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Title: CROP-MILK CYCLES IN BAND-TAILED PIGEONS AND LOSSES OF SQUABS DUE TO HUNTING PIGEONS IN SEPTEMBER

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Howard M. Wight

The production of crop-milk in band-tailed pigeons was investigated to estimate losses of squabs that occur from hunting pigeons during September.[1] Living birds held captive were examined with a cystoscope and pigeons killed by hunters were examined in the field to determine changes in gross appearance of crops and the timing of these changes through the reproductive cycle.

Two cycles in the production of crop-milk were found, a daily cycle and a seasonal cycle. The seasonal cycle extended from the time an egg was laid, through fledging of the squab, until an egg in the next cycle was laid. Four phases were identified in the seasonal cycle; inactive, developing, active and regressing.

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[1] This study was supported by the Bureau of Sport Fisheries and Wildlife, U.S. Fish and Wildlife Service, and the Oregon Agricultural Experiment Station, Corvallis.

Crop-milk was produced during the active phase in a daily cycle for approximately 30 days. The daily cycle had five characteristic phases, but crop-milk was found in only two or three, indicating that crop-milk was not a consistent criterion for identifying pigeons with active crops. Daily cycles of crops of males and females appeared not to be synchronized.

Sixty-two percent of 614 pigeons killed by hunters had active crops, 31 percent were inactive, 5 percent were regressing and 2 percent were developing.

The ability of one parent to fledge a squab was determined by removing the other parent at various stages of incubation and brooding. Squabs could not be fledged in the normal length of time (22 to 24 days of brooding) by one parent if the other parent was removed prior to the 9th day of brooding.

Losses of productivity that occurred from hunting pigeons in Oregon during September were estimated using two methods. Minimal estimates were 3.5 percent and 5.0 percent, and the maximal estimates were 5.8 percent and 7.2 percent, respectively. These data indicated that hunting pigeons in September may not affect productivity of these populations significantly.

Crop-Milk Cycles in Band-Tailed Pigeons and Losses of Squabs Due to Hunting Pigeons in September

by

Don Leslie Zeigler

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Mr. Marlowe W. Jenks kindly allowed me to examine pigeons killed by hunters at the Crawfordsville mineral spring.

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CROP-MILK CYCLES IN BAND-TAILED PIGEONS AND LOSSES OF SQUABS DUE TO HUNTING PIGEONS IN SEPTEMBER

I. INTRODUCTION

This is a report on the frequency of milk-producing crops in band-tailed pigeons, Columba fasciata, killed by hunters in September, and on the biological implications of this occurrence to the productivity of these populations.

The band-tailed pigeon is a migratory game bird of the family Columbidae. Birds of this family produce crop-milk, a curd-like substance formed in the lobes of the crops of both parents, which is regurgitated and fed to the young.

Most research concerning the lobes of the crop was done on the domestic pigeon, Columba livia. These investigations were primarily histological and physiological in nature (Litwer, 1926; Beams and Meyer, 1931; Riddle and Braucher, 1931; Patel, 1936; Weber, 1962; Dumont, 1965). Studies concerning seasonal variations in crop activity were conducted on wood-pigeons, Columba palumbus, (Ljunggren, 1969). March and Sadleir (1970) were first to report on seasonal activity of crops of band-tailed pigeons. Research involving the relation of parental behavior to development of the crop was conducted on ring doves, Streptopelia risoria, (Lehrman, 1955, 1964) and mourning doves, Zenaidura macroura, (Laub, 1956).

Band-tailed pigeons are commonly hunted during part of their nesting season (Neff and Niedrach, 1946; Einarsen, 1953; Smith, 1968; Silovsky, 1969; March and Sadleir, 1970), but the effect of killing adults that are producing crop-milk on the productivity of populations has not been measured. Therefore, the objectives of this study were:

1. To develop criteria for separating crops which were inactive or in various phases of the production of crop-milk.
2. To determine the frequency of phases of production of crop-milk in a sample of band-tailed pigeons killed by hunters.
3. To determine the fate of squabs when one parent was removed during incubation or brooding.
4. To estimate the reduction of productivity which may have occurred from killing adult pigeons which were producing crop-milk.

II. METHODS

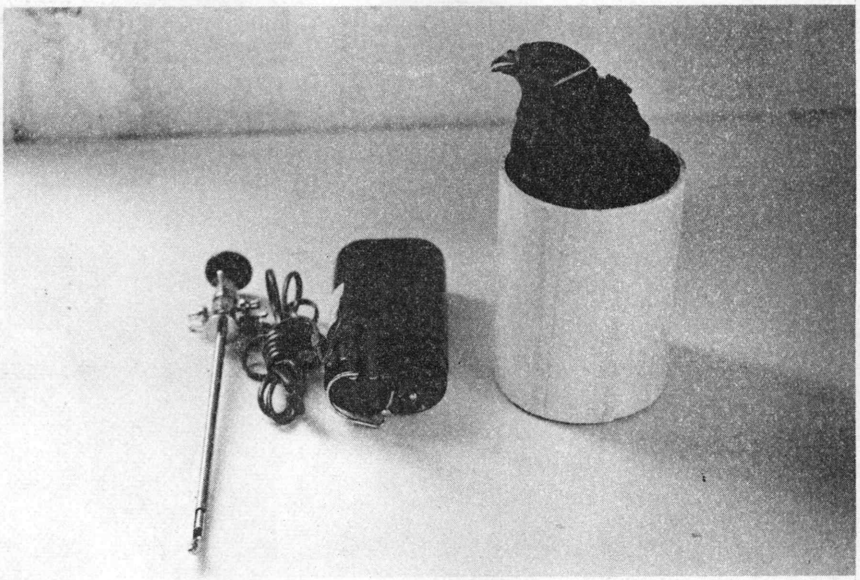
A breeding flock of captive band-tailed pigeons was maintained 5 miles west of Corvallis, Oregon. Ten pairs, each composed of a male and a female bird, and several additional birds of both sexes were housed in 11 outdoor pens, 12-x 6-x 6-ft. Each pair was placed in a separate pen and all additional birds were placed in one holding pen. A small tree, usually a Douglas fir, _Pseudotsuga menziesii_, was enclosed in each pen to provide a nesting site. Two nest cones (9 inch diam) constructed of ¼-inch hardware cloth were placed in different locations in the tree to offer the birds a choice of nest sites. Each pen was provided with commercial pigeon feed, water, calcium grit, and small sticks for nesting material. All 11 pens and an observation shack were enclosed by a 1 x 2 inch mesh fence, 4-ft high. On the exterior of the mesh fence, a two-strand electric fence was mounted to discourage climbing by mammalian predators.

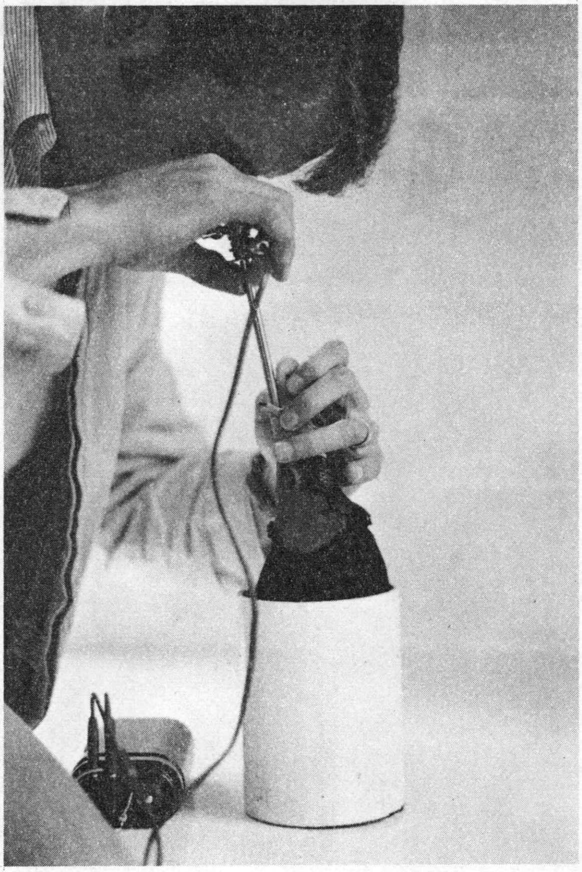
Examination of Crops by Living Birds

Crops of living birds held captive were examined with a cystoscope (Figure 1, ACMI model 24 F) to determine changes in gross appearance, and the timing of these changes through the reproductive cycle. During examinations, birds were restrained by placing them in a nylon stretch sock, which had been modified by cutting a hole in the

Figure 1. Cystoscope, power unit, and band-tailed pigeon ready to be examined.

Figure 2. Examining the lobes of the crop of a band-tailed pigeon with a cystoscope.





toe to allow the head of the bird to protrude. The bird was supported in an upright position by placing it in a piece of irrigation pipe (6 inch x $3\frac{1}{2}$-inch inside diam). The cystoscope was then inserted down the esophagus into the lumen of the crop (Figure 2). Each crop lobe could be examined by rotating the cystoscope.

Large amounts of grain hampered examination of the crop with the cystoscope by obscuring visibility. I found it expedient to make examinations of incubating and brooding birds prior to the time that they were relieved by their mates in order for them to feed. At these times, the amount of grain in the crop did not interfere with the examination. The feed was removed from the pens of birds whose squabs required infrequent brooding 6 to 8 hours prior to examining their crops with the cystoscope in order to prevent recently ingested grain from interfering with examinations.

Histological Studies

Histological studies were initiated in 1969 to facilitate differentiation of crops from birds in different stages of the reproductive cycle. Due to the limited size of the flock of captive band-tailed pigeons, domestic pigeons, which exhibit the same cycles of the crop as do band-tailed pigeons, were used for additional histological study.

Tissue samples were taken from the crops of living birds by making an incision in the external wall of the crop, removing a small piece of the lobe, and then suturing the incision. Samples were taken from the same bird whenever possible and at approximately the same time of day. Tissue was also taken from the crops of birds that were sacrificed. Samples were taken from birds at 10, 12, and 14 days of incubation; 1, 5, 10, 15, and 20 days of brooding; and 7 days after the squabs fledged. All tissue samples were fixed in 10% formalin and stored in 5% formalin. Tissues were frozen to -13C and sectioned with a cryostat. Five sections from each sample were stained in Harris' haematoxylin and counterstained in eosin y. Two sections from samples of developing and regressing crops were stained in Ehrlich's haematoxylin and sudan IV to demonstrate neutral fats (A. Owczarzak, personal communication).

Disruption of Nests

The capability of one parent to fledge a squab was determined by removing the other parent at various stages of incubation and brooding. Parents were removed at 11, 9, 6, and 4 days after squabs hatched. Two males were removed in the evening after the females began brooding, and four females were removed in the morning after the males began brooding.

Examination of Pigeons Killed by Hunters

Pigeons killed by hunters at a mineral spring near Crawfordsville, Linn County, Oregon, were examined to determine the frequency of various crop phases in the sample. This area was closed to hunting at 1 p. m. each day. The crop of each adult pigeon was opened and classified according to: (1) the occurrence of crop-milk in the crop, (2) the condition of the crop-milk (i. e. intact on the lobe or sloughed into the lumen), and (3) the degree of fusion of the folds (i. e. no fusion, partial fusion, complete fusion). Representative photographs were taken of all identifiable crop phases. The lobes of the crop were then excised and preserved for further study.

An attempt was made to examine birds soon after they were killed by hunters to determine the frequency of various crop phases, by time, through the morning. Most hunters were checked several times during the morning.

III. RESULTS AND DISCUSSION

Anatomy and Physiology of the Crop

Anatomy

The wall of a pigeon crop is composed of four distinct layers: (1) an outer layer of fibrous connective tissue, (2) a muscular layer, (3) a tunica propria, and (4) a stratified epithelium (Litwer, 1926; Beams and Meyer, 1931; Patel, 1936; Weber, 1962; Dumont, 1965; March and Sadleir, 1970). The germinal layer of the stratified epithelium is capable of rapid proliferation which pushes newly formed cells away from their blood supply into the superficial layer. These cells, which eventually slough into the lumen of the crop, constitute the crop-milk (Beams and Meyer, 1931).

Physiology

The development of the crop epithelium is controlled by the pituitary hormone prolactin (Riddle, Bates and Dykshorn, 1932). This hormone acts directly on crop tissue and not through any intermediate mechanism (Riddle and Bates, 1936; Lehrman, 1955). Lehrman (1964) concluded that reciprocal interrelations between the endocrine system and stimuli from the external environment act to control the entire reproductive cycle. Thus, external stimuli initiate hormone secretion which elicits changes in behavior, that may in turn be a further source of stimuli.

Davies (1939) analyzed crop-milk from domestic pigeons and found it was composed of 28.5% dry matter which was 58.6% protein, 33.8% fat, 4.6% ash, and 3.0% starch. Young chickens fed a supplemental diet (5 g per chick per day) of crop-milk showed remarkable growth gains over a control group fed a standard ration (Pace, Landlot, and Mussehl, 1952). The growth promoting factor in crop-milk was though to be a complex of vitamins (Reed, Mendel, and Vickery, 1932).

Cycles of the Crop

Seasonal Cycle

The seasonal cycle of the crop extends from the time the egg is laid, through fledging of the squab, until the egg of the next cycle is laid. The seasonal cycle was divided into four phases on the basis of crop activity and appearance (Figure 3):

(1) Inactive

The crop appeared thin-walled and transparent for the first 10 to 12 days of the seasonal cycle.

(2) Developing

The first noticeable hypertrophy of the crop occurred after

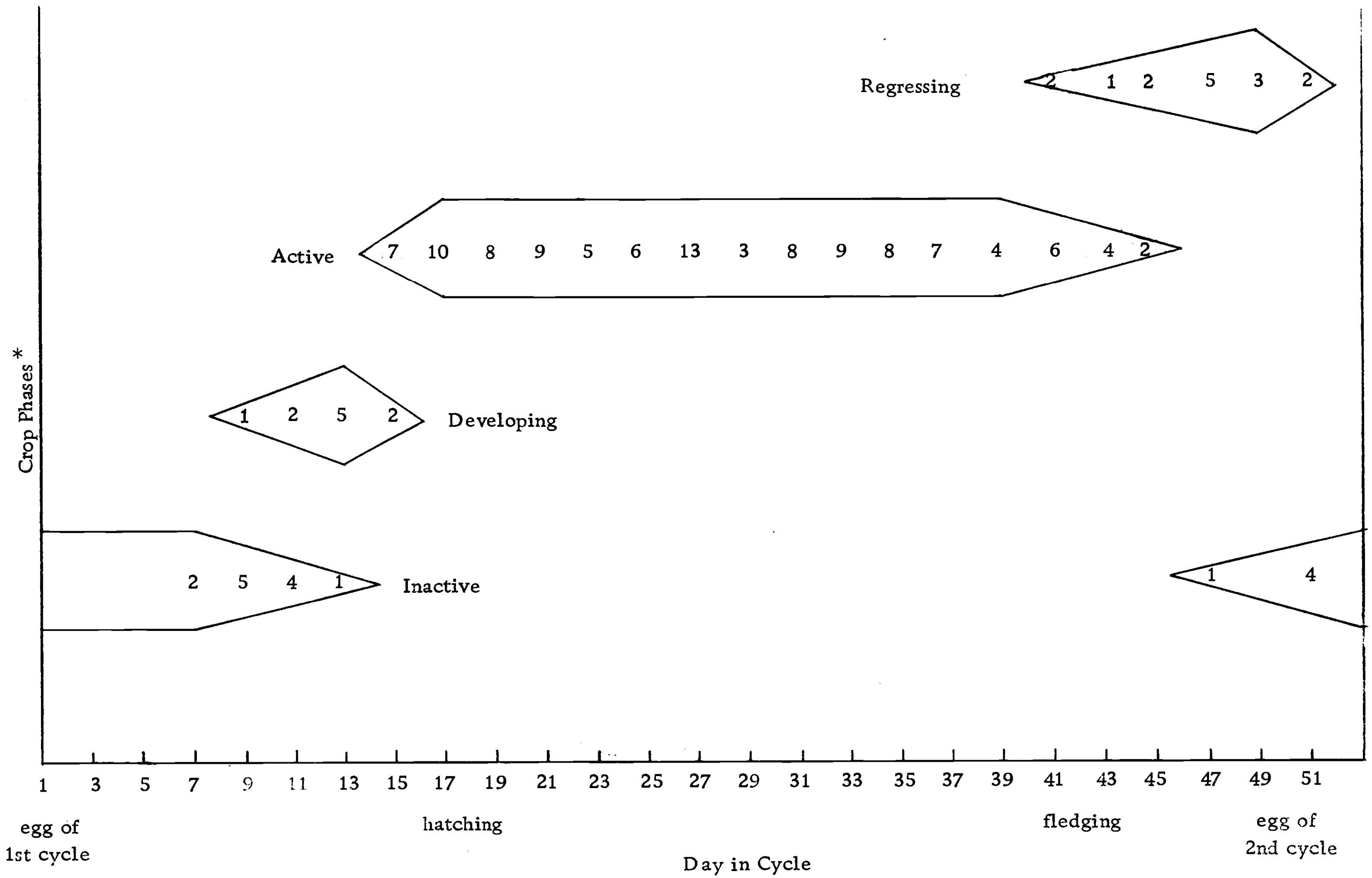


Figure 3. Seasonal cycle of crops of captive band-tailed pigeons based on 151 observations with a cystoscope.+

* For description of crop phases see pages 9-14.

\+ Total observations for each day can be determined by adding the numbers positioned perpendicular to the day.

birds incubated for 8 days (Beams and Meyer, 1931). At this time an increase in the blood supply was evident, and the lobes became thickened so that distinct folds were visible. The thickness of the lobes continued to increase, and by the 15th day of incubation, the greatly enlarged folds began to fuse. This process of fusion was described by Beams and Meyer (1931) as, "an increase in the thickness of the folds produced by rapid division of the cells in the proliferating layer, thus increasing the width of the epithelium and decreasing the space between the folds." Prior to hatching of the squabs (about 18 days incubation) the crop lobes reached their greatest development. The folds were fused completely, and the smooth surface of the crop represented several layers of crop milk. The crop-milk sloughed into the lumen of the crop before the squabs hatched (Patel, 1936).

(3) Active

The crop began to produce crop-milk and the process of crop-milk formation described by Beams and Meyer (1931) was repeated in a daily cycle.

Daily Cycle. Researchers in the past have not reported that crops of pigeons and doves undergo a daily cycle in the production of crop-milk. However, Beams and Meyer (1931) described the developmental phases in the formation of crop-milk, March and Sadleir (1970) reported that active crops were varying in appearance, and Murton (1965) found that crop-milk was sloughed from the lobes of the crop in one mass at periods when nestlings were due to be fed.

The existence of a daily cycle was substantiated by examining the crop of the same bird with a cystoscope at different times during the day, and by examining and photographing crops of female birds that were sacrificed at different times of the day and night (Figure 4). The crops in Figure 4 are characteristic phases in the daily cycle of the production of crop-milk. These phases are described as:

Phase I- The lobes are thin, heavily folded, and rosy red in color; they sometimes contain small pieces of crop-milk.

Phase II- The lobes are thicker; the folds are fused partially and mottled pinkish-white in color.

Phase III- The lobes are still thicker; the folds are fused completely, and the surface of the lobes is nearly smooth and off-white in color.

Phase IV- The lobes reach their maximum thickness in the cycle; the surface of the lobes is a smooth layer of intact crop-milk, pale yellow in color.

Phase V- The crop-milk has sloughed into the lumen; the thin, heavily folded lobes can be seen under the masses of crop-milk.

Phase V is not a true developmental phase in the daily cycle of the crop, but merely represents a time during which the lumen of the

Figure 4. Characteristic phases in the daily cycle of crops of band-tailed pigeons. All crops were taken from female band-tailed pigeons.

Phase I- collected at 7:30 a. m., nest stage unknown.

Phase II- collected at 1 p. m., 4 days brooding.

Phase III- collected at 6 p. m., 9 days brooding.

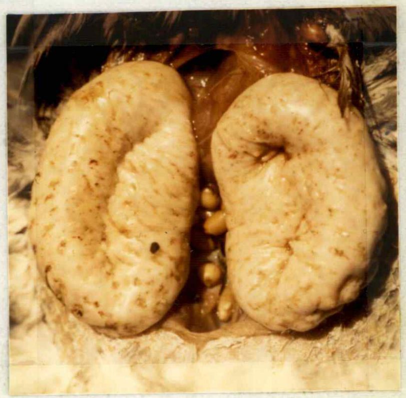
Phase IV- collected at 1 a. m., 2 days brooding.

Phase V- collected at 4 a. m., 4 days brooding.

I

II

III



IV

V

crop contains crop-milk. The lobes of the crop appear as Phase I. The interval between the process of sloughing and the feeding of the squab determines the interval that the crop will be found in Phase V. Small amounts of crop-milk sometimes are found in the lumen and on the lobes during Phase I and Phase II.

Daily cycles of crops of males and females appeared not be be synchronized (Table 1, Figures 5 and 6).

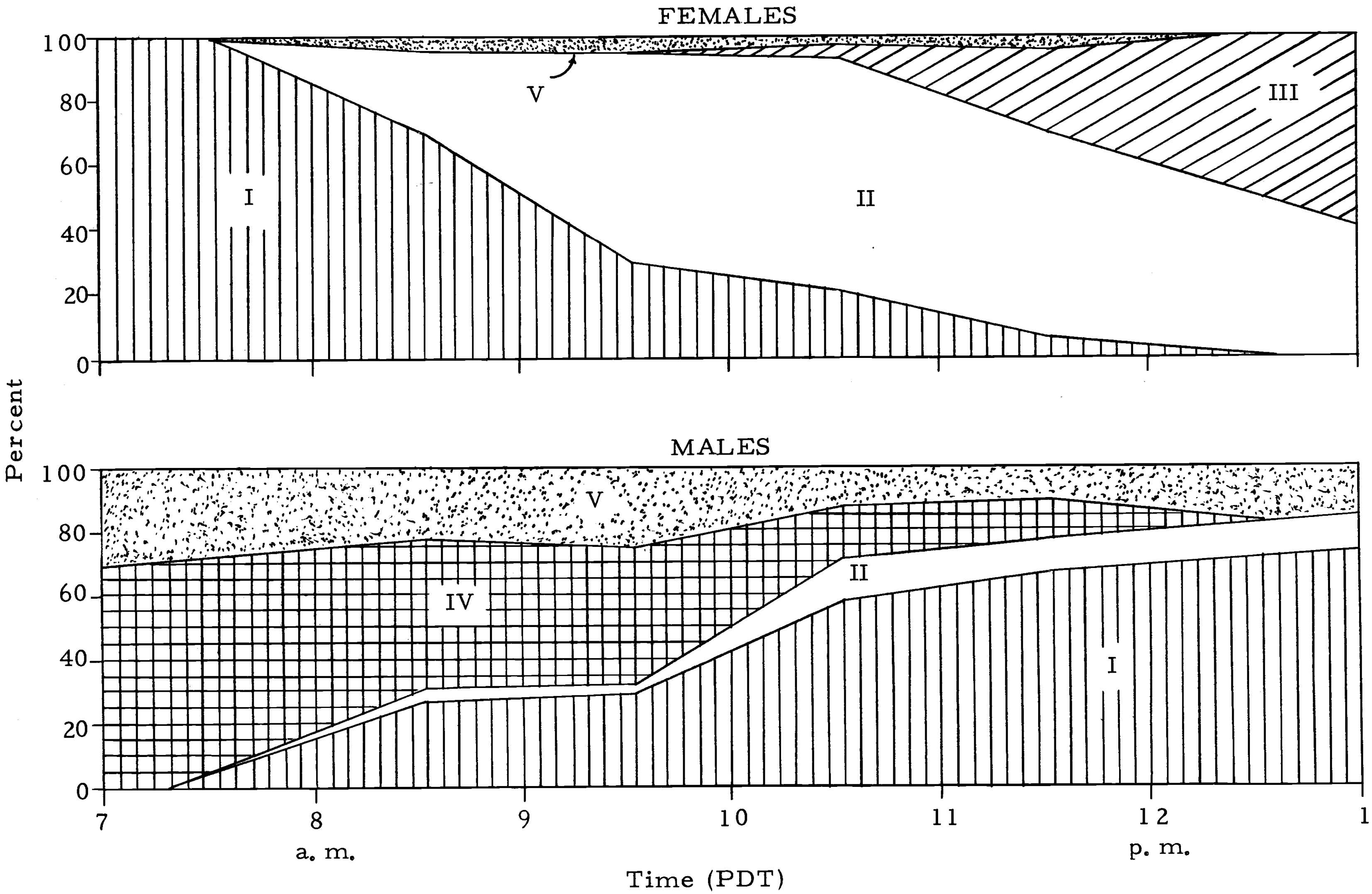
The period in the seasonal cycle when the crop is actively producing crop-milk seems to vary with the different species of columbids. Band-tailed pigeons produced crop-milk for approximately 30 days, beginning 2 or 3 days before the squab hatched, and ending 2 or 3 days after the squab fledged (Figure 3). Domestic pigeons had active crops from shortly before the squab hatched until the 16th or 17th day of brooding (Litwer, 1926; Patel, 1936). Mourning doves produced crop-milk from a few days after the mid-point of incubation until 6 to 8 days after the first young hatched (Laub, 1956).

(4) Regressing

The lobes of crops in early stages of regression (4 to 6 days after fledging) appeared thin with shallow furrows and contained small bits of crop-milk (Figure 3). In later stages of regression (6 to 10 days after fledging) the lobes were very thin, and the folds appeared vermicular. Regression of the lobes was usually complete 10 days after squabs fledged (Figure 3). Regression of crops of domestic

Figure 5. Percent distribution of active crop phases of 189 male and 192 female band-tailed pigeons killed between 7 a.m. and 1 p.m., September 1-10, 1968 and 1969, near Crawfordsville, Linn County, Oregon.

Phase I-	lobes thin, heavily folded, rosy red.
Phase II-	lobes thick, folds partially fused, pinkish-white.
Phase III-	lobes thick, folds completely fused, surface smooth, white.
Phase IV-	lobes very thick, surface smooth, pale yellow.
Phase V-	feeding phase, crop-milk in lumen, lobes appear as Active I.



FEMALES
MALES
Percent
100
80
60
40
20
0
I
II
III
IV
V
7
8
9
10
11
12
1
a. m.
p. m.
Time (PDT)

Figure 6. Schematic representation of the daily cycle of crops of band-tailed pigeons based on observations of crops of captive birds with a cystoscope, photographs of crops of birds sacrificed at different times of the day and night (Figure 4), and the frequency distribution of active crop phases in a sample of pigeons killed by hunters (Figure 5).

Phase I- lobes thin, heavily folded, rosy red.

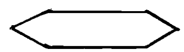
Phase II- lobes thick, folds partially fused, pinkish-white.

