

PHYSICAL AND BEHAVIORAL FACTORS IN SOCIALITY
AND EVOLUTION OF CERTAIN PARROTS (*ARATINGA*)

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THE concepts of species-specific characteristics and social releasers as developed by ethologists (see Tinbergen, 1951; 1959: 318–330) have intrigued animal behaviorists as much as any concept in the science of ethology. Utilizing these concepts, I have been engaged since 1959 in studies of the behavior of parakeets of the genus *Aratinga*, primarily *A. c. canicularis*, the Orange-fronted Parakeet, and also recently other forms. The acquisition, in 1960, of captive birds of *A. c. eburnirostrum* and, in 1962, of 12 *Aratinga astec*, the Aztec Parakeet, made possible experiments and observations on the function of morphological and behavioral characteristics which are involved in sociality. The results of these studies have bearing upon our understanding of psittacid evolution.

Elsewhere (1963) I have described the epigamic and reproductive biology and (1965) the flock social behavior of *A. canicularis*. This parakeet is highly social in the wild except during the nesting season, when pairs disperse to nest. Flocks of 5 to 50 birds are otherwise common throughout the species' range, and groups of up to 12 or 15 birds typically wander about between scattered feeding areas and resting sites. The range of the species extends from northern Sinaloa, Mexico, south into the Central American lowlands and the foothills of the Pacific coast in tropical deciduous forest. Three well-marked populations occupy this range. These are designated subspecifically as *clarae* in the north, *eburnirostrum* from Michoacán to Oaxaca, and *canicularis* in the south (Friedmann, *et al.*, 1950: 126). The last two races mentioned are to be considered here. They are easily separable, the former having less orange on the forehead and a blackish splotch on the lower mandible, while the latter has a large patch of orange on the forehead and only the faintest wash of gray on the lower mandible (see extreme left and right subjects in "Step 7," Figure 1).

Aratinga astec may be considered the ecological counterpart of *A. canicularis* in similar (but more mesic) habitat on the Atlantic slopes of Mexico and Central America. *A. astec* averages slightly smaller and is generally similar to *A. canicularis* in plumage, but lacks markings of orange, blue, and black on the head. In *Aratinga astec*, only a tuft of orange feathering is found above the cere. In captivity, the two species as observed by me were much alike in habits, including feeding, degree of sociality, agonism, epigamy, and voice. Although little published information is available concerning *Aratinga astec*, its biology in the wild state probably is closely similar to that of *A. canicularis*. All evidence in-

dicates that the two species have been derived recently from a common ancestor.

METHODS

All birds were housed in aviaries and cages at the Moore Laboratory of Zoology, Occidental College. From 1960 through 1962, I observed mixed groups of *A. c. canicularis* and *A. c. eburnirostrum*. For one-half of this time, 12 of the latter occupied cages or outdoor aviaries ($6 \times 20 \times 12$ feet high) with from 8 to 10 of the former. I kept notes on sociality in these cages. In autumn, 1962, a cage (approximately $3 \times 3 \times 4$ feet) was used in the laboratory for the experimental isolation of various combinations of individuals of the different species, races, and flocks. I made observations on interspecific, interracial, and interflock behavior.

OBSERVATIONS AND EXPERIMENTAL RESULTS

From 1960 through 1962, no social relationship developed between members of the two races of *A. canicularis*, except when single individuals of each race were placed together in an isolated cage for a period of several days. In the mixed flock of the two races a few birds did not have mates or partners; in addition the sex ratio in the *canicularis* racial group was at one time one male to six females while the *eburnirostrum* members included six males and five females. Yet, even these imbalances did not induce interracial socialization. Finally, interracial agonism was not as common as intraracial agonism.

In the following designation of individual birds, A equals species *astec*, C equals species *canicularis*, subscript E equals race *eburnirostrum* of species *canicularis*, and subscript C equals race *canicularis* thereof. Birds were marked by a colored aluminum band on one leg; thus, R and L equal right and left. Colors are indicated by lower case letters: r, red; bl, blue; bk, black; y, yellow; p, purple; pi, pink; and g, green. A formula is thus available for any bird. (I think it is important to refer to individuals herein by band color in the event that color bands might in the future be shown to play a role in recognition.) Terms descriptive of behavioral components of agonism and ambivalence will be found in Hardy (1963, 1965); for the most part these are self-descriptive. The experiment proceeded in a number of stages, which may be referred to as steps 1 through 11 in the first phase of the study.

Step 1.—On 16 November 1962, a male, C_ELbk, was removed from a flock of 10 of his own race housed in an indoor cage and placed in a similar cage in the same room with four female Aztec Parakeets, ARg, ARp, ARy, and ALbl. All *A. astec* in this study were then less than one year old. The four Aztecs had been in a cage with eight of their own species. In the new cage, C_ELbk could both see and hear his flock-mates, while the

