the absence of a male. Female Rock Doves (*Columba livia*) and Woodpigeons apparently do not undergo final ovarian development if a male is not present (Bartelmez 1912, Murton and Isaacson 1962). Ovaries of both females remained granular (follicles less than 2.0 mm in diameter) until the period 1 April to 1 May 1972, when they increased to 5.0 and 4.2 mm. They reached maximum follicular diameter in June (6.4 mm, 6.8 mm), then began to decrease gradually until September, when they were once again classified as granular. Bartelmez (1912) stated that in Rock Doves a follicle would not exceed 5.5 mm before pair bond formation. Others have used this 5.5 mm criterion as a measure of breeding activity in other species of pigeons (Lofts et al. 1966, March and Sadleir 1970). While our observations also suggest a male must be present before final follicle development can occur, follicles can increase to a size greater than 5.5 mm.

DISCUSSION

Band-tailed Pigeons breed in Colorado from at least May through August. The season may start even earlier, but no birds were collected in March or April. In New Mexico the breeding season is similar, except that fall breeding may occur in southwestern New Mexico. The length of the breeding season is not a latitudinal response *per se* as suggested by March and Sadleir (1970), but almost certainly is a response to environmental conditions (i.e. acorn production). Two populations of pigeons sampled in September 1972 at the same latitude (33° N), but

150 miles apart, document this. Specimens from one population were in breeding condition, the others were not.

Also, as shown by this study, testes from birds collected in 1970 and 1971 were not significantly different with respect to size, yet were significantly larger than testes in birds collected in 1969 and 1972. We considered 1971 as the poorest year studied of pigeon production (only 288 (7%) of 4006 pigeons banded were immature), and 1970 as one of the best years of pigeon production (548 (17%) of 3292 pigeons banded were immature). Testes from these adult birds (both 1970 and 1971) remained larger for a longer period of time (Fig. 2B). If environmental conditions are favorable, it is conceivable that pigeons could continue breeding for a longer period of time. If conditions are poor, pigeons may retain breeding capability longer so that late nesting could occur if mast or berry crops develop. Both situations could result in testes remaining larger for a longer time period. As fall breeding occurred in 1972 in southwestern New Mexico, both hypotheses may be valid.

The testis data for the years 1969 and 1972 may represent a normal breeding season with average production of young. If this is the situation, the breeding season may be considered as normally ending in mid-August. In years of either favorable or unfavorable environmental conditions breeding may be extended or delayed. It is probable that Band-tailed Pigeons are opportunistic, breeding whenever favorable conditions occur. Food seems to be of major importance in timing of breeding attempts.

Band-tailed Pigeons in Colorado and New Mexico remain sexually competent until mid-August. As the incubation period is 19 days and nestling life is about 20 days (MacGregor and Smith 1955), the birds could easily bring off two broods per year. Also, this bird in captivity will occasionally lay eggs in a nest containing a nestling (Braun MS). If this is a common occurrence in nature, it would considerably shorten two nesting cycles.

Enlarged ovarian follicles are a general indicator of breeding condition. March and Sadleir (1970) did not find more than one enlarged follicle in any ovary ($n = 90$), suggesting that pigeons from British Columbia lay only one egg per clutch. Of the females we examined, 8% had two or more enlarged follicles suggesting that a small percentage of interior pigeons lay two eggs. We do not believe that Band-tailed Pigeons lay three eggs, although specimens containing three or more follicles greater than 7.0 mm were recorded. This supports the findings of experiment 5 that follicles may attain a size greater than 5.5 mm without ovulation taking place. Neff (1947) and MacGregor and Smith (1955) reported clutches of two eggs, although these were not common.

Band-tailed Pigeons may attempt to breed three times in years of favorable environmental conditions, as suggested by fall breeding in at least one population. MacGregor and Smith (1955) reported one pair that successfully reared three broods in one year.

Acorns were locally abundant in southwestern New Mexico in 1972 and Band-tailed Pigeons may have bred in the fall in response to abundant acorns. Ligon (1971) found Piñon Jays (*Gymnorhinus cyanocephalus*) breeding in fall in southwestern New Mexico, presumably in response to an abundance of piñon pine (*Pinus edulis*) seeds.

Nomadic behavior of Band-tailed Pigeons in response to mast production has been suggested by Neff (1947) and Smith (1968), but Braun (1972) found that Colorado pigeons have a high fidelity to a given area. The production of acorns and piñon seeds in the Southwest is not predictable. As Band-tailed Pigeons may not have a true refractory period, they may move until they find a food supply large enough to support a breeding effort, regardless of increasing or decreasing daylength. Reproductive success must be considered the ultimate factor in the control of any species' breeding cycle. Food as well as light probably interact as proximate factors that trigger breeding in Band-tailed Pigeons.

