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EPIGAMIC AND REPRODUCTIVE BEHAVIOR OF THE ORANGE-FRONTED PARAKEET

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The Orange-fronted Parakeet (*Aratinga canicularis*) occurs in tropical deciduous and scrub-thorn forests of Pacific mountain slopes and lowlands from Sinaloa, México, to Costa Rica. Within that range, this small parrot is often nomadic but probably nonmigratory; it is highly social in flocks, abundant, and conspicuous.

In the present study, birds of three distinct populations (named as *A. c. clarae*, *A. c. eburnirostrum*, and *A. c. canicularis*) were investigated. The first of these is northernmost in distribution, primarily in the state of Sinaloa, México, the second occupies an intermediate range from there south to northern Oaxaca, while the last occurs from the Isthmus of Tehuantepec, Oaxaca, southward. The study was divided into three parts: observation of nesting habits in Sinaloa (*A. c. clarae*), observation of postbreeding flock behavior in Chiapas (*A. c. canicularis*), and observation of behavior of captive birds in aviaries (*A. c. canicularis* and *A. c. eburnirostrum*).

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MATERIALS AND METHODS

In observation of nesting in the wild, a blind was often employed, and in examination of nest contents a small mirror, described later, was useful. Experiments on breeding of captive birds involved construction of simulated termitaria made of plastic and of cork.

About one-half the parrots held in captivity in aviaries by me were purchased from Mexican bird dealers in the market places of Tuxtla Gutierrez, Chiapas, and Tehuantepec, Oaxaca, in July, 1959. A second group of 12 individuals was obtained in October, 1960, from the University of California Medical School, San Francisco.

Observations of captive birds were usually made from outside the aviaries and normally consisted of a one- to three-hour period each morning in the first year of the study. In the second year, 20-minute observation periods, usually two or three successively, were used three to five mornings per week. Occasional and brief observational periods were sometimes undertaken in afternoon and evening hours and rarely also at night. In the third year, when studies were made of breeding in captivity, several

10- to 12-hour observation periods were arranged so that attentiveness at the nest could be assessed. I entered the aviaries only to clean them, provide food, or occasionally for photographic purposes. In the first year, birds were housed in an indoor aviary at the University of Kansas; in the second year, they were housed in two aviaries on the roof of the Life Science Building, University of California, Los Angeles. Beginning in January, 1962, all birds were housed in an aviary at Occidental College. The parakeets were color banded and sexes determined by laparotomy.

Besides direct observation and the recording of notes, motion and still pictures were often made of specific behavioral aspects, and typical vocalizations were recorded on magnetic tape.

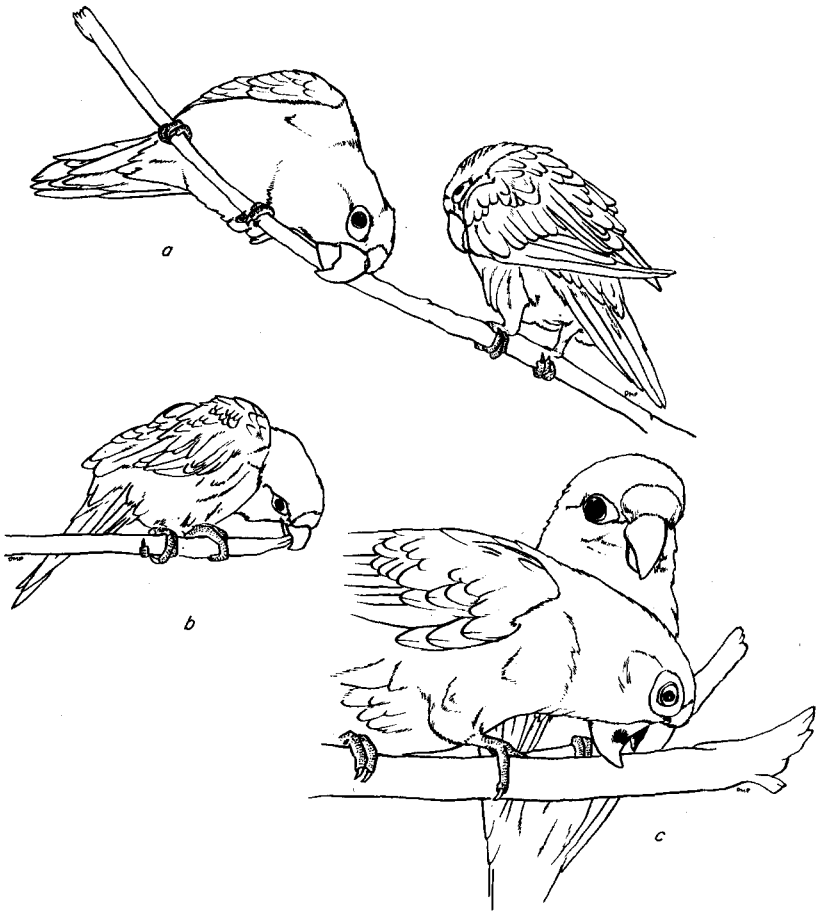

Fig. 1. Displays of the Orange-fronted Parakeet (*Aratinga canicularis*). a, Bill-wiping; b, perch-biting; c, high-intensity perch-biting; note constriction of pupil of eye.

EPIGAMIC AND ASSOCIATED BEHAVIOR

Described here are behavioral components of several types, including relatively pure epigamic activities, ambivalent activities wherein epigamic and other tendencies are represented in approximate "balance," and behavior that may be termed appeasement activity. The word component is used herein to denote a discrete behavior or act, one that is an integral part of a display or other behavioral sequence.

Components of Courtship Feeding Display

Dilger (1960:679–680) believes that in the African love-bird parakeets (*Agapornis* sp.) courtship feeding is not sexually motivated but is rather a means of enforcing the pair bond. He cites the fact that courtship feeding occurs at all times of the year, that it may often immediately follow successful copulation, and that in some species (*Agapornis cana* and *A. taranta*) females frequently feed their mates in captivity. Whether the latter behavior exists in nature is unknown. In captive *Aratinga canicularis*, females may perform courtship feeding in homosexual pairs. In the case of these homosexual pairs, either female of a given pair performed the feeding. This agrees with Lack's (1940:176) information for the Psittaciformes. I do not know whether females feed males in *Aratinga canicularis* in nature.

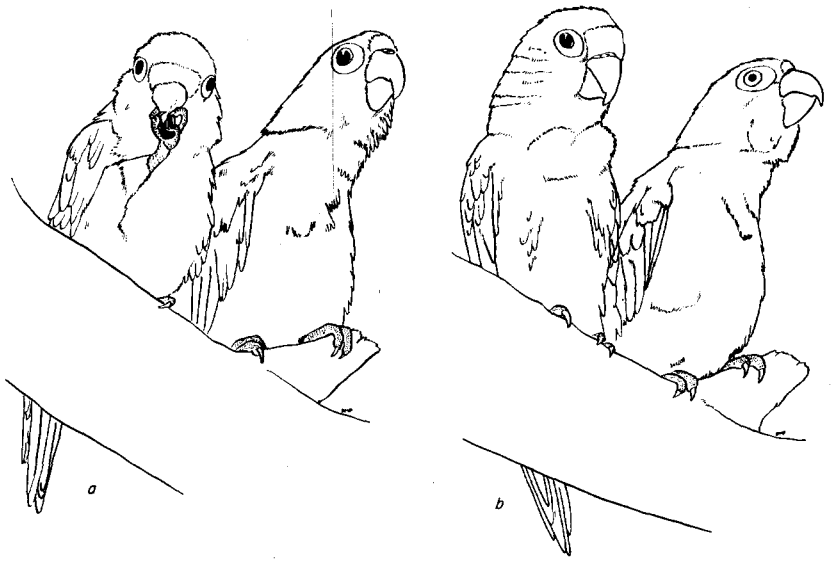

Fig. 2. Preparatory components of courtship feeding in Orange-fronted Parakeet. a, Bird on right displays with head erect, malar feathers fluffed; b, bird on right still with head up, malar feathers puffed, but now with pupils constricted, revealing yellow irides.

In the Orange-fronted Parakeet, courtship feeding consists of a series of components, some of which, although often associated with the display, are of highly ambivalent character and reflect other tendencies than courtship or consummation of courtship feeding. They usually occur early, in the weak stages of courtship feeding, when conflict of epigamic tendency with other tendencies are expectedly greatest (see Morris, 1956; Dilger, 1960:673–674). Other behavior, functional components of courtship feeding, seems necessary to successful completion of the act. Although it is here recognized that this latter behavior is in no sense "pure," there is relatively little evidence in it of conflicting tendencies.

In a typical act of courtship feeding, two birds perch side by side. One may bite the perch, or alternately bite the perch (fig. 1*bc*), rub or wipe its mandibles against the perch (fig. 1*a*), or head-waggle. Such activities seldom stimulate the partner. Next, the displaying bird may cease manipulation of the perch and suddenly erect its head, fluffing the malar feathers (malar-puff). Then, as quickly, the bird may return to kneading the perch in its bill, causing a popping sound. This may be followed by erection of the head, fluffing of the malar feathers, crane-peering, pupil-flexing (fig. 2*ab*),

and bill-vibrating or snapping. The preceding components usually cause the partner to move closer, fluff, or also to vibrate or snap the mandibles. The first bird may then perform quickly several courtship feeding components: head-up chin-out, head-bobbing, bill-grasp, bill-hold, and head-jerk. The last named component completes the courtship feeding act. Following is a description and discussion of each component of this ritual.

Displacement head-waggling.—In this behavior, a parakeet rapidly wags the head. Two birds may head-waggle simultaneously, interspersing this with bill-wiping, bill-rubbing, and perch-biting, in very weak expression of courtship feeding. Head-waggling, unlike bill-wiping, rubbing, and perch-biting, also occurs in other contexts, along with pupil-flexing and the inflected whistle. In courtship feeding, however, these highly ambivalent behavioral components are not associated, head-waggling appearing early in the expression, pupil-flexing and the whistle late in the pattern. The trophic expression of the head-waggling motor pattern occurs in feeding, wherein the motion is used in flinging off particles of sticky foods from the bill.

Displacement bill-wiping.—Autochthonously, bill-wiping is employed to clean the mandibles of adhering food particles, such as when fleshy fruit is being consumed, or in freeing earth and wood particles when the nest cavity is being excavated. Allochthonously, bill-wiping becomes highly exaggerated: each side of the beak, with mandibles slightly agape, is brought alternately into a wide-sweeping contact with the perch as the parakeet faces its partner. The act is rapid and repeated several times.

Displacement bill-rubbing.—In this behavior, the parakeet places one broad side of the mandibles against the perch and works this side back and forth or up and down against the perch. Autochthonously, bill-rubbing is a honing operation frequently engaged in for minutes at a time; a bird may perch beside the trunk of a rough-barked tree and hone against it. Allochthonous bill-rubbing is exaggerated and frequently interspersed with erection of the head, bill-wiping, and pupil-flexing.

The appearance of these weakly aggressive tendencies may result from the fact that bill-wiping, bill-rubbing, and perch-biting usually do not elicit full acceptance of courtship feeding by the partner but merely serve to excite the displaying bird itself. Thwarting, except from the standpoint of apparently self-stimulating effects of the components, thus stimulates erection of the head and pupil-flexing, both of which are components possessing some agonistic meaning.

Displacement perch-biting.—In this behavior, the perch is seized firmly between the mandibles and bitten or chewed and twisted (fig. 1*b*). Perch-biting is a frequent leisure activity of psittacines, and aviculturists know that providing the aviary with an ample supply of twigs and soft branches encourages the birds to the pass-time behavior of chewing on these rather than alternate activities such as feather pulling. The parakeets thus gather in small groups several times a day to engage in this behavior. When displaced, perch-biting is much exaggerated (fig. 1*c*) and interspersed with bill-rubbing, popping, and components of weakly aggressive, agonistic, quality.

Popping.—This is an especially remarkable component; in it the perch is grasped in the bill and bitten rapidly. The mandibles are moved up and down and back and forth on the object, producing by this kneading action a vibrating, popping sound, not unlike the rapid-fire noise made by the pecking of a woodpecker. The bill motion in popping is like that in bill-vibrating and bill-snapping.

When a parakeet engages in popping, it draws attention to itself. Other birds in the flock become quiet and watch the displaying bird, although usually it is possible to determine toward which other individual the display is being directed. Components in

the sequence preceding popping frequently do not give way to subsequent stronger elements in the behavioral series leading to courtship feeding. However, with the popping component, a behavioral stage is reached in which further components (at least one or two) in the series may be expected. The origin of popping is not clear. As such, it does not occur in other contexts; it perhaps is a very strong version of perch-biting.

Bill-vibrating.—In this component, the head is suddenly held erect from the perch-biting or popping posture, the plumage of the head and sometimes of the body is slightly fluffed, and the bill rapidly opened and closed. The mandibles do not meet, so that the motion is noiseless. The pupils of the eyes may be slightly constricted as in bill-snapping, revealing the yellow irides. The behavior seemingly draws attention to the bill of the displaying bird and, perhaps, to the tongue.

Bill-snapping.—This is an intense form of the previous component; here, the mandibles come in contact producing an audible snapping sound. Again, the pupils may be half-flexed, and there is often an associated inflected whistle (see below). Bill-snapping, pupil-flexing, and the inflected whistle often occur together, displaced in ambivalent states created when a parrot is suddenly frightened. There they may serve a function of forestalling attack.

Crane-peering.—With the head erect, a parakeet, crane-peers by cocking its head from side to side and looking hurriedly in various directions, all in a very jerky, mechanical toy-like fashion. The malar feathers are strongly fluffed. I have not seen crane-peering outside the context of the precourtship feeding sequence. Again, as with popping, crane-peering may serve to draw attention to the head of the displaying bird and may lead directly to bill contact and courtship feeding.

Malar puff.—As indicated by the term, the feathers of the malar region are fluffed, producing a bilaterally bearded appearance (fig. 2*ab*). Malar-puffing strongly emphasizes the area around the bill and is usually a component of the display pattern involving pupil-flexing, when components indicating threat, defense, flight, and courtship may all occur nearly simultaneously. In the context of courtship feeding, this is usually early in the pattern before a stimulatory effect has been produced in the partner or at times when the response of the partner is such as to thwart the displaying bird. There is no indication by Dilger (1960) that specific fluffing of the malar feathers occurs as a display in *Agapornis*.

Pupil-flexing and inflected whistling.—These two components are typically associated with each other; although birds may flex their pupils without whistling, the whistle is almost always accompanied by pupil flexion. Many, if not all, species of parrots have the ability to constrict or expand the size of the pupils in relation to factors totally apart from the direct stimulus of sudden change in light intensity. Voluntary shortening of the focal length, for example, is accompanied by a marked reduction in pupil size. Of course, change in size of pupil with change in focal length is probably correlated with light condition also: when distant objects are being viewed, the pupil must be larger than when near objects are being viewed, if the optical stimulus in each case is to be the same.

The action of pupil flexion can be voluntary. Walls (1942:647) mentions both the sphincter and dilator muscles in the iris. Rochon-Duvigneaud (1950:225–227) describes extensive circular and radial striated muscles in the irides of birds, stating that some of these are specifically directed to changing the size of pupils while others are used in accommodation. Thus, the existence of appropriate striated musculature in the irides of birds indicates that the pupils can be flexed voluntarily. My own histological examination of the iridial musculature in *Aratinga canicularis*, as well as in other parrots, confirms the existence of striated muscles therein.

When an Orange-fronted Parakeet suddenly constricts and then expands the pupils, the irides are flashed in a manner truly startling to an unsuspecting observer (fig. 2*b*). This pupil flexion display is often accompanied by other components, as has been mentioned; in the context of epigamy, these include extending the head (or erecting it), bill-snapping, and head-fluffing, while in agonistic context, head-waving or head-waggling are associated components. Pupil flexion may be full, in which case the pupil is first but a pinhead in size and then suddenly nearly the diameter of the entire eye, or flexion may be only partial, as in the less intense displays.

The pupil flexion display is not confined to *A. canicularis*. Widely differing species throughout the order are known to employ the mechanism in some ritualized fashion. For example, Tavistock (1929:562; 1931:283) mentions the constriction of the pupil by the male of *Psittacula derbiana* in courtship. In this species, according to Tavistock, pupil constriction accompanies a deep bow toward the female.

Pupil flexion display is much more prevalent outside epigamic contexts in circumstances having the following factors in common: a bird has been taken unaware while involved in relaxed behavior such as casual feeding, sleeping, or preening, or the object (other bird or human) has suddenly appeared and/or is rapidly approaching. The normal reaction of the intruder to the display is to pause, turn away, or otherwise be deterred from a course toward the surprised, displaying individual.

Apparently for reasons of survival, a rapidly approaching or suddenly appearing object is treated as potentially dangerous by the bird. In order properly to deal with this potential danger, the ability to change focus rapidly would naturally be selected for, the process involving an appreciable change in the size of the pupil. Although the ability to change the size of the pupil is known in many birds, there is evidence, in parrots at least, that the ritualization of this mechanism into a display that serves to forestall intraspecific attack has accompanied the evolvement of or has been fortuitously associated with the morphological condition of pale-colored irides that contrast with dark pupils. In the Yellow-headed Parakeet (*Aratinga jendaya*) of South America and the Orange-chinned Parakeet (*Brotogeris jugularis*) of México and Central America, both kept captive by me, the irides are dark brown, and no pupil flexion display is present in these species. Nor does Dilger (1960) mention the display in *Agapornis* which have dark irides. Such a display is present in a Red-crowned Parrot (*Amazona viridigenalis*) in my aviary. The evolution of the display and the pale irides may thus be correlated.

Inflected cry and inflected whistle.—An inflected vocalization nearly always accompanies pupil flexion display in the Orange-fronted Parakeet. The whistle-like version is easily imitated by a human whistle. It varies from a shrill whistle to a cry richer in quality, something like *crooooo*. Figure 5*b* is a spectrographic illustration of this call. The vocalization probably enhances the effect of the flexion by calling attention to the displaying bird from a greater distance.

Head-up chin-out.—This and the following components in courtship feeding display are steps in returning liquid matter to the mouth from the esophagus or crop or in the transmittal of the matter to another bird. The hypothesized purpose of courtship feeding is affirmation or strengthening of the pair bond. Even though ritualized, the motor pattern may still, although probably unnecessarily, function as a feeding mechanism. An actual regurgitant seems to be passed from one adult to the other. The motor pattern of the display is apparently identical to that involved in feeding of the young.

The head-up chin-out component is a low intensity regurgitating action. It rarely leads directly to the head-jerk but gives way, in growing intensity, to the head-bob or, when intensity wanes, to behavior of other context. The behavior resembles movements

made by a man attempting to avoid the constricting effects of a tight collar without benefit of hands. Weak gaping accompanies the movements.

Head-bob.—The head-bob is high-intensity regurgitating behavior. It often leads directly to the consummatory act of the head-jerk. Readers familiar with pumping movements of bitterns (*Botaurus*) will perforce have an idea of the head-bob of this parakeet. The action is not so severe as in bitterns, but the "rippling" out-thrust of the neck and head is similar, and the peristalsis-like effect on the upper alimentary tract forces liquid regurgitant to the mouth.

Dilger (1960:674–675) discusses the homologous behavior in *Agapornis*, terming it head-bobbing. He found variation in number of head-bobs and in rapidity of performance among several species. The performance in *Aratinga canicularis* apparently resembles closely that which Dilger found in his white-eye-ringed forms, the number of bobs being less numerous and the performance relatively slow. Dilger mentions a possible direct correlation in *Agapornis* between bare or white circumorbital area and slow bobbing with few bobs. It is well to note that in *Brotogeris jugularis*, which possesses no white or bare area around the eyes, the head-bob is rapid and consists of more bobs than in *Aratinga canicularis*.

Bill-sparring.—In order to feed its partner, a parakeet must manage to grasp the bill of that bird with its own. The gaping of the bill and concurrent movement toward the partner is similar to an agonistic motion, and, if performed suddenly, often elicits a defensive response from the partner, so that momentarily the birds seem almost to fight with their bills. Rarely, the result is a brief fight; usually the head feathers remain fluffed and after a brief period of bill-sparring, one bird quietly holds the bill of the other. Since either bird may perform the feeding operation in homosexual pairs, of which there are several in my aviary, it is possible that bill-sparring sometimes occurs at times when both birds are stimulated to perform feeding. Bill-sparring is not, it should be emphasized, an agonistic act, and it occurs only between members of pairs or partnerships. Bill-sparring is the act, then, of grasping at the partner's bill whenever any conflict of tendencies occurs. In aggressive encounters between members of pairs, a subordinate bird may employ vague bill-sparring motions that effectively reduce agonistic tendencies of its mate. Thus in agonistic context the effect is appeasement. The bill-fencing of *Agapornis* (Dilger, 1960:661) is of an entirely different nature, being a component of agonism, as it is in *Aratinga*.

Bill-grasping.—When bill-grasping occurs successfully, it requires participation of both members of a pair or partnership. The bills of the two birds are slightly open and interlocked at right angles to each other as in *Agapornis* (Dilger, *op. cit.*:680, not illustrated).

The head of one bird, usually the dominant of the two (if one is in fact dominant) and almost always the one that has initiated the act, is higher than that of its partner. The tongues of the two birds touch each other. Occasionally, the birds cease movement when the bills are interlocked and merely "hold-bills," as it were. Such behavior is not frequent enough to rate consideration as a typical component of courtship feeding, however.

Head-jerk.—This component is the consummatory act of courtship feeding. With the bills interlocked, the heads of the two birds move rapidly back and forth from two to six or a few more times. This movement is a rapid "push-pull" one, but, in fact, the bird being fed seems responsible for most of it. Evidence for this comes from young birds of the species that, when fed with an eye-dropper, gape and respond with jerking motions when no movement is supplied by a person providing the food. The

head-jerk may occur several times in quick succession with incipient components being omitted between the subsequent feedings.

