

MIXED SPECIES FLOCKS IN PATAGONIAN FORESTS, WITH REMARKS ON INTERSPECIES FLOCK FORMATION

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Mixed species flocks of birds have received renewed attention in recent years. Short (1961) emphasized rightly that two different questions have been asked about mixed flocks. He suggested that "gregariousness or individuals' motivation to associate" provided the answer to the "how" of flocking, and that advantages such as increased foraging efficiency, protection from predators, and "mutual aid in finding food" are the answers to the "why" of flocking. Moynihan (1962) discussed these points in greater detail and also gave a model for the origin and probable evolution of mixed flocks of passerine birds. This model stressed that the first step in flock formation should be the development of "specialized social bonds between a species that shows a high degree of intraspecific gregariousness and one or a few other species that do not show a high degree of intraspecific gregariousness."

In order to test the validity of this model, and to analyze the actual course of flock formation, one would need to study mixed flocks in early stages of evolution, in which there were few and preferably unrelated species, only one of which would exhibit marked intraspecific gregariousness. In other words, one should examine a "simple" mixed flock and explain why the component species had an initial tendency to flock before selection acted to reinforce the flock. It appears that neither the flocks observed by Short (1961) nor those studied by Moynihan (1962) possess these characteristics.

Mixed flocks that seemed to fit the description of the postulated first stage of flock formation were seen in the *Nothofagus* forests of southern Argentina and southern Chile from 6 February to 4 March 1965, and from 25 March to 3 April 1965. The flocks were composed of two ovenbirds, including *Aphrastura spinicauda*, a small bird, and the larger *Pygarrhichas albogularis*, in addition to a small woodpecker, *Dendrocopos lignarius*, and a medium-sized tyrant flycatcher, *Xolmis pyrope*. Table 1 gives an indication of the relative frequency and abundance of these four species.

DESCRIPTION OF THE BEECH FORESTS

The following four major types of beech forests were visited:

1. Wet lowland forest composed of tall evergreen *Nothofagus dombeyi* and conifers (*Saxegothea*, *Fitzroya*, *Pilgerodendron*), with a dense undergrowth of bamboos (*Chusquea*) and evergreen shrubs (Puerto Blest and Laguna Frías in Parque Nacional Nahuel Huapi, Río Negro, Argentina; Peulla and Ensenada, Llanquihue, Chile).

2. Mesophytic *Nothofagus dombeyi* forest from lowlands up to about 1200 meters, lacking the conifers and the majority of evergreen shrubs found in wet forest, but having usually a dense bamboo undergrowth (several localities in Parque Nacional Nahuel Huapi, Argentina, especially Cerros Otto, Goye, and Carbón).

3. Mesophytic *Nothofagus pumilio*-*Araucaria araucana* forest with bamboo undergrowth, at altitudes from 1300 to about 1600 meters (Volcán Llaima, Cautín, and Lonquimay, Malleco, Chile).

4. Montane forest of deciduous *Nothofagus pumilio* from about 1200 meters up to timberline at 1600–1800 meters, lacking bamboos and becoming quite stunted at

the higher elevations (several localities in Parque Nacional Nahuel Huapi, Argentina, especially Cerros Lopez, Catedral, and Vilchadero, and Termas de Chillán, Nuble, Chile).

It is important to realize that there is no sharp boundary between one type of forest and the next; floristically and physiognomically the transitions are gradual and usually correspond to climatic gradients. It is, therefore, not surprising to find that the avifauna inhabiting the Patagonian beech forests is so uniform in composition and varies but little from one forest type to another.

DESCRIPTION OF THE FLOCKS

As mentioned above, four species of birds were found in mixed flocks in Patagonian beech forests. Two of them (*Aphrastura spinicauda* and *Pygarrhichas albogularis*) can be considered true forest species. *A. spinicauda* occurs in every type of forest, but *P. albogularis* favors tall forest, regardless of how dense or open, and avoids stunted forest. The third species, *Dendrocopos lignarius*, prefers open types of forest or the edge of dense forest, but can also be seen in the interior of tall, wet forest. Finally, the fourth species, *Xolmis pyrope*, is a forest-edge species entering the forest only rarely or occasionally; I saw it inside the forest on three days, but in edge situations on eight days.

The small, rather plain-colored *Aphrastura spinicauda* is an arboreal species occupying two foraging niches, being a foliage as well as a trunk gleaner. *A. spinicauda* is very social and is usually encountered in small flocks of four to seven individuals, although flocks of 12 to 15 birds or more are not rare. During my stay in southern South America, which was at the end of the breeding season of the forest species, I saw an isolated individual of *A. spinicauda* only once. These intraspecific flocks are a characteristic feature of the bird life of the *Nothofagus* forests, usually from the lowlands to about 1300 meters, but also up to timberline as high as 1800 meters.

The birds in a flock move about incessantly and rapidly in search of food, which according to Goodall, Johnson, and Philippi (1957:253) consists only of insects. With quick and nervous motions they either cling acrobatically to twigs in the manner of titmice (*Parus*), or climb tree trunks exactly like treecreepers (*Certhia*).

Every flock moves through the forest as a tight unit, within which the single birds usually have individual distances of between 1.5 and 2 meters. "Contact" between birds is kept by constant calling. Four kinds of vocalizations were noted, but I could not devote enough time to make a study of the behavioral context of each. The vocalizations can be summarized as follows: (1) simple "contact" call, (2) low intensity and (3) high intensity threat displays, and (4) a "chorus call," which may correspond to Moynihan's (1955) infectious "exemplary" displays.