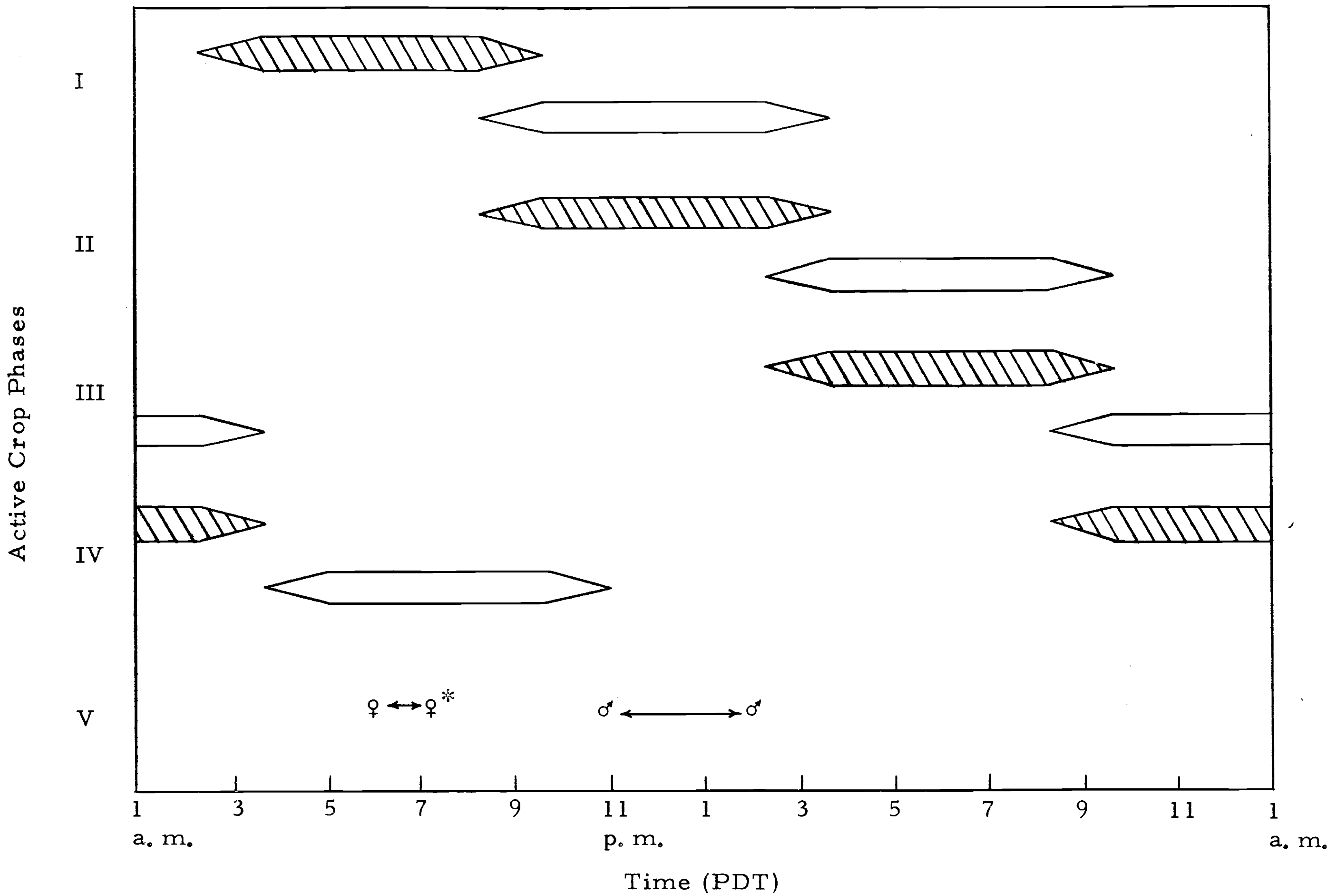
Phase III- lobes thick, folds completely fused, surface smooth, white.

Phase IV- lobes very thick, surface smooth, pale yellow.

Phase V- feeding phase, crop-milk in lumen, lobes appear as Phase I.

Females 

Males 



* The interval between the symbols represents the period of time in which a squab was observed being fed by a male or a female band-tailed pigeon.

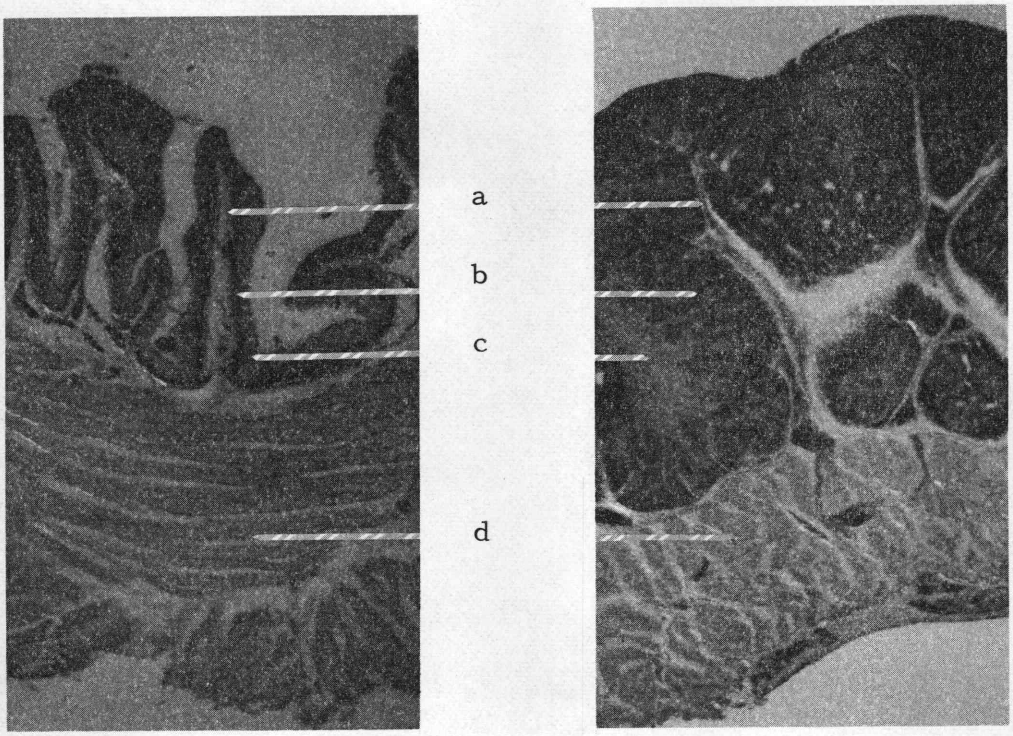
Table 1. Percent distribution of various phases of active crops of band-tailed pigeons killed between 7 a.m. and 1 p.m., September 1-10, 1968 and 1969, near Crawfordsville, Linn County, Oregon.

			Crop Phases (percent)									
	No. Examined		Phase I		Phase II		Phase III		Phase IV		Phase V	
Time	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
a.m.												
7	18	5	5.5	100.0	0.0	0.0	0.0	0.0	66.7	0.0	27.8	0.0
8	26	23	26.9	69.6	3.8	26.1	0.0	0.0	46.2	0.0	23.1	4.3
9	38	41	29.0	29.3	2.6	65.8	0.0	0.0	42.1	0.0	26.3	4.9
10	56	82	57.9	22.2	14.0	74.1	0.0	1.2	15.8	0.0	12.3	2.5
11	49	50	67.4	6.0	10.2	66.0	0.0	24.0	12.2	0.0	10.2	4.0
12												
p.m. 1	18	8	72.2	0.0	11.1	50.0	0.0	50.0	0.0	0.0	16.7	0.0

* See page 12 for description of crop phases.

pigeons began about 1 to 2 weeks after squabs hatched and was usually complete on the 25th or 26th day of brooding, or before the eggs of the next cycle were laid (Litwer, 1926; Beams and Meyer, 1931; Patel, 1936). Lehrman (1964) weighed crops of ring doves through the seasonal cycle and found they regressed to normal weight about 17 days after the squabs hatched (3 days after fledging).

Throughout this study an attempt was made to develop a method to differentiate between crops taken on different days of the seasonal cycle. Crops in early stages of development (8 to 13 days) and late stages of regression could usually be distinguished from active crops by the thickness of the lobes. Developing crops could usually be distinguished from crops in early stages of regression by small pieces of crop-milk which remained in the lumens and on the lobes of regressing crops. Developing crops could not be reliably differentiated from crops in late stages of regression by gross appearance of the lobes. Histologically, developing crops and those in late stages of regression appeared separable by three differences (Figure 7): (1) the epithelial layer of developing crops was much thicker than the epithelial layer of regressing crops; (2) the germinal layer of the stratified epithelium, distinguished by deep staining cells (Patel, 1936), occupied a much larger portion (over half) of the stratified epithelium in developing crops; and (3) developing crops contained much larger quantities of fat globules in the stratified epithelium. These results were



(1) (2)

Figure 7. Photomicrographs of tissue from crops of domestic pigeons. (1) regressing tissue removed from a male pigeon 7 days after it's squab fledged. (2) developing tissue removed from a male pigeon at 10 days incubation. a) tunica propria, b) germinal layer of the stratified epithelium, c) superficial layer of the stratified epithelium, d) muscular layer. Fat globules are not visible. X30.

corroborated by March and Sadleir (1970). Crops taken from pigeons on different days during the active phase of the seasonal cycle could not be differentiated by either histological or gross appearance.