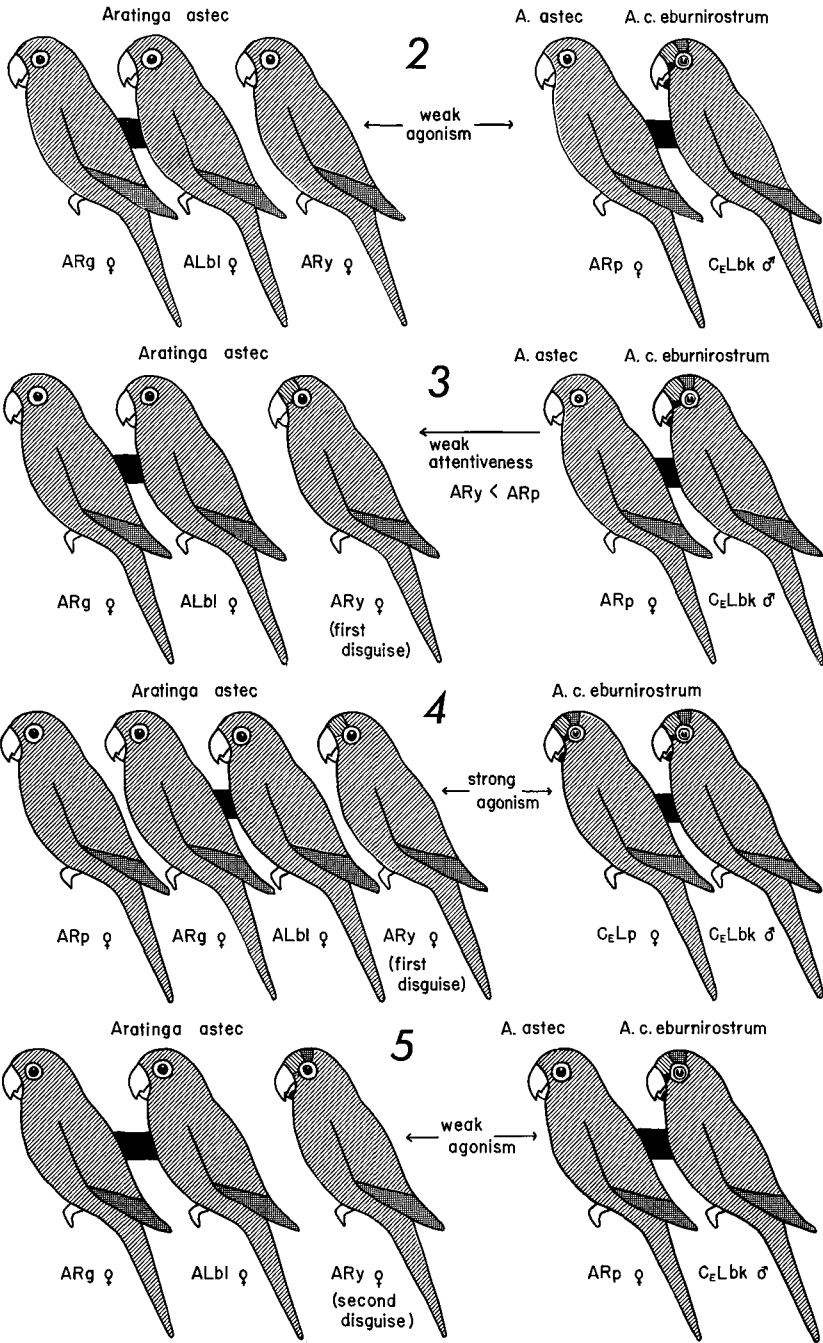
four Aztecs could only faintly hear others of their own species. This situation was maintained until 26 November; during this period, I noticed no interspecific sociality between these birds. C_ELbk for the most part clung to the cage wall and seemed to watch his former flock-mates. The four Aztecs freely associated with one another, often in pairs, mutually preening, nuzzling, and bill-sparring (see Hardy, 1963: 170–178 for discussion of these terms). Step 1 is not illustrated in Figure 1.

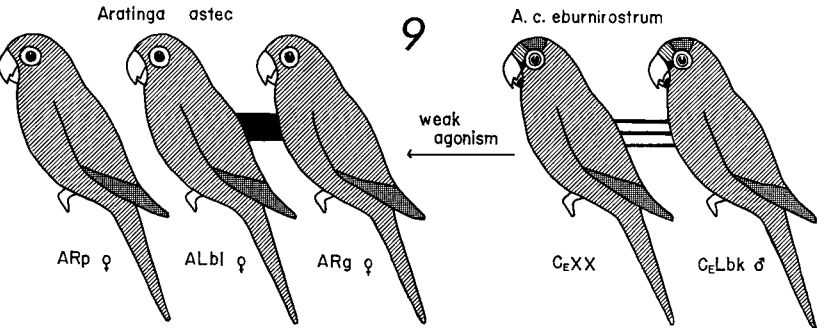
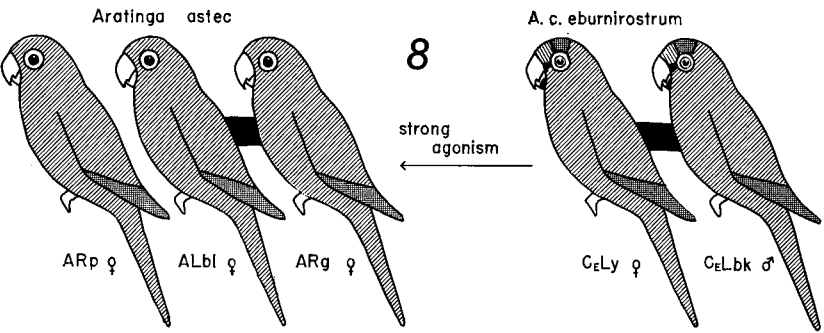
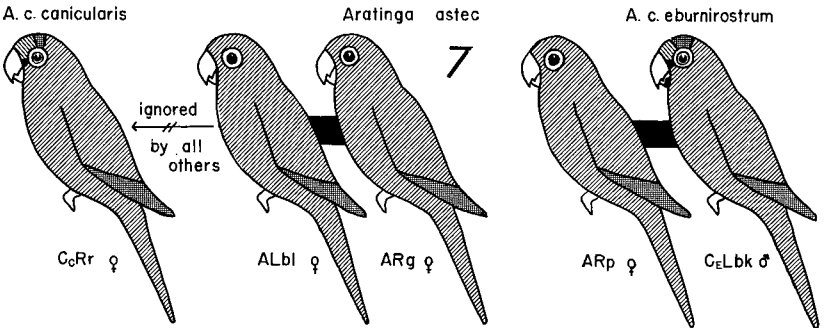
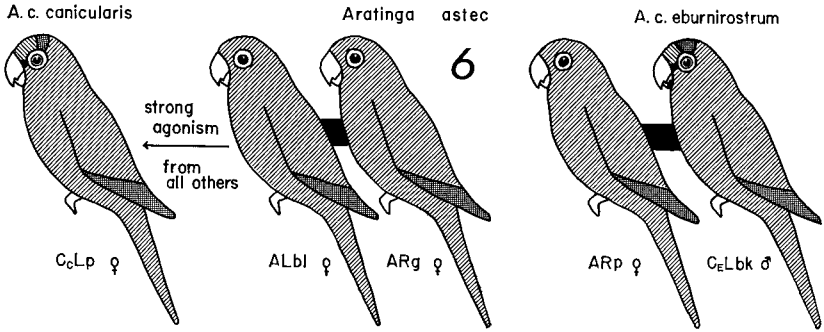
Step 2.—On 26 November, the experimental cage was removed to another room. The new position of the cage prevented C_ELbk from seeing, but not from clearly hearing, others of his flock. The four Aztecs could probably not hear others of their species and definitely could not see them. There was no immediate change in the attitude of the birds toward each other, but on 29 November, C_ELbk and ARp were noted bill-sparring as they clung to the screen of the cage. On 30 November, these two birds had apparently established a strong pair relationship (Step 2, Figure 1); C_ELbk preened ARp's cheek, performed weak bill-holding, and remained close beside the female. Thereafter the relationship persisted until the next step in the experiment. C_ELbk always initiated interaction between the two and seemed to dominate ARp. Courtship feeding was never observed (it is uncommon except in spring and summer in captive *A. canicularis*). A "pair relationship" also obtained between the two females, ARG and ALbl; ARy often was alone. No interaction except occasional agonism (at feeding times and when the birds were frightened by humans) occurred between C_ELbk and the Aztecs other than ARp. Likewise, rarely did any sort of interaction occur between ARp and the other Aztecs.

