

THE CONDOR

VOLUME 64

NOVEMBER-DECEMBER, 1962

NUMBER 6

NUPTIAL BEHAVIOR OF THE BAND-TAILED PIGEON IN THE SAN FRANCISCO BAY AREA

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In the summer of 1960 Band-tailed Pigeons (*Columba fasciata*) were found nesting for the first time in Strawberry Canyon on the campus of the University of California, Berkeley, California. Winter visitant flocks had been recorded irregularly in this area for a number of years (Grinnell and Wythe, 1927:77). Relatively little has been published on the nuptial behavior of this pigeon. Consequently effort was concentrated on this aspect of its life history. Study was begun on April 6, 1961, and terminated in mid-August, when nuptial activity had ceased. Additional observations were made in the spring and summer of 1962.

I am indebted to Alden H. Miller and Ned K. Johnson for assistance and guidance in the pursuit of this study. Frank A. Pitelka, Richard C. Banks and Gene M. Christman have made helpful suggestions.

STUDY AREA AND METHODS OF OBSERVATION

The study area encompassed Strawberry Canyon and its branches. The canyon is approximately one mile long and three-fourths of a mile wide. Elevations range from 500 feet at the canyon floor to 1200 feet along the hill tops. Due to slope exposure, the north side is almost entirely grass-covered, save for some oak-laurel woodland in the draws, a redwood grove at the Botanical Gardens, and an extensive eucalyptus forest at higher elevations. The south slope is covered with various types of vegetation, the most important of which are stands of exotic conifers, oak-laurel woodland, and moist chaparral.

Conifers include redwood (*Sequoia* sp.), knobcone pine (*Pinus attenuata*), and Monterey cypress (*Cupressus macrocarpa*). At lower elevations, woodland consisting of coast live oak (*Quercus agrifolia*) and California laurel (*Umbellularia californica*) predominates. Chaparral occurs intermittently throughout the south slope and virtually takes over toward the east end of the canyon; prominent species are coyote-bush (*Baccharis pilularis*), poison oak (*Rhus diversiloba*), thimble-berry (*Rubus parviflorus*), and elderberry (*Sambucus glauca*).

Observations were made at all times of the day, with emphasis on late afternoon hours when nuptial activity was at its peak. Although the pigeons were ordinarily very wary, they did not notice the observer if he kept very still. This circumstance, as well as the mobility of the birds, particularly that of the unmated males, made the construction of a blind impractical. In 1962, two nests were observed during incubation and rearing of the young in order to record the behavior of the adults. Mated as well as unmated birds were followed in their movements throughout the canyon; from certain vantage points, several birds in different areas could be observed simultaneously.

Sex determination was based on the behavior and, primarily, on the color of the breast and head of the individual bird. In the male, these parts are decidedly more deeply rosy, compared to the much more subdued sienna or umber brown in the female.



Fig. 1. Band-tailed Pigeon (*Columba fasciata*). Female (left) and male.

Drawings of pigeons are from sketches made in the field at the time of observation. They were checked for accuracy on subsequent occasions.

FLOCKING PERIOD

Whereas the majority of pigeons observed between April 6 and May 21, 1961, was congregated in flocks, paired birds were seen frequently during the first days of observation, from April 6 to 15. These pairs, however, assembled daily into flocks of 12 to 16 birds and eventually integrated with a large flock. By April 17, various smaller bands had united into a flock of more than 80 birds, consisting of both adults and immatures; the latter were identified by the browner aspect of their plumage and by the buff edges of the contour feathers. On May 21, the adults were still randomly dispersed among the immature individuals, which outnumbered the former in a ratio of approximately 3:1.

The presence of single pairs of pigeons between April 7 and 17 and their subsequent integration into a large flock suggest a propensity for flocking which apparently may even supplant sexual activity. Further evidence of this propensity appears in the communal feeding of incubating females whose relief schedules coincide and in the immediate flock formation after the young have fledged (see pp. 464, 466).

Movements.—Daily movements were largely confined to flights to and from food sources and roosts. As such, these movements followed a rather rigid schedule. At the first light of dawn, about 6 a.m., while still at the night roost in a eucalyptus forest, the birds became restless. Several individuals began walking to and fro on the limbs, particularly those of the highest branches. After approximately 15 minutes, these birds took flight and circled overhead; the pigeons that had perched lower in the trees now hopped or fluttered up to higher limbs, and, after walking back and forth several times, also flew off and joined the already circling birds. Within a few minutes, all pigeons followed this procedure, and the entire flock, after circling once more, flew off to feed. This departure took place almost noiselessly, in marked contrast to situations where the pigeons were frightened, as, for example, by the sudden appearance of a hawk; on such occasions, all birds took to the wing simultaneously, sharply clapping their wings as they flew off. This wing-clapping was also observed in single pigeons under similar circumstances. Both Cooper and Sharp-shinned hawks (*Accipiter cooperii* and *A. striatus*) elicited this reaction, whereas Red-tailed Hawks (*Buteo jamaicensis*) were generally ignored. Usually, when the flock was frightened off by the appearance of a hawk, the birds circled several times above the grove before settling down again. Feeding or roosting was resumed after about ten minutes, first by a few individuals, then by the entire flock.

Feeding.—With the onset of activity at dawn, feeding commenced as soon as the pigeons arrived at the food trees. Prominent food items included the terminal buds of the coast live oak, blossoms and young leaves of the madrone (*Arbutus menziesii*) and black locust (*Robinia pseudacacia*), and the fruit of the Carolina cherry laurel (*Prunus carolinensis*). During the morning hours, various areas were visited and a variety of these foods was taken. Feeding was leisurely and unhurried, and the pigeons moved frequently from one location to another.

While feeding on the blossoms of a stand of madrone on the steep south slope of the canyon, the pigeons started at the top of the grove, dropping down singly or in small groups. As the birds advanced down the hillside, the individuals from the rear moved to the front of the flock; this rotation continued until the lower end of the grove was reached. Gilman (1903:134) reports similar behavior in ground-feeding Band-tails.

When the pigeons were feeding in small isolated stands of oaks, they spread out fairly evenly throughout the crowns and, after the most accessible buds had been picked, moved on to the next grove.

Between 11 a.m. and noon, feeding generally slowed down, and the flock flew back to the redwood grove at the Botanical Gardens, a favorite roosting place, or to the night roost in the eucalyptus forest. Between 2 and 3 p.m., feeding was resumed in a stand of locusts within the redwood grove (see fig. 2). The pigeons fed on young leaves and blossom buds and ignored the already open blossoms. Whereas feeding was slow and intermittent at first, it accelerated toward late afternoon; by 5 p.m., the birds were in a veritable frenzy and fed rapidly, moving steadily from branch to branch.

During this activity, a nasal, grunt-like call, lasting approximately two seconds, was heard frequently, reminiscent of the snoring of a man. This "grunt" was given by an individual when physical contact resulted from crowding by another pigeon. One bird,

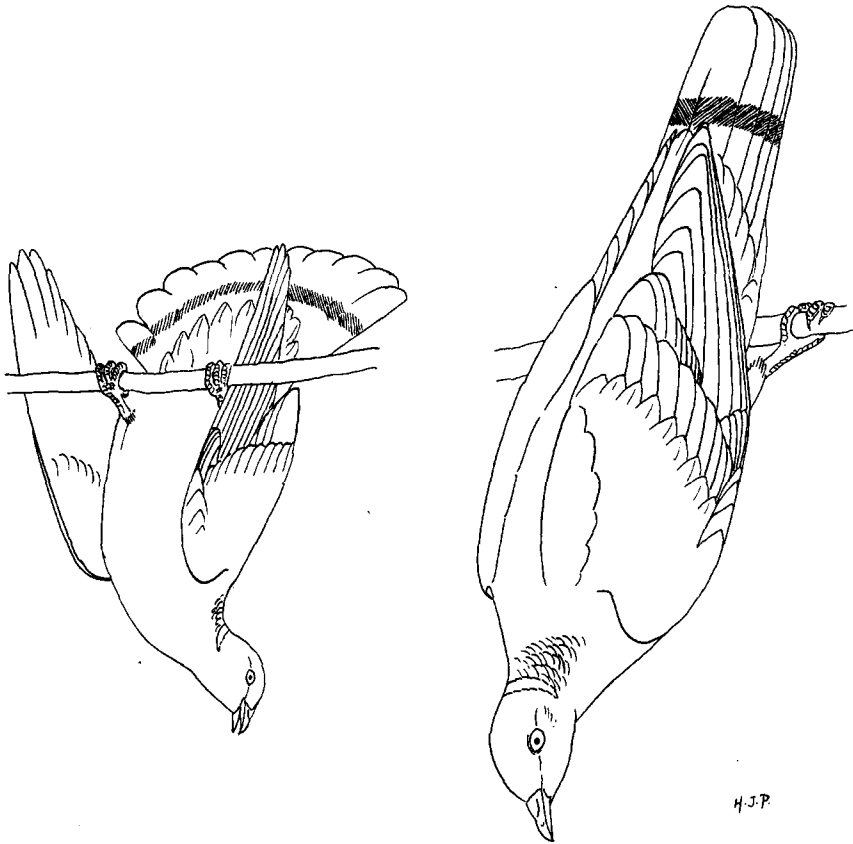


Fig. 2. Hanging positions assumed by Band-tailed Pigeons while feeding on locust blossom buds.

while leaning forward to reach a cluster of flower buds, would be temporarily off balance; a second pigeon, reaching for the same cluster, would nearly push the first bird off the branch. The crowded bird then grunted in protest, which caused the newcomer to step back and either fly to another branch or settle down to rest. Toward the beginning of May, as the buds became progressively scarcer, this grunt was heard with increasing frequency.