Feeding of the Young

Band-tailed pigeons were reported feeding squabs at sunrise, between 8 and 9 a. m., 12 and 2 p. m., and at sunset (Neff, 1947), and between 11 a. m. and 2 p. m. (Peeters, 1962). All observers reported either two or three feedings a day for the first week after the squab hatched; thereafter feedings varied. Females were reported feeding squabs at sunrise and sunset and a male was reported feeding a squab between 8 and 9 a. m. (Neff, 1947).

A pair of captive band-tails was observed every 5th day from the 1st day after the squab hatched to the 20th day of brooding (Figure 8). During the first week of brooding, feedings were timed with the cycling of the crop (Figure 6). The female fed the squab once or twice at sunrise, and the male fed it several times between 11 a. m. and 2 p. m. From the 10th to the 20th day of brooding, the feedings were more frequent, usually 6 to 8 times per day. The female continued to feed the squab at sunrise, but the male fed it earlier in the morning, between 7:30 a. m. and 9 a. m. During the remainder of the day the parents alternated feedings at 1 to 2 hour intervals.

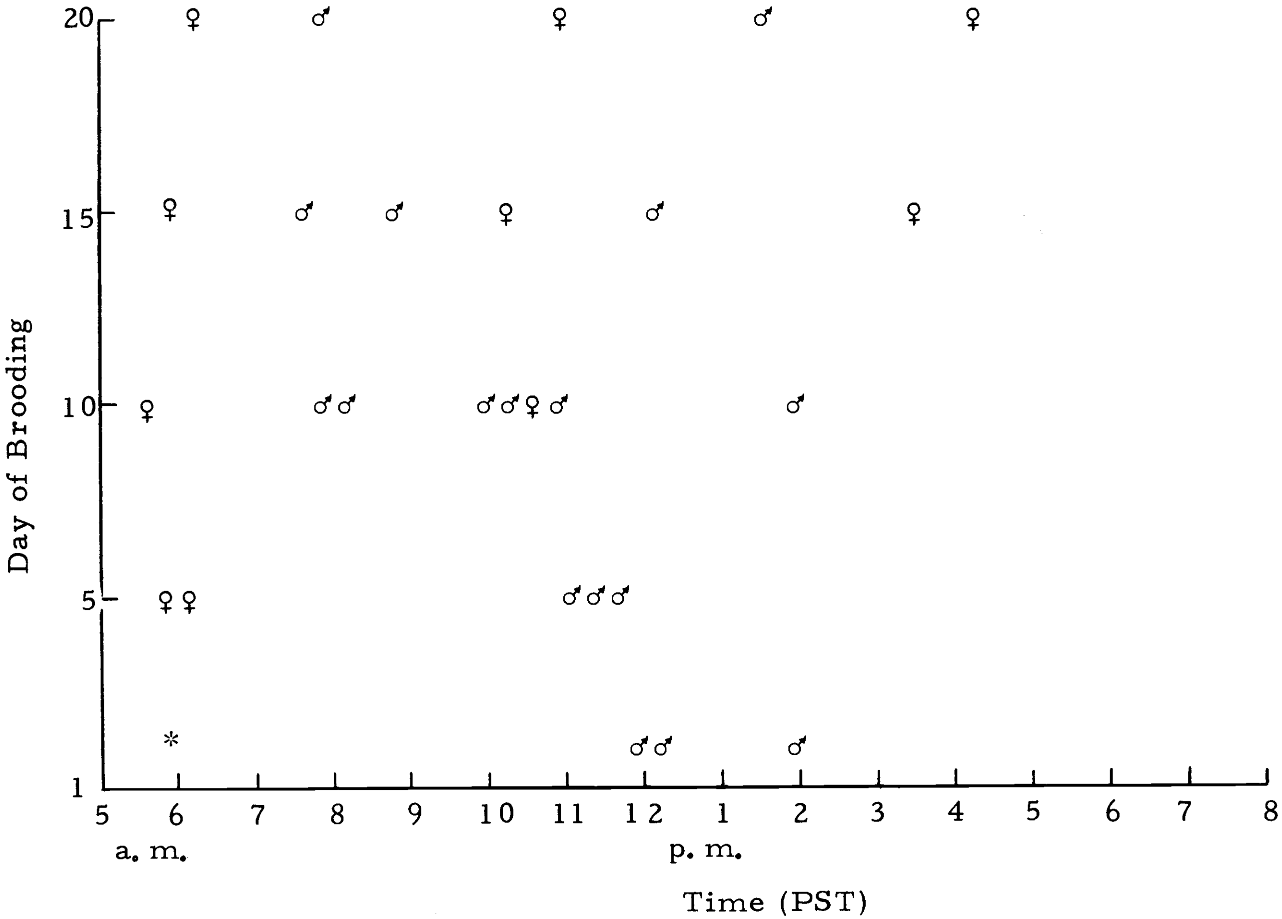


Figure 8. Frequency and timing of feeding of a squab by a pair of captive band-tailed pigeons through the period of brooding (each symbol represents one feeding).

* Poor lighting conditions prevented observation of the nest. However, it is probable that the squab was fed at this time since day 1 was the first day after the squab hatched and most altricial birds absorb their yolk before the egg hatches (Welty, 1963).

Frequency of Active Crops in Pigeons Killed by Hunters

The various appearances of phases involved in the daily cycle of the crop have caused confusion in identifying pigeons and doves with active crops (Caldwell, 1957; Silovsky, 1969). Band-tailed pigeons with active crops were killed by hunters during September in Colorado (Neff and Niedrach, 1946), California (Smith, 1968), Oregon (Einarsen, 1953; Silovsky, 1969), and British Columbia (March and Sadleir, 1970). Smith (1968) and Silovsky (1969) reported 60 to 68 percent, respectively, of the band-tailed pigeons they examined had crops in some stage of development, crop-milk production, or regression, but the percentages of pigeons with active crops in their samples were undetermined. March and Sadleir (1970) found that active crops varied in appearance, thus the percentages of pigeons with active crops in their samples, 57% of 197 in 1968 and 70% of 59 in 1969, are probably accurate.

Sixty-two percent of 614 band-tailed pigeons killed by hunters in this study had active crops (Table 2). Pigeons with developing and regressing crops made up a small part of the sample (2% and 5%, respectively). Thirty-one percent of the pigeons killed had inactive crops. There was a significant difference ($p < 0.10$) between the number of males, 78 of 294 (26.5%), and females, 109 of 320 (34.0%), with inactive crops ($\chi^2 = 2.834$, 1 d.f.). I found no evidence

Table 2. Percent distribution of seasonal phases of crops of band-tailed pigeons killed between September 1-10, 1968 and 1969, near Crawfordsville, Linn County, Oregon.

Crop Phase (percent)	1968 Males	1968 Females	1968 Totals	1969 Males	1969 Females	1969 Totals	Combined Years Males	Combined Years Females	Grand Total
	(159)*	(163)	(322)	(135)	(157)	(292)	(294)	(320)	(614)
Inactive	26.4	34.3	30.4	26.7	33.8	30.5	26.5	34.0	30.5
Developing	3.1	1.9	2.5	2.2	1.9	2.1	2.7	1.9	2.3
Active	64.2	58.9	61.5	65.2	61.1	63.0	64.6	60.0	62.2
Regressing	6.3	4.9	5.6	5.9	3.2	4.4	6.2	4.1	5.0

* Numbers of birds examined are in parentheses.

during my study that would serve to explain this difference. However, Ljunggren (1969) suggested that female wood pigeons may stop feeding squabs earlier in the seasonal cycle than do males. He observed increased ovarian activity in females near the end of the seasonal cycle indicating they were preparing to lay a new clutch of eggs. March and Sadleir (1970) found similar evidence in band-tailed pigeons. It is common for domestic pigeons and wood pigeons to lay a new clutch of eggs while the previous brood is still being fed (Whitman, 1919; Murton, 1965). When this occurs the female loses interest in her young and begins to incubate the new clutch of eggs, while the male continues to feed the young (Whitman, 1919).

Disruption of Nests

Survival of Squabs

When one parent of a pair of nesting pigeons or doves is killed, the survival of the squab (s) depends upon the ability of the remaining parent to provide sufficient nourishment and brooding. Band-tailed pigeon squabs could not survive under the care of one parent if the other parent was removed prior to the 6th day of brooding (Table 3).

Goforth (1964) reported a male mourning dove fledged two squabs after the female was removed from the pen on the 4th day of incubation. The squabs required several additional days for fledging and

Table 3. Success of nests of captive band-tailed pigeons that were disrupted by removing one parent at various stages of incubation and brooding to test the ability of the other parent to fledge the squab, 1968, 1969, and 1970.