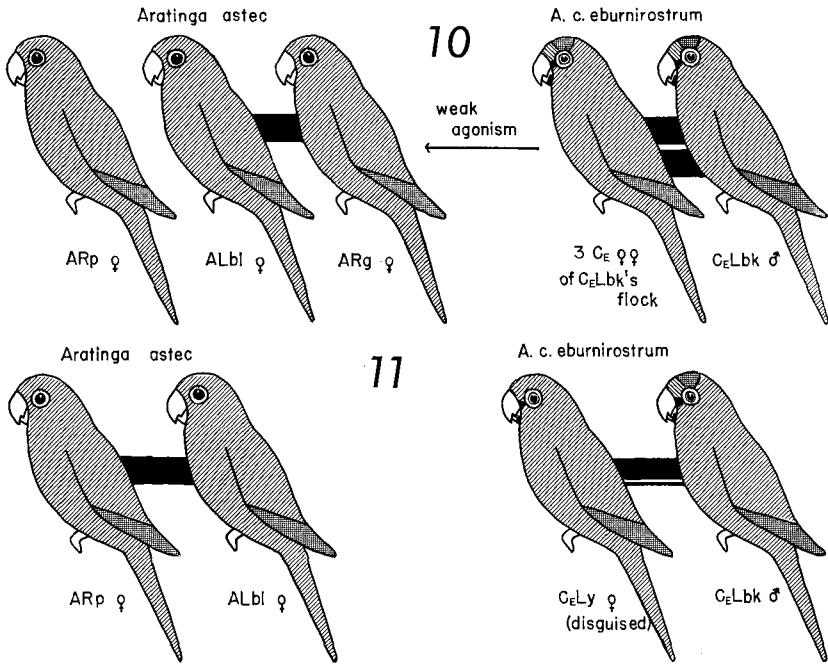
Step 3.—C_ELbk had readily commenced a relationship with ARp when neither could see others of its own kind. The relationship seemed authentic and as strong as between any two birds within either species. In Step 3, I attempted to assess the significance of an obvious species-character—the orange forehead—of *A. canicularis* and the strength of the interspecific pair bond when tested against this stimulus. On 6 December, ARy, the one bird in the cage without a partner, was removed and its forehead colored orange with oil paint. On 7 December, ARy was returned to the experimental cage. C_ELbk immediately moved toward ARy and gave a threat display consisting either of extension of the head, gaping, and pecking, or of lunging without making contact. C_ELbk's mate, ARp, in-

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Figure 1. Shown herewith (pp. 69–71) are the results of steps 2–11 (large numerals) of the initial experiment. Black bars connecting birds represent pair bonds. A single broad black bar indicates that the bond was formed with ordinary speed; three narrow bars (as in step 9) indicate delayed formation; one broad and one narrow bar (as in step 11) indicate slightly delayed formation; two broad bars (step 10) indicate very rapid formation. See text for further details.







tervened within moments and several times in the next hour was weakly attentive to ARy, preening her head just above the orange patch and remaining near her. C_ELbk showed no further aggressive action toward ARy. After these initial acts, C_ELbk and ARp remained paired and no further interaction was observed between either of them and ARy (Step 3, Figure 1).

Thus, the stimulus of the painted orange forehead of ARy was not sufficient to cause dissolution of the interspecific pair bond. Perhaps, however, ARp's attraction to ARy indicates that the interspecific pair bond of ARp and C_ELbk was as much due to ARp's attraction to the orange forehead of C_ELbk as to C_ELbk's reaction, in the absence of his flock-mates, to a bird of a different species. Such an attraction as ARp demonstrated is perhaps roughly comparable to the reaction of some birds to the "super-stimulus," as in the case of the European Oystercatcher (*Haematopus ostralegus*) attracted to eggs similar to but larger than its own (Tinbergen, 1951: 4-5).