After completion of the head-jerk, the performers usually are quiet for several minutes; they may, however, follow head-jerking, with a few moments of erecting the head, flexing the pupils, and normally associated behavior, before becoming quiet.

Components of Mutual Preening and Appeasement

It is the well-developed habit of mutual preening (figs. 3*a*, 4*ab*) that, to me, seems

Fig. 3. a, Three parakeets engaged in preening and chewing behavior. Bird on left preens neck of middle bird, which preens itself, as bird on right chews and cleans its foot. b, Nuzzling behavior, an appeasement component of attentiveness. Bird on left pushes bill against side of mate's head. Note closed eyes and fluffed head feathers of bird on right.

the strongest behavioral device for actual maintenance of the pair-bond throughout the year. Mutual preening, in which actual or potential members of pairs or partnerships preen each others' plumage, is indulged in daily throughout the year, with no apparent change in frequency in any season. An elaborate set of components involving elicitation, direction of preening, and the use of the habit in appeasement (very important in a peaceful relationship outside of the breeding season) is present in *Aratinga*. In comparison to preening in *Agapornis*, the development of the habit in *Aratinga* seems much greater. In the former, preening only of the head is indulged in by adults (young birds often preen other areas), whereas in *Aratinga canicularis* mutual preening is directed to the head, wings, and tail areas.

Fig. 4. a, Bird on left preens neck of mate which lifts head to indicate area to be preened. b, Bird on right now cocks head for nape to be preened.

A few components serve only to calm the aggressive tendency of the partner, not to redirect it or to elicit another positive response. These components are seen, additionally, in the context of mutual attentiveness when other components are employed to elicit preening or feeding, or possibly a copulatory response.

In typical activity involved with appeasement and mutual preening, two birds may fluff the plumage, draw close to each other and withdraw their heads, while closing or nearly closing their eyes. One bird may then cock its head to solicit preening, or the other may begin to preen the first bird and meet with a defensive response. When the latter occurs, the bird that has offered to preen may nuzzle its excited opponent to calm it. A second attempt may then be made to preen the calmed bird. Successful initiation of preening may call forth reciprocal preening or merely the direction of the place to be preened. This is accomplished by the preened bird slowly turning its head or turning slightly to expose the side, undertail, or area beneath the wing.

These last three movements are like head-cocking but serve merely to direct preening to other parts of the body. Any action of agonistic nature by either bird may elicit nuzzling behavior by the partner. Dilger (1960) does not describe nuzzling behavior for *Agapornis*.

Purely appeasive components of behavior are combinations of or elaborations of normal resting or roosting postures and movements. The first three of the following components are of such nature.

Fluffing the plumage.—Parakeets always fluff the plumage when assuming resting state. Similar fluffing occurs or is maintained in all non-agonistic interaction of individual birds. If a parakeet exhibits fluffed plumage to an aggressive opponent or to its mate, the latter's fierceness of approach or attack is visibly reduced; aggressive agonistic tendency may in fact be altogether lost quite suddenly. Additionally, a bird that exhibits high-intensity threat components but is even slightly fluffed is unlikely to be successful in an attack or in maintaining whatever aggressive demeanor it had toward another bird. Plumage may be fluffed very gradually or fluffing may be initiated by a rather violent ruffling action combined with assumption of a drooped-wing, lowered-tail posture.

Withdrawing the head.—Withdrawing the head connotes complete relaxation and lack of any readiness to move in a quick manner. Always combined with it is drooping of the wings and lowering of the tail. These three acts compose the second stage of assuming full rest posture or the roosting state. Birds at the lower end of the social order are more often seen in some stage of this behavior than they are in any other.

Closing the eyes.—This signifies nearly complete absence of agonistic tendency. Birds of reticent demeanor often keep their eyes less than fully open and often bat their lids, especially in the presence of a socially superior bird. A parakeet may close its eyes but not show any other signs of subordinate state or appeasiveness while engaged in otherwise intense agonistic interaction. But, no matter how active the bird with drooping eyelids or closed eyes may appear in an encounter, the bird's quick defeat is thereafter a certainty.

Nuzzling.—This and the following components serve appeasement function but are also components in solicitation of preening from another individual.

A bird may nuzzle its partner with the eyes open (fig. 3*b*) or closed. An individual is appeasive only toward its partner, typically edging close to the latter and gently pushing with the bill in the feathers of the partner's neck, breast, back, or rarely, abdominal region. A bird that is behaving ambivalently toward its partner utilizes nuzzling to allay the latter's agonistic (either defensive or aggressive) behavior, stimulated by the appeaser's alternately aggressive demeanor. Once the partner becomes "contented," the appeaser then abandons nuzzling, assuming an attentive attitude, often gradually becoming so fierce in this attentiveness as to require again the appeasive nuzzling. This may continue for several cycles.

Wing-up, tail-up.—When a parakeet lifts a wing but does not spread it or bends forward slightly lifting the tail, the bird thereby solicits its partner to preen the sides and underwings or the tail area. In the latter area either the rectrices or the coverts may be preened in response to the tail-up. Frequently, if the solicited bird's preening tendency is not great, the wing-up stimulates agonistic leg-grabbing or, in the case of the tail-up, pulling of the tail feathers.

Pre-mating or Pre-copulatory Components

Switch-sidle and pushing.—In this behavior, a parakeet, as Dilger (1960:674) has described in *Agapornis*, "sidles along the perch toward or away from the female, repeat-

edly turning around as he does so." If the partner exhibits no sign of interest in sexual behavior when a parakeet approaches by switch-sidling, the approaching bird turns away. When the partner indicates by fluffing, stooping, or leaning forward, that approach is favored, the other parakeet "edges in" and, turning so that it is parallel to the partner, pushes against the latter's side with the wrist area of the wing. The wing may be completely folded or slightly to fully extended; in the latter state, the sides of the two birds may be in contact and the open wing slightly over-hanging the bird being pushed.

Clawing.—This action is only superficially a clawing motion and has no relationship to any agonistic behavior. In clawing, a parakeet raises the foot closest to the partner and gently waves it in the air or places it on the back, wing, or side of the partner. Clawing is weak incipient mounting behavior in *A. canicularis*. On two occasions I have observed it to be followed by somewhat stronger attempts to mount in seeming preparation for copulation. On one occasion it was seen to precede copulation. Rarely, clawing occurs in appeasement behavior: when an individual is attacked it may accompany this with fluffing, closing the eyes and other typically appeasive behavior.

The foregoing accounts complete the description of components of epigamic and reproductive behavior except for two, dueting and display flight. These were not observed in captive birds but were seen occasionally in the wild by me (see p. 188).

Vocalizations

A detailed analysis of vocalizations in Orange-fronted Parakeets is now underway, but the basic call patterns are mentioned here. One vocalization, the inflected whistle and call, associated with ambivalent behavior, has been discussed previously (p. 174).

Like most parrots, *A. canicularis* has a large vocabulary, the size and flexibility of which can only be appreciated by those who have kept a flock of these birds in captivity. The complexity of this vocabulary makes phonetic notation frustrating. Certain call-groups are distinguishable immediately, however; two are typical of agonistic behavior, while others connote appeasement, content, epigamic tendencies, and alarm. The character and significance of these vocalizations are as follows.

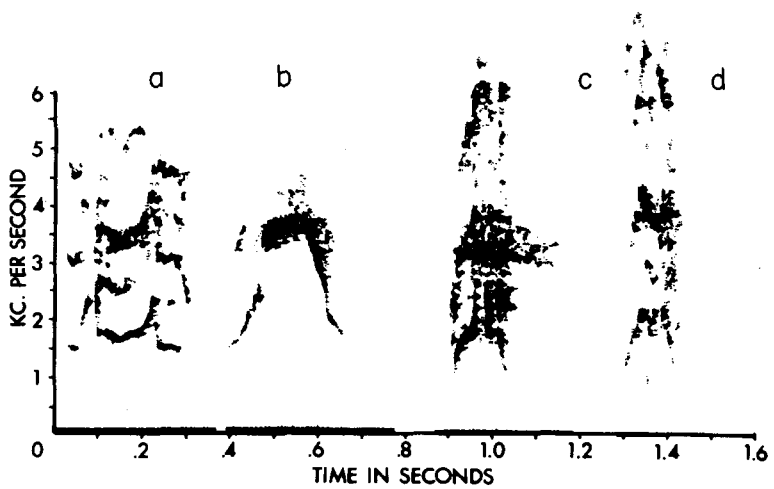

Fig. 5. Sonagrams of four vocalizations of the Orange-fronted Parakeet. a, Epigamic song-like call; b, inflected whistle; c, d, two versions of the *peach* call associated with initiation of flock activity such as feeding. (All narrow band filter.)

Group I. *Annoyance squawks.*—These are associated with agonistic behavior, not considered in this paper. Squawks usually accompany the ultimate component of intimidatory action. They may, however, signify almost any kind of annoyance and thus are frequent in the context of intense courtship display, associated there with ambivalence and thwarting. The lowest intensity squawks resemble short scolding notes of finches, whereas higher intensity forms are broader in frequency spectrum and harsher. Figure 6*d* illustrates squawking. Note that the patterns shown are almost pure noise, revealing no distinct harmonic waves.

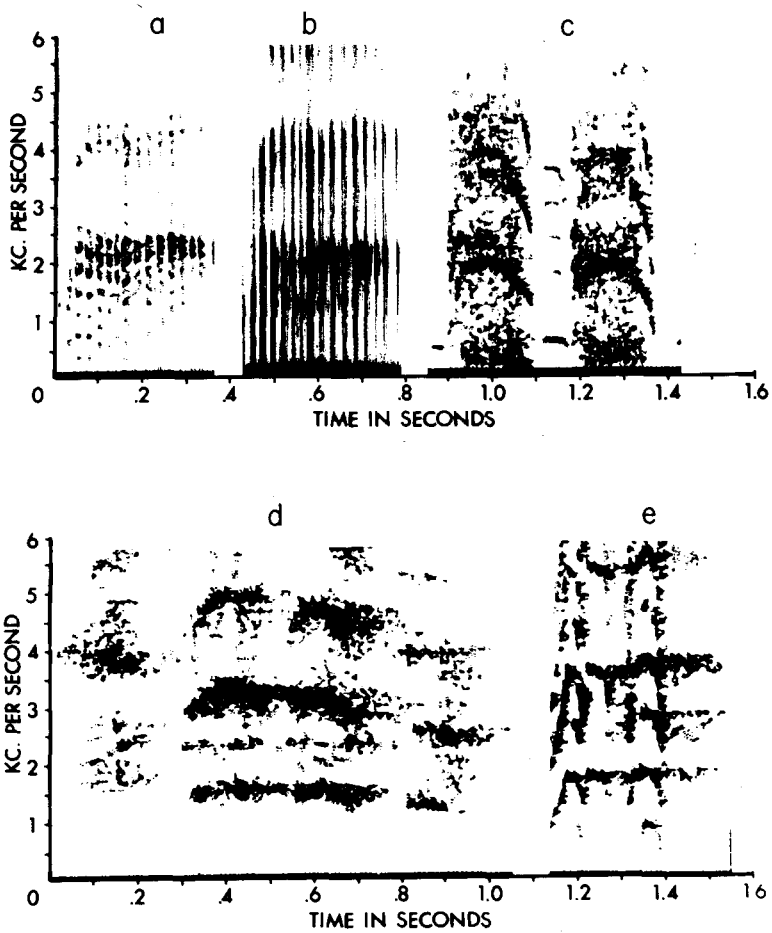

Fig. 6. Upper: Sonagrams of two warning or alarm calls of the Orange-fronted Parakeet. a, b, Low-intensity alerting "mutter," narrow band and wide band filter, respectively. Note steep wave front and marked segmentation of this call as revealed in b. c, High-intensity alarm call.