Pen Number	Sex of Parent Remaining	Date	Nest Stage	Results
1	Female	9-19-68	16 days incubation	*Egg hatched, squab was brooded for 5 days and found dead in the nest on the 6th day after hatching. It's crop was full of crop-milk.
1	Male	9-28-69	4 days brooding	Squab was found dead in the nest 6 days after the female was removed. It's crop contained a small amount of crop-milk.
10	Female	9-19-69	6 days brooding	Squab was fledged 29 days after hatching.
7	Female	7-27-69	9 days brooding	Squab was fledged 22 days after hatching.
9	Female	8-18-69	9 days brooding	Squab was fledged 22 days after hatching.
7	Male	4-25-70	9 days brooding	Squab was fledged 24 days after hatching.
10	Female	7-25-69	11 days brooding	Squab was found dead in the nest 3 days after the male was removed. It's crop was empty; the female had laid another egg in the nest.

*This experiment was initiated when a male bird was killed during an examination with the cystoscope.

were markedly underweight. One of the squabs died 3 days after it fledged. Males of four other pairs did not complete incubation after removal of the female on the 4th day. Laub (1956) removed one parent at various stages of incubation and brooding from 65 dove nests and found that nestlings were 6 to 8 days old before one parent could fledge them. This information cannot be compared directly to Table 3 because mourning doves hatch after 12 days incubation, and the nestlings fledge about 12 days later (Laub, 1956). Laub (1956) found no correlation between the sex of the parent removed and survival of squabs. Results of this study agreed with those of Laub's (1956).

The Factor of Brooding in the Survival of Squabs

The time in the nesting cycle when Laub (1956) found that two nestling doves could be fledged by one parent (6 to 8 days brooding) closely coincides with the development of thermoregulation in that species. Thermogenesis in mourning doves begins about 6 days of age (Breitenbach and Baskett, 1967). There is no experimental evidence indicating when thermogenesis begins in band-tailed pigeons. However, captive band-tailed pigeons rarely brooded squabs 9 to 12 days old. Similar observations were reported in ring doves, 4 to 8 days old (Lehrman, 1955), and domestic pigeons, 7 days old (Whitman, 1919). Stannard (Neff, 1947) observed a nest in which a band-tailed pigeon squab, approximately 1 week old, was not brooded at night.

Other altricial birds exhibit various degrees of thermogenic development with age. Eastern house wrens are able to regulate their body temperature slightly at 3 to 6 days of age (Sturkie, 1965). Eastern field sparrows and eastern chipping sparrows are essentially homeothermic at 7 to 10 days of age (Sturkie, 1965).

Thermogenesis is only one factor in the development of thermoregulation in altricial birds. Young mourning doves underwent a marked thermogenic change between 6 and 9 days of age (Breitenbach and Baskett, 1967). This change was largely attributed to the development of the insulative feather coat. Another important factor is the decreasing body surface to mass ratio with growth of the young bird (Sturkie, 1965).

The Factor of Nourishment in Survival of Squabs

Laub (1956) concluded that the most important factor limiting survival of squabs that had lost one parent was the inability of the other parent to provide sufficient crop-milk. Since band-tailed pigeons rarely have to care for more than one squab (Macgregor and Smith, 1955; Glover, 1953) and produce crop-milk for the entire brood period, it seems unlikely that insufficient crop-milk would be the most important factor limiting survival of squabs. The inability of one parent to provide sufficient brooding would appear to be an equally important factor limiting survival of squabs in disrupted nests of band-tailed pigeons.

Estimating the Loss of Productivity Due to Hunting in September

Shooting band-tailed pigeons with active crops undoubtedly results in a loss of nestlings. To determine this loss, the following information concerning productivity of populations was needed:

1. The annual production prior to the hunting season, defined as the number of squabs per 100 females produced prior to September 1.
2. The annual production during the hunting season; defined as the number of squabs produced during September per 100 females alive August 31.
3. The potential annual production; defined as the number of squabs per 100 females that could be produced in an entire breeding season if there was no loss due to hunting.

Nesting Studies

There have been few nesting studies of band-tailed pigeons, consequently there is little known concerning productivity of populations. It was generally thought that band-tailed pigeons reared no more than one brood per season (Grinnell, 1913; Glover, 1953), but Macgregor and Smith (1955) reported age ratios from pigeons killed in California in December that could be explained only by a production of greater than one young per pair, or by differential migration and/or vulnerability between young birds and adults. They also reported observations of 26 nestings, 65% of which were considered successful in fledging squabs. One pair of birds attempted four nestings and fledged three squabs in one nesting season. March and Sadleir (1970) found evidence that band-tailed pigeons in British Columbia were producing two clutches of eggs during the breeding season.

Multiple Nesting by Pigeons in Oregon

There is no direct evidence of multiple nesting by band-tailed pigeons in Oregon, but it seems probable that most of the population sampled is attempting at least two nestings. This appears true for several reasons.

First, evidence that pigeons nest from April through August in Oregon was obtained by back-calculating the ages of immature pigeons killed by hunters (Figure 9). Ages of immature pigeons can be determined by noting the stage in molt of primary feathers and knowing how long after hatching that stage occurs (G. D. Silovsky, personal communication).

Second, considering the time required to complete the seasonal cycle, it is possible for a pair of band-tailed pigeons to fledge two squabs between June 1 and September 1 in Oregon (Figure 3). Murton (1965) reported that wood pigeons in England could rear three broods of young from July through October. He accounted for some overlap

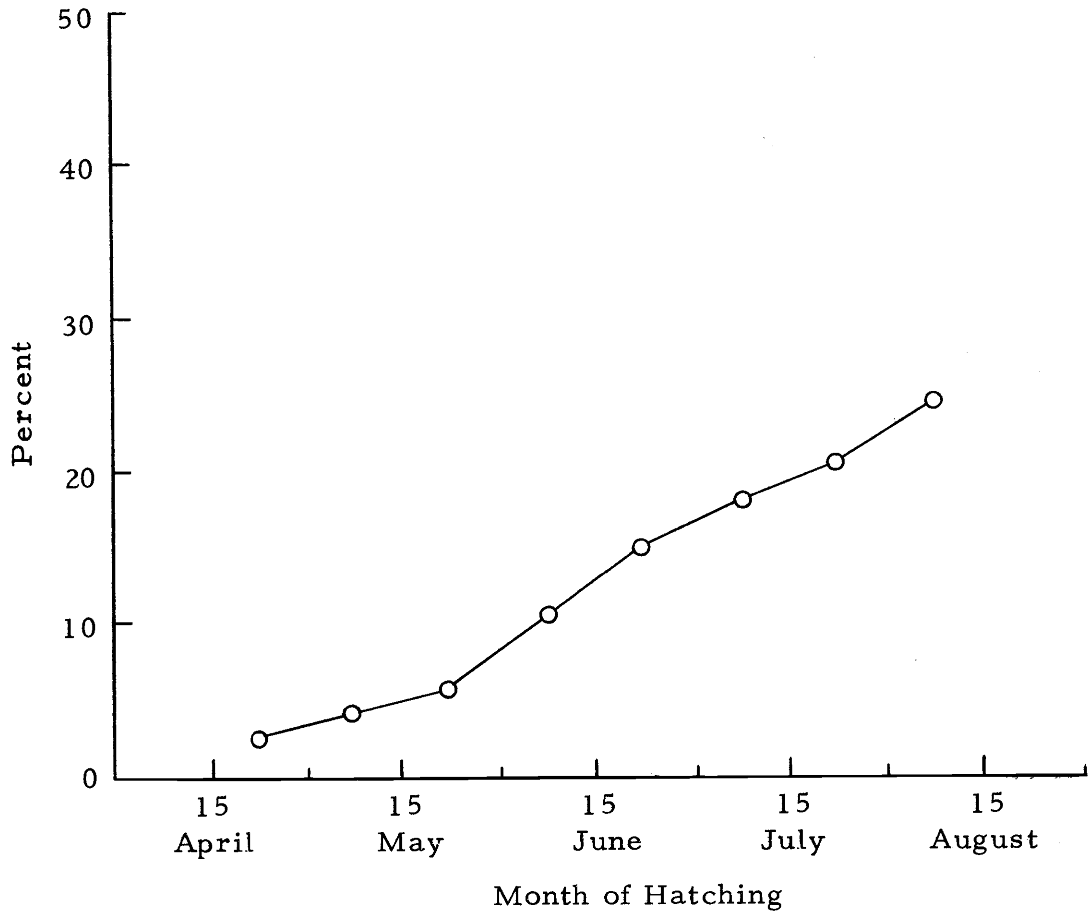


Figure 9. Apparent distribution of the hatch of immature band-tailed pigeons by 15 day periods. Hatching dates were determined by back-calculating the ages of immature pigeons killed by hunters (Silovsky, 1969).

in cycles, because he observed fresh eggs being laid and incubated before the previous brood was fledged. March and Sadleir (1970) suggested that there is also some overlap between seasonal cycles of band-tailed pigeons, and concluded that pigeons laying eggs in May could fledge two broods in one nesting season in British Columbia.

Third, it seems unlikely that 65% of the population would still be nesting in September if only one squab per pair were produced. It is also unlikely that the population could remain stable with such low productivity. Silovsky (1969) estimated that a population of band-tailed pigeons must produce 1.28 squabs per pair to remain stable under mortality rates he computed for pigeons in Oregon.