If we now summarize the various characters of *A. spinicauda* that are relevant to flocking, we find that this species is endowed with some attributes considered by Moynihan (1960) to be among the most significant for interspecies flocking. It is a restless, very vocal species, performing hostile-type displays (perhaps mostly vocal). Finally, this species is drab-colored, although it does have a wing pattern that could be thought of as flash pattern (especially since a bird flicks open its wings in and out while climbing a tree).

All these characters would, therefore, make *A. spinicauda* highly suited as a nuclear species in mixed flocks. I was consequently very much interested to discover that about 60 per cent of the flocks of *A. spinicauda* in the forests of southern

TABLE 1
RELATIVE FREQUENCY AND ABUNDANCE OF THE FOUR SPECIES OF BIRDS OBSERVED IN MIXED FLOCKS
IN PATAGONIAN *Nothofagus* FORESTS

Species	Frequency ^a	Abundance ^b
<i>Aphrastura spinicauda</i>	25 (89%)	5-8
<i>Pygarrhichas albogularis</i>	18 (64%)	0.7-2
<i>Dendrocopos ligniarius</i>	5 (18%)	0
<i>Xolmis pyrope</i>	3 (11%)	0

^a Number of days on which the species was observed. Total = 28.

^b Number of individuals met along 1-km line transects through two forest tracts in the Nahuel Huapi National Park.

Argentina and southern Chile are in fact accompanied by another furnariid, *Pygarrhichas albogularis*, and that about 8 per cent of the flocks also have, in addition to *P. albogularis*, a small species of woodpecker, *Dendrocopos ligniarius*. In one instance, a flock containing the above three species was joined for a short while by a fourth species, the tyrannid *Xolmis pyrope*. The association between *A. spinicauda* and *P. albogularis* was noticed earlier by Krieg (1951:146).

Let us now examine the three species that associate in flocks with *A. spinicauda*. The furnariid *P. albogularis* behaves in many ways exactly like a nuthatch (*Sitta*), an observation already made by Goodall, Johnson, and Philippi (1957:266). It is a larger bird than *A. spinicauda*, with a more conspicuously patterned plumage. Usually *P. albogularis* is present in *A. spinicauda* flocks only as a single individual, but I have seen up to four birds in a flock. *P. albogularis* has two kinds of vocalizations, a high-pitched call sounding quite similar to vocalization (1) mentioned for *A. spinicauda*, and a loud, bisyllabic and often repeated *tikup*. Because *P. albogularis* is less abundant and more difficult to observe than *A. spinicauda*, I was not able to detect in what behavioral context these calls were uttered. Hostile behavior is very inconspicuous in *P. albogularis*. Only once did I see two birds actually engaged in a chase; the performance was remarkably quiet, no calls were emitted, and the birds resumed their foraging activity immediately after the chase; I did not notice any posturing.

The woodpecker *Dendrocopos ligniarius* resembles the small European *D. minor* in foraging behavior and in voice. The only calls I ever heard were (apparently) emitted by both male and female, and could be described as a trill. In two out of five days on which *D. ligniarius* was observed, one and two individuals, respectively, were seen to follow a flock of *A. spinicauda* and *P. albogularis*.

The last species seen in company of *A. spinicauda* is *Xolmis pyrope*, a common forest-edge tyrannid of southern South America. I saw *X. pyrope* follow a flock only once, when two or three birds were in the wake of a flock moving along a clearing, and containing about 10 *A. spinicauda*, one or two *P. albogularis*, and one ♂ *Dendrocopos ligniarius*.

None of these three species (*P. albogularis*, *D. ligniarius*, and *X. pyrope*) occurs in intraspecific flocks, although loose groups (possibly families?) of four to five *X. pyrope* were seen on occasion, after the breeding season. None of these species was ever seen showing any "interest" in *A. spinicauda* when individuals of this species were nearby, nor was any *A. spinicauda* ever observed making any social contact with any of the three species. For example, I never saw the supplanting attacks frequently noted by Moynihan (1962).

DISCUSSION

If we use Moynihan's (1962) classification to describe the social role of the above species, it is obvious that *A. spinicauda* is a passive nuclear species, and that *P. albogularis*, *D. ligniarius*, and *X. pyrope* are attendant species. Further, *P. albogularis* is a regular member of the flocks, while *D. ligniarius* and *X. pyrope* are probably only occasional members.

Ecologically, the various species of the flocks occupy complementary foraging niches, although the niches present a great deal of spatial overlap. For example, three of the four species seen in the flocks forage on tree trunks and consume insects. However, the large differences in bill size and bill shape and in foraging methods would not only insure the minimum amount of competition but actually would allow a maximum efficiency in exploiting the food source provided by all the different kinds of insects living on tree trunks. This point raises the question of whether the selective advantages of feeding in mixed flocks are of importance for the formation of the flocks. In the case of the *Nothofagus* forest flocks, it is probably significant that the regular attendant species (*P. albogularis*) occurs mostly in mixed flocks. I saw *P. albogularis* associated with *A. spinicauda* on 15 out of 18 days of observation of the species (83 per cent). It seems, therefore, probable that *P. albogularis* actively seeks the company of *A. spinicauda*. But this still does not decisively answer the question asked above. In other words, the feeding association is obviously advantageous now to both species, but the flock formation might not necessarily owe its origin to selection pressures provided by more efficient exploitation of a food source.

Of greater significance, however, is the fact that the nucleus species (*A. spinicauda*) occurs almost as frequently in monospecific flocks (10 days out of 25, or 40 per cent) as in mixed flocks (15 days out of 25, or 60 per cent). The difference could well be a result of insufficient sampling (sample size is 25 days), so that the true frequency would probably be nearer 50 per cent. Intraspecific flocking tendencies of *A. spinicauda* are probably a result of selection for better exploitation of a source of food. In turn, these flocking tendