

INTER-SPECIFIC RELATIONS BETWEEN SOME ANDEAN BIRDS

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INTRODUCTION

It is becoming increasingly evident that the social relations between individuals of different species of similar ecology occupying the same or adjacent habitats may be as complex as the relations between individuals of the same species. This point is illustrated in a particularly striking way by four types of "honeycreepers" occurring in the Quito region of central Ecuador, namely three flower-piercers, *Diglossa lafresnayei lafresnayei*, *D. carbonaria aterrima*, *D. cyanea cyanea*, and one conebill, *Conirostrum cinereum fraseri*. These names are assigned according to Hellmayr (1935). For convenience, the birds will be called by their subspecific names alone throughout the following account. Some of the inter-specific reactions of these birds are not only particularly complex but also very distinctive.

The birds were studied during four short field trips to the Quito region: 4-9 August 1959, 20 May-2 June 1960, 21-27 May 1961, and 19-25 May 1962. The total time spent in observation was approximately 250 hours. The observations in 1959 were made during the first part of the rainy season. The other observations were made during dry seasons.

The birds were observed in three areas, a few miles apart: in Quito itself and the adjacent suburbs, at an altitude of approximately 9,000 feet; on the western slopes of Cerro Pichincha (west and northwest of Quito), near the towns of Nono and Lloa, at altitudes between 9,000 and 10,000 feet; and on the northern slopes of Cerro Atacaso (southwest of Quito), near the town of San Juan, at an altitude of approximately 11,000 feet. (Nono, Lloa, and the summit of Atacaso are all shown on the map in Chapman 1926). Every area was visited repeatedly during every field trip, and approximately equal amounts of time were spent in each area.

aterrima and *fraseri* were observed in all three areas; *aterrima* was always much more abundant than *fraseri*. *lafresnayei* was observed only on Atacaso, where it was even more abundant than *aterrima*. *cyanea* was observed only near Nono and Lloa. In both places, it was much less abundant than *aterrima*, but probably slightly more abundant than *fraseri*. The populations of all the species in any given area seemed to be essentially the same during all periods of observation. This would suggest that all or most individuals are largely or completely sedentary.

On Atacaso, all the birds were found in narrow "hedges" of scrub along roads and irrigation ditches. The birds near Nono and Lloa were found in similar environments and in broader patches of more or less dense vegetation in ravines along natural water-courses. The birds in Quito itself were found in gardens, abandoned scrub-covered fields, and eucalyptus plantations.

Although no specimens were collected, and no certain copulation attempts were seen, it was obvious that at least some of the birds were breeding during some of the periods in which observations were made. A few fledglings of *aterrima* were seen in both 1961 and 1962. (These young birds still had short rectrices and remiges, and followed and begged from a parent very frequently.) Older individuals of *aterrima* in "juvinal" plumage (see comments below) were abundant during the periods of observation in 1959, 1960, and 1961, but were less common and/or less conspicuous in May 1962. Fully fledged individuals of *lafresnayei* in juvenal plumage were abundant in August 1959, but less common and/or less conspicuous during the other periods of observation.

Obviously-adult individuals of *aterrima* performed high intensity displays and unritualized hostile activities most frequently during the first days of observation in May 1960. The frequency of such patterns definitely declined during the last days of May and the first days of June of that year. Adult *lafresnayei* performed high intensity displays and unritualized hostile activities most frequently in August 1959. Displays and territorial disputes between individuals of *fraseri* were seen most frequently in May 1960 and May 1961. Displays of adult *cyanea* were seen most frequently in May 1962. The observed behaviour of all these birds when their displays and unritualized hostile activities were most frequent was very reminiscent of the corresponding behaviour of some individuals of *D. carbonaria gloriosa* which were studied in the mountains of western Venezuela at a later date, and which were definitely known to be performing successful copulations at the time of observation.

Some of the characteristic features of the behaviour of the honeycreepers of the Quito region may be affected by their appearance.

1. *lafresnayei* is the largest of the four forms, and *fraseri* is the smallest. *aterrima* and *cyanea* are similar to one another in size, but *aterrima* appears to be plumper and shorter-bodied.

2. Adult individuals of *lafresnayeri* are blackish, with conspicuous pale blue humeral patches. Typical adults of *aterrima* are blackish without humeral patches. Although the blackish adults of these two forms are similar, they are not difficult to distinguish in the field. They differ in proportions, voice, and other display patterns (see below) as well as in size and the presence or absence of humeral patches.

3. Some individuals of both *lafresnayeri* and *aterrima* are largely dull grey, and most of these are certainly young. All the fledglings I have seen were grey. None of the specimens in grey plumage in the collections of the U.S. National Museum or the American Museum of Natural History is noted as having had enlarged gonads when collected. There are some indications, however, that some individuals of *aterrima* may show reproductive behaviour while in grey plumage—see below. For this reason, observed birds of this species in grey plumage that were not obviously fledglings will be referred to as “apparently immature” throughout the following pages. Birds in black plumage will be referred to as “obviously adult”.

4. Adult individuals of *cyanea* are medium blue, with black faces and lighter blue or whitish crowns. Adults of *fraseri* are largely greyish above and buffy below, with whitish superciliary stripes and white wing-patches. Young birds of *cyanea* and *fraseri* are similar to their parents, but duller (very much duller in the case of *cyanea*).

It will be convenient to refer to all these birds, as a group, as the “*Diglossa-Conirostrum* complex”, but it must be emphasised that the phrase in the following pages refers only to the Quito region, although the group may have a wider distribution than this.

NOTES ON ECOLOGY

Every form of this complex may be said to compete with every other form of the complex with which it is in contact.* At least, the forms compete insofar as they may all use, or try to use, certain features of the environment which cannot be used twice or cannot be used by two individuals simultaneously. The presence of one form in an area must render the area less favourable (at least in some respects) for the other forms. In particular, the forms must compete for certain foods and some other features of the environment such as song perches.

All the forms occurring in any given area are found in all or most of the same habitats, and appear to take almost or exactly the same *ranges* of foods. They all are partly insectivorous and partly nectarivorous. It is very common to see individuals of two or three of these forms feed in rapid succession on the flowers of the same plant. The three local forms of *Diglossa* extract nectar from flowers with tubular corollas by the same method as *D. baritula* described by Skutch (1954). Holding the tube by the hook of the upper mandible, an incision is made by the lower mandible, and the nectar is then (apparently) secured by inserting the tongue through the incision. Although the bill of *C. c. fraseri* is much less specialized in shape, it seems to extract nectar from many of the same tubular flowers by a similar method. At least, I have seen cone-bills pecking at the base of tubular corollas, apparently inserting their bills, and then found incisions in the corollas after the birds had flown away. This species may use its mandibles and tongue

* The rather general term “form” will be used instead of “species” or “subspecies” throughout much of the following discussion for several reasons. It will be used instead of “species” because the behaviour of the Quito birds may be different from that of other birds of the same species in other regions. It will be used instead of “subspecies”, in some passages, for the sake of clarity and brevity. In some contexts, the term “subspecies” would have to be accompanied by more or less lengthy qualifying phrases, in order to make sure that discussions of the relations or differences between sympatric subspecies of different species were not confused with comparisons between different, allopatric subspecies of a single one of the same species. Such phrases as “the four subspecies of the *Diglossa-Conirostrum* complex of the Quito region . . .” would be particularly liable to misinterpretation.

The meaning of the term “form” should be clear in any given context in the following discussions without qualifying phrases.

during feeding in much the same way as the Bananaquit *Coereba flaveola* which has an equally unspecialized bill and also makes incisions in the corollas of flowers (Skutch 1954). All the forms of the *Diglossa-Conirostrum* complex also tend to hunt for insects on the same plants by the same methods, i.e. probing at the bases of leaves and leaf-clusters and in crevices in bark. Thus, the presence of one form of the complex in an area must reduce the amount of food available to other forms of the complex in the same area.

It is obvious, however, that the severity of this competition must be mitigated by certain other factors. Although all the forms occurring in any given area may be found in all the same habitats, this does not mean that their habitat preferences are absolutely identical. The forms inhabiting the same areas do not usually occur in the same habitats with exactly the same relative frequencies. *fraseri* is primarily a species of moderately open, and usually relatively low, thickets and shrubbery. It occurs in areas of very dense shrubbery relatively (if not actually) infrequently. Individuals of this form usually tend to remain in or near the upper layer or surface of the scrub or shrubbery they inhabit; but apparently never go very high in tall trees.

The preferences of *cyanea* are more varied. Most individuals of this form spend at least half their time in thickets and shrubbery. They often occur in shrubbery that is somewhat denser and/or higher than the scrub preferred by *fraseri*. They seem to occur quite frequently in all parts of the shrubbery, deep and low inside as well as in the upper layer. They also show a definite tendency to visit trees, where they may feed, display, and perform many other activities. They frequently go much higher in trees than either *fraseri* or *aterrima* in the same areas. Most of my observations of *cyanea* were made near Nono. In this area, individuals of *cyanea* frequently visit the upper parts of imported eucalyptus trees, approximately 30 to 40 feet above the ground.

The habitat preferences of *aterrima* and *lafresnayeii* are partly intermediate between those of the other two forms. Both *aterrima* and *lafresnayeii* are primarily birds of dense, and usually moderately high, thickets and shrubbery. They visit trees less frequently than *cyanea* and occur in relatively open scrub comparatively (if not actually) less frequently than *fraseri*. On Atacaso, where *lafresnayeii* and *aterrima* occur in the same general area, all or most individuals of *aterrima* inhabit sites which are exposed to direct sunshine shortly after dawn; while individuals of *lafresnayeii* inhabit sites which are in the shadow of the crest of the mountain until 8.00 a.m. or later, in addition to the same sites as *aterrima*.