Step 4.—Although the orange paint caused ARy to look remarkably like an Orange-fronted Parakeet, the blue crown, the black splotches on the lower mandible, and the yellow irides of *A. canicularis eburnirostrum* had not been matched in the disguise. On 17 December, to test the effective-

ness of the artificial coloring (or the importance of it in the absence of other "specific" characters) and the strength of the interspecific pair bond still further, a female *A. canicularis eburnirostrum*, C_ELp, a former flock-mate of C_ELbk, was introduced to the experimental group. ARy, still weakly disguised, was left therein, also. The response was spontaneous and dramatic. C_ELbk immediately approached C_ELp and began the intense greeting-recognition display, which he continued for one minute. The head was rapidly raised, head feathers were fluffed, the pupils expanded and contracted (pupil flexion of Hardy, 1963) frequently, the bill rapidly snapped, and the head waggled and wagged. The birds also frequently bowed their heads and grabbed the perch before rapidly raising them to display. Mention should be made here that the display just described serves in courtship display between long-paired Orange-fronted Parakeets. The components indicate various degrees of ambivalence and I judge them to be seral components "leading" toward courtship feeding—the act prior to copulation (Hardy, 1963: 171–173).

At the conclusion of the above encounter C_ELbk and C_ELp were close together and remained partners thereafter (Step 4, Figure 1). Their further attentiveness was, however, delayed for the next several minutes by certain events: at the beginning of the display between the two birds, the four Aztec Parakeets became aggressive toward the Orange-fronted Parakeets. At first ARp attacked them by flying at them with gaping mouth. Thereafter ARy led the other Aztecs in persistent threats of aggression which prevented the two Orange-fronts from occupying either one of the perches in the cage. They consequently remained clinging to the cage screen.

Thus C_ELbk, when confronted with a female from his former flock-mates, broke his interspecific relationship immediately. This seemingly took place as a response not only to recognition of physical characteristics possessed by C_ELp but to the female's response to C_ELbk's greeting-recognition display. The subsequent aggressive attitude of the Aztec Parakeets may be explainable as follows: from the beginning of the experiment, C_ELbk had been the only Orange-fronted Parakeet in the cage. Before he assumed partnership with ARp, he was quiet and comparatively inactive, only weakly displaying species-specific behavioral characteristics. He was, therefore, ignored until he gradually assumed a close but not highly demonstrative relationship with ARp. Interaction between the two birds was mostly mutual preening and weak bill-holding and did not include other components of courtship feeding or precopulatory behavior. In other words, C_ELbk was not, in a sense, an Orange-fronted Parakeet, or sufficiently one behaviorally to evoke interspecific aggressiveness by the Aztec Parakeets. Placing C_ELp in the cage evoked the highly char-

acteristic social attitudes of both the Orange-fronts toward each other, thus establishing a positive and, we might say, competitive social system (two birds of the same kind socially interacting would comprise a species in this sense), to which the Aztecs reacted aggressively and strongly. Their aggressiveness was not forthwith countered, seemingly because $C_E Lbk$ and $C_E Lp$ were too "interested" in each other to pay attention to the Aztecs. It was predictable that once their relationship was established, they, too, would behave agonistically toward the Aztecs. Such was the case by the second day—in fact to the extent that the two Orange-fronts usually dominated the Aztecs completely.

Since it was now established that a "complete" Orange-fronted Parakeet of the same flock as $C_E Lbk$ was sufficient to induce strong greeting, pairing, and dissolution of an established interspecific pair bond, the next steps in the investigation were designed to reveal just what characters $C_E Lbk$ had reacted to in $C_E Lp$. These could be (1) physical characters not included in the disguised Aztec (ARy), but characters of the species *canicularis* as a whole; (2) subspecific physical and behavioral characters (specific plus characters of plumage not found in *A. c. canicularis*); or (3) recognition factors having to do with flock or individual idiosyncrasies (i.e., was $C_E Lbk$'s strong reaction to $C_E Rp$ a result of his having recognized the individual as a former flock-mate or a result of his having recognized some generalized flock-characteristic in the individual?).

Step 5.—On 20 December, $C_E Lp$ was transferred to another room, and ARy was removed to be repainted. This time, the forehead was painted even more vividly, and in addition, the crown was tinted with blue, the circumorbital skin with yellow, and the sides of the lower mandible given a blackish spot, thereby duplicating all salient physical characteristics of *A. c. eburnirostrum* except the yellow irides. Three hours later, ARy was returned to the cage with $C_E Lbk$ and the other Aztecs. $C_E Lbk$'s reaction was immediate and identical to that evoked by $C_E Lp$, but significantly ARy did not respond to $C_E Lbk$'s greeting-recognition display. $C_E Lbk$ abruptly discontinued his display, did not approach, and thereafter ignored ARy as before. Again, the latter received some attention from an Aztec (not ARp) at first, but within a few hours this too ceased.

No further changes were made in the birds in the cage and, by 24 December, $C_E Lbk$ had resumed his interspecific relationship with ARp (Step 5, Figure 1).

From the results of Step 5, it may be inferred that the combination of orange forehead, black bill markings, yellow circumorbital skin, and blue crown (or one of these characters) is sufficient to evoke species-specific greeting-recognition display, but that continuation of a relationship de-

pends either upon additional characters (most probably the yellow irides, so plainly seen in the pupil flexion display) or cooperative behavior probably including participation in the greeting-recognition ceremony or both. The pupil flexion behavior and the pale irides of course comprise a physico-behavioral factor; the yellow color has no importance unless the pupils are flexed and the flexion probably lacks importance unless the irides are pale, since dark irides suddenly revealed produce no flashing effect.