At this time, the pigeons commonly resorted to hanging by their feet while feeding on the buds; Willard (1916:111) writes of Band-tails feeding on acorns in Arizona: "They would walk out on the slender branches till they tipped down, then, hanging by their feet, would secure an acorn, and drop off to alight on a branch lower down." While feeding on the blossom buds, the pigeons maintained themselves in this head-down position anywhere from 18 seconds to two minutes, picking all the buds off one cluster. With feet placed about three inches apart, and legs slightly flexed, they swung vertically from the branches, some of them half-spreading their wings and tails to stabilize themselves. After dropping to a lower branch, the pigeons repeated this procedure until they reached the lowest blossom-bearing branches; then, flying back to the top of the tree, or to that of an adjacent one, they descended again in the same fashion. The trees were eventually stripped completely of all blossom buds, and the ground beneath the trees was littered with open blossoms that had been knocked off.

Observations of the food habits of the pigeons were verified by the crop and stomach contents of two birds collected on May 10. One individual had eaten 11 plums of the Carolina cherry laurel, ovoid drupes about three-fourths of an inch long and one-half inch wide. The crop and stomach of the second bird were filled with the blossom buds of the locust. The spilled crop contents of two pigeons killed by predators also consisted entirely of these food stuffs.

Among the foods taken by the pigeons in this area, the blossom buds of the black locust seem to be the only item not previously recorded. This is probably due to the fact that this tree is not native to the range of the Band-tail and is only sparingly cultivated.

Neff (1947:68) states that the stomachs of pigeons which have been feeding on hard-pitted fruits, such as cherries and dogwood seeds, do not contain gravel; "apparently the pits are softened by the digestive juices and broken by muscular action, the fragments then serving as grinding material." In the present study, however, large quantities of whole pits of the Carolina cherry laurel were found under roosts. One would think that the digestion of such soft fruits would not require the presence of grinding material.

The ability of the Band-tail to hang by its feet for prolonged periods is surprising, and periods of up to 2 minutes of suspension seem extraordinary for such a heavy-bodied and relatively weak-legged species. I could not ascertain whether other columbids with similar arboreal habits have this ability also, and I have not found it reported in the literature.

Dispersal.—On May 15, 1961, nearly a third of the flock disappeared; the remaining birds, about 50 individuals, continued to frequent the same localities as before. On May 21, at 2 p.m., the pigeons were clustered in and around the large pine above the locust grove. The birds seemed to be highly agitated; some individuals were walking to and fro on limbs, others fluttered from branch to branch and to adjacent trees. Periodically, small groups of 10 to 12 birds took to the wing and flew back and forth above the grove. After a few minutes, they alighted again, and presently, another group flew off. Both adults and immatures participated in these movements. At approximately 7 p.m., this activity subsided somewhat, and at 7:37 p.m., the flock moved to the eucalyptus forest for the night. The following day, at 2:15 p.m., only 12 adults were present at the locust grove; thereafter, the large flock was no longer seen, nor were immature birds. The adults remained together until May 23. In the afternoon of that day, one of them cooed for a short period. By the following day, these pigeons had dispersed throughout the canyon.

The depletion of the locust blossom buds, the major food item, apparently initiated this behavior, and the restlessness of the winter-visitant flock just prior to leaving the study area was striking. It appeared as if the birds were "warming up" for the major flight. While adults participated in these movements, it is not known whether the pigeons that remained to nest were also present in the flock at that time. Presumably they were, since they continued to frequent the roosts used by the flock after the disappearance of the latter. The leaving of the winter-visitant flock apparently contributed to the onset of nuptial activity.

In 1962, the departure of the main flock was not witnessed; however, approximately twice as many pigeons as in 1961 remained and nested.

Molting.—Small body feathers were found in large numbers beneath food trees and roosts when this study was begun, and primaries and rectrices appeared on April 19,

1961; thereafter, molting birds with gaps in tail and wings were seen throughout the period of observation.

The two birds collected on May 10 were males, one immature and the other adult. In the immature, primaries 1, 2, and 3, and the corresponding greater coverts were new, and 4 and its covert were half-grown. The adult showed no molting activity; however, on both wings there were six secondaries (3-8) which were older than the other remiges. These were apparently feathers that had not been replaced during the previous molt.

The unusual seasonal timing of this molt is somewhat puzzling. Neff (1947:5) states that, according to Bendire, juvenal birds apparently molt during their first fall. Considering the prolonged nesting period of this pigeon, such molts could conceivably occur in spring, also, before the onset of nesting activity. Witherby *et al.* (1949) state that molting juveniles of the Wood Pigeon (*Columba palumbus*) may be found at all times of the year. They attribute this fact to the extended nesting period of this species. However, adult birds in the migratory flock appeared to be molting also, and "adult-colored" primaries and rectrices were found under the roost. During late spring and summer, molting seemed to be erratic, and relatively few flight feathers were found in the vicinity of nests, in spite of the considerable time spent there by the birds during incubation and brooding.

NUPTIAL BEHAVIOR

The earliest reported nesting date for California seems to be February 1 (Macgregor and Smith, 1955:318), and the latest date is apparently represented by an observation of Allen (1941:157) who saw a young bird leave the nest on November 1. In the present study, in 1961 nesting activity did not commence until May 28, in marked contrast to the spring of 1962, when mated pairs occupied nest groves as early as April 7. In this year, prenuptial displays were also observed for the first time, whereas such displays were apparently altogether absent in the preceding year.

The testes of the adult male collected on May 10, 1961, appeared enlarged and measured 15.2 mm. in length, compared to a length of 4.3 mm. for the testes of the immature male. However, these measurements are at present of little value in determining the breeding status of these birds, because the maximum size of the testes in this species is apparently unknown.

VOCALIZATIONS

Outstanding among the features of the courtship of this pigeon are the vocalizations.

The crowding grunt.—This utterance has been described previously (p. 447). This call was given by one, or occasionally two, birds when another individual came in physical contact while trying to reach the food already chosen by the first bird.

Cooing.—Best known of the vocalizations of this species, the coo has been described by a number of authors (Bailey, 1902:139; Grinnell, 1905:382; Swarth, 1904:5). Wales (1926:42) writes in detail about the male beginning to coo: "When the male pigeon starts this performance he usually maneuvers around for a firm footing and perhaps opens his bill slightly once or twice. Next he stretches his neck out in a line parallel with the axis of his body, and bends his head down at a right angle. With his bill open a crack he gives one gasp which fills out the skin of his neck until about three times natural size, and at the same time utters a faint *oo* which is not usually audible over twenty feet. All of these are preliminary actions, as directly following the

first sound comes the *whoo-oo*." In the present study, all these preliminaries were not observed. The lowering of the head is reminiscent of the "head-swinging" performed by the male prior to cooing during courtship (see page 456); however, all observed males "inflated" their necks more gradually than indicated in the above quotation. When alone, the birds cooed with the front part of the body tilted up at about a 45° angle, the neck upright, and the head in a vertical position so that the bill rested on the throat. In the presence of a female, and particularly prior to copulation, the male maintains the entire body in an almost vertical position while cooing.

Solitary unmated males preferred to coo from the tops of high trees, often using rather precarious perches. On June 15, 1961, the lone male L1 performed on the vertical terminal shoot of a 40-foot pine, which waved violently in a strong wind. Upon returning from display flights, the bird was forced to alight by turning on his side, seizing the shoot with both feet and bending it into a horizontal position. After each flight, the pigeon thus struggled for several seconds while trying to gain his balance.

Elevated or otherwise prominent perches were not required by mated males. The male of pair P1 which subsequently nested in the redwood grove at the Botanical Gardens invariably cooed from very inconspicuous locations in the dense canopy of the trees.

The coo of the Band-tailed Pigeon has been described as owl-like (Bailey, 1902:139; Glover, 1953:398). To this writer, however, the coo appears in quality quite similar to that of other pigeons, such as *C. livia*. The coo is tonally low and weak and carries little more than 50 yards, particularly in dense forest. Single coos are heard rarely and are perhaps easily overlooked. Actively vocalizing males commonly uttered series of 3 to 12 coos, each coo consisting of two syllables lasting 2 seconds. On June 15, 1961, male L1 vocalized continually from 5:05 p.m. until 6:30 p.m., only stopping occasionally for a display flight. Series of five coos were given 2 to 3 minutes apart, with the second syllables of the two terminal coos in each series noticeably shorter than the preceding ones. Each series thus sounded somewhat like this: *whōō-hōō—whōō-hōō—whōō-hōō—whōō-rōō—whōō-rōō*. The pitch dropped sharply at the ends of these shorter syllables.