Estimating Production

Because of the lack of knowledge regarding productivity of populations of band-tailed pigeons, a theoretical population of 100 pairs of pigeons was created to estimate annual production and potential annual production. Estimates were based on the following assumptions: (1) All pigeons begin nesting June 1, (2) the interval between the laying of an egg in a successful nest and an egg in the succeeding nest is 50 days, (3) the interval between egg laying and fledging of the squab is 42 days, (4) nexts which failed to produce young were incubated for an average of 15 days. Most failures of nests of white-winged doves and wood pigeons occurred in the egg stage (Murton, 1965; Cottam and Trefethen, 1968),

(5) 8 days are required between a nest failure and the laying of another egg (renest), (6) 65% of the pairs, per nesting attempt, are successful in fledging squabs (Macgregor and Smith, 1955). On the basis of these assumptions, the potential annual production was diagrammed (Figure 10).

To estimate the annual production that occurred during the hunting season, the following additional information was needed:

a. The approximate day in the seasonal cycle of crop activity of each pigeon killed by the hunters.

b. The potential for survival of eggs and squabs under the care of one parent.

c. An estimate of the mortality of adult pigeons due to hunting in September.

d. An estimate of the percentage of pigeons nesting during the hunting season.

a. Estimating the Stage in Nesting of Pigeons. The approximate day in the seasonal cycle of most adult pigeons killed by hunters could not be determined by examining the crop. Therefore, it was assumed that the pigeons were evenly distributed through the days in the seasonal cycle of crop activity, and that seasonal crop phases were found in the same proportion in the adult population as they were in the seasonal cycle. The inactive phase comprises about 10/50 of the seasonal cycle; developing, about 5/50; active, about 30/50; and

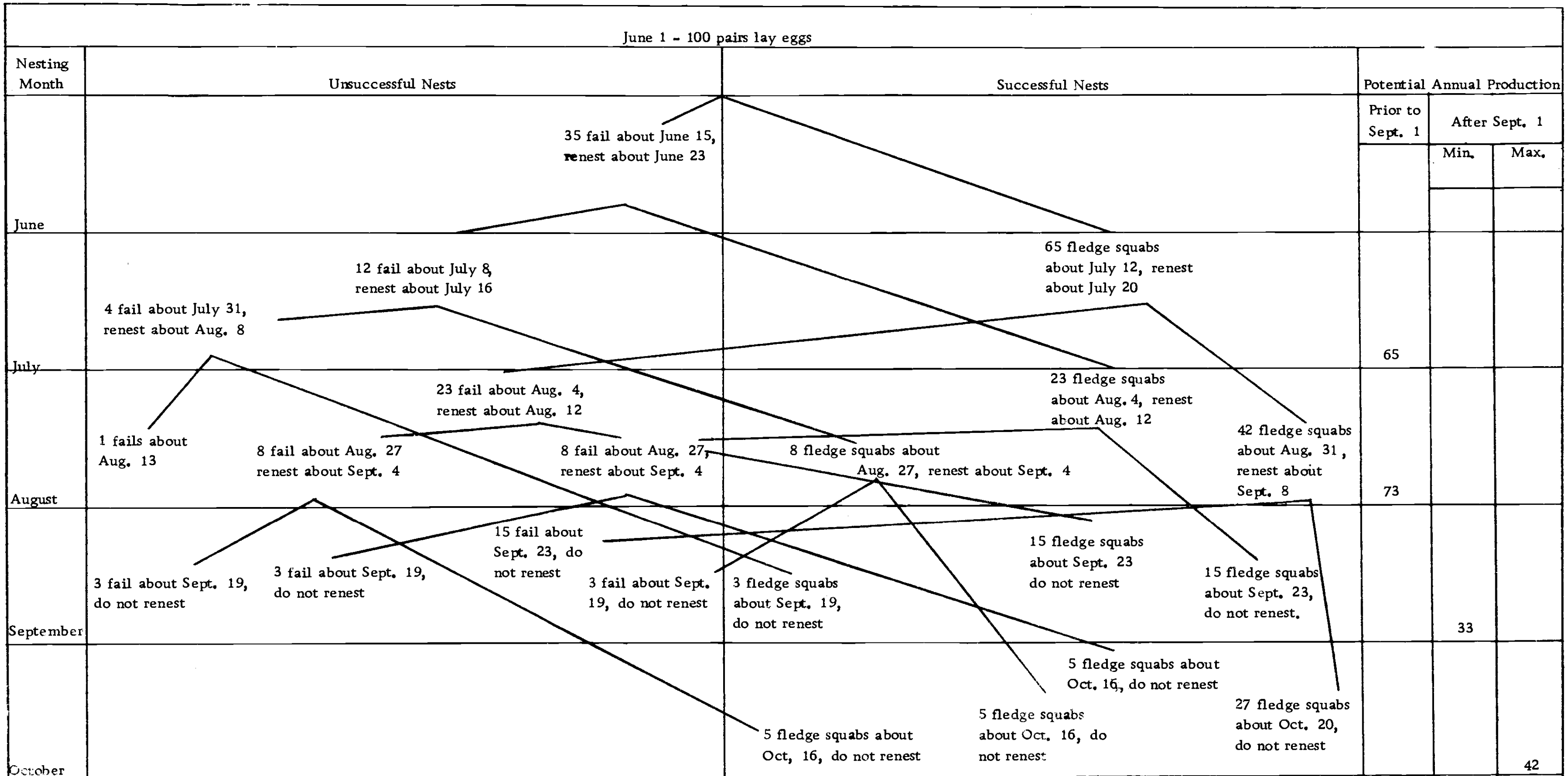


Figure 10. Diagrammatic representation of the potential annual production of 100 pairs of band-tailed pigeons that begin nesting June 1. This figure is based on the following assumptions:

1. The interval between the laying of an egg in a successful nest and the laying of an egg in the succeeding nest is 50 days.
2. The interval between egg laying and fledging is 42 days.
3. The interval between a nest failure and a renest is 8 days.
4. The mean time for a nest failure is 15 days incubation.
5. 65% of the pairs, per nesting attempt, will fledge squabs.

	Prior to Sept. 1	After Sept. 1 Min.	After Sept. 1 Max.
TOTALS	138	33	42
Total annual potential production (minimum)		171	
Total annual potential production (maximum)			213

regressing, about 5/50 (Figure 3). A comparison of the observed and expected frequencies of crop phases of adult pigeons is found in Table 4. The percentage of inactive crops was higher than expected, and the percentage of developing crops was lower than expected. This suggests that due to the lateness of the nesting season, fewer birds than expected were incubating eggs, and birds that had recently completed a nesting cycle were not starting another. The percentage of

Table 4. Observed and expected frequencies* of seasonal crop phases of adult band-tailed pigeons killed between September 1-10, 1968 and 1969, near Crawfordsville, Linn County, Oregon.

Crop Phases (Percent)	Observed Frequency	Expected Frequency
Inactive	30.5	20.0
Developing	2.3	10.0
Active	62.2	60.0
Regressing	5.0	10.0

* Derived from the proportion of the seasonal cycle represented by each of the crop phases (Figure 3 and p. 32 and 34).

regressing crops was lower than expected and was probably due, in part, to classifying some crops in late stages of regression as inactive crops.

b. Survival Potential of Eggs and Squabs. The potential for survival of eggs and squabs under the care of one parent was extrapolated from Table 3. Squabs had to be 9 days old when a parent was removed in order for the remaining parent to fledge them. One squab fledged after a parent was removed on the 6th day of brooding, but it required 5 or 6 extra days to fledge and was quite small.

c. Mortality of Adult Pigeons in September. Mortality rates for pigeons banded in Oregon were computed by Wight, Mace and Batterson (1967) and Silovsky (1969). These authors proportioned the adult first year mortality into a percentage due to hunting and a percentage due to natural causes by using the method of Hickey (1952). To compute hunting mortality using this method, the natural mortality is subtracted from the first year mortality, thus the hunting mortality measured is an annual rate. Because I was concerned only with the hunting mortality during September of adult pigeons that survived to the start of the hunting season, Hickey's (1952) method was inappropriate. Therefore, the following formula was used to estimate hunting mortality (W. S. Overton, personal communication):

$$M = [1 - \frac{a}{b}] \times c$$

where M = The hunting mortality during September of adults surviving to the start of the hunting season.

a = The proportion of adults surviving the first year after they were banded.

b = The proportion of adults surviving to the start of the hunting season.

c = The proportion of the band recoveries that occur during September.

To use this formula the assumptions must be made that band reporting rates are constant and that all natural mortality occurs prior to the hunting season, or between October 1 and August 31.

Sixty-eight percent of recoveries of 2313 pigeons banded near Reedsport, Oregon, were recovered in Oregon (56.6%), Washington (10.5%), and British Columbia (0.9%) during the September hunting season. Thirty-two percent of the recoveries occurred in California after the September hunting season. The population of adult pigeons banded near Reedsport had a first year mortality rate of 30.6%, and a natural mortality rate of 9.4%. If this information is applied to the formula

$$M = \left[1 - \frac{(1 - 0.306)}{(1 - 0.094)}\right] \times 0.680 = 0.159$$

the estimate of hunting mortality that occurs in September is 15.9%.

To determine the number of pairs in the population that would lose one or both members due to hunting, the estimate of hunting mortality was applied to a probability checkerboard (Table 5). It was assumed that there was no differential mortality between the sexes. About 29% of the nesting pairs will lose one or both members (2.6% lose both members, 13.4% lose a male member, and 13.4% lose a female member).

Table 5. Probability checkerboard showing the percentage of pairs of band-tailed pigeons that would be expected to lose one or both members with a hunting mortality of 15.9%.

			Males (percent)	
			shot (15.9)	survive (84.1)
Females (percent)	shot	(15.9)	2.6	13.4
	survive	(84.1)	13.4	70.6

d. <u>Estimates of the Percentage of Pigeons Nesting During September</u>. Estimates of the percentage of pigeons nesting during the hunting season were derived from Figure 10. Because 33 squabs fledged during September, a minimal estimate of the number of pairs nesting would be 33 of 100. Band-tailed pigeon nests containing eggs have been found in late September in Oregon (Neff, 1947) so it is possible that some squabs are fledged in October. A maximal estimate of the number of pairs nesting would be 75 of 100 because 42 additional squabs could be fledged in October (Figure 10).

The percentage of pigeons nesting during September was also estimated from observed frequencies of seasonal crop phases in pigeons killed by hunters (Table 4). To use these estimates, the assumptions were made that none of the adults migrated prior to the hunting season, and the frequency of crop phases in the sample was representative of the population. Of each 100 adults shot during the hunting season, 62 had active crops and two had developing crops. It was assumed that each pigeon shot represented one member of a pair, thus 64 of 100 pairs were assumed to be nesting. About 2.6% of the pairs would be expected to be represented by both members (Table 5), but this would not change the percentage of the population nesting. This was a minimal estimate of the percentage of pigeons nesting because 31 birds classified as having inactive crops could have been in early stages of another seasonal cycle (Table 4). A maximal estimate would include these 31 birds.

Estimates of Production and Losses of Production

Estimates of the annual production that occurs during the hunting season and the loss of potential annual production were computed using two methods.

Method I. The minimal estimate of the number of pigeons nesting was derived from Figure 10. About 26.8%, or 9 of 33 pairs of pigeons nesting in September, would lose one member due to hunting; and 2.6%, or one pair, would lose both members. Of the 9 pairs losing only one member, none were expected to fledge young if the loss occurred prior to the 9th day of brooding. About 75% would be expected to fledge young if the loss occurred after the 9th day (Table 3). The following losses in production would be expected from the 9 pairs if it is assumed that they were evenly distributed through the developing and active phases of the seasonal cycle of crop activity (pigeons with inactive and regressing crops were considered to have completed nesting for the season. The active and developing phases comprise 35 days of the seasonal cycle):

all pairs with developing crops	5/35 = 14%
all pairs in the first 3 days of the active phase (late incubation)	3/35 = 9%
all pairs in the next 8 days of the active phase (early brooding)	8/35 = 23%
25% of the pairs in the remainder of the active phase	25% of 19/35 = 14%
	60%

Total loss =	60% of the production of 9 pairs =	5
	plus one pair with no production =	1
		6

Pairs nesting during September	= 33
Squabs lost due to hunting	= 6
Production during September	= 27/100

The annual production that occurred during September was added to the annual production that occurred prior to the hunting season to estimate the annual production:

$$138/100 + 27/100 = 165/100 .$$

The minimal loss in production was computed by subtracting the annual production from the minimal estimate of the potential annual production and then by dividing by the minimal estimate of the potential annual production (Figure 10):

$$\begin{array}{r} 171 \\ -\underline{165} \\ 6/171 = 3.5\% \end{array}$$

Several approaches can be employed in estimating the maximal loss of production: (1) It can be assumed that pigeons continue nesting into October, and the maximal estimates of percentages of pigeons nesting during September can be used to estimate the loss; (2) it can be assumed that all pairs of nesting pigeons that lose one or both members due to hunting will not fledge squabs, or (3) a combination of the first two approaches. I chose the second approach because it appears doubtful that many pigeons would still be nesting in October in Oregon (Neff, 1947; Smith, 1968), and my data on the ability of one parent to fledge a squab are limited and based on experiments conducted in an aviary.

> If none of the 10 pairs of pigeons losing one or both members fledged squabs during September, the annual production during September would be 23/100 and the annual production,161/100.

The estimate of the maximal loss was,

$$\begin{array}{r} 171 \\ -\underline{161} \\ 10/171 = 5.8\% . \end{array}$$

<u>Method II.</u> The minimal estimate of the percentage of pigeons nesting (64%) was derived from the observed frequency of seasonal crop phases in pigeons killed by hunters (Table 4). If there was no loss due to hunting, 42 squabs would be produced by 64 pairs nesting

during the hunting season (65% nest success x 64 pairs). These squabs would be added to the annual production that occurred prior to the hunting season to provide a minimal estimate of the potential annual production:

138/100 + 42/100 = 180/100

Estimates of loss of production were computed as before. About 26.8%, or 18 of the 64 pairs, would lose one member due to hunting; and 2.6%, or two of the 64 pairs, would lose both members.

Total loss =	60% of the production of 18 pairs	=	11
	plus two pairs with no production.		2
			13

Pairs nesting during September	=	64
Squabs lost due to hunting	=	13
Annual production during September	=	51/100

The production of 51 pairs with a 65% nest success (33 squabs) was added to the annual production that occurred prior to the hunting season to estimate the annual production:

138/100 + 33/100 = 171/100

The minimal and maximal estimates of loss of production were computed as before. The minimal estimate was,

$$\frac{180 - 171}{180} = 9/180 = 5.0\%.$$

If none of the 20 pairs of pigeons losing one or both members fledged squabs during September, the annual production that occurred during September would be 65% (nest success) of 44/100, or 29/100, and the annual production, 167/100.

The maximal estimate of the loss of production was,

$$\begin{array}{r} 180 \\ -\underline{167} \\ 13/180 \end{array} = 7.2\%.$$

Estimates of losses of production made in this study are subject to numerous assumptions, and the validity of these assumptions will determine the accuracy of the estimates.

IV. CONCLUSIONS AND RECOMMENDATIONS

Conclusions

Two cycles in the production of crop-milk were found in band-tailed pigeons; a seasonal cycle and a daily cycle. The seasonal cycle was divided into four phases on the basis of crop activity and appearance; inactive, developing, active, and regressing.

During the inactive phase, which occupied the first 10 to 12 days of the seasonal cycle, the crop appeared thin-walled and transparent. The crop was developing through the next 5 to 7 days of the cycle.

During the active phase, crop-milk was produced in a daily cycle for approximately 30 days. The daily cycle was characterized by five identifiable phases. Crop-milk was found in the crop during two or three of the phases. Daily cycles of crops of males and females appeared not to be synchronized.

Regression of crops was usually complete about 10 days after squabs fledged.

Crops in early stages of development and late stages of regression could usually be distinguished from active crops by gross appearance of the lobes. This method also served to differentiate between developing crops and crops in early stages of regression. Developing crops could not be reliably differentiated from crops in late stages of regression by gross appearance of the lobes. However, they appeared separable by histological appearance. Active crops taken from pigeons on different days during the seasonal cycle could not be differentiated by either histological or gross appearance.

Parents fed a squab three to five times a day during the first week of brooding and the feedings were timed with the cycling of the crop. For the remainder of the brooding period, feedings were more frequent, usually at 1 to 2 hour intervals.

The various appearances of phases involved in the daily cycle, have caused confusion in identifying pigeons and doves with active crops. The presence or absence of crop-milk in the crop was not a valid criterion for differentiating between band-tailed pigeons with active or inactive crops.

Sixty-two percent of 614 pigeons killed by hunters in this study had active crops. Thirty-two percent had inactive crops. Pigeons with developing and regressing crops made up a small part of the sample (2% and 5%, respectively).

Band-tailed pigeon squabs could not survive under the care of one parent if the other parent was removed prior to the 6th day of brooding, and they could not be fledged in the normal length of time (22 to 24 days brooding) if a parent was removed prior to the 9th day.

Estimates of the loss of productivity that occurred from hunting pigeons during September were computed using two methods.

Minimal estimates were 3.5% and 5.0%, and maximal estimates were 5.8% and 7.2%, respectively.

Recommendations

Results of this study indicate that hunting band-tailed pigeons during September may not have a significant effect on productivity of populations. However, band-tailed pigeons have a low reproductive potential, thus they are not as resilient as most populations of game birds. This fact would suggest the need for intensive inventories to determine the status of populations. If populations decrease to a level that would necessitate restricting the hunting regulations, their recovery would be enhanced by an increase in the size of spring breeding populations, due to not only the survival of some pigeons that normally would be shot, but also by an increase in the annual production of the previous year.

There is need for further studies concerning the productivity of populations. The annual production cannot be determined from age ratio data until the differentials in migration and/or vulnerability between adult and immature pigeons are known.

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