These differences in habitat preference are supplemented by certain temporal differences in feeding habits. Most individuals of *aterrima* and *lafresnayeii* seem to spend more time feeding on nectar, and less time feeding on insects, than most individuals of the other two forms. All or most individuals of *cyanea* seem to feed on nectar more frequently than all or most individuals of *fraseri*. (Skutch (1954) says that *cyanea* eats fruit also; but I never saw this myself.)

Thus, even if two or more forms in an area take the same range of types of food, they probably usually take different amounts of the different types. This tendency may be enhanced by other factors. There are indications, for instance, that the habitat preferences of both *lafresnayeii* and *aterrima* may change with age. Most individuals of both forms in grey "juvenile" plumage seem to spend almost all their time deep inside thickets and shrubbery. In the case of *aterrima*, at least, this is just as true of fully grown and completely independent birds as of fledglings just out of the nest. Obviously adult birds spend considerably less time in such environments. They range throughout all the types of vegetation inhabited by their species, coming out with considerable frequency to the top and/or the outer edges of shrubbery, where they may perform a variety of activities, including both feeding and singing, as well as in trees. Such partial segregation might be advantageous in any one of several different ways. Inexperienced young

birds may be less exposed to predation deep inside shrubbery than in the outer or upper layers of vegetation. They may also be less exposed to attack by other members of their own species (see below). Perhaps more important, such segregation must help to reduce competition for food between the inexperienced young and both adults of their own species and the individuals of *fraseri* that also occur in the same areas.

I have seen very few traces of any similar partial segregation of apparently immature birds in either *fraseri* or *cyanea*. This difference may help to explain why the population densities of *lafresnayeii* and *aterrima* near Quito are much higher than those of either *cyanea* or *fraseri* in the same areas.

All these birds must have other competitors in addition to other members of their own complex, the most important being humming birds. Large numbers of many species of humming birds occur in almost all parts of the Quito region (see Chapman 1926).

Some more closely related species may be almost equally important. Near Nono, for instance, two common warblers, *Basileuterus nigrocristatus* and *Myioborus melanocephalus ruficoronatus* feed on insects in many of the same places as the local forms of the *Diglossa-Conirostrum* group. (The names of these warblers follow Blake (1957), those of the tanager and finch cited below follow Hellmayr (1936 and 1938 respectively).) *M. m. ruficoronatus* is essentially arboreal and competes with *cyanea* and, to a lesser extent, *aterrima*. *B. nigrocristatus* inhabits shrubbery and thickets, and competes with *fraseri* as well as *cyanea* and *aterrima*. There are also a few warbler-like tanagers of the species *Thlypopsis ornata* (see Hellmayr 1936) near Nono. These birds seem to be primarily insectivorous and inhabit much the same shrubbery as *B. nigrocristatus*; but they may also take nectar. I have seen at least one individual of this species pecking at the base of tubular flowers in much the same way as *fraseri*. Flowers of this type are very abundant in the Quito region, and it is not surprising that many different types of birds have evolved methods of exploiting them.

It seems unlikely that any other species competes with any of the forms of the *Diglossa-Conirostrum* complex as frequently as the latter compete with one another; but they must make appreciable inroads on the total amount of food available in many areas.

On Atacaso, I caught a few glimpses of one or two individuals of *Diglossa indigotica*, in both 1959 and 1960. These individuals were seen in the same area as *aterrima* and *lafresnayeii*; but they certainly were not permanent residents. They were probably strays from lower altitudes to the west of Atacaso.

INTRA-SPECIFIC REACTIONS

Some aspects of intra-specific behaviour are very different in different forms of the *Diglossa-Conirostrum* complex. Pairing behaviour may be cited as an example. Pair-bonds between males and females must be very brief indeed in both *lafresnayeii* and *aterrima*. I never saw two obviously adult individuals of either *lafresnayeii* or of *aterrima* remain associated with one another for more than a few seconds. Whenever two obviously adult individuals of the same form did happen to come close to one another, one always attacked the other almost immediately. As far as I could tell, every obviously adult individual of both forms adopts its own individual territory, and defends this territory against all other obviously adult birds and most apparently immature birds of its own form.

I did see a few examples of associations between one obviously adult individual of *aterrima* and one individual of the same form in grey plumage which were somewhat more long-sustained, lasting a few minutes or more. In some cases, the grey bird was obviously a fledgling. In other cases, however, it was fully grown and made no attempt

to beg from its black companion. In at least one of the latter cases, certain reactions between the two birds were somewhat similar to some of the partly hostile "courtship" patterns of other honeycreepers and tanagers. This might suggest that some individuals of *aterrima* may pair up while still in "immature" plumage.

I also saw one *aterrima* in grey plumage uttering "advertising songs" similar to those of obviously adult birds. It is conceivable, therefore, that at least some individuals of *aterrima* retain the grey "immature" plumage after they have become mature in all other respects. If this is typical of some but not all members of the population, the variations in plumage development of *aterrima* would be similar to those of the hummingbird *Florisuga mellivora* described by Zimmer (1950). The two species may be responding to similar selection pressures.

The pair-bonds of *cyanea* and *fraseri* seem to be less brief than those of *aterrima* or *lafresnayeri*. Approximately half the individuals of *cyanea* observed, and almost all the individuals of *fraseri*, were grouped in pairs. Although the sexes of both species look alike in the field, it is overwhelmingly probable that all or most of these pairs were composed of one male and one female. All the pairs observed were maintained throughout the whole period during which I was able to watch them in any given year. The members of such pairs remain in close proximity to one another even when they are not engaged in mutual display.

These differences in pairing behaviour may be functionally related to the slight differences in feeding behaviour noted above. Brevity of associations between males and females seems to be characteristic of many or most primarily or largely nectarivorous species (e.g. humming-birds).

All the forms of the *Diglossa-Conirostrum* complex show a remarkable amount of intra-specific aggressiveness. Both pairs and single, apparently unmated, individuals of *cyanea* and *fraseri* adopt territories, and defend them against other birds of their own species as vigorously as do single individuals of *aterrima* and *lafresnayeri*. It is just as rare to see more than two individuals of *cyanea* or *fraseri* together as it is to see more than one *aterrima* or *lafresnayeri* at any given site.

They all defend their territories against other members of their own species by means of purely or primarily hostile "advertising songs" and a small variety of more active movements and/or ritualized threat displays.

The advertising songs of all four forms are twittering or warbling phrases (rather like the songs of some humming-birds of the same region in tonal quality, although probably not in basic structure). The phrases of *aterrima*, *fraseri*, and *cyanea* consist of a rapid, jumbled series of notes. The phrases of the first two of these forms are always at least very similar, and sometimes quite indistinguishable (to human ears). The basic phrases of *cyanea* are also very similar to those of *aterrima*, but they are frequently preceded by one or two call notes which are usually or always lacking before the phrases of the other forms. The phrases of *lafresnayeri* are the most easy to distinguish. They are appreciably less rapid and jumbled than the phrases of the other forms.

Some aspects of the advertising songs of *fraseri*, *cyanea*, and *lafresnayeri* would seem to have been evolved as special adaptations to an environment that is dominated by *aterrima* (by far the most common of the four forms in the Quito region as a whole). It is obvious that individuals of each form can distinguish between their own form and all others; but there is reason to believe that it would be disadvantageous for them to react to individuals of the other forms of the group as if they were completely unrelated (see below). In these circumstances, it is surely not coincidental that the songs, feeding habits, and physical appearance of *fraseri*, *cyanea*, and *lafresnayeri* are correlated in such a way that any difference from *aterrima* in one respect is counterbalanced by a similarity in some other respect. *fraseri* is very different from *aterrima* in appearance and rather different in feeding habits, but has a very similar song. *cyanea* is less different from *aterrima* in

appearance and feeding habits, but has a more easily recognizable song. *lafresnayeri* is most similar to *aterrima* in appearance and feeding habits, but has the least similar song. As a result, *fraseri*, *cyanea*, and *lafresnayeri* are all approximately equally, but not very greatly, different from *aterrima* in what might be called "immediately obvious" characters.

The probable importance of *aterrima* as a "standard for comparison" in this situation is shown by the fact that there is no similar correlation between the immediately obvious characters of any other single form of the group and the corresponding characters of all its associates. This lack of correlation is most significant in the case of *fraseri*, as it overlaps and reacts with all the other forms of the group in much the same way as *aterrima* (see also below).

All or most adult birds of all four forms utter advertising songs quite frequently. As far as I could tell, obviously adult males and females of *aterrima* probably sing with approximately equal frequency, and so do adult males and females of *lafresnayeri*. Mated females of *cyanea* and *fraseri* tend to sing less frequently than their mates. When there are no intruders of their own form actually within or very near the boundaries of their territories, individuals of all four forms tend to utter many advertising songs while perched on favourite "stations" near the centres of their territories. As the territories of all these forms are usually rather small, neighbouring territory owners can hear one another very clearly (if there is no interference from other sources—see below). It is obvious that the timing of the songs uttered by any given individual is greatly affected by the timing of the songs uttered by all other individuals of the same form within ear-shot. Sometimes the sound of one bird singing seems to stimulate or release singing by other bird(s) of the same form. This releasing effect is almost always very rapid; the responding bird(s) beginning to sing within a few seconds after the first bird starts. At other times, the sound of one bird singing seems to inhibit singing by other bird(s) of the same form. As a result of these contradictory effects, the songs of neighbouring birds of the same form are usually almost synchronous or do not overlap at all.

When intruders of their own form actually invade their territories, individuals of all forms usually rush to repel the intruders. Individuals of *aterrima* usually attack such intruders immediately; but individuals of the other forms tend instead to perform hostile displays (including songs and/or closely related vocalizations), or at least display for a few seconds before attacking.

Individuals of all four forms become engaged in overt short-range disputes with other birds of their own form rather frequently. (The term "overt short-range disputes" may be used to include all encounters in which opponents come close to one another, and perform hostile displays, as well as actually attack and fight. Such disputes may be contrasted with long range "song duels".)

INTER-SPECIFIC REACTIONS

Throughout the whole of the Quito region, the territories of individuals of any one of these forms usually overlap territories of one or two of the other three forms. Sometimes they overlap completely. As far as I could tell, the boundaries of the territories of one form are seldom or never determined, or even affected, by the location or boundaries of the territories of other forms. In some areas, the territories of two or three of these forms tend to coincide exactly; but this occurs only when the boundaries of all the territories are strictly determined by the same factors of the physical environment, such as pronounced gaps in the shrubbery. Sometimes individuals of two or three forms will use the same tree or bush as a station from which to deliver their advertising songs. They may even use the same perches. In view of this overlapping, and the fact that individuals of all the forms in any given area frequently feed in exactly the same places, it is most remarkable that individuals of different forms seldom or never occur close

together. They may feed and sing in exactly the same places, but almost never simultaneously. The average distance between individuals of different forms varies with the nature of the vegetation. In some areas, birds of different forms may occur about 8 to 10 feet apart from one another rather frequently. In other areas, they usually stay at least 20 to 25 feet apart.

This sort of "micro-spatial" separation between different forms inhabiting the same area may be facilitated by a number of factors; but its immediate cause is usually nothing more than the reluctance of individuals of one form to approach individuals of other forms. The sight and/or sound of an individual of any form of this complex seems to inhibit close approach by individuals of any other form of the group normally occurring in the same area.

Although the method by which this separation is achieved may appear to be basically simple, it is not always easy for a bird to maintain the separation and still carry on other necessary activities. Any bird desiring to sing or feed at a spot already occupied by an individual of one of the other forms must remain constantly alert in order to occupy the spot as soon as it is vacated, before it is occupied by another bird of another form or re-occupied by its previous occupant. All birds must be pretty constantly aware of the location of all individuals of the other forms in their neighbourhood at any given time. In many cases, a bird must keep an eye on several individuals of other forms which may be occupying different desirable spots, and be prepared to replace any of them instantly if they move. All or most individuals of all four forms of the group in the Quito region are really engaged almost constantly in complicated social manoeuvres. This manoeuvring is seldom obvious at first glance, as the individuals involved are usually rather far apart, and two birds of different species seldom or never rush to occupy the same spot simultaneously. Overt competition for particular positions are rare because a bird seldom or never rushes to occupy a vacant spot if it sees that a bird of another form has already started for the spot or is closer to the spot and making intention movements of going there. The whole procedure works only because all the birds of all four forms are very active and restless, almost never staying in the same spot, no matter how favourable, for more than a few seconds. Any given spot is always frequently available for new occupancy.

This method of maintaining separation between individuals of different species must be highly specialized. Individuals of many or most passerine species are probably usually at least slightly attracted to individuals of most other species (Moynihan 1962). Most of them certainly do not usually deliberately refrain from approaching individuals of other species of approximately the same size. Even more significant is the fact that none of the four forms of the complex shows any definite tendency to refrain from approaching other passerine birds of other groups that are common in the same region. Individuals of this complex do, in fact, occur in close proximity to individuals of species of other groups with appreciable frequency, while feeding and performing other ordinary activities.

The individuals of *lafresnayei*, *aterrima*, and *cyanea* near Quito are somewhat exceptional, among passerines, in never showing definite signs of being positively attracted (in a non-hostile way) to individuals of any other species. They may occur in close proximity to individuals of species of other groups without hostility; but they never seem to seek such encounters, which occur only when individuals are joined or followed by individuals of other species, or when they themselves happen to meet individuals of other species while for example in pursuit of a perch or a source of food. They apparently never try to join or follow individuals of other species for purely "friendly" purposes.

It must be stressed that this type of relationship is fundamentally different from the relationship between individuals of different forms of the complex which definitely avoid one another. Individuals of *lafresnayei*, *aterrima* and *cyanea* near Quito do not avoid

individuals of species of other groups. They simply do not make special friendly attempts to approach such individuals. The two types of behaviour must be produced by different internal factors.

The very slight development, or absence, of positive gregarious tendencies in the three common forms of *Diglossa* near Quito may be correlated with their nectarivorous habits. At least, most humming-birds are equally "non-gregarious" in the same way. (The lowland honeycreepers that are frequently associated with mixed flocks are probably more frequently insectivorous and/or frugivorous than most humming-birds or the three species of *Diglossa* near Quito.)

fraseri differs from the species of *Diglossa* near Quito, and is more like most other passerines, in its reactions to some other species of other groups, tending to follow some other small birds (such as *Basileuterus nigrocristatus*) for brief periods of time in an apparently friendly manner. It will be recalled that *fraseri* seems to be less of a nectar-feeder than the other forms.

The tendency of the four forms of this complex to refrain from approaching one another may be essentially similar to some poorly understood reactions of lowland tanagers which have been called "inter-specific aversions" (Moynihan 1962).

One might have expected that the social separation between the forms of the complex would be maintained or facilitated by inter-specific hostility of a conventional type. This may be true to some slight extent (see below), but overt or obvious attack and escape reactions are very seldom the immediate cause of the separation. I saw only one overt short-range dispute between individuals of different forms of this complex during all my periods of observation. In this exceptional case, an obviously adult *aterrima* supplanted a single *cyanea* several times within a few minutes.

The almost complete absence of overt short-range disputes between these four forms is probably another highly specialized feature of their behaviour. This is quite evident in the case of *aterrima*, individuals of which are often remarkably aggressive toward all or almost all other small birds except *lafresnayei*, *cyanea*, and *fraseri*. Among the species attacked most frequently are *Basileuterus nigrocristatus*, the Andean Sparrow *Zonotrichia capensis*, and all the small to medium-sized humming-birds of the region. The variety of these species is significant. They are so diverse in appearance and behaviour as to suggest that almost anything may stimulate the attack drive of *aterrima*. This, in turn, would suggest that attacks by *aterrima* on *lafresnayei*, *cyanea*, and *fraseri* must be prevented or suppressed by some special mechanism, probably some direct inhibition, rather than "fear", since individuals of *aterrima* seldom or never retreat or escape from individuals of *lafresnayei*, *cyanea*, or *fraseri*. The inhibitory stimuli presented by the latter forms must be some aspect(s) of their appearance and/or their ordinary behaviour. They never direct special appeasement displays toward *aterrima*.

The extreme aggressiveness of *aterrima* toward most other species is another character reminiscent of humming-birds. It is generally accepted that *Diglossa* has been derived from some warbler-like or tanager-like form. There is also evidence that *Conirostrum* is closely-related to *Diglossa* phylogenetically (this will be discussed in a later paper). The general trend of evolution in this group would seem to have been in the direction of increasing reliance upon nectar as a principal source of food, with the development of special structural characters and behaviour patterns to facilitate access to as many sources of nectar as possible. The group as a whole is obviously convergent toward humming-birds. *aterrima* would seem to have progressed farther in this direction than any other species of *Diglossa* whose behaviour has been studied. In almost all the behavioural characters in which it differs from its congeners it is more humming-bird-like than they are. The series *fraseri*—*cyanea*—*lafresnayei*—*aterrima* is certainly not a real phylogenetic line, but it may well illustrate successive stages in the evolution of a humming-bird-like "habitus".

Individuals of all four forms of the complex usually or always react to the advertising songs of individuals of all other forms of the group. They may react to these songs in either one or both of the same two, contradictory, ways that they react to the songs of other individuals of their own species; but the relative frequencies of the two types of reactions are quite different in interspecific and intraspecific situations. The sound of a song by an individual of one form of the complex almost always inhibits songs by individuals of the other forms. Only very rarely does it release songs by the latter. Thus the songs of individuals of different forms are much less frequently synchronized, and much more frequently separated in time, than are the songs of different individuals of the same form.

As far as I could tell, birds of different forms do not sing in regular sequence. In any given area, the first bird to sing may belong to any of the forms present, and it may be followed by any other individuals of the same form, or any individuals of any other form(s) of the complex, in any order.

The mutual inhibition of song by the different forms of the *Diglossa-Conirostrum* complex is probably quite as specialized as their other types of mutual inhibition. All individuals of all forms of this complex usually ignore the songs of all or most species of other groups (i.e. the timing of their songs is seldom directly correlated, in any way, with the timing of the songs of the latter species). If they do respond to the songs of other species of other groups in some conspicuous manner, they are usually stimulated to sing rather than inhibited. In such cases, they usually start to sing before the other bird(s) stop (i.e. they seldom engage in "duets", alternating song phrases, with species of other groups). When they do respond in this way, they show little or no preference for any particular type of song.

The mutual inhibition of songs by the forms of the complex probably serves to maintain the effectiveness of the songs as *intra*-specific signals. If birds of two or more forms frequently sang simultaneously, there would be many chances for confusion, as the songs of one bird might tend to drown the songs of the other(s). The individuals of a bird's own species, toward which all or most of its songs were "directed" or which the songs were designed to influence, might have difficulty in hearing and/or recognizing them. Many songs might produce little effect, or unnecessary or undesirable effects on individuals of the wrong species. Confusion would be particularly likely to occur in this group simply because the songs of all the forms (even *lafresnayei*) are more or less similar.