Glover (1953:398) reports that most cooing in his study area in Humboldt County occurred in the early morning hours, particularly between 10 and 11 a.m. In the present study area, however, the males seldom vocalized during morning and early afternoon hours. This time was largely devoted to feeding and roosting. Toward 5 p.m., cooing was heard with increasing frequency, becoming constant at about 5:45 p.m., and subsiding after 6:30 p.m. Of the 8 males observed, all followed this schedule during the period of vocalization.

In paired males, cooing stopped abruptly with the onset of incubation.

Chirping.—This vocalization is heard during the display flight of the male. It has been described as a "peculiar wheezing noise" by Swarth (1904:5), or as a modified chirp of a cricket (Pearse, 1935:71). This writer found that the call is quite similar to the "creaking door" call of the Steller Jay (*Cyanocitta stelleri*), except that it seems to be somewhat higher pitched and is sustained longer. A good imitation may be obtained by slowly running one's finger over the teeth of a comb.

There has been some speculation as to how this sound is produced. Pearse (*op. cit.*) theorizes that it may be caused by "the wing feathers coming in contact with those of the tail." However, there is no evidence to support this theory, because during the display flight, both wings and tail are fully spread and never touch. Swarth (*op. cit.*), who at first also believed that the sound was caused by the wing feathers, mentions

that a captive bird uttered the same sound, "evidently by means of his vocal organs, as we had ample opportunity of observing." While this call is being given, the bill is kept closed; this fact, together with the peculiar quality of the vocalization, may easily lead to the theory that it is of mechanical origin.

Pearse (*op. cit.*) mentions a second type of vocalization, a "wheezing noise." This, he states, is distinctly different from the "chirping" described above; he observed this on one occasion during which the pigeon flew from tree to tree in display flight fashion. This sound, Pearse states (p. 72), might be caused by "movement of the quills of the tail feathers." In the present study this display was observed only once. Pair P1 continued to remain together after its first nest had been presumably robbed. The pigeons stayed together constantly and were apparently inseparable. However, on July 2, 1961, at 3 p.m., only the male was present in the redwood grove; for 27 minutes, the bird flew from tree to tree in a radius of about 40 feet, his wings and tail fully spread, moving with quick shallow beats in display flight fashion. During these short flights, he uttered a call reminiscent of "chirping," except much higher pitched. Finally the female appeared between the treetops, and both birds flew off together.

Thus it seems highly unlikely that the tail feathers are the source of this sound, particularly in the light of Swarth's statement in regard to "chirping." During the flights, the tail was constantly fully spread, and there was no perceptible movement of the rectrices.

Miscellaneous notes.—Neff and Niedrach (1946:74) mention that while the male pigeon brooded the young, he greeted the female with "guttural [sic] exclamations" when she was unusually late in returning to the nest. This was also observed in the present study. When the female of pair P3 approached the nest later than usual, the brooding male half-raised himself, extended his neck forward and uttered short, low-pitched calls sounding somewhat like *croo*.

The young, just prior to being fed, utters a begging call, described by Neff (1947:5) as a thin piping note. In the present study this call was heard only twice, possibly because it is quite weak and is barely audible 20 feet away.

On several occasions, males were heard uttering a short soft *whoo* when slightly alarmed by my presence near the nest. This call sounded like a sudden expulsion of the air from the lungs and was accompanied by a stretching of the neck and peering about. When the birds were fully alarmed, they at once flew off with loud wing claps.

Discussion.—The principal vocalizations may be divided into two major categories, (1) cooing, and (2) excitement calls. Cooing appears separated from all other vocalizations functionally as well as tonally. Its primary function seems to lie in pair formation and in courtship, and hence it is given by both mated and lone males. In the case of the latter, the display of the brilliant neck plumage is probably of at least equal value in signaling the female and in announcing the sex of the bird.

Cooing also seems to be directly associated with the early stages of sexual activity. With the onset of incubation, this vocalization stops abruptly.

Excitement calls include the crowding grunt, chirping, and the call heard once from the mated male during the absence of the female. All these calls are very similar tonally, resembling mechanical sounds rather than vocalizations, and have a rattling or buzzing quality, as if produced by a stiff membrane. These calls are heard when the birds are in a state of excitement other than sexual.

The crowding grunt is apparently a note of protest; it is the lowest pitched of the three types and is uttered in short bursts. Expressing protest, or annoyance, seems to be its only function.

Somewhat higher pitched, and apparently of territorial nature, chirping accompanies the advertising and exploratory flights of both mated and single males. Compared to cooing, this sound carries amazingly far, up to 150 yards, and is sustained for the period of the flight. During communal announcement flights, when several males are circling above their nest groves at the same time, they can most probably hear one another, or at least their closest neighbors. Visual contact is probably important in bringing about the utterance of this call.

The call uttered by the mated male in the absence of the female is still higher pitched and almost shrill. The short flights, during which this call is given, seem almost like a formalized search for the female.

Only the crowding grunt has been heard from both sexes. The two other excitement calls are given solely by males.

PAIR FORMATION AND COURTSHIP

The unmated male.—With the dispersal of the flock, numerous areas which were used for nesting during the previous year were reoccupied at once by pigeons that apparently were paired. However, a number of single birds remained in the canyon and were relatively easily distinguished because, prior to incubation, paired pigeons remain together constantly.

In the course of this study, three unmated males were observed. On June 11, 1961, at 1:45 p.m., a male (L1) was seen flying up the canyon from the west. After traveling about 100 yards in a straight line, the bird suddenly set his wings and glided in a wide circle, about 100 yards in diameter, in the fashion of the display flight. The pigeon then continued up the canyon, only to repeat the maneuver after another 100 yards. Continuing, the bird arrived at the Botanical Gardens, where he turned and started back down the canyon, only to circle once more. Thereafter he flew into a stand of pines and disappeared from view. Identical performances by this same individual, which could easily be identified by the molt pattern of his flight feathers, were witnessed on June 12, 14, 16, and 19. On this latter date, the bird encountered an unmated female.

These exploratory circling flights resulted, in the case of two solitary males, in the selection of a "cooing perch." Male L1 chose the terminal shoot of a tall pine topping an adjacent grove of coast live oaks and growing on the embankment of a well-traveled road. Male L3 selected the top of a 40-foot larch in the Botanical Gardens. Both these perches were located in areas wholly unlike those used for nesting by paired pigeons.

From these trees, the birds struck out in various directions, performing display flights; however, unlike mated males, L1 and L3 circled two or three times during each flight, each circle overlapping the previous one. Invariably, at least one of these circles was performed over woodland suitable for nesting, such as the redwood grove northwest of the Botanical Gardens.

Between these flights, the birds cooed vigorously from their selected perches, each time returning to them. While circling, the chirping call was given. Typically, this behavior was not restricted to a particular time of day, as were the display flights of the paired males.

These exploratory flights of single males are apparently a search for an unoccupied nest grove. The flights carry the birds over suitable areas, as seen in the flights of the lone male L3 (see fig. 3). The three successive circles over potential nest sites seem to be equivalent to the announcement flights of the paired male, except that they are probably only a tentative delineation of such an area. The lone male apparently anticipates opposition from a resident male. Male L1, upon first seeing an unmated fe-

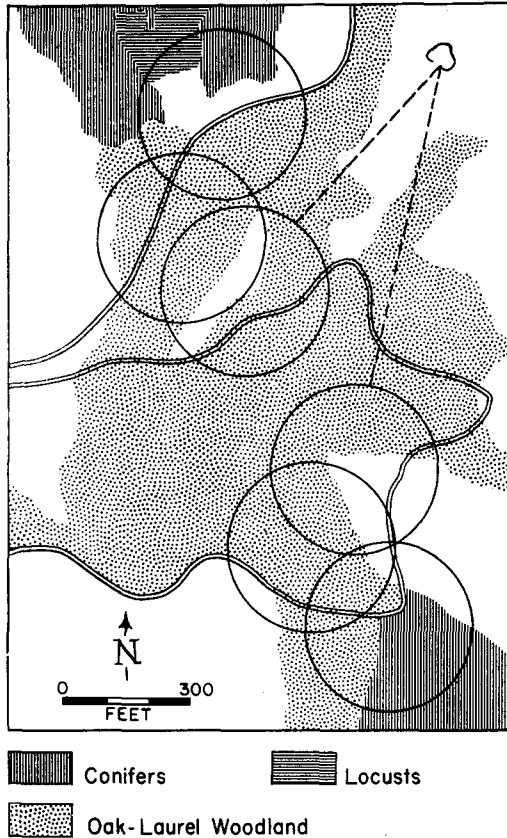


Fig. 3. Two exploratory display flights of male L3 on June 29. Dotted lines and circles mark path of each flight. Note inclusion of conifer groves in the terminal circles.

male, approached her cautiously with a series of circles, chirping continually (see p. 455). After these flights, he withdrew for 15 minutes before he joined her, giving the other bird ample time to announce territorial ownership, should it have been a male.

Pairing.—There is some evidence suggesting that Band-tails remain paired throughout the year. In the large winter-visitant flock, the adults seemed randomly dispersed among the juveniles; however, the presence of single pairs prior to their integration into the flock, and the banding together of such pairs are reminiscent of the behavior of the Canada Goose (*Branta canadensis*) which flocks annually during migration but apparently has a permanent pair bond. Also, after the dispersal of a flock of Band-tails, no unmated males were seen in groves which had been used for nesting during the previous year. Instead, these areas were at once occupied by pairs. Unfortunately, it is not known whether these were the same birds that had occupied these areas during the previous year.