Lower: Sonograms of two vocalizations of the Orange-fronted Parakeet. d, Annoyance squawk; e, intra-pair call (*chee-chee*). Narrow band filter.

Group II. *Warning cries.*—Vocalizations of this category are stimulated by predators or predator-like stimuli. Two basic intensities are common and are shown in figure 6. The low intensity alerting signal (fig. 6*ab*) may be described as a "stuttering

mutter." It is represented in illustration by both narrow and wide band filter analysis. Wide band analysis reveals the marked segmentation characteristic of calls with steep wave fronts. This alerting signal is stimulated by incipient recognition or discovery of a predator. In captivity, detection of the human observer often elicits it. It accompanies termination of activities and is accompanied by movements indicating uneasiness, such as peering, shifting movements of the feet, edging of the birds along their perches, crouch, and waving of the wings; the last two are intention movements of flight. Any sudden change in the activities or attitude of the supposed predator following low intensity alerting may cause the parakeets to break into high intensity alarm cries. As suggested in figure 6*c* the loud alarm cry is the "noisiest" of all vocalizations. Tape recorded examples of this vocalization played to the captive birds cause them to exhibit fear reactions, sometimes including flights of panic if the vocalizations are presented suddenly and with no previous warning of danger.

Group III. *Epigamic calls.*—There are many variations in these calls, but all are melodious or "sweet." The inflected whistle call often associated with ambivalence in courtship is illustrated in figure 5*a*. This is the song-like calling most frequently heard in conjunction with high-intensity activity around the nest. Prolonged utterance of such calls by a pair I have termed dueting.

Dueting of *A. canicularis* is performed by members of a pair while in slow, almost hovering, flight toward the nest tree. It is seen only occasionally and occurs in the early stages of the reproductive cycle. Both birds vocalize in chattering fashion simultaneously, there being no alternation of calling. In *Brotogeris jugularis*, dueting in captivity is performed while the pair is perched and there is alternation of the calls: one bird calls *chew*, the other *chee* at slightly higher pitch. The rapid utterance results in *chew chee chew chee chew chee*, in sing-song fashion with no overlap in the sequential syllables.

Group IV. *Conversation and activity calls.*—These vocalizations, especially at high-intensity, resemble epigamic dueting, except that many or all members of a flock may indulge in them simultaneously. In addition, such calls may be stimulated by either epigamic activities of a pair or conflict between two birds or two pairs of birds. In the latter context, the chattering flock conversation is given mostly by the birds not engaged in fighting. Lower-intensity chatter—a stuttering conglomeration of highly varied melodious "conversation"—accompanies flock feeding (where it is interspersed with harsher annoyance squawking as individual distance is maintained), excavation of the nest-cavity, and other active, but generally non-agonistic, non-flight behavior. Such vocalizations may, thus, precede assumption of roosting position and the birds' attempt to reach favored roost sites.

Group V. *Activity initiation call.*—Represented in figure 5*cd* the *peach* call is a type of social flock vocalization that accompanies initiation of feeding or other flock activity and is not heard outside this context. It is not a flight call, but accompanies change in activity in the wild while a flock is perched in a tree. In captive birds the *peach* call accompanies the climbing or flying of the birds to food trays and ceases shortly after feeding has commenced.

Group VI. *Flock social or assembly calls.*—These calls are not shown in spectrographic illustration, but resemble intrapair signals (fig. 6*e*) although they are more prolonged and complex. Members of flocks exchange such calls in flight, flocks in trees similarly call to flocks flying overhead, and a stray individual gives this call while flying about attempting to locate its fellows. Aviary birds answer vociferously when flock social calls are played to them via a tape-recording. A flock which I maintain in an aviary is rather more vocal than normal in daylight hours because its members seem

to receive stimulation to call from the echoes of their own flock social call reverberating from a building 200 feet away.

Group VII. *Intra-pair signals.*—These consist of two- or three-note calls (fig. 6*e*), something like *chee chee* or *chee chee chew*, exchanged by members of a pair in flight or between the male outside the nest and the female inside. The female may utter such notes just after entering the nest or shortly before leaving the nest. The male may give such a call upon arriving near the nest after an absence of several minutes. Both birds may utter the call as they fly past the nest, possibly as a signal to the young inside.

Group VIII. *Content-rest calls.*—At rest diurnally and while roosting, these parakeets seldom cease vocalization for more than a few minutes at a time. Two types of content-rest calls are given, and each is associated with specific resting movements. The "breath squeak" is normally given only in diurnal rest periods. It is a short whimper, consisting of a single note, given very softly with each exhalation, for periods of a few seconds to several minutes. Certain individuals in my captive flock are more prone than others to indulge in this vocalization. These birds seem otherwise not clearly distinguishable from the non-squeaking members of the flock, behaviorally or from the standpoint of health factors. Breath-squeaking accompanies complete resting behavior, often including sleep.

Parakeets more or less continually indulge in yawning and gaping when at rest or roosting. A vocalization here termed the yawning call accompanies this habit. A flock at roost in the dark is conspicuous because of this vocalization. Yawning is also interspersed with other gaping, tongue movements, and chewing, which movements cause audible, mechanically produced sounds from the roosting birds.

BREEDING BEHAVIOR

The distribution of the Orange-fronted Parakeet closely approximates that of the colonial termite *Eutermes* (*Nasutitermes*) *nigriceps*. The correlation is a natural one, because these parrots most frequently construct their nests by digging out cavities in termitaria. Where these termitaria are abundant, the parrots seem almost wholly dependent upon them for nest sites. Dickey and van Rossem (1938:205) state that old woodpecker nest cavities and natural hollows in trees are used. Nonetheless, *A. canicularis* seems not to be found breeding outside the geographic range of the termite, and it thus may be postulated that the parrot is not capable of maintaining populations without symbiotic association with the termite. Throughout most of its range, this parrot competes with few other birds for these nest sites. *Brotogeris jugularis* and some trogons such as the Citreoline Trogon (*Trogon citreolus*) use termite nests occasionally but apparently do not compete successfully with *Aratinga canicularis*, whereas the Green Parakeet (*A. holochlora*), which also uses termite nests habitually, occurs in slightly different habitat for the most part. On the other hand, competition with other birds for woodpecker holes is undoubtedly more severe.

Von Hagen (1938) was the first to give a detailed account of the biology of *Eutermes*, basing this account on observations of *E. nigriceps* in Guerrero and Oaxaca, México, and elsewhere in the New World tropics. He devotes one section of his treatise to a discussion of the parakeet-termite relationship, discussing briefly the digging by the birds and other aspects of nesting that bear importantly on the biological success of the termite.

Readers are referred to Von Hagen's work for information on the details of the life history of the termite, the essences of which are important for appreciation of the ecology of *A. canicularis*.

I spent a period of three weeks, March 6 to 27, 1961, in central Sinaloa, México, observing the nesting habits of the Orange-fronted Parakeet. The locality of my studies was approximately 5 miles toward San Ignacio from Coyotitán, which is situated near the main north-south highway from Nogales to Mazatlán. The hills in this area are precipitous, with many rocky outcroppings. The vegetation is tropical deciduous forest with thorn-scrub in the more exposed places. In early March, the dry season is about half over, and the trees are nearly leafless, except in the arroyos. Only a few miles farther north in these hills, the Orange-fronted Parakeet and the termites previously mentioned reach their northern limits. Also, the tropical deciduous forest gives way there to arid thorn-scrub and desert, except along rivers. The transition is an abrupt one, so that the parrots and termitaria extend commonly to the northern periphery of the deciduous forest.

Description of the Termitarium

Before describing the breeding cycle of the parakeet, it is important to have some idea of the termite colony. Information is taken in part from Von Hagen's work and in part from personal observation. According to Von Hagen, *E. nigriceps* has social castes; there is a queen, many workers, worker-soldiers, and soldiers, besides larval stages. The termitarium is called a "ballo" by the Mexican natives and hereinafter is often referred to as such; it is constructed of agglutinated feces and wood debris formed into concentric ligneous layers. A mature ballo resembles a wasps' nest, being roughly globular in shape and attached to a limb or trunk of a tree, or rarely to a rock. The frontispiece shows a ballo, containing a nest cavity of a parrot. The outer portions of the mass of a ballo are relatively hard, the inner layers more humid and friable. The color of the substance is dark brown. The matrix is completely traversed by a system of tortuous canals which interconnect and lead to the central chambers where the queen remains and the eggs and larvae are cared for.

The entire structure is covered by a "wood paste wrapper," as Von Hagen terms it. This wrapper is maintained by the termites. No canals open in its surface, and breaks are quickly repaired by the workers. Its color is a light or medium sandy brown. If a hole is made in the wrapper, the termites swarm out. The insects are normally not visible diurnally at the colony, unless they are stimulated to repair the wrapper.

So far as is known, the parakeets never utilize deserted ballos for nesting. Ballos not in use become dry and crumble, the wrappers fall away, and the substance, since it is dry, becomes much more difficult to dig into without resulting disintegration of the ballo.

The Nesting Season

At northern latitudes, the breeding season of the Orange-fronted Parakeet probably commences in February. Lamb (Mexican Check-list, Pac. Coast Avif., 1954) collected two specimens (now in the Moore collection, Occidental College) near San Ignacio, Sinaloa, in mid-March, 1934; these birds were in breeding condition. One contained an egg in the oviduct. The beaks of both of these birds bore brownish particles indicating that the parakeets had been excavating a termitarium.

Although the height of the nesting season is in the first half of March, 15 to 20 fully-fledged young were brought to my camp on March 26, proving the commencement of nesting by early February. These captive young had been obtained farther into the foothills by men who were taking them to the market places. At the locality of my own studies, I observed no young leaving or briefly out of the nest at this same time. Yet I found one nest being dug, one with an egg, and one with young. The season, thus, may have been somewhat retarded in comparison to the locality farther inland.

Epigamic Behavior

As previously discussed, no obvious behavioral method of pair formation or of competition for mates was seen in captive parakeets. Therefore, I expected that in early spring in the wild I might be able to discover some evidence of pair formation activity. But this was not the case in Sinaloa. Because such behavior had not been observed in the confines of aviaries, it was suspected that the normal behavior might involve flight display inhibited by cages.

My observations of flight display involving 3 or 4 Lilac-crowned Parrots (*Amazona finschii*) and Red-crowned Parrots further contributed to my prediction that a flight display occurred in pair formation in *Aratinga canicularis*. On several occasions I did note what seemed to be brief "chases" involving 3 or 4 parakeets, but they were of such short duration and seen so few times that I doubt their importance in pairing.