On 1 January, ARy was removed permanently from the experimental procedure, since its plumage had been damaged by the paint. ARy was not replaced by another bird.

Step 6.—It will be recalled that in an aviary containing a mixed flock of *A. c. canicularis* and *A. c. eburnirostrum* no interracial sociality occurred. A female *A. c. canicularis*, C_CLp, which had been a member of this mixed flock, was placed in the experimental cage on 2 January. C_CLp had a history of strong aggressiveness, low sociality, high position in the peck order, and femaleness in interpair behavior. C_ELbk immediately approached C_CLp, and pupil-flexed and bill-snapped; C_CLp did not react. Then suddenly C_ELbk commenced strong intimidatory behavior toward C_CLp. Six successive times, C_ELbk flew at C_CLp and supplanted her, each time gaping and pecking at her. Then the three Aztecs showed aggressiveness, and in the next hour C_CLp was repeatedly pecked at, supplanted, and chased, so that only occasionally could she rest, clinging to the screen. Although the aggressiveness ceased thereafter, for the remainder of the time that C_CLp was in the cage (until 14 January) she was ignored by all other birds. C_ELbk continued his relationship with ARp, although the attentiveness between these two involved little mutual preening (Step 6, Figure 1). Thus, seemingly, C_ELbk's initial greeting to C_CLp was stimulated by well-developed, species-specific markings of the latter; but when C_CLp did not in turn react toward the greeting, C_ELbk followed by attacking C_CLp. These events probably account for the fact that the three Aztecs did not turn on C_ELbk as they had when the latter had formed a partnership with one of his old flock-mates.

Step 7.—Because of C_CLp's history in captivity of strong aggressiveness, high position in the peck order, and femaleness, I decided to replace her in the cage with C_CRr, also a female, but one with a history of docility, highly social nature, low position in the peck order, and little tendency toward maleness (except toward the lowest bird in the peck order). C_CRr tended to adjust well to small cages because she was pinioned; she was brilliantly marked like C_CLp. From her introduction to the cage (14 January) to her removal (25 January), no interaction of any kind was observed between her and the other birds in the cage (Step 7, Figure 1).

This indicates that lack of positive reaction by C_ELbk to C_CLp was not due wholly to C_CLp's lack of reaction to C_ELbk's greeting, but may have been based partly on the fact that these birds were of a different racial type or of different flocks.

Step 8.—To test the possibility that C_ELbk had by now developed such a strong bond with ARP that I was not really assessing the attractability of the birds being introduced into the cage, C_CRr was replaced on 25 January by C_ELy, a former flock-mate of C_ELbk. As previously, C_ELbk greeted the bird, she returned the greeting, there was a period of display that persisted for over an hour, and which was accompanied by marked aggression by both birds toward the Aztecs. Thereafter, until C_ELy was removed from the cage, a strong bond existed between the two Orange-fronts and no further relationship obtained between C_ELbk and the Aztecs (Step 8, Figure 1).

Step 9.—It now seemed beyond reasonable doubt that the difference in the reactions of C_ELbk to individuals of the race *canicularis* and individuals of the race *eburnirostrum* that were additionally his old flock-mates was a real difference. Step 9 partially reveals the comparative values of a bird being of the same race and of the same flock, in achievement of the relationships just described between C_ELbk and other birds. On 4 February, an Orange-fronted Parakeet, which had never been seen by any of the experimental birds, and which was of the race *eburnirostrum*, was obtained. This bird was designated C_EXX. C_ELy was removed from the cage and C_EXX placed therein. C_ELbk immediately approached and gave a strong greeting including bill-snapping, head-wagging, and pupil-flexing. Approaching closely, he gave the loud annoyance call, whereupon C_EXX reacted with weak bill-snapping. After two minutes, C_ELbk withdrew and chased the Aztecs twice. No apparent relationship developed between C_ELbk and C_EXX immediately. C_ELbk occasionally showed weak interest in C_EXX and was never strongly aggressive toward the strange bird. C_EXX was quiet and very docile. On 6 February, the two birds were seen sitting side by side. Thereafter, the two were usually together, although C_EXX was "uncooperative" and C_ELbk several times was noted pecking at her after attempting to bill-hold. On 12 February, mutual preening was observed between the two and the pair bond seemed firmly established (Step 9, Figure 1). Thus, C_ELbk had seemingly reacted strongly to C_EXX's visually perceptible characters and, although frustrated in immediate attempts at association, had within a week established a strong bond. This indicates that the rapidity with which C_ELbk had established partnership with the other individuals of the race *A. c. eburnirostrum*, was in part due to prior familiarity with them, and that seemingly, also, the differences in subspecific physical and behavioral char-

acters between *A. c. canicularis* and *A. c. eburnirostrum* are significant in establishment of interracial social relationships.

Step 10.—Within a period of a week following Step 9, three additional females, all former flock-mates of C_ELbk, were placed in succession in the cage with him and the Aztecs. Each time, he immediately accepted them and the partnerships were formed (Step 10, Figure 1). This would indicate that C_ELbk and these former flock-mates were recognizing each other by some generalized characteristic(s) possessed by all members of the flock, rather than by some individual characteristic(s) familiar through close prior association. It is impossible to rule out the last basis entirely, but other studies by me have shown that there is never free association among all members of a given flock. Rather there are social subgroups within the flocks. Thus, it is unlikely that C_ELbk “knew” each former flock-mate because of prior close relationship.

It was now necessary to remove ARG from the experiment because ALbl had begun plucking feathers from her head by over-zealous preening. No bird was substituted for ARG.