On June 19, 1961, what appeared to be the formation of a new pair was observed. The lone male L1 had been observed almost daily during the preceding week, and all evidence suggests that this was his first encounter with an unmated female. At 5:15

p.m., a single female was seen flying up the southeastern arm of the canyon; about 100 yards past the Botanical Gardens, she perched atop a lone dead tree protruding above the brush-covered south slope. Upon alighting, she assumed the crouching position commonly observed in resting pigeons. At 5:56 p.m., the lone male L1 appeared near the Botanical Gardens and flew toward the female; about 150 feet from her, he circled once in display-flight fashion, then flew toward an extensive stand of pines, some 200 feet southwest of the female, where he circled again. Turning back toward the female, he circled a third time, now almost above the other bird, then flew past her and disappeared in a large bay tree farther up-slope. Fifteen minutes later, he rose steeply out of the tree and flew down toward the female, alighting about one and a half feet away from her in the dead tree. During this descent, as well as during the preceding flights, he constantly uttered the chirping call. The female appeared entirely uninterested until the male alighted. The ensuing behavior of both birds was identical with the courtship display.

Apparently the passive behavior of the female was decisive in sex recognition, a situation also observed in other largely monomorphic species, and pair formation seems to take place via a trial and error method on the part of the male. Once contact with the female is established, pre-copulatory displays apparently "seal" the bond.

Courtship display.—Almost all activity concerning courting and nesting took place in the late afternoon, most frequently after 5 p.m. Exceptions to this timing are preliminary displays. The male seems to initiate the displays, and they always take place in trees.

The preliminary display is reminiscent of the courtship display proper in that it contains some of the elements of the latter, although in reduced form. The following account seems to be representative of this behavior. On April 7, 1962, at 3:10 p.m., a pair of pigeons was observed perched on a flat, top branch of a Monterey cypress in a large stand of these trees. This was possibly the same pair (P2) which occupied that grove in 1961. While the female was preening, the male arose from his resting position every 8 to 15 minutes, rapidly bobbed his head several times at the female and walked, rather than strutted, in a small circle, whereupon he settled down again. Meanwhile the female continued to preen. At 4:03 p.m., after having remained still for about 10 minutes, the male flew off and performed a series of display flight circles. He then alighted at some distance from the female. It was noted that at this time several other males were also performing display flights over other areas of the canyon. After approximately 15 minutes of perching silently, the male cooed softly, and the female flew up and joined him.

Preliminary displays were not observed in 1961. That year the pigeons occupied the nest groves almost two months later (toward the end of May) than in 1962 and proceeded to copulate and nest immediately.

Although the display flight of the male has been regarded as being intimately connected with courtship and has consequently been called a nuptial flight, evidence in the present study suggests that this is not the case. Display flight is discussed in detail under the section on territoriality.

Courtship was observed in its entirety in three pairs. In one case, the encounter of male L1 with the female, it did not result in coition. Observation of the display was at times difficult, since most of the activity took place in the dense crowns of conifers. The behavior of pair P4 was found to be representative, however, and is described here.

On June 22, 1961, at 5:12 p.m., the male of this pair initiated the courtship display by cooing several times while perched in a pine some 10 yards from the female. The

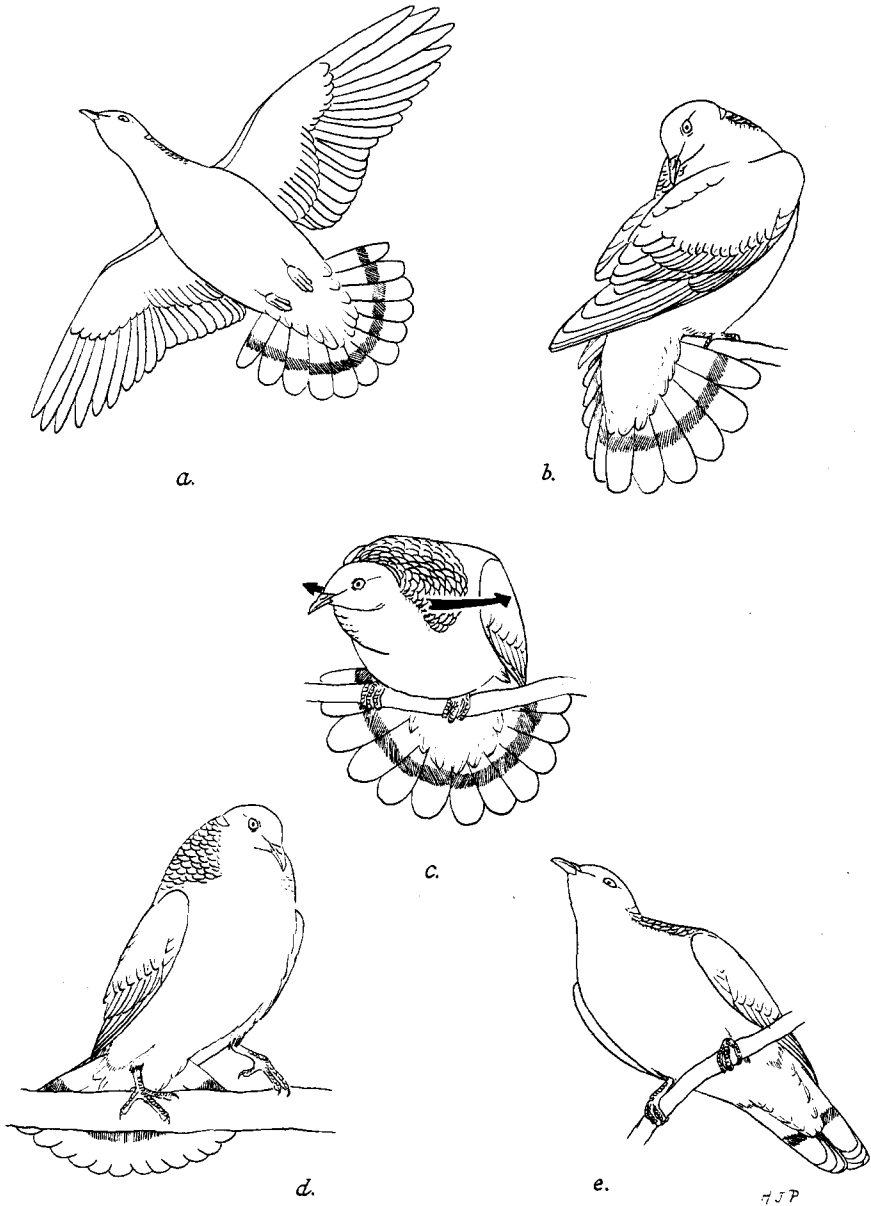


Fig. 4. Displays of the male Band-tailed Pigeon: a, display flight; b, wing-billing; c, head-swinging; d, pre-copulatory strut; e, post-copulatory pose.

bird then flew toward the female and perched about one foot from and slightly below her. Having alighted, the male immediately turned toward the female and leaned forward, so that his head and entire body were parallel to the branch on which he was perched. He now distended his neck, then swung his head slowly at first to the left, then to the right side. By now, the female had stood up and was watching the male intently. The latter now fluttered up and past her, alighting once more about one foot

away from her, his neck still inflated. He stood stiffly erect, pressed his beak against his throat and cooed twice.

The female rapidly bobbed her head at the male, who, still very erect, quickly strutted toward her. When he had almost reached her, she apparently attempted to seize the base of his bill with her bill. He backed away a few inches, half-raised his left wing and quickly pecked behind it at the axillar region. Again he cooed and advanced once more. The female took a step away from the male, who followed her immediately and mounted her. Now the female half-raised her wings to stabilize the male, and the latter beat his wings slowly. Copulation lasted about four seconds and was terminated by a short, rapid downward movement of the tail of the male. Upon dismounting, the male pointed his bill upward and flew to a neighboring tree in display flight, his wings and tail fully spread. Both birds then commenced to preen.

During the display, the male maintained his tail in a depressed position at all times.

So-called "driving," which commonly occurs in other pigeons (Whitman, 1919:12) was observed only once in the present study. The male of pair P1, in the afternoon of May 28, 1961, perched close to the female in the crown of a redwood and cooed twice, his neck distended. He then turned away from the female and rapidly walked along the limb, his tail depressed and fanned, and he uttered a soft, high-pitched *coor-r-r*. Returning to the female, he touched her with his breast and slowly beat his wings. The female flew to the next tree, with the male following her at once, and again he pushed her on. This was repeated four times, both birds flying from tree to tree in a semicircle. Copulation finally took place as described above.

Driving was observed a second time in this pair but not in connection with courtship. The selection of a nest site apparently resulted from this second performance.

TERRITORIALITY

Glover (1953:399) in writing about nesting Band-tailed Pigeons in Humboldt County, California, several times refers to their "nesting territories." His basis for this designation is, however, not clear, unless he deduces the existence of such territories from the wide spacing of the nests.

A number of authors have stated that the nests of this pigeon are usually well spaced; however, an interesting reference to colonial nesting is supplied by Neff (1947:12). He mentions a note he received from H. Garvin Smith of the United States Forest Service, Tucson, Arizona: "He says that in 1933, while camping in the Magdalena Mountains of New Mexico, he found 14 bandtail nests in one large Douglas fir near a spring, and that in 1934 in the same tree he found 17 nests."

Neff also states that when he and Peterson inspected a recently deserted community nesting ground northwest of Nogales, Arizona, they found that the nests were irregularly spaced, sometimes within a few yards of each other, but usually fairly well separated. This appears inconclusive evidence of colonial nesting, since the nests were deserted and hence not necessarily those of simultaneously nesting pairs. This writer has found that the nests, flimsy as they are, may easily last as long as one year. Be that as it may, there was no evidence of communal nesting in the Strawberry Canyon study area. Furthermore, certain aspects of the pigeon's behavior are apparently of a territorial nature.

Announcement flight.—With the onset of sexual activity, it was soon noted that the presumed nuptial flights were not necessarily connected with that activity. Frequently, paired males were performing these flights while their mates roosted in another part of the nesting grove.

The male begins the flight by gliding out horizontally from his perch, his wings on a plane with his body. The first 30 to 40 feet are covered in a straight line, and the bird flies slightly downward, gathering momentum. Then, swerving to either the right or left, the pigeon begins to glide in a circle which may be anywhere from 50 to 200 yards in diameter. At this point, the chirping call begins and is subsequently sustained throughout the performance. Wings and tail are fully spread and in a horizontal position. The head is extended forward, giving the bird a somewhat long-necked appearance.

After completing one-half or three-fourths of the circle, the pigeon begins to move his wings with rapid, shallow, almost quivering beats. Only the primaries appear to move up and down, as if only the distal segments of the wings, from the wrists out, were involved. While giving these vibrating beats, the bird slows down considerably and moves very haltingly as he completes the circle.

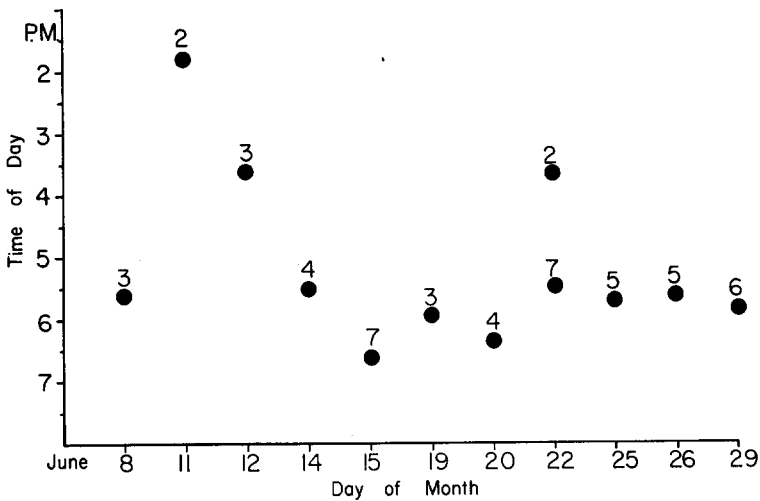


Fig. 5. Simultaneous display flights of male Band-tailed Pigeons. Figures above circles show number of participating males.

As the nesting groves were occupied by paired birds at the beginning of June, 1961, these flights occurred randomly throughout the afternoon. Soon, however, as most breeding pairs were established, flights took place in the late afternoon, particularly after 5 p.m.

From a vantage point on the north slope, which afforded a view of the flights of as many as eight males, the following behavior was observed several times. Between 5 and 6 p.m., one male would appear, circling. Seconds later, while this bird was still in the air, several males would perform display flights throughout the canyon. The effect was one of a trigger reaction. As soon as one male began his flight, the other males which could see him also took to the wing. Frequently, this communal performance took only seconds and occurred only once a day, particularly toward the end of June, just prior to the onset of incubation in most of these birds (see figs. 5 and 6). On June 26, 1961, for example, five males flew out almost simultaneously at 5:25 p.m., one taking to the wing after another. One minute later all had disappeared again. On that day, no other flights were seen prior to or after that time.

Evidence thus suggests that the so-called nuptial flight is territorial in nature. The successive circles flown by the males roughly covered either the entire nest grove or

the side of the grove which faced the canyon and was hence in view of other pigeons. The simultaneous performance of several males would occur during the peak of flight activity, a rather curious coincidence if the flights were solely related to part of the courtship. The rather odd time of day, for a diurnal species, might be explained by the absence of several pairs from their nest groves at other times of the day, when they were feeding. By 5 p.m., the pigeons had usually returned to their respective groves, and the sight of the announcement flight of one male may have stimulated other males to do likewise. The fact that the exploratory flights of lone males occurred at all times of the day seems to support this interpretation.

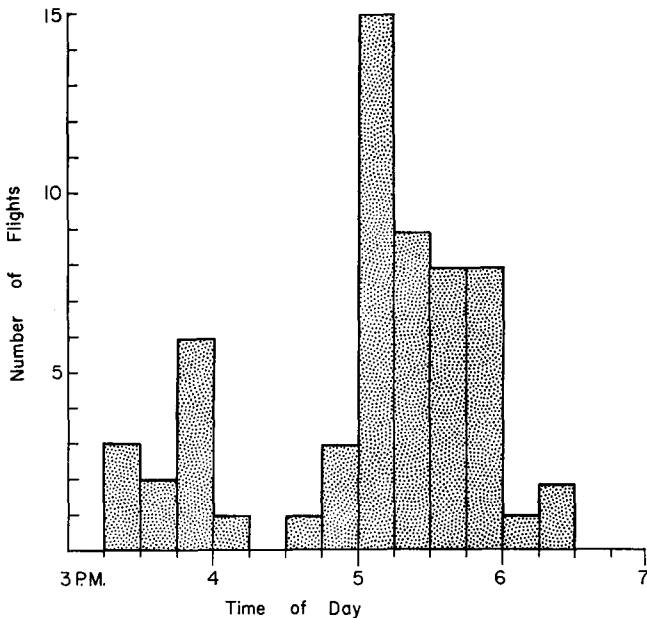


Fig. 6. Number of display flights performed by seven male Band-tailed Pigeons on June 17, 1961.

Aggressive behavior.—On June 19, 1961, pair formation involving male L1 was observed (see p. 454). After the courtship display, both he and the female settled down, preened, then roosted quietly. After about 20 minutes, the writer imitated the coo of the male. The latter at once arose and bristled the feathers on his back while bobbing his head in the direction of the sound. After another coo, he flew off, gliding in a straight line toward me. His wings and tail were spread, and the bird uttered the chirping call. Passing by within a few yards, the pigeon continued to glide down the canyon and flew out of sight. Except for the line of travel, this flight possessed all the elements of the display flight. The female remained oblivious to this activity.

While engaging in exploratory flights in the afternoon of June 29, 1961, male L3 passed over the redwood grove occupied by pair P1, which had just resumed nuptial activity. When the lone male approached the site where the pair was roosting, the resident male flew up and directly at the intruder, which at once turned back. After giving chase for approximately 50 yards, the resident male flew back into the grove in display flight fashion. He returned to his cooing perch and looked about for a few minutes, then cooed. Once more he flew off, circling. This time he headed toward the south slope

of the canyon. After three circles, he flew toward another redwood grove, where he apparently planned to perch on a particularly tall tree. He had almost reached it when two pigeons flew up and chased him also for about 50 yards before returning to the grove. This time, the male continued flying down the canyon and disappeared from view. A subsequent check at the site where the two pigeons had been seen revealed a nest containing a very young bird.

Aggressiveness toward intruders also suggests strong territoriality. The exploring lone male L3 was driven away by the resident male at the redwood grove, and the caution exercised by L1 while approaching the female seems to be further evidence.

Nature of the territory.—Most of the California nests, as reported by Grinnell, Bryant, and Storer (1918) were in oaks. In my study area, in 1961, conifers were chosen

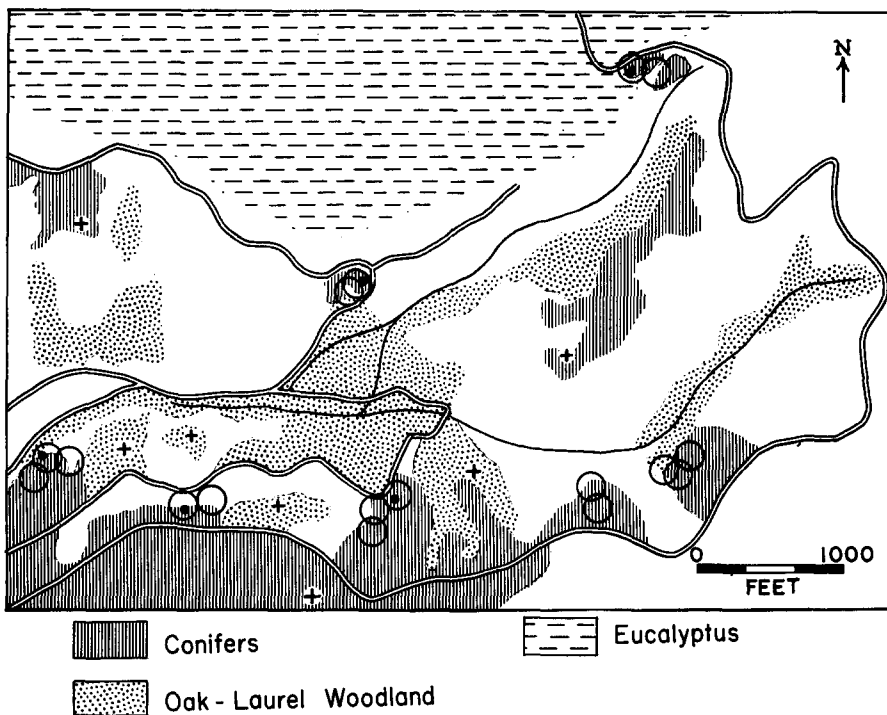


Fig. 7. Nest locations of Band-tailed Pigeons in Strawberry Canyon, Berkeley, California. Open circles mark areas covered by announcement flights; smaller solid circles indicate nest sites in 1961. Crosses indicate additional nesting areas used in 1962.

in nine out of ten cases, in spite of the presence of fairly extensive oak groves. In 1962, with the number of nesting pairs approximately doubled, oaks were also utilized, apparently as a second choice to conifers. Macgregor and Smith (1955:316) who studied nesting Band-tails at Carmel, Monterey County, California, also found that 62 per cent of the nests were built in Monterey pines (*Pinus radiata*).