Although the inhibition of the songs of one species by the songs of another is obviously particularly advantageous when the inhibitory effect is reciprocal, it is not difficult to see why such an inhibition might be selected for, in a single species, even in the absence of reciprocal effects. Even when they do not actually suppress the songs of other species, the songs of a bird which sings only when birds of other species are silent may still be clearer and therefore (presumably) more effective as *intra*-specific signals, at least in the short run and on the average than the songs of other birds of the same species which frequently sing at the same time as birds of other species.

If prevention of confusion is advantageous, it might be wondered why some mechanism similar to the mutual inhibition between members of the *Diglossa-Conirostrum* complex has not been evolved to prevent confusion between the songs of different individuals of the same species or between the songs of members of this complex and those of species of other groups. The obvious answer is that refraining from singing must have disadvantages as well as advantages, and the former may outweigh the latter in some situations.

The songs of all or most species of other groups in the Quito region are more or less distinctly different, in form or tone, from the songs of species of the *Diglossa-Conirostrum* complex. This, in itself, must help to reduce the frequency of confusion between such

songs, even when complete overlapping occurs. Thus the advantages which an individual of the *Diglossa-Conirostrum* complex would secure by refraining from singing during the songs of species of other groups would be relatively minor. And the disadvantages would probably be very great. If a bird refrained from singing during the songs of all other species in its environment, it might be able to sing only very rarely. In this case, its songs would still be clear and presumably very effective when actually uttered, but they might be uttered too infrequently to be very useful in the long run. This might disturb many aspects of reproductive behaviour, as songs may attract mates as well as repel rivals of the same sex.

Refraining from singing during the songs of other members of the same species might be particularly disadvantageous because songs are often used to maintain or secure territories. It may be vital for a bird to answer the songs of other members of the same species as soon as possible in order to avoid losing its own territory.

The fact that mutual inhibition of song among the members of the *Diglossa-Conirostrum* complex has been selected for, in the course of evolution, would seem to be conclusive proof that it does not reduce the frequency of songs too much and does not reduce their frequency in particularly crucial situations.

As the songs of all the forms of the *Diglossa-Conirostrum* complex near Quito are usually or always at least partly hostile, it is quite possible that they are inhibited by the same mechanism(s) that inhibit overt short-range disputes between different forms.

DISCUSSION

The most recent review of the evolutionary and functional aspects of sympatry among closely related species is by Hamilton (1962). By his criteria, the overlapping forms of the *Diglossa-Conirostrum* group are a good, if not perfect, example of "habitat co-occupancy".

Hamilton suggests that habitat co-occupancy usually develops *after* related forms have come into contact with one another. This would seem to be confirmed, indirectly, by some of the characters of the *Diglossa* and *Conirostrum* species near Quito. It has already been mentioned that a variety of characters of *lafresnayei*, *cyanea*, and *fraseri* seem to have evolved in the presence of *aterrima*. It seems very unlikely that such adaptive correlations of characters, or the peculiar behavioural interactions between all the forms of the group, could have reached their present state of refinement in a very short period of time.

It is quite possible, however, that some of the adaptations to facilitate sympatry among these forms began to evolve in somewhat different social environments, in the absence of some forms and/or the presence of additional species, perhaps in other areas. All the forms that are common in the Quito region at the present time belong to wide-spread polytypic species. Some of the other forms of the same species are very different from the Quito forms, at least in appearance. Many of these forms probably overlap one another, and/or several other closely related species, in many different regions. Unfortunately, little or nothing is known of the social or ecological relations between most of these forms. Observations of their behaviour in the wild might help to explain some of the problematical aspects of the inter-specific relations observed in the Quito region, and give some indication of the probable sequence(s) in which various adaptations to facilitate sympatry have developed. It is hoped to begin such observations in the near future.

The most specialized inter-specific reactions of the forms of the Quito region seem to be adaptations (or the indirect results of adaptations) to keep individuals of different species at least a few feet apart, at any given moment, by some method other than actual fighting or other active expressions of hostility.

Keeping apart may provide either one or both of two advantages. It may help to reduce the intensity of ecological competition between species; and/or may help to reduce the frequency of attempts to hybridize or form mixed pairs. The relative importance of these two advantages may differ in the case of different species and in different areas. The forms of the Quito region are so well segregated, now, that they provide no indication of any sort as to which, if either, of these two possible advantages might have been more important during the early stages of the evolution of sympatry in the group.

Actual fighting must have one or two disadvantages. It is likely to produce physical injuries and/or exhaustion in the combatants. It may also consume too much valuable time, to the complete exclusion of other necessary activities. A bird engaged in fighting can hardly do anything else simultaneously; but a bird that is only refraining from approaching another bird can usually feed, sing or perform a variety of maintenance activities while it watches or listens to the other bird (the combination of such activities may be difficult, as noted above, but it is obviously not impossible in many or most cases).