Step 11.—The last step was designed to assess roughly the comparative value of behavior and these visually perceptible characters from another viewpoint. C_ELp had been the first individual of C_ELbk's flock-mates placed in the experimental cage. She had immediately been accepted (see Step 4). In Step 11, C_ELp was disguised, her forehead and crown being painted green so that she resembled an Aztec Parakeet. Her circumorbital skin remained yellowish, the black mandible markings were not concealed, and, of course, the color of her irides remained yellow. On 27 February, C_ERp was removed and the disguised C_ELp placed in her stead. The reaction of C_ELbk was similar to that which he displayed when confronted with C_EXX. Bill-snapping, however, did not occur in the first encounter. At first the two birds remained apart. All displays were initiated by C_ELbk and included head-wagging, dueting, fluffing, and bowing. C_ELp was cooperative, but C_ELbk did not approach closely at first. When he finally did, he gaped several times and pecked at C_ELp. But C_ELp continued to return the greeting-recognition display of C_ELbk, and after one-half hour, C_ELbk finally performed the bill-snapping component of display. An hour from the time C_ELp was placed in the cage, she and C_ELbk were together, although several times, when C_ELp turned toward C_ELbk, the latter reacted by raising his head, gaping, and pecking at her. However, on 1 March, ambivalence had disappeared, and C_ELbk was twice observed performing courtship feeding of C_ELp—a stronger form of pair behavior than he had demonstrated to any of the previous experimental introducees (Step 11, Figure 1). The advance of the season possibly was a contributing factor to this fact.

ADDITIONAL EXPERIMENTS

Immediately following Step 11 of the present series of experiments, I attempted to repeat them employing another male in place of C_ELbk, plus the four female Aztec Parakeets as in the original experiment. However, the new male ignored and was ignored by the Aztecs under all circumstances. A third *Aratinga canicularis* placed with the Aztecs also ignored and was ignored by them, until three of the Aztecs were removed. Thereafter a weak association existed between the two remaining birds. I felt strongly that gonadal condition associated with the breeding season (February–May) was responsible for this decreased interspecific sociality, and that replication of the experiments above reported should be attempted again only in autumn, winter, and early spring in order to be significant in testing the initial results and conclusions.

Therefore, beginning 1 November 1963, repetition of the foregoing work was commenced. It was not possible to use an entirely different group of individual birds in the second set of experiments. Fortunately the significant interactions that occurred in the second set were largely between different individuals of the two species than in the previously described work. Because of the small supply of birds on hand, it was necessary to disregard the actual sex of some individuals and to assume that in homosexual pairs one bird assumes the role of the male, the other of the female, and that behavioral events between such birds are those typical of heterosexually paired birds. Observations of *Aratinga canicularis* over a five-year period indicate that this is a safe assumption.

Symbols for and sexes of birds referred to in the following account are as follows: C_ELbk ♂, C_ERp ♂, C_ELbl ♀, C_ERr ♂, C_ELp ♀, C_CLbl ♀, C_ERpi ♀, ALg ♂, ARo (o = orange) ♀, ARp ♀, ARr ♀.

RESULTS.—Between 1 November 1963 and 14 January 1964, several combinations of single male *A. canicularis* and three or four *A. astec* were caged together, sometimes in view of other parakeets, sometimes isolated from such view. In this period, any four Aztecs used always formed two pairs, regardless of actual sexes involved. On 8 January 1964, C_ELbk (the male of the previous steps) had been housed with four Aztecs, ARr, ARo, ALg, and ARp (C_ELbk's interspecific mate in the previous steps), for a period of 26 days. On the final day, C_ELbk was observed in mutual attentiveness with ALg. C_ELbk was promptly removed and C_ERp was placed in its stead.

On 14 January, C_ERp and ALg were seen together, engaged in mutual preening; ALg seemed dominant as if having assumed the male role.

On 20 January, ARr, a fifth bird, was disguised to look like an Orange-fronted Parakeet; the forehead was colored orange, the crown blue, the circumorbital skin yellow, and the sides of the lower mandible blackish. (Because water-base paints were employed, feather texture was little affected, and thus the disguise was more natural than any achieved the previous years.) After alteration, ARr was allowed to become calm and was then introduced into the experimental cage. C_ERp immediately per-

formed an intense greeting display, including pupil-flexing, bill vibrating and snapping, and gave the *chee-chee* greeting call, but did not approach ARr. ARr did not respond, and within one minute, C_ERp ceased displaying. Then AL_g approached the disguised ARr, the latter turned to face AL_g, and AL_g fled! ARo and ARP thereafter weakly flight-supplanted ARr several times. One hour after ARr had been placed in the cage, C_ERp and AL_g were observed together. They maintained their bond until 21 January.

On 21 January, C_ELbl, a former flock-mate of C_ERp, was disguised to resemble an Aztec Parakeet. The orange forehead was painted green, feathers bordering the cere were colored dark brown, and the circumorbital skin was colored white. The bird was then placed in the experimental cage with the other five birds. C_ERp immediately gave the greeting call but *did not* display toward C_ELbl. The latter, likewise, did not display. Twelve minutes later, C_ERp climbed to where C_ELbl had clung since her entry. The two birds first bill-sparred briefly but then interaction ceased. One hour later, C_ERp was seen to engage in ambivalent behavior, including perch-biting, head-wagging, a variety of intermixed annoyance and social calls, the head-up chin-out display, and plumage fluffing, while perched within a few inches of C_ELbl. C_ELbl did not respond.