The limits of the territory seemed to conform largely to the physiognomy of the vegetation (see fig. 7). For this reason, there was some variation in the actual size of the territories. Each territory, however, covered a fairly well-defined stand of conifers, and the size of these stands varied from two to four acres approximately. Glover

(1953:402) found that nesting territories apparently varied in size according to the irregularity of terrain, abundance of forest cover, and proximity of a permanent water source. The latter factor was not prominent in the present study area, probably because water sources are easily reached from all parts of the canyon.

All conifer and oak groves that were used for nesting in Strawberry Canyon grow on slopes varying from 30° to 45°. Within such a grove, one of the birds, presumably the male, selected the actual nest site. If this site was located near the upper edge of the grove, the announcement flights of the male took place directly above the grove; if at the lower edge, the male performed in front of the grove, that is, the side facing the canyon. In 1962, with the larger number of nesting birds, males simultaneously performed display flights both over the lower oak groves and the conifers farther up-hill, suggesting partial vertical territoriality.

All nuptial activities took place in these groves. Here the pigeons also roosted. The only activity taking place outside the grove was feeding, which, however, also took place within the confines of the canyon.

East nest grove consisted more or less of the same species of tree. Those used were stands of coast live oak, redwood, knobcone pine, Monterey cypress, and Douglas fir (*Pseudotsuga menziesii*). In all cases, mature trees 25 or more feet in height were used. Density of the groves varied from one tree per one and one-half square yards to one tree per five square yards.

Open areas within and adjacent to the groves were used by the pigeons as flyways.

NESTING AND INCUBATION

Nest location.—Eleven occupied and two old nests were found in the course of this study, six of the former in 1962. The new nests as well as one of the old ones were located in the above-mentioned conifers and oaks. Only one nest, apparently one used the previous year, was built in an alder (*Alnus* sp.).

Heights of nests from the ground varied from seven feet of that in the alder to 40 feet in a pine. Six of the nests were between 15 and 20 feet above the ground. Without exception, the nest tree stood above a small precipice or slope, giving the pigeons additional height when flying from the nest. Neff and Niedrach (1946:73) mention similar nest locations in Colorado. This requirement of location accounts for the lowness of the nest in the alder. Actually, the nest branch grew out over a small but very steep precipice some 14 feet in height.

Each nest tree was adjacent to or within a few feet of a clearing. The latter facilitated access to the nest, and the pigeons used it regularly rather than maneuver through the dense crowns of the conifers.

Most nests were built on horizontal branches at points 2 to 5 feet from the trunk. Only two nests were located at the trunk; these were near the tops of the trees. In all cases, the nests were well hidden from above, and only two nests could be seen clearly from below.

Construction of the nest.—The following evidence suggests that the male selects the nest tree. The nest building of pair P1 was observed on May 30, 1961. At 4:07 p.m., the male drove the female in a semicircle toward a particular tree in the redwood grove; then both birds rested, perched close together. Suddenly the male arose and flew off but turned at once and alighted again in the same tree, about 15 feet beneath the female. He walked back and forth four times on the limb he had alighted on, then broke off a small dead twig with his bill. The bird then hopped up the tree from limb to limb, spiralling the trunk. After the male had climbed in this fashion about seven

feet, the female, which had watched him intently, flew down and perched three feet from him. The male walked toward her and presented the twig, which she accepted. She then put down the twig awkwardly, simply placing it at the junction of the limb and two smaller side branches. The male broke off another twig, which the female also accepted and placed on the limb. The male now brought a twig from a neighboring tree, then another, both of which the female promptly incorporated into the small platform. The male then stopped and wiped his bill on the limb he was perched on. He cooed twice, and strutted toward the female, which took to the wing. The male followed her at once, and both birds flew out of sight.

No further nest building was observed until June 1, when the female was seen at 5:17 p.m., adding more twigs to the platform. On June 2, at 6:30 a.m., there was an egg in the nest.

Willard (1916:110-111), writing about Band-tails in Arizona, states that apparently only the female builds the nest. This was certainly the case in this study also, although the male played a definite role in bringing about this activity. Willard also states that six days elapsed between the beginning of nest construction and the appearance of the first egg. In the present study, the interval was found to be only three days.

The nest.—All nests were found to be mere platforms of twigs which varied from one-eighth to one-fourth of an inch in diameter. Actual measurement of dimensions of the nests was not attempted because of the disorderly arrangement of the building material. Grinnell, Bryant, and Storer (1918) state that the average diameter is six or eight inches, excluding several protruding sticks. The depth was found to be about four inches. The nests observed in this study were nearly completely shaded at all times of the day.

Kitchin, as quoted by Bent (1932:354) states that "the birds are fond of their old nesting sites and are insistent in using the site selected. They not only come back to the same tree but will use the same limb as they used the previous year, even if the first nest has been disturbed." This was also observed in the present study. In 1962, the nest tree used by P1 in the previous year again held a nest, slightly higher than the old one, and perhaps built by the same pair.

Incubation.—When the egg in the nest of pair P1 was found at 6:30 a.m. on June 2, 1961, the female was already incubating. At 2:30 p.m. of the same day, the male was on the nest. On subsequent days, a definite schedule was observed. On June 4, the male took over at 10:26 a.m. and incubated until 5:14 p.m. when the female returned. This approximate schedule continued until the nest was robbed on June 21. Whereas the male was very punctual in taking over, always arriving between 10 and 10:30 a.m., the time of the female's return in the afternoon varied between 4:17 and 5:30. Neff and Niedrach (1946:74) report a similar schedule and delay in the female's return in a pair brooding a young bird in Colorado.

The egg was turned on the average of three times a day during early incubation. Toward hatching time, however, turning became increasingly more frequent. On June 18, between 6:08 a.m. and 7:26 p.m., the egg was turned nine times, that is, at approximately two-hour intervals.

Because the nest of pair P1 was robbed, no exact figures for the length of the incubation period could be obtained. Possibly the egg hatched on the day of its disappearance, on June 21, 18 days after it was laid. Neff (1947:12) states that the length of incubation varies from 18 to 20 days.

TABLE 1
SCHEDULE OF INCUBATION AT NEST OF PAIR P1

Date	Arrival ¹ (a.m.)	Male		Arrival ¹ (p.m.)	Female		Number of times egg was turned by either male or female ²
		Hrs.	Min.		Hrs.	Min.	
June 3	5:25	17	01
4	10:26	6	48	5:14	16	49
5	10:03	7	04	5:05	17	07	3
6	10:12	6	35	4:47
7	5:12
8	4:36	17	38	3
9	10:02	7	12	5:14	17	04	3
10	10:18	6	54	5:12	16	57
11	10:09	6	08	4:17
12	5:26	16	36
13	10:02	7	28	5:30	16	42	5
15	10:12	6	51	5:03	16	48
16	10:15	7	06	5:21	16	54	8
18	10:15	6	53	5:08	17	20	9
20	10:28	6	45	5:13

¹ Arrival of either bird coincided with the leaving of its mate.

² Figures based on four or more hours of observation per recorded day.

Behavior of adults during incubation.—Approaching the nest, the adults always alighted from 4 to 10 feet beneath it, usually on the opposite side of the tree. The pigeons then hopped up from limb to limb, usually spiralling the trunk, until the nest branch was reached. Prior to this ascent, the birds sometimes perched quietly for considerably lengths of time and peered about. Once the nest branch was reached, the adults walked out to the nest with quick steps.

The changing of places between male and female was rapid. When one bird had arrived, the other vacated the nest at once and either flew to an adjacent tree or out of sight. The newly arrived pigeon settled down on the egg immediately. When the female delayed in returning in the afternoon, the male uttered soft cooing sounds upon her appearance.

While incubating, the adult faced toward the trunk of the tree, perhaps because of potential danger from squirrels. This is also found to be the case in other incubating and brooding pigeons. Because of its immobility, the incubating bird is probably fairly immune to detection by avian predators and hence does not face the adjacent clearing.

Defense of the nest against a possible predator was observed on June 4, at 11:55 a.m. A fox squirrel (*Sciurus niger*), while crossing the tree at nest level, noticed the incubating male. The squirrel at once climbed on to a limb above the pigeon and peered down at it. Then the squirrel dropped beneath the nest and sniffed at the latter from below. Finally it climbed to the nest limb and advanced toward the pigeon. When it had almost reached the bird, the latter half-raised himself, drooped his wings and bristled the lesser wing coverts. Then, opening its bill slightly, the pigeon hissed and struck out with the bends of its wings. The squirrel at once retreated and left the tree.

Occasionally, the female returned earlier than usual in the afternoon. She then perched in trees about 20 to 30 feet from the nest for as long as a half-hour before taking over. The male also frequently perched for nearly an hour in the vicinity of the nest after having been relieved by the female. During this time he actively looked around, possibly making sure there were no predators in the vicinity.

On four occasions, when female P1 left to feed, she was joined by the female of pair P2 which nested at the Monterey cypress grove at the east end of the canyon and evidently followed a similar incubation schedule.

On one occasion, in 1962, when I climbed to a nest in a redwood, the incubating male tolerated approach within six feet, then tumbled and flopped to the ground, obviously feigning injury. This behavior, rather surprising for a tree-nesting species, was observed on only this occasion.

CARE OF THE YOUNG

On July 1, the nest of pair P3 was found; it contained a very young bird. By comparison with the data of Neff and Niedrach (1946:74), it was concluded the nestling was one day old.

Brooding and feeding.—These aspects were found to be nearly identical with the information in the Neff accounts (1947:14-15). The nestling was brooded regularly by both parents until it was 19 days of age. Neff reports 20 days as the brooding period in his birds. The female brooded all night, and the male took over during most of the day, arriving between 10:45 and 11:30 a.m., and leaving between 5 and 5:30 p.m. This schedule was remarkably similar to the incubation schedule of pair P1.

After the nineteenth day, the parents returned to the nest only to feed the nestling. This took place between 11 a.m. and 2 p.m., as did the feedings when the nestling was still being brooded.

During the first five days of observation, the young bird was fed about three times per day; thereafter, feeding varied, and after brooding ceased, the nestling was fed twice and occasionally only once per day.

Measurements of the nestling were not taken, because the necessary disturbances would have interfered with the normal behavior of the adults. Neff (*op. cit.*) furnishes detailed, and apparently accurate, data on the growth and development of the young.

The young bird remained in the nest until July 28, when it ventured out onto the branches surrounding the nest. Flights to adjacent trees occurred on the following day, and on July 30, at 7:15 a.m., the bird had left the area.

Behavior of adults at nest with young.—When approaching the nest, the adults alighted beneath it and hopped up to it in the same fashion as they did when incubating. Grinnell (1928:126) observed a slightly different approach while watching a Band-tail feed its young in Yosemite. He states that the bird "alighted on a branch of the nest tree, on a level with the nest but on nearly the opposite side of the trunk. After remaining perched quietly for awhile, the old bird then walked along the branch lengthwise to the trunk, hopped across, fluttering some, to the base of the nest branch, and walked out on it to the nest." The short period of quiet perching before going to the nest was also observed in this study.

Aggressiveness was observed only once when both adults drove away the intruding male L3.

Both parents were exceedingly secretive at and in the vicinity of the nest. Vocalizations were limited to soft cooing sounds when the brooding male welcomed the return of his mate in the late afternoon. In the early morning, while the female brooded the nestling, the male frequently visited the nest area and perched atop a nearby tree while scanning the surroundings. This behavior ceased abruptly four days after the brooding of the nestling had stopped.

Due to the limited view of the nest, which was well hidden by surrounding branches, the behavior of the young bird was difficult to observe. After brooding had ceased, the

bird remained practically motionless almost all day. When being fed, it vigorously beat its wings. At first, feedings took about a half to one minute each. After the parents stopped brooding and the young was fed only twice a day, each feeding lasted from one to two minutes. The feeding procedure itself was found to be identical with that described by Macgregor and Smith (1955:323): the adult seizes the bill of the young bird near the base in a cross-wise position; the old bird then gulps up and down 15 to 25 times (18 to 25 times in the above-mentioned study). Apparently the entire crop contents are passed to the young. After feeding, the adults frequently shook their heads from side to side.

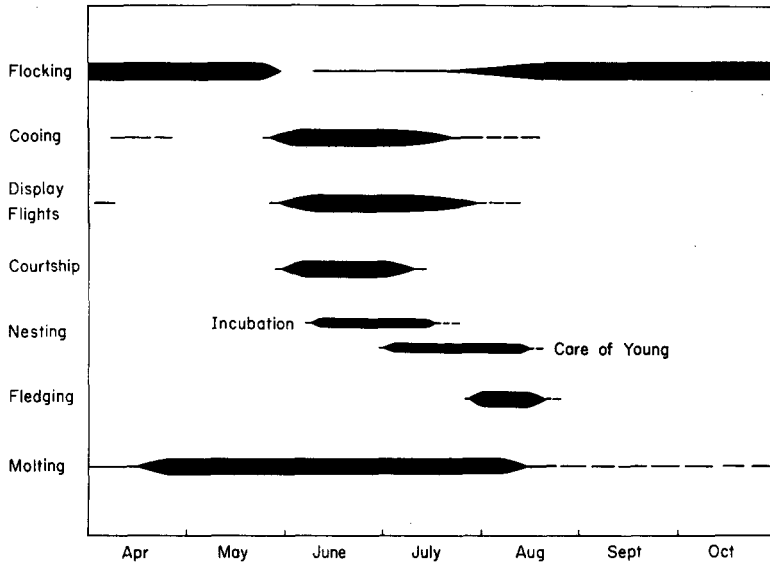


Fig. 8. General pattern of activity of Band-tailed Pigeons during period of observation. Length of bars indicates duration of a particular activity; width of bars shows amount of activity.

The nestling watched during this study was highly inactive until shortly before fledging. Prolonged periods of preening did not occur until the bird was 25 days old; then the young bird spent from 30 to 45 minutes at a time arranging its plumage and pulling sheath-flakes off the feathers. The lack of concern on the part of the adults after the young bird was 19 days of age is apparently a common situation in other pigeons.

In 1962, a high incidence of mortality among nestlings was observed. None of the young of six watched nests survived, either because of falling out of the nest (2), or because of predation by a Cooper Hawk and a Great Horned Owl (*Bubo virginianus*), which took one bird each. The two other nestlings disappeared from their nests at an early age. In the preceding year, only two known nestings were unsuccessful.

Food of adults.—During the entire nesting season, the only foods observed to be taken by the pigeons were the blossoms and fruit of the elderberry. Due to the great abundance of this bush in the canyon, large quantities of this food were available. At the onset of nesting, the blossoms were taken. The pigeons alighted on the tops of the bushes and fed leisurely for 15 or 20 minutes on the most easily reached clusters, then moved on to another bush. When green berries began to appear, the birds switched to

these. Paired birds which were no longer incubating or brooding fed together. Toward mid-August, when most nestlings began to fledge, the elderberries had ripened, and family groups banded together, forming small flocks of 6 to 12 birds. As during nesting, the pigeons fed entirely within the confines of the canyon.

The use of the blossoms of the elderberry as food, as well as of the green and ripe fruit suggests that the pigeons settle on an abundant food as a staple. Undoubtedly there is much variation in this summer staple in different nesting localities.

COMPARISON WITH THE NUPTIAL BEHAVIOR OF THE EUROPEAN WOOD PIGEON

There appears to be no record of the pair formation of the Wood Pigeon (*Columba palumbus*). The call of the male has been described by Witherby *et al.* (1949:132) as a series of syllables sounding like "coo-cooo-coo, coo-coo."

During the display flight, the male rises fairly steeply, then sets his wings approximately horizontal and glides back down, often repeating this performance, so that he follows an undulating course. Near the top of the rise, the bird commonly claps his wings vigorously one to three times.

The display of the male in the presence of the female apparently takes place either on the ground or on a limb. The male bows until his breast touches the limb or ground and raises his tail nearly vertically, fanning it. This position is held for several seconds. The bird then returns to normal, closing and lowering his tail (Witherby *et al.*, *op. cit.*).

Haverschmidt (1932:10-11) has described the pre-copulatory ritual of this pigeon in detail. Both birds pass their bills over their own backs and peck behind their wings, then bill one another. This may be repeated several times, and the male's bill may be widely opened when he withdraws it from behind the wing. The female then crouches and raises her wings a little to support the mounting male. The male then dismounts, and the female once more raises her wings a little, distends her neck, and coos softly. Her head is lowered during this display. The pre-copulatory behavior may now be repeated, or the birds may preen one another's head and neck feathers. Heinroth and Heinroth (1926-1928) state that the male also occasionally follows the female about, his tail depressed and fanned.

Goodwin (1947a:221) described the behavior of this pigeon during the selection of the nest site. The male's hindparts and tail are more or less raised, and he calls continually. He nods his head, and his closed wings twitch spasmodically. The female now joins him, and the birds bill each other's heads and twitch their wings.

The Wood Pigeon may build its own nest or may use the old nests of Jays (*Garrulus glandarius*) and other corvids, or squirrels. Two eggs form the normal clutch.

Generally, one may say that the nuptial behavior of the Band-tailed Pigeon is less complex than that of the Wood Pigeon, particularly the behavior following coition. This difference in complexity may be due to the fact that *C. palumbus* "requires" more isolating mechanisms to maintain itself against two sympatric species, *C. oenas* and *C. livia*, whereas the Band-tail is the only representative of its genus in its North American range, with the possible exception of the Rock Dove, which, however, is not found in the habitat of the Band-tail and which, of course, is a recently introduced species. The importance of a number of isolating mechanisms in the Wood Pigeon is underlined by the fact that under abnormal conditions, such as captivity, where not all facets of behavior may appear (the display flight, for example), *C. palumbus* will copulate with *C. livia*, and the latter in turn hybridizes with *C. oenas*. Only one *C. livia* x *C. fasciata* hybrid, apparently produced in captivity, is briefly mentioned in the literature (Miller, 1956).

The bowing and head-swinging of the male Band-tail prior to copulation is reminiscent of the bowing of *C. palumbus*, but it is certainly not the same. Wing- and mutual-billing, prominent in the Wood Pigeon, is barely indicated in *C. fasciata*. The male merely touches his wing, and the female only reaches for the base of the male's bill.

Unfortunately, there is virtually no information on the behavior of other American members of this genus. Certain aspects of the nuptial and territorial behavior of the Band-tail are different enough from those of Old World species to invite similar investigations of other New World columbids. From the scant literature it appears that territoriality, for example, evidently also occurs in *C. squamosa*. Fighting breaks out if a male, after a display flight, alights too close to another male (Wetmore, 1927). Such pronounced territoriality apparently does not occur in European species, although squabbles may arise between neighbors in a colony. Demléé (1954) states that male Stock Doves defend tiny territories, that is, the nesting cavity and its immediate vicinity, but that even the display flights are performed communally. The Wood Pigeon is also known to nest communally on occasion, as around the Zoological Garden in Berlin (Fehringer, 1926:82).

TABLE 2
COMPARISON OF SOME BEHAVIORAL AND REPRODUCTIVE FEATURES
OF *Columba fasciata* AND THREE EUROPEAN PIGEONS*

Species	Display flight	Copulatory behavior		Nest and clutch size
		Male	Female	
<i>C. fasciata</i>	Wide circle, $\frac{3}{4}$ glide, $\frac{1}{4}$ quick shallow wing-beats; apparently announces ownership of territory; wings horizontal; chirping.	In tree; bowing head-swinging; erect posture; cooing strut; indication of wing-billing; after coition, beak pointed up, display flight to next tree.	Largely inactive; indication of billing with male; wings half-raised during coition.	Nests well-spaced; self-built. 1 egg, rarely 2.
<i>C. palumbus</i>	Steep rise with wing-beats, glide down; wings approximately horizontal; wing clapping.	Tree or ground; repeated wing-billing; bills female after coition, may preen head and neck of female.	Wing-billing; bills male repeatedly; raises wings a little; after coition, distends neck and coos, head bent down; or preens head and neck of male.	Spaced or colonial; self-built, or uses nests of other species; in tree. Usually 2 eggs.
<i>C. oenas</i>	Up and down; "sweeps and circles"; communal; gliding with wings dihedral; often rapid and with spurts; wing-clapping.	Tree or ground; strutting with folded wings held out horizontally; wing-billing; or same as <i>C. palumbus</i> ; after coition, displays to female, bowing with raised and spread tail; and cooing.	Wing-billing, bills male, same as <i>C. palumbus</i> .	Singly, but often colonial, in natural and artificial cavities, in trees. Usually 2 eggs.
<i>C. livia</i>	Slower wing-beats than normal, then glide with wings strongly dihedral; semicircles; wing-clapping.	Ground; repeated wing-billing, false feeding of female; after coition, struts off with feathers raised, tail spread and depressed; or display flight with female.	As above; after coition follows male, imitates his posture; or display flight with male.	Usually colonial; self-built in houses, cliffs. Usually 2 eggs.

* Data on European species from Demléé (1954), Fehringer (1926), Goodwin (1947a, 1947b, 1948), Haverschmidt (1932), and Witherby *et al.* (1949).

As seen in table 2, the behavior of the Band-tailed Pigeon differs considerably from that of European columbids in several aspects: (1) the display flight differs functionally as well as in execution and is accompanied by vocalization; (2) in the pre-copulatory ritual, wing and mutual billing are barely indicated; (3) the male's tail is always depressed; (4) post-copulatory displays are virtually absent; (5) the female is largely inactive throughout courtship; and (6) a definite nesting territory seems to exist. It is also noteworthy that all European species are inclined to use already present nesting facilities, whereas the Band-tail apparently invariably builds its own nest. Two eggs are the exception with the latter species, but the clutches of the Old World birds regularly consist of two or even more eggs.

SPECIES RELATIONSHIPS

Goodwin (1959) has subdivided the genus *Columba* into several species groups, and these into sub-groups, all on the basis of plumage characteristics, including those of the neck. He feels that American and Old World species cannot yet be separated, and that this could be done only on osteological and biochemical characters. Furthermore, he states that "colour pattern is usually a better guide to relationship than actual colour." However, an examination of the skins of four Eurasian species, *C. palumbus*, *C. oenas*, *C. livia*, and *C. rupestris*, at the Museum of Vertebrate Zoology shows that all four species have purplish red iridescent and viridian-green iridescent neck plumage; the colors in all species are precisely the same and always occur together. Only *C. palumbus* has "added" white neck patches. It seems to be more than a curious coincidence that these colors, either alone or together, evidently are not found in the American members of the genus.

Johnston (1962:71) has placed all present members of the genus *Columba* into a number of infrageneric groups, employing two previously unremarked characters, the presence or absence of a trailing fringe on the tenth remex, and the angle on the skull at the frontal hinge. He believes that the superspecies of American band-tailed pigeons belong to the Afro-Eurasian genus *Columba*, whereas the other New World species are assigned to two other genera. While this classification may be justified, the behavior of *C. fasciata* certainly does not suggest a close relationship to the European species, any two of which are behaviorally more similar to one another than to the Band-tail.

Perhaps an investigation and comparison of other New World pigeons with Old World species as to behavior could shed some more light on the problem of generic relationship. While it would be premature to draw any conclusions at this point, striking differences in the behavior of the Band-tailed Pigeon and that of European species suggest a basis for further work in this area.

SUMMARY

A wintering flock of Band-tailed Pigeons and subsequent breeding pairs were observed in Strawberry Canyon on the campus of the University of California at Berkeley.

Whereas in 1962 paired birds occupied nest groves in early April, in 1961 the migratory flock remained until late May. Between April 7 and May 21, 1961, the flock followed a fairly rigid schedule of roosting and feeding. Major food items not previously reported were the blossom buds of the black locust. When the supply of buds neared exhaustion, the pigeons resorted to hanging by their feet in order to reach otherwise inaccessible bud clusters.

Body feathers were molted throughout the period of this study. Rectrices and primaries of apparently both adults and immatures began to appear beneath the roosts on April 19.

The large flock in 1961 left on May 22, and a smaller one of 12 adults, as well as some single birds, remained. Nuptial activity began on May 28, when some pairs had occupied nest groves used during the previous year.

Two major types of vocalization were recorded, cooing and excitement calls. The latter include display-flight chirping, the crowding grunt, and the temporarily deserted mated male's call. Cooing was most frequently heard in the afternoon, particularly after 5 p.m.

Unmated males apparently conducted searches for unoccupied nest groves while also looking for single females. Certain perches were selected for cooing and as starting points for exploratory display flights.

Pair formation was observed once. Evidently the behavior of the female is the determining factor in sex recognition. The courtship display apparently plays an important role in pair formation. Preliminary displays may precede the courtship proper.

The courtship display seems to take place always in a tree and includes bowing and head swinging as well as cooing on the part of the male. After coition, the latter momentarily points his beak up at an angle, then flies to an adjacent tree in display flight fashion. Wing- and mutual-billing are barely indicated. The female is largely inactive throughout the display.

Evidence suggests the defense of sexual and nesting territories. Such areas consisted of coniferous groves. Intruding single males were chased away by the resident male or by both resident birds. The display flight of the male seems to be territorial rather than nuptial. When nearly all nest groves were occupied, such flights occurred only once a day and were performed by several males simultaneously.

With one exception, nests were located in coast live oaks and conifers. All nest trees grew on steep slopes or on small precipices within the nest groves. Nest height from ground varied from 7 to 40 feet. Usually, the nest was placed on a horizontal limb, several feet from the trunk.

Both adults participated in incubation. The female incubated during the night, and the male took over during part of the day. A fairly regular schedule was followed by both birds. On one occasion, a male flushed from the nest exhibited injury-feigning.

The nestling was brooded and fed by both parents. Brooding ceased abruptly when the young was 19 days old, and feedings were reduced from three to two times daily. The young left the nest area two days after fledging. Parents and their fledged young subsequently formed small flocks.

During the nesting period, the only food items observed to be taken by the pigeons were the blossoms and the green and ripe fruit of the elderberry.

A comparison with the nuptial behavior of the Wood Pigeon (*C. palumbus*) reveals significant differences between the two species. Further studies of the behavior of other New World pigeons could possibly contribute to a basis for generic distinction.

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Museum of Vertebrate Zoology, Berkeley, California, March 20, 1962.