Pair formation, then, is probably a very subtle product of social interaction in the flocks that form in late summer, involving no special flight or other display. This hypothesis is supported by the fact that birds which I purchased in market places of México in July, 1959, soon paired, even in the tiny cages in which I transported them, and despite the fact that they had not been members of a natural flock preceding their initial capture. The birds were, in fact, mostly young-of-the-year. Pairing in these cases took place while displays and postures occurred that I have described in the first part of this paper. My observations, thus, indicate that pair formation is like that described by Dilger (1960:667) for *Agapornis*.

General Social Behavior in the Nesting Season

Orange-fronted Parakeets are less social in the breeding season than at other times of year. Although Dickey and van Rossem (1938:205) report two or three pairs of parakeets nesting in one ballo, this habit is apparently rare and was not observed by me in Sinaloa. There, it may be due to the fact that most ballos are simply not large enough to accommodate two normal-sized nest cavities. Pairs in Sinaloa remained apart while engaged in breeding activities, but more often than not joined their fellows to form small flocks of 4 to 8 birds to feed at frequent intervals in the day. Often while a pair of birds frequented their nest location, other parakeets fed or rested not far away and could be heard chattering. The pair upon leaving its nest usually flew directly to these other birds.

Although other parakeets were aware of nest locations, I did not observe any birds except the owners nearer than several hundred feet to the nest sites.

Nest Building in the Wild

Captive Orange-fronted Parakeets, as a rule, do not breed until they are two years old. In the wild, a small number of birds that consistently frequented the vicinity of my camp were possibly not breeding birds, although it is also possible that they had completed breeding. These birds were usually present in certain food trees and always flew about together, indicating no intermittent breeding duties. Some birds in these flocks did, however, seem paired. I collected one of these pairs with a single shot on March 8. Their gonads were slightly enlarged (testes 8 mm. in length; largest ovum 3 mm. in diameter).

Positive information on the division of duties in the nesting cycle are available for captive birds in the San Diego Zoo through Mr. K. C. Lint, from my observations in the wild, where sexes were only tentatively determined, and from observations of breeding of a pair in my aviary in the spring of 1962.

Conclusions concerning excavation of the nest are based on observations at a single nest in the wild and on activities at three nests in my aviary. Both members of the pair participate in excavation, although the male performs most or all of the work until completion of the entrance tunnel and the commencement of digging of the nest chamber proper. In the wild, I ascertained only that one bird (sex unknown) did most of the digging of the tunnel. In the captives, one heterosexual pair excavated in two simulated termitaria, and one homosexual pair excavated only the tunnel portion of a third. In the captive pairs,the individual consistently in the behavioral role of the male excavated the tunnel. In the wild pair, on the estimated second day of digging, one bird was digging at the time of my arrival and continued to do so for over an hour (9:00 to slightly after 10:00 a.m., March 7). The birds remained together constantly; while one dug, the other sat close by, sometimes clinging to the side of the ballo, sometimes perching on a limb nearby. The parrots dig only with their bills. The process does not involve much movement of the body or head of the bird, so that from a distance a digding bird seems merely to be clinging and perhaps feeding on the ballo. The motion of excavation is the biting and chewing a person so often sees in the captives as the birds mutilate the framework of the aviary.

Although usually the parrots are quiet in the vicinity of the nest, they occasionally engage in conversational exchange and less often in harsh screaming. A loud harsh chatter also usually accompanies flight to the nest, but all vocalizations cease on appearance of an observer or predator, although excavation may continue normally.

Pairs excavate periodically throughout the day, for several minutes to an hour or slightly more at a time. In these periods they frequently stop to preen or merely sit silently. Courtship activity when the tunnel is being dug usually includes some mutual preening and rarely courtship feeding which was observed only once at the nest in the wild. On March 8, the following sequence of activity occurred between 8:51 and 11:15 a.m., in the wild pair.

8:51. Bird clings to entrance, the other on limb nearby.
9:00. Warning calls from digger who flies up beside its mate. Both call harshly (a series of regular squawks), then fly away.
9:30. Pair returns but perches down canyon with two others.
9:40. All fly away.
9:42. Pair returns to nest and stares at me.
9:43. One to limb of tree nearby, other to dig.
10:17. Birds switch places.
10:30. Switch again. Outside bird sits fluffed and yawns.
11:00. No change.
11:15. End observation, with bird that began digging at 10:30 inside tunnel, sometimes out of sight.

In the captive pairs, the males performed all digging until a bird could enter the tunnel and was out of sight; thereafter the females spent a few minutes (compared to several hours for males) per day in excavation, usually relieving their mates for a short period. In the wild, excavation from the outside is begun low on the side of the ballo and is directed first upward at an angle for from eight inches to a foot. When the friable central part of the ballo is reached, the birds veer downward in making the actual nest cavity, which when completed is roughly spherical and is about 10 inches in diameter. The size and shape of the cavity and the tunnel vary, of course, with the size, shape, and placement of the ballo on a limb.

I have previously mentioned that breaks in the wood paste wrapper of the ballo stimulate the photodermatic senses of the resident termites, causing workers and soldiers immediately to move to the break and begin repairs. The termites are obviously

stimulated to repair the excavations made by the parakeets at first. The birds seem to be only mildly irritated by the insects, which they shake off with rapid head-waggling motion as they dig. Later, the insects resort instead to sealing off canals leading into the tunnel and cavity. The passage of the tunnel from a downwardly facing entrance upward at an angle probably causes as little light as possible to be shed on the broken tunnelway made by the parrots. Thus, as Von Hagen pointed out, the termites are not so greatly stimulated to fill in the tunnel as they might be if the break or tunnel were on the upper side of the ballo, where exposure to direct rays of the sun would be possible. In addition, the relationship of the passage way to the nest cavity makes it difficult for any but the most highly adapted and persistent of predators to reach the eggs or young without exposure to the added irritation of the swarming termites that become active when the ballo is broken.

I suspect that old but suitable nest cavities are often reused, because it seems to me that the supply of termitaria would otherwise be depleted rapidly. The pair in captivity readily accepted a nest cavity already excavated. According to Von Hagen, and my own personal observations, once a parakeet nest cavity is dug, the termites never fill it up.

The pair of birds that I discovered in the wild had excavated by March 8 far enough for a bird completely to enter the tunnel. Although in three days the work seemed nearly half finished, they continued to visit the nest and seemingly continued to dig until March 14. After March 14, however, their visits became sporadic and brief; I did not find them digging again or entering the tunnel. However, I did discover on March 19, that the pair were returning to roost in the nest. Their lack of attentiveness to the nest in diurnal hours indicated that egg laying had not commenced. The birds apparently roosted in the nest cavity from at least March 19 until shortly before my departure from the study area. On the evening of March 25, I collected the pair and found them on the verge of reproductive activity: the female's ovary contained a nearly full-sized ovum about ready to rupture from its follicle; the male's testes measured 8 by 10 mm. Dissection of the ballo the following day showed the nest cavity complete. Perhaps such delay in laying is characteristic of the species. If it is, future investigations should explore the possibility, or perhaps the probability, that the delay allows the termite population to adjust to the cavity by first evacuating it completely and then sealing off canals leading into these chambers. Perhaps only then can the birds nest satisfactorily.

Nest Building in the Aviary

Captive parakeets were provided with three simulated termitaria in the spring of 1962. Each of these was satisfactory in certain respects. First, on January 25, the birds were offered a ballo made of styrafoam plastic, a white, granular material, which I had coated with a thin layer of brown vegetable dye to encourage the birds to begin excavation more readily. This brown layer was removed by the birds, revealing the unnatural white coloration of the plastic. The potential breeding pair of parakeets and several other birds participated in this generalized digging, and the pair began to fashion a tunnel vertically upward against the back foundation board to which the ballo was glued. They thereby used the board much as parakeets in the wild use a limb to which the termitarium is attached, namely as a structural frame which might prevent the widening of the entrance by a predator.

At about the time the nest chamber proper was commenced, the male's pattern of excavation seemed to disintegrate, and he thereafter widened the entrance, so that it was nearly as wide as long. I attribute this breakdown in digging action to the white color-

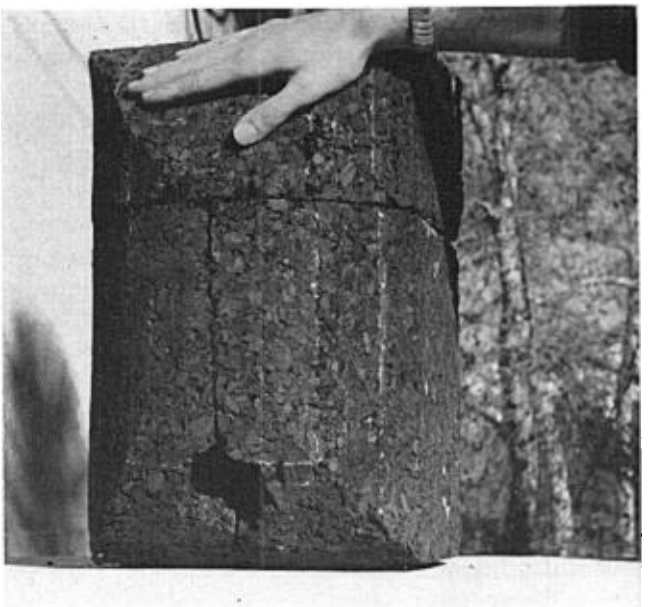

Fig. 7. Cork termitarium with entrance, tunnel, and cavity already fashioned, and removable lid constructed. Parakeets laid two clutches of eggs herein in the aviary.

ation of the plastic, the light reflecting and transmitting properties of which prevented the birds from creating a dark nest chamber merely by digging deep into the ballo.

At this time, February 23, I supplied the birds with a ballo made of thick, spongy cork which was soft, dark brown, and easily chewable (fig. 7). The potential breeding pair immediately abandoned all interest in the plastic ballo and, along with a homosexual female pair, began excavation in the cork. On March 14, I decided to bypass further excavation studies, because competition between the two pairs was severe; the homosexual pair had dominated the potential breeders and the "male" of this pair had completed a tunnel about 10 inches into the cork.

I then removed the homosexual pair and replaced the deserted plastic ballo with a new cork one, this time with a nest cavity and tunnel already fashioned. This second cork ballo was immediately accepted by the potential breeding pair, which began to enter the chamber and investigate it periodically in daylight hours. Beginning on March 15, the birds habitually spent from a few minutes to an hour or more in the ballo several times a day. The male, as during excavation, continued to initiate all activity at the nest, entering and leaving first and being the only bird to sit inside alone. While inside, the birds excavated the chamber, removing the back cork wall as far as the foundation board in the first week. Particles freed, in this reshaping of the chamber, were periodically scooped out the entrance, but enough of them were left in the chamber floor to make it two or three inches shallower and flatter than such chambers are in the wild.

By March 20, the nesting pair was roosting in the chamber, and, as in the wild, commencement of roosting closely correlated with the disappearance of the sun (see later discussion). The male continued to lead the way in activities at the nest until March 27, when the female was first noted entering the nest followed by her mate.

Thereafter the female tended to lead the way to and from the nest and frequently she sat inside without her mate. Abortive attempts at copulation were also noted on March 27, two days before the first egg was discovered in the nest.