Although the results of the greeting ceremony between C_ERp and C_ELbl were seemingly equivocal, on the next day it was apparent that the bond between C_ERp and AL_g had ceased to exist and that C_ERp and C_ELbl had formed an associational bond. This bond was not characterized by any mutual attentiveness and was marked instead by displays of ambivalence, as described above, on the part of both birds. I think that the disguise of C_ELbl interfered with the achievement of a more attentive relationship.

The same day, C_ELbl was removed from the experimental cage. ARr was necessarily removed also, since in the single day in which relationship between C_ERp and AL_g had not existed, ARr and AL_g had begun an association.

By 27 January, C_ERp and AL_g had again assumed an attentive relationship. On that day, C_ERr, a former flock-mate of C_ERp, was placed undisguised in the experimental group. C_ERp immediately gave a strong greeting display which was returned by C_ERr. Within two minutes, marked by continuous greeting and recognition behavior, the two birds were firmly paired and engaged in high intensity aggression with the Aztec Parakeets. Fighting continued for several minutes, both species pecking, flight-supplanting, and rushing their opponents.

On 28 January, I removed C_ERr from the experimental group. Within a day, C_ERp and AL_g had re-established their bond. The group was left unaltered until 4 February.

On 4 February, C_ERr, which had been with a flock of its fellows for eight days, was again placed in the experimental group. This time, however, it was painted to resemble an Aztec Parakeet. The disguise, however, did not prevent the immediate resumption of a bond between C_ERp and C_ERr.

On 8 February C_ERr was again removed from the group, and by 9 February C_ERp and AL_g were back together.

On 11 February, C_ELbk was painted white on the forehead and introduced to the experimental group. Immediately, C_ERp and C_ELbk formed a bond. C_ELbk was immediately removed from the cage and within a day C_ERp and AL_g were together.

C_CLp, a member of the race *A. c. canicularis* and not a flock-mate of C_ERp, had been caged with approximately six individuals of *A. c. eburnirostrum*. She had become partially integrated in that group to the extent that she fed easily with it, al-

though as far as observed she did not otherwise engage in social behavior with its members. On 18 February, C_CLp was introduced to the experimental group. C_ERp quickly greeted C_CLp. The latter did not respond but did not seem intimidated. Instead she moved easily about the cage. C_ERp then approached C_CLp and the two bill-sparred, pecked at each other, and fluffed their feathers in a display of ambivalence. Such behavior occurred intermittently for an hour.

From 19 to 27 February, no attentiveness was noted between C_ERp and C_CLp, although they were together about 90 per cent of the time of observations. Otherwise, C_ERp frequently was alone or near the Aztec Parakeets, although she was never observed in attentiveness with ALg in this period. In addition, throughout this period, the flock's social behavior was characterized by extremely nervous, noisy behavior, many aggressive encounters, and ambivalent display, with this usually involving C_CLp and C_ERp.

On 27 February, C_CLp was removed from the experimental group, and on 28 February, C_ERp and ALg were together and engaged in mutual preening.

On 2 March, C_ERpi, a newly acquired individual belonging to the race *A. c. eburnirostrum* never before seen by any of the experimental group, was placed in it. C_ERp greeted this bird weakly, and the Aztec Parakeets attacked C_ERpi furiously. After several minutes of this, C_ERp attacked the Aztec Parakeets, and the two Orange-fronted Parakeets defended themselves separately. Aggressive behavior decreased in 15 minutes, and then C_ERp approached C_ERpi and bill-sparred once. No further interaction was observed between the two birds, but between 3 and 5 March a strong bond developed between them with C_ERp in the dominant, male role.

On 6 March, C_ERpi was removed, and C_ERp and ALg resumed their association.

Finally, on 7 March, C_CLbl was removed from a flock of its fellows and placed in the experimental group. C_ERp greeted her but did not approach. C_CLbl did not respond and was attacked several times by the Aztec Parakeets. She defended herself well; C_ERp was also stimulated to attack the Aztec Parakeets. Although on the evening of the same day, C_ERp and C_CLbl were together at the time of roosting, on the following day C_ERp and ALg were together, and no further association between C_ERp and C_CLbl occurred. Experimentation was terminated on 17 March.

In comparing the two sets of experiments, work of the second year seems to support the results of the previous year. Once again, prior associations between two birds seemed to take precedence over other factors in the re-establishment of such associations. Interspecific pair bonds form easily, but only in the absence of a potential partner of the same race. Although birds of the same species exhibit weak interspecific recognition, no firm pair bonds seem to form unless the birds are of the same race. Color alteration, when carefully and properly done, usually creates an initial complication in the recognition ceremony, but this is always temporary. Again there was delay in the assumption of relationship by the isolated bird with an introduced bird of the same race, but with which it had had no prior association, but the delay was, as in the first experiments, short and perhaps not significant. Nonetheless, no such delays occurred in establishment of relationships with prior associates having unaltered color and patterns.

Finally, a step in the 1963-64 procedure not included in the first set of experiments indicates that a bird of different racial type from the isolated bird may achieve a tentative bond if this is preceded by a period in which the bird to be introduced into the experiment is "conditioned" to members of the isolate's race while simultaneously deprived of its own kind. Thus, C_CLp and C_ERp had a weak association, but C_CLbl and C_ERp did not.