The time factor may also help to explain why all or most hostile displays are not used to help keep individuals of different forms apart. It is also impossible to feed or perform maintenance activities while performing displays. It is conceivable that individuals of some or all of the forms of *Diglossa* and *Conirostrum* near Quito are sometimes repelled by the advertising songs of other forms; but these songs are certainly primarily intra-specific signals. The birds must utter advertising songs even if there are no individuals of other species present. Thus, the use of advertising songs to help keep individuals of different species apart should not "waste" any more time than has to be "wasted" anyhow.

Speaking of the sympatric species of *Parus* in Europe, Hamilton (1958 : 313) suggests that "for members of this genus occupying the same habitat . . . selection has favored . . . traits of behavior which promote disregard of non-conspecific individuals". Apparent disregard of non-conspecific individuals is probably the general rule whenever closely related species occupy the same habitat; but this appearance may be deceptive. The non-conspecific individuals of *Diglossa* and *Conirostrum* in the Quito region certainly appear to disregard one another, as they seldom react positively or actively to one another; but this apparent lack of response is possible only because they actually "regard", i.e. watch and listen to, one another almost constantly.

A system of inter-specific relations such as that of the forms of the *Diglossa-Conirostrum* complex must be remarkably stable in some ways. As long as the forms continue to compete with one another, and it continues to be advantageous for individuals of different forms to keep slightly apart, there probably will be strong selection pressure against either further divergence or convergence of the forms. If any one of the forms should become very unlike the others in appearance and/or behaviour, it probably would fail to produce the correct inhibitions in the other forms, which would tend to react to it in the same ways that they react to species of other groups. Similarly, if any one of the forms should become very much more similar to one or more of the others in appearance and/or behaviour, the more similar forms would probably fail to produce the correct inhibitions in one another. They would tend to react to one another as if they were all members of the same species.

In an earlier paper (Moynihan 1960 : 535), the suggestion was made that "It will usually be advantageous for any reaction between any two species to be as definite as possible, either positive or negative—if only because a definite response of any kind will usually be more rapid than any kind of inconclusive or ambivalent reaction". This suggestion may be re-phrased in slightly different terms as a result of observations of the species of *Diglossa* and *Conirostrum* in the Quito region, and recent work on "friendly" and hostile inter-specific reactions within mixed flocks (Moynihan 1962). It will usually be advantageous for any two species which frequently come into contact

with one another, and whose feeding or other habits affect one another in any way, to react to one another as rapidly as possible. In order to ensure rapidity, all inter-specific reactions, whatever their original nature (positive, negative, or ambivalent), will usually tend to become stereotyped in form. In this respect, there is no qualitative difference between inter-specific and intra-specific reactions.

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SUMMARY

Four types of partly nectarivorous and partly insectivorous "honeycreepers", *Diglossa lafresnayei lafresnayei*, *D. carbonaria aterrima*, *D. cyanea cyanea* and *Conirostrum cinereum fraseri* are more or less common near Quito, Ecuador. They compete with one another to a very considerable extent, since their ranges are broadly overlapping, they occur in many of the same habitats, and they feed on many of the same flowers and types of insects in exactly the same places.

The relations between these birds are so distinctive and so obviously specialized that they may be considered to form a special social group or "complex". Some of the reactions between individuals of different species in this complex are quite different from both their intra-specific reactions and their reactions to other species (not belonging to the complex). This differential responsiveness is shown in three ways.

1. Individuals of different species of this complex never (or almost never) come close together, due to the fact that they deliberately refrain from approaching one another. They also keep apart from other individuals of their own species (except members of the same family group), but they do this by defending territories against such individuals, not merely by refraining from approaching them. They do not refrain from approaching individuals of any other species.

2. Individuals of different species of this complex never (or almost never) become openly aggressive toward one another; but they do show such hostility toward most other individuals of their own species and (usually to a lesser extent) individuals of all other species.

3. Individuals of different species of this complex usually refrain from singing simultaneously. They do not show the same degree of restraint when other individuals of their own species are singing, and they usually ignore the songs of other species.

All the distinctive features of the behaviour of the different species of this complex toward one another seem to be adaptations (or the results of adaptations) to permit them to live in the same areas and habitats, during the same general periods of time, and still remain segregated from one another at any given moment. There is reason to believe that this type of segregation may be more advantageous than inter-specific fighting.

It seems likely that the members of this complex have been in contact with one another for a long time. Some of the morphological and behavioural characters of *lafresnayei*, *cyanea*, and *fraseri* seem to be adaptations to the presence of *aterrima*. Theoretical considerations would suggest that there will be strong selection pressure against both further divergence and convergence of these forms as long as it continues to be advantageous for them to maintain the same inter-specific relations with one another.

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