It is to be noted that the captive pair did not show a period of inactivity at the nest chamber as had the pair in the wild. The lack of termites in the simulated ballo may have made the nest chamber immediately suitable for use by the birds.

Correlation of Habits with Type of Nest Cavity

Most species of birds that dig their own nest cavities make them large enough barely to accommodate only one adult and the eggs or young. This is the case in some parrots, such as *Amazona finschii*; these cavities are occasionally so small that it is difficult to believe that an adult bird could incubate the eggs or brood the young therein. However, *Aratinga canicularis* builds a large cavity, about 10 inches in diameter; this is correlated with the facts that (1) the matrix is soft, allowing easy excavation without undue expenditure of energy and (2) the members of the pair perform most of their duties at the nest simultaneously. As mentioned, the pair is present when the nest is excavated, and both roost in it as soon as it is large enough or otherwise suitable; later both birds continue to roost in the cavity throughout the nesting period and visit the nest together in bringing food to the young.

Flight Display and "Dueting"

In the period between digging of the nest and laying of the eggs, the pair observed in this phase in the wild several times made hovering unison flights to the nest from trees 50 to 100 feet away. Rarely such flights were from tree to tree merely in the vicinity of the nest. Such flights were accompanied by a chattering vocalization that was not so harsh in quality as alarm calls but resembled instead the melodious assembly calls given in a simultaneous, stylized fashion by both members of the pair.

In addition, the pair occasionally perched in the vicinity of the nest site to engage in mutual attentiveness. At these times, the unison chattering vocalization became, it seemed to me, a more cooperatively unison effort, that may be called "dueting." I have previously mentioned the alternate-syllable dueting of pairs of *Brotogeris*. Dueting in flight has been absent in my captive *Aratinga,* although occasionally birds duet as they perch on or near the nest.

Copulation

I have not observed copulation in this species in the wild. The captive pair which had begun use of the cork termitarium in the aviary were seen in strong but unsuccessful attempts at copulation several times on March 27, shortly before the first egg was discovered. Apparently successful copulation was observed on March 31 at 4:48 p.m., when the clutch contained two eggs. The many abortive attempts at copulation were accompanied by much bill-wiping, courtship feeding, vigorous preening of the male by the female, and the clawing attempts to mount previously mentioned.

Behavior preceding successful copulation was as follows: the pair emerged from the nest at 4:35 p.m. They indulged in mutual preening, after which the male fluffed, perch-bit, raised the head, crane-peered, and made several futile attempts to mount (clawing). He then head-bobbed several times, performed courtship feeding, and when the female fluffed and crouched in receptive posture, with tail elevated and head slightly raised, he again attempted to mount. Both birds fluffed strongly just previous to this mounting attempt. This time copulation seemingly was performed. In it, the male does not completely climb upon the female but is about half on her back, half perched beside her.

Nevertheless, cloacal contact is achieved. The act lasted approximately one minute and thirty seconds. Courtship feeding occurred once in this time. No vocalization accompanied the act. Other birds in the flock were at rest during this time and exhibited no reaction to the behavior of the pair. The pair engaged in no special behavior following copulation but joined their fellows to rest and feed. The female re-entered the nest at 5:30 p.m., her mate joining her at 5:40 p.m.

Copulation as observed in this one pair of the Orange-fronted Parakeets resembles copulatory behavior in *Agapornis* (Dilger, 1960:677–678) as follows: female solicitation is similar in that the wings are not quivered, and in strong solicitation the head and wings are raised slightly above the horizontal; the male mounts by stepping on the female with one foot (two in *Agapornis*), rather than flying to the position; no vocalizations accompany solicitation or copulation. However, to contrast behavior in the two, in achieving cloacal contact during prolonged copulation, the male Orange-fronted Parakeet does not switch from side to side of the female as does the male of *Agapornis*; no wing raising occurs in *Aratinga* in solicitation; mounting is incomplete; and no wing flapping accompanies copulation.

Since copulation has been observed only once in *Aratinga canicularis*, the foregoing comparison of the act in the two genera is, of course, tentative. However, the normally stereotyped pattern of such behavior makes the comparison of some value.

Laying

I made no observations concerning laying in the wild. In the two clutches laid in the aviary (both by the same pair in spring, 1962), eggs were seemingly laid every other day; it is possible that they may on occasion be laid at three-day intervals. In one instance such an interval was noted, although an egg could have been laid after the check of the nest on the second day. Time of day of laying has not been determined. Laying of each clutch spanned approximately eight days.

Incubation

Only the late phases of incubation were observed in the wild. The entire incubation period of the captive pair was studied. Incubation begins with the first egg, after the laying of which the incubation patch of the female is immediately discernible when she leaves the nest to feed and rest. Growth and age differences in young birds of the same brood in the wild also indicate commencement of incubation with the laying of the first egg. Both in the wild and in captivity, seemingly only the female incubates. The male develops no brood patch; the male when in the nest chamber seems always to occupy a position at the end of the tunnel.

As has been stated, both male and female previous to laying spend frequent periods in the day sitting in the nest chamber. Nine hourly checks of the aviary on March 26 revealed that the pair was inside the nest four times and out of the nest five times. Thus the birds spent slightly less than half their time in the nest chamber in the week preceding laying. The pair was observed continuously over a 12- to 13-hour period once a week beginning with Saturday, March 31, when there were two eggs of the first clutch in the nest. Figure 8 summarizes per cent of attentiveness of the adults on four successive Saturdays in the incubation period. The time spent by the female in the nest rose from approximately 50 per cent at the beginning to around 90 per cent at the end of two weeks. The male, which was attentive to his mate, spent about one-half of his time in the nest in this period. When he was out of the chamber, the male divided his time about equally between occupying a guard perch three feet from the nest, feeding the female, and engaging in such activities as preening, chewing on twigs, and resting. In

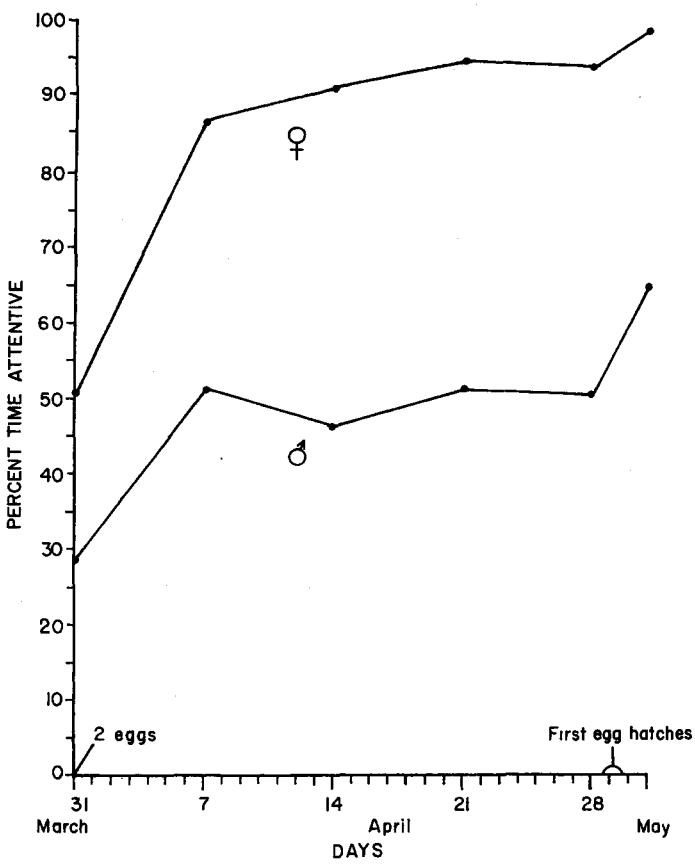

Fig. 8. Graph depicting per cent of attentiveness of male and female captive parakeets during incubation of first clutch.

contrast to the prelaying period, the male spends no time in the nest when the female is not inside. When the female is out of the nest, she typically feeds and rests briefly, although in early morning and late afternoon hours she may preen, engage in mutual attentiveness with the male, indulge in twig-chewing, or dig in another "termitarium" in the aviary. Table 1 provides information on lengths of periods in the nest for both male and female.

The only observations made on the incubation period in the wild occurred at one nest during the last two days of incubation. Since the duties of the male were at variance with those of the captive male, a summary of those observations in the wild is important. In the wild pair, the female was more sparingly attended by her mate than was the female in the captive pair. The wild male roosted in the cavity but diurnally accompanied his mate only when she left the chamber to feed at intervals of from two to three hours, sometimes longer. This male usually remained perched in a nearby tree as the female incubated, but on occasion he stationed himself farther away, out of the observer's sight but not out of audible range of his mate. When she grew restless, she called, using the intra-pair signal *chee chee*! or *chee chee chew*! Thereupon, the male either answered and flew to a nearby tree to await her exit or chased after her as she erupted from the entrance to the nest in strong flight.

On the day preceding hatching in this nest, the female was observed to remain in the chamber for a period of two hours, from 10:00 a.m. to 12:00 noon, during which time her mate did not appear. On the same day, she flushed from the nest twice and each time returned minutes later with her mate. However, on the succeeding day, when I approached the nest at 2:00 p.m., I noted an eggshell on the ground below the nest, and both birds flushed from the ballo.

With a small mirror device I examined this nest and could see only a single young, just hatched, and no eggs. In another nest there were two half-grown nestlings. The

TABLE 1

TIME SPENT IN NEST BY CAPTIVE MALE AND FEMALE ORANGE-FRONTED PARAKEETS DURING INCUBATION OF FIRST CLUTCH

	March 30		March 31		April 7		April 14		April 21		April 28	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
Minutes in nest during a complete attentive period						80						85
						60		18			58	125
			40	50	80	138		37			40	268
			41	110	95	45		102			100	45
			95	110	38	163		47			100	92
	90	80	20	78	88	45	65	10		145	15	13
	20	20	10	10	130	110	45	35	80	205	65	18
Average time in nest (hrs. and minutes)	:55	:55	:41	1:01	1:06	1:32	:55	:42	1:20	2:55	1:03	1:40

contents of still another which were brought to me consisted of three young. These were seemingly the full complements in each of these nests. Mr. Lint of the San Diego Zoo states that three to five eggs is the usual clutch size in captives of this species. The eggs are plain white and measure 2.67 × 2.03 (average of three); they are short subelliptical in shape (see Preston, 1953:166). The length of the incubation period is approximately 26 days ± 1 day, as determined from my captive pair.

CARE OF THE YOUNG

In the first days of care of young in the wild, brooding is frequent and apparently performed only by the female. As during incubation, the male awaits his mate but more often perches outside near the nest site rather than leaving the area as he did during incubation. If the female remained in the nest cavity for more than five minutes, however, the male often flew farther away and then made periodic visits to the nest to perch in the vicinity for from a few moments to approximately 10 minutes.

The single egg in the nest mentioned on page 183 hatched about noon of March 23. By March 25, the male had begun to enter the nest cavity and remain in it as long as 35 minutes, which is normal for both members of the pair on most visits to the nest later in the care of young.