Nomadism is a reasonable response to local shortages of food. The great mobility of these pigeons can be considered as an adaptation that allows breeding in an environment with an unpredictable local food supply. Numerous observations of nomadic behavior in this pigeon have been made in southwestern New Mexico (Ligon MS). In this respect the biology of the Band-tailed Pigeon is similar to that of the extinct Passenger Pigeon (*Ectopistes migratorius*) (Schorger 1955). Most of Braun's (1972) study was made near agricultural areas (e.g. small grains, orchards) where food supplies may have been more constant, which could well explain his birds' high site fidelity.

Gonadal cycles of interior and British Columbia Band-tailed Pigeons are similar (see March and Sadleir 1970). In Britain the Woodpigeon, Stock Dove (*Columba oenas*), and Rock Dove exhibit similar gonadal cycles (Lofts et al. 1966). Woodpigeons depend on cereal grains and Stock Doves on weed seeds during the breeding season (Lofts et al. 1966). As in these columbids, Band-tailed Pigeons undoubtedly also respond to food as a proximate factor. This is also the case in many other birds (Lofts and Murton 1968).

Other columbids, e.g., the Woodpigeon, Stock Dove, Rock Dove, and possibly the Mourning Dove (*Zenaida macroura*), show no refractory period like that noted in many passerines (Cole 1933; Lofts et al. 1966, 1967b, 1967c; Lofts and Murton 1968). Another columbid, the Turtle Dove (*Streptopelia turtur*), does show a refractory period (Lofts et al.

1967a). Although not absolutely documented, the Band-tailed Pigeon may also lack a true refractory period.

The fact that Band-tailed Pigeons are responsive to photoperiods as short as 10 h (1 January at 35° N) helps to explain the breeding records from Mexico in December and January (Thayer 1909, Lamb 1926, Braun MS). As daylength is always greater than 10 h in Mexico, the pigeons presumably try to breed there if the proximate factors of food and weather are favorable.

The pigeons kept in outdoor aviaries showed a gradual testis regression from September until December. Testis size increased rapidly between 30 November 1972 and 4 January 1973. Absence of further growth during January and February may have been the result of overcrowding in the aviaries. In any case, after this situation was relieved on 1 March testis growth resumed. Females in outdoor aviaries remained sexually inactive until the period 1 March 1973–3 April 1973 when a large increase in follicle size was noted. These data help to explain prior reports of the ability of the Band-tailed Pigeon to attempt unseasonable breeding or to show extended breeding seasons as a response to environmental conditions (Neff 1947, MacGregor and Smith 1955, Fitzhugh 1970).

ACKNOWLEDGMENTS

M. K. Gutiérrez provided assistance in all phases of the research and was essential to the success of the project. J. D. Ligon served as the senior author's major professor and critically reviewed the manuscript. A. S. Leopold, J. Davis, and D. W. Duszynski also reviewed the manuscript. S. Cito helped construct aviaries and P. W. Day provided ketamine hydrochloride and technical assistance. J. A. White, J. E. Kautz, B. Petersen, and S. Amend provided technical and field assistance.

We acknowledge financial support of the Colorado Division of Wildlife and New Mexico Department of Game and Fish, Federal Aid in Wildlife Restoration Projects W-88-R and W-104-R, respectively, and the Accelerated Research Program of the U.S. Fish and Wildlife Service.

SUMMARY

Band-tailed Pigeons breed in Colorado and New Mexico from at least May through August and may attempt two nestings per season. Normally one egg per clutch is laid, although a small percentage lay two eggs.

Photoperiod studies indicate that gonadal stimulation occurs with light periods as short as 10 h a day. Band-tailed Pigeons may not exhibit a characteristic refractory period. Gonadal regression begins in September with a rapid decrease in testes volume. Further regression takes place slowly in October and November. Significant gonadal development, presumably in response to increasing daylength was observed by 4 January 1972 in birds kept outdoors, and full breeding capability was reached in March.

The response to photoperiod stimulation and the probable response to other environmental cues (i.e. food availability) explain the reports of winter nesting and the unusually long and varied breeding seasons sometimes recorded for this pigeon.

The Band-tailed Pigeon apparently responds to proximate environmental cues, particularly mast production, in parts of its range (southwestern New Mexico) and fall breeding may occur. This response is not latitudinal *per se* but may be influenced by environmental conditions. If conditions are unfavorable in a given region, these pigeons may show nomadic behavior, like that of the extinct Passenger Pigeon, until they find food adequate to sustain breeding.

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Department of Biology, University of New Mexico, Albuquerque, New Mexico 87131; *Colorado Division of Wildlife, Wildlife Research Center, Fort Collins, Colorado 80521*; and *New Mexico Department of Game and Fish, Albuquerque, New Mexico 87108. Present address of first author: Museum of Vertebrate Zoology, University of California, Berkeley, California 94720.* Accepted 26 August 1974.