DISCUSSION

Peters (1937: 141–273) lists 81 genera and over 330 species of parrots. The family is known in tropical and subtropical regions throughout the world, excepting some oceanic islands. Gray (1958: 142–177) records hundreds of cases of hybridization and alleged hybridization (almost all in captive birds) involving over 100 species and subspecies and 36 genera of psittacids. Most of these are intrageneric, but intergeneric hybridization is frequent and inter-subfamily crosses are of rare occurrence (for example: *Melopsittacus* × *Agapornis*, Gray, 1958: 143). The few reports of psittacids hybridizing in the wild are of two types. The first type includes unsubstantiated reports, some based on hearsay and some on “guesswork” unsupported by specimens. Tavistock (1930: 40) suggests possible wild hybridization of *Alisterus s. scapularis*, the King Parakeet, and *Aprosmictus e. erythropterus*, the Crimson-wing Parakeet, but his “evidence” involves a rather complicated comparison of his captive hybrids with a color plate of a parrot originally described as a species but now considered to be a hybrid between the King and Crimson-wing. The second type of report of wild hybrids is of interbreeding between the well-marked allopatric populations of certain Australian parakeets which Keast (1961: 343–344) terms the *Platycercus elegans* superspecies and the *P. eximus* superspecies. The significance of the interrelationships in these superspecies is suggested below, following discussion of psittacid evolutionary mechanisms in the next five paragraphs. There is one last point to be made before that discussion: many *sympatric* species of parrots are never known to hybridize in the wild but do so readily in captivity. These facts, especially the last one, taken together with my observations on captive *Aratinga* seem to me to bear strongly on an understanding of psittacid evolutionary mechanisms as shown in the following suggested explanation.

1. There is no order of birds in which the species are more diversified in color and color pattern than the Psittaciformes. Even members of the same genus, although they may number over 20 species (as in *Aratinga*) or of the same superspecies (as in *Agapornis*; see Dilger, 1960) are instantly distinguishable on the basis of coloration of either sex or of young birds fully feathered. Yet, the ease with which hybridization occurs in the aviary (intrageneric hybrids are apparently no more difficult to obtain than normal breeding *per se*) when male and female are isolated from others of their own kind, reveals that the variation in plumage color obscures a contrastingly small amount of diversity in those characters having to do with interspecific compatibility.

2. In the wild, as opposed to the aviary, some factors obviously must act to reduce or prevent hybridization. Where two or three species of the same genus are sympatric, apparently utilizing similar foods and nest sites, or where ranges of similar species meet, hybridization seldom occurs. In Mexico, for example, *Amazona viridigenalis*, *A. autumnalis*, and *A. ochrocephala* occur together in southern Tamaulipas. South America has several species of *Amazona* and many of *Aratinga* ranging from sympatry to allopatry in distributional relationships. No wild hybrids are known, but in *Aratinga*, for example, six interspecific hybrid types are known from captive matings (Gray, 1958: 153–154).

The behavior of parrots used experimentally in this study seems to point out a mechanism sufficient to account for isolation of the species in the wild and indicates further a mechanism promoting genetic divergence accompanying even the slightest geographic isolation: so long as an individual parrot has others of his own *kind* with which to associate, he tends not to socialize with other kinds. "Kind" is emphasized here because, from the experimental steps just outlined, the reaction of a given parrot toward others of his own flock is, other things being equal, markedly more positive than toward similar individuals of a different subspecies type, or even toward seemingly identical individuals not before seen.

I do not here mean to imply that, because of physico-ethological barriers between subspecies and between flocks, sympatric subspeciation or speciation is possible, but it is easy to see that such barriers would tend, as previously stated, to re-enforce the effects of geographic isolation. Thus, for example, we might imagine two flocks of a given form of parrot inhabiting during the nesting season the two sides of a broad river. Occasionally in the non-breeding season, when pairs are gradually being formed, especially among young of the year, the flocks might in their wanderings encounter each other. At these times, they would always have available others of their own kind. Because of clannishness, as demonstrated in the present experiments, there would be little chance that birds of the two flocks would be attracted to each other. Therefore, the effects of minor geographic isolation would be re-enforced. The previously mentioned "superspecies" of Australian parrots (Keast, 1961: 341–347), considering the variable but limited interaction of their geographically distinctive forms, may be near to showing the "end" speciation result of such a combination of ecological, ethological, and genetic factors.

In conclusion, I hypothesize that behavioral peculiarities similar to those described in this paper have been a major factor in the marked phenotypic divergence characteristic of the Psittaciformes, and that this constitutes an effective barrier to hybridization in the wild.

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SUMMARY

Orange-fronted Parakeets of two races and Aztec Parakeets were observed in aviaries and confined in a cage in various combinations to reveal the importance of specific, racial, and individual characteristics in sociality. A male Orange-front of the race *eburnirostrum* paired with an Aztec female when deprived of the sight of his own kind. These two birds maintained their bond, except when other individuals of the race *eburnirostrum* were placed in the cage, whereupon the male always paired with them. The male typically ignored Orange-fronted Parakeets of the race *canicularis* except to greet them. Apparently greeting is evoked by species-specific physical characters (orange forehead, for example) but further progress toward sociality requires cooperation by the bird toward which the display is directed. An Aztec Parakeet (other than the one with which the male paired) was painted variously to resemble an Orange-fronted Parakeet. The disguise evoked only incipient greeting and recognition.

An individual of the race *eburnirostrum* never before seen by the male used in the experiments was accepted only after a period of several days, while all of the male's former flock-mates, when introduced into the cage, were immediately accepted by the male. This indicates that the male recognized the latter birds by individual or flock characteristics. A female *eburnirostrum* of the same flock as the male and previously accepted by him in the experiment was painted with green paint to conceal the orange forehead. Acceptance of the disguised bird by the male was delayed for an hour and the greeting-recognition display of the male was interspersed with threat. Replication of the experiments was conducted and results substantiated the initial hypotheses.

Parrots have diverged phenotypically much further than their inter-specific fertility in captivity would indicate. Few wild hybrids are known, however, and it is hypothesized that the phenotypic variety together with clannishness and ability to recognize individuals or flock-mates accounts for isolation of species in the wild. It is hypothesized that these factors

promote rapidity of evolution by re-enforcing the effects of slight geographic isolation.

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