Following is an outline of events at the nest soon after the egg hatched:

2:00 p.m. Both adults flew at my arrival, flushing from the nest. Examination reveals one young.
3:00 Adults return, one to tree, the other to nest and in after brief hesitation and conversational notes between birds.
3:07 Other adult (presumably the male) flies away.
3:42 Bird brooding (?) out and away.
4:05 Both adults return, one to tree, one to nest, then almost immediately both depart.
5:01 Adults return; one in at 5:05; other leaves.
5:30 Second adult back.
5:40 Second adult in.

On March 25, the following sequence occurred:

9:45 a.m.	One adult inside.
10:54	Gives *chee chee* social call. Immediately, male (?) answers down the hill.
10:55	Adult flies past nest and lands in nearby tree.
11:00	Bird inside goes out and leaves screaming, followed by mate.
11:15	Both back to tree. There they converse.
11:16	One bird to nest and in.
11:20	Second bird in. They both call *chee chee* and then are quiet.
11:55	Both birds out and leave.
12:45 p.m.	End of observation period, neither adult present.

Care of the young when they are from two to three weeks of age was studied at one nest, from March 12 through March 24. Figures 9 and 10 depict attentiveness at this nest at that time. Although my time was necessarily divided among several duties connected with this study, an attempt was made at this nest to include observations over most of the range of diurnal activity of the birds. From the two figures it may be seen that there are probably three to five visits to the nest by the adults each day. The

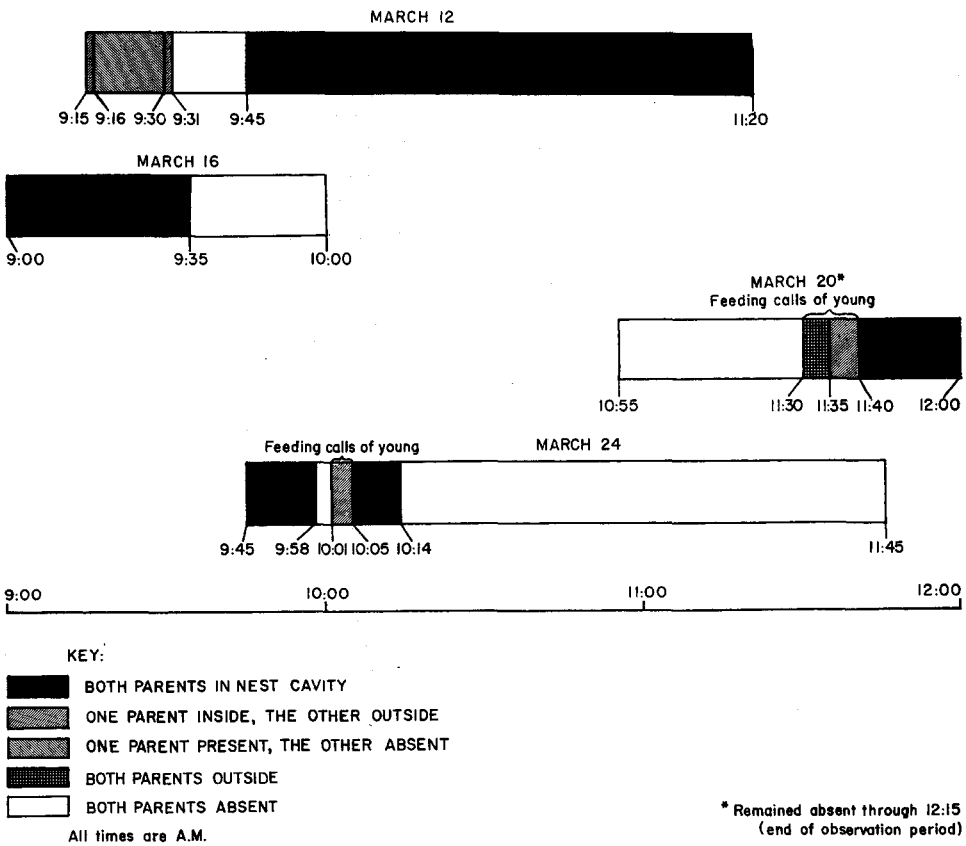

Fig. 9. Record of attentiveness at nest of Orange-fronted Parakeet in morning hours during care of young in wild. Total minutes of observation: 385; minutes both adults were near or in the nest: 215; minutes both adults were absent from nest: 170.

parents usually arrive and depart together, or nearly so. Sometimes they enter together, but more often one enters, feeds, and remains while the other enters after one to five minutes. Following this, there is a period of quiet, when both adults occupy the cavity with the young. This period may last from less than ten minutes to more than two hours. Periods away from the nest are similarly long.

Seemingly, only particulate matter in liquid, regurgitable form is fed to the nestlings. Foods included at this time of year, as evidenced by my observations of the adults feeding in the area, included small fleshy fruits of unidentified trees and flowers of a scandent shrub, *Combretum farinosum* (family Terminaliaceae), which was in full bloom during my stay in Sinaloa. *Combretum* was especially attractive to the parakeets, as well as to other birds such as Magpie-jays (*Calocitta*), White-necked Robins (*Turdus assimilis*), and Scarlet-headed Orioles (*Icterus pustulatus*). The flowers of this woody vine are bright orange and full of nectar. The flower parts are fleshy and when pressed between the fingers assume a gummy consistency. This sticky quality resulted

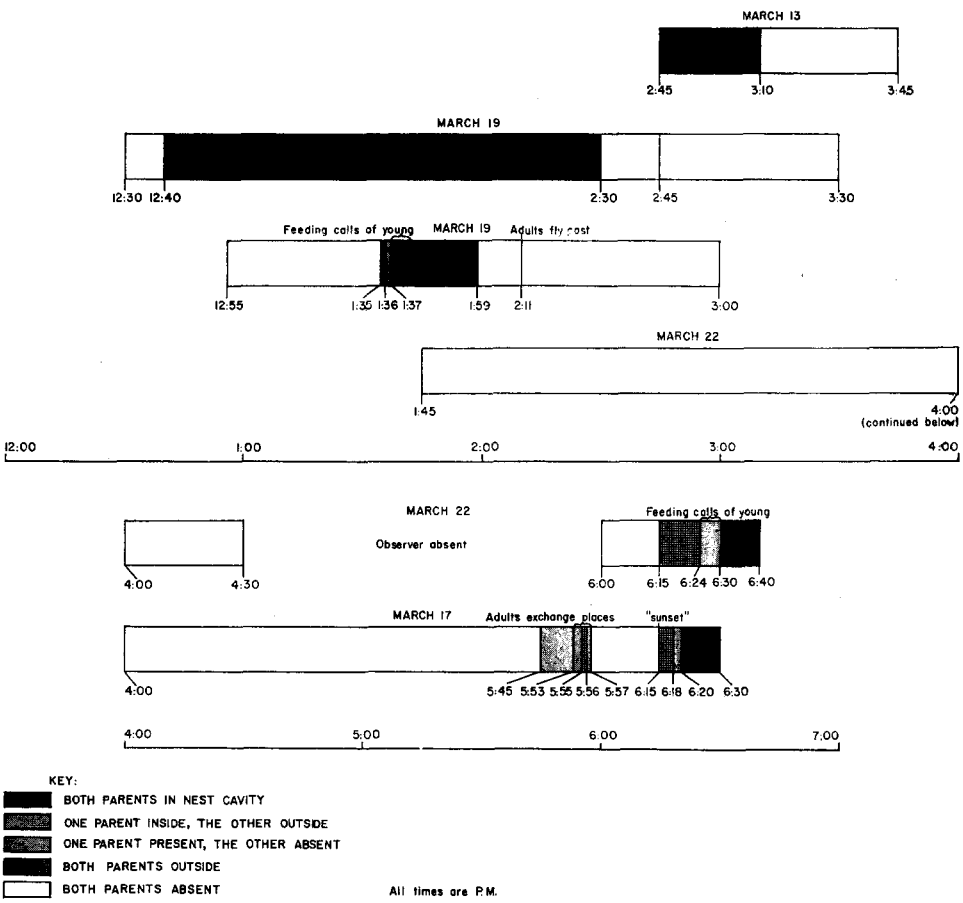

Fig. 10. Record of attentiveness at nest of Orange-fronted Parakeet (same nest as in fig. 9) in afternoon and evening hours during care of young in wild. Total minutes of observation: 720; minutes adults were near or in the nest: 226; minutes adults were absent from the nest: 494.

in orange-stained feathers around the bills of the birds. From the frequency with which I observed the parakeets feeding on the flowers and from the succulent character of the blossoms, I suspect that they were an important constituent of the liquid food given to young parakeets. Several especially heavy concentrations of these flowers in treetops in the study area were almost never without a small flock of parakeets feeding on them. I mashed *Combretum* flower parts into a weak milk solution, to which they imparted a faint orange tone, and fed the substance to captive young parakeets; they seemed to relish it.

Although the concealed situation of nests prevented me from observing activities in the chambers, it appears from knowledge of other parakeets that the manner of feeding of the young by the adults is as follows: the adult grasps, with its own bill, the upper mandible of the young bird, the holding points being roughly either side of the upper mandible near the commissure of the gape. Such action by the adult triggers an immediate gaping response and a vocalization, which written phonetically is *ya ya ya ya yayayayaya* given with a nasal rasping quality. In captive young parakeets, the vocalization always accompanied gaping and was not given otherwise. Gaping by captives was elicited by the gentle placement of thumb and finger on either side of the base of the mandible while simultaneously projecting a weak stream of fluid into the bird's gullet using an eyedropper. Apparently this artificial feeding process resembled the natural feeding method. No amount of poking with the eyedropper at the bill of a young bird evoked any gaping response, unless such poking became vigorous enough that a defensive gape was provoked. I assume that each time I heard the feeding vocalization in the nest cavity regurgitant was being transmitted to the young, and I further assume that the mechanics of the process are as I have described because of the nature of the courtship feeding ritual described earlier in this paper.

Only the first egg hatched in the first clutch laid in the aviary. Of the other three eggs of this clutch, two were fertile; the three unhatched eggs were removed from the nest approximately 35 days after they were laid and after the female had ceased incubating them. The two dead embryos measured 8 and 13 mm. in total length, respectively, compared to 45 mm. for the nestling at an age of two days. The embryos must have died previous to the hatching of the first egg, considering their developmental stage. The larger was comparable to a six or seven day old chick embryo in appearance.

The single young that hatched survived into the third day but then died. It apparently had not been fed.

Development of the Young

At hatching, the young are sparsely downy, the down being of a wispy, fine character and whitish in color. Dilger (1960:651) reported a second coat of down replacing the natal one soon after hatching in *Agapornis*. I detected no such down in *Aratinga canicularis*, in young of one to 12 days of age. Instead, the juvenal plumage begins to emerge at the latter age. In one specimen about 12 days old the feet are anisodactyl. Dilger (1960:652) depicts all ages of young *Agapornis* as zygodactyl. I have discovered no other information as to the condition of the foot in other species of parrots.

Juveniles may be distinguished from adults in *Aratinga canicularis* by their dark brown irides in comparison to the yellow irides of mature birds. It is not known when the change in color occurs, but birds about ready to leave the nest retain brown irides. I have no information on postjuvenal molt in the wild, but juveniles obtained by me in July molted in captivity during August and September. These juveniles had been clipped prior to purchase, and I therefore plucked their remiges shortly after acquisition. The

August–September molt involved the entire body and took place while the birds were acquiring new remiges. In normal postjuvenal molt, probably the juvenal remiges are not replaced.

According to Lint young remain in the nest in captivity until they are approximately six weeks of age. No other information is available on the length of this period.

Pair Bond Maintenance

Although frequent mutual attentiveness exists prior to hatching of the eggs, I observed no indication of courtship feeding, mutual preening, or other maintenance activity while the young were being cared for in the wild. However, I was unable to follow the activities of the adults when they were away from the vicinity of the nest; therefore, such behavior may occur at this time in the breeding cycle.

The strength of the pair bond may be maintained merely by the attentiveness of the adults. In species such as the Blue Jay (*Cyanocitta cristata*), for example, in which the role of the male in actual duties of nest, egg, and nestling care are less than those of the female, evidences of courtship manifest themselves throughout the nesting period, serving to enforce the bond of the male to the events of the reproductive cycle subsequent to the initiation of nest building. In the Orange-fronted Parakeet, such traces of epigamy, once nidification has begun, would seem unnecessary and soon replaced, as previously mentioned, by (1) nearly constant association of the adults, (2) equality of duties in care of the young, and (3) roosting of adults in the nest cavity from its completion to the departure of the young from the nest.

Roosting Behavior

On each occasion that I observed the adults of nest N-2 going to roost, their retirement at from 6:18 to 6:30 p.m. was closely associated with the time the sun disappeared below the horizon from the viewpoint of the nest of the birds. At two other nests, both with higher western horizons from the viewpoint of the nest locality, a similar correlation with disappearance of the sun was noted. At nest N-1, located in a ravine and with the nest entrance pointed downward toward the south, the adults arrived shortly after 5:00 p.m., perched near the nest by 5:25, and on the two occasions recorded went to roost by 5:30, about the time the sun disappeared. At nest N-5, roosting time was observed only once and was correlated with disappearance of the sun at about 5:10.

The two captive parakeets using the nest chamber at night also began roosting in correlation with disappearance of the sun on clear days, but entered the nest cavity on overcast days as much as 45 minutes prior to that time, depending on the heaviness of the cloud cover. Thus, it seems that initiation of roosting may be dependent upon light intensity. In the wild, weather conditions during the nesting season rarely include cloud cover in the evening hours.

After the birds retired there usually ensued a short period of from one to five minutes of conversational chatter, but there was no vocal response to the calls of other birds outside.

Contrary to the situation in the evening, the parakeets began activities in the morning before the sun appeared, although they did not become very active in their movements until full daylight prevailed in the ravine between 7:30 and 8:00 a.m.

Spacing of Nests

Dickey and van Rossem (1938:205) reported, as previously mentioned, the occasional utilization of a termite nest by two pairs of parakeets simultaneously in El Salva-

dor. In Sinaloa, each of the three active nests discovered were single, while each of an additional five termitaria contained a single parakeet excavation. Characteristically, active termitaria were rather widely spaced through the woodland, no two being closer together than approximately 1000 feet in a direct line. Thus, the parakeet nests were of necessity not found in close proximity to each other. Most ballos having a diameter of one foot or more contained excavations made by parakeets. However, these included mostly old diggings not in use by the birds. I discovered 10 termitaria that were active and large enough to accommodate the parakeets, within the study area; of these termitaria, eight had been excavated and four had active parakeet nests. The two mentioned previously that were approximately 1000 feet apart were in two different ravines. Approximately equidistant between them was a well-excavated inactive nest, apparently available for use. Seemingly, there is no tendency for the birds to place their nests close together if adequate nesting sites and space permit otherwise.

Correlated with placement of nests, the individual pairs do not associate near the nest sites or show any inquisitiveness about each other's nests. Away from the nest, the pairs associate as freely as they do in the nonbreeding season.

Flock Balance and Breeding in Captives

Aviculturists generally believe that in order to obtain breeding results in *Aratinga canicularis* in the aviary, one must isolate the potential breeding pair in an aviary six to eight feet wide by about 24 feet long. Moreover, breeding may not occur even then until the birds have been allowed to grow accustomed to their surroundings for two or three years. When attempts have been made to breed the species in aviaries containing many individuals, competition for nest sites, diversion of attentiveness of the breeders by nonbreeding social activities, and general crowding have apparently inhibited reproductive behavior.

In the present study, although young have not, at this writing, been successfully reared by captive pairs, the factors just listed which possibly contribute to failure have largely been eliminated or shown to be unimportant.

My single breeding pair has nested in an aviary 6 by 16 feet in the presence of 12 other birds of the species. Of these 12, 9 are of a different race (*A. c. eburnirostrum*); these birds are comparatively wild, poorly adjusted to captivity, and, perhaps as a result, socially subordinate to other birds in the cage. The three individuals in the aviary of the same race as the breeders (*A. c. canicularis*) are relatively tame, all females, and all with a past history of subordinance to the breeders. Thus, a social situation similar to that found in nature has been achieved: the breeders, chiefly the male, have no trouble defending the nest site, competing for food, or, at intervals during the day, consorting with others of their kind in nonbreeding, noncompetitive social activities. As a probable result, even though these birds were placed in the aviary as recently as January, 1962, they have become immediately adjusted and have commenced prenesting activities that have continued to this writing (May, 1962), at which time a second clutch of eggs is being laid.

Relationships with Other Animals

The Orange-fronted Parakeet associates with no other species of birds as is frequently true in other kinds of parrots. Regarding predators, Beebe (1905:181) observed a flock of these parakeets sitting in a treetop and suddenly being attacked by a falcon; although one of their number was taken, the remainder of the flock sat still and quiet, as if they had not perceived the attack at all. My own observations with captive birds

reveal that these parakeets have no fear of life-like mounts of a Long-eared Owl (*Asio otus*) or a Sharp-shinned Hawk (*Accipter striatus*). The parrots actually climbed on these mounts and chewed on them as they do with other inanimate, but chewable, objects. However, parakeets in the wild in Sinaloa often reacted to a hawk overhead with nervous muttering (low intensity alerting signal) and then loud screams (high intensity alarm cries) and flight when the raptor drew nearer. I observed a Gray Hawk (*Buteo nitidus*) sailing about up high with a parakeet clutched in its talons; other parrots of this and other species were excited by this and flew about screaming. I observed no predation or evidence of it at the nests of the parakeets. I assume that snakes might be successful predators on the nest contents, but probably most other potential predators, for example, small mammals, would be discouraged or thwarted in attempts to enter the nest by the termite swarms that occur when the termitarium is broken.

SUMMARY

Orange-fronted Parakeets (*Aratinga canicularis*) inhabit tropical deciduous forests of the Pacific slopes of México and central America. Studies reported here were made of epigamic and nesting behavior of captive birds and of nesting habits in the wild.

Components of courtship feeding display include, among others, bill-wiping, bill-rubbing, perch-biting, popping, bill-vibrating, bill-snapping, crane-peering, malar-puffing, pupil-flexing and inflected whistling, all of which precede the act of courtship feeding, in various combinations. Pupil-flexing display is performed in conjunction with an ambivalent emotional state at the sudden appearance or rapid approach of another bird or other creature and serves to divert this approach or to forestall it. Pupil flexion is evidence of high-intensity, conflicting tendencies frequent in epigamic context. Actual courtship feeding has several components, including head-up chin-out, head-bobbing, bill-sparring, bill-grasping, and head-jerking. Head-jerking is the act of courtship feeding wherein a liquid regurgitant is probably passed from one bird to the other; the act is homologous to that of feeding the young by the adults. Mutual preening and associated behavior is regular throughout the year; courtship feeding is prevalent from midwinter to early summer. Clawing and switch-sidling, regarded here as precopulatory behavior, are likewise common components only in midwinter to late spring months.

The vocal repertoire includes annoyance squawks, alarm cries, epigamic calls, ambivalent calls, feeding calls, pair and flock social signals, activity-conversation, and content-rest calls. Sonagraphic analyses of some of these categories are presented.

Breeding behavior of the species was studied in Sinaloa, México. The range of the parakeet roughly coincides with that of an arboreal, colonial termite, in the termitaria of which the parakeets excavate their nest cavities. There is no discrete time of courtship display or of pair formation immediately preceding nest building. Pair formation probably occurs in late summer, and pair bonds are evident throughout the year.

Pairs probably begin nesting in early February, and the peak of the breeding season occurs in March in Sinaloa. Excavation is accomplished by both members of a pair and requires approximately one week. A parakeet can enter the nest cavity after three days of excavation.

For a period of approximately one week following excavation, the pair in the wild does not visit the nest, possibly allowing the termites to evacuate the nest cavity area of the termitarium. When nesting begins, pairs remain apart when involved in breeding duties, but they form small flocks when feeding. Courtship behavior accompanies early phases of nesting but thereafter it decreases sharply.

When the nest cavity is complete, both birds begin to roost inside the nest. Frequent attempts at successful copulation occur at this time. In the act, the female does not solicit by quivering the wings but raises the head and tail. The mounting is only partial, the male placing one foot on the female's back. In the single complete copulatory act observed in this study, courtship feeding occurred and the act lasted one minute and thirty seconds.

Clutch sizes in captivity vary from three to five eggs, and complete clutches of one to three were noted in the wild. The eggs are dull white in color and are laid every other day. Only the female incubates. The male in the wild enters the nest only to roost and accompanies his mate when she leaves the nest to feed. The captive male in this study frequented the nest diurnally in the incubation period.

The incubation period is approximately 30 days. Incubation begins with the first egg. Upon hatching, the shells may be carried from the nest or left inside it. The male in the wild now begins to visit the nest and with his mate to feed the young. Only the female broods. In middle to late stages of care of young, parents leave and return to the nest together to feed the young. The close association of the members of the pair probably enforces the pair bond, obviating necessity of courtship-type behavior during nesting.

The time the young remain in the nest was not determined by me but according to Lint (personal communication) it is about six weeks in captivity. The young at hatching are downy, altricial, and anisodactyl. They weigh approximately 2 grams. The first plumage begins to emerge toward the end of the first week. The young are feathered by approximately the middle of the third week and are then also zygodactyl. The plumage is identical in pattern and color to that of the adults, but the irides are dark brown and the circumorbital skin is whitish.

Young parakeets are fed regurgitated food. Flowers of the shrub *Combretum farinosum* are apparently an integral constituent of this regurgitant. Young birds gape for feeding when each side of the mandibles is grasped and not in response to other stimuli.

Roosting time of the adults commences at and seems correlated with the disappearrance of the sun below the horizon from the viewpoint of the nest site or with comparable light intensities on cloudy days.

Nests in the area of study were discovered only in active termite colonies and were thus never closer to each other than about 1000 feet. Most active termitaria had excavations by parakeets but of ten excavations discovered only four contained active nests.

Orange-fronted Parakeets associate with no other species of bird. Predation by the Gray Hawk was noted, and it is thought that only snakes could successfully prey on nest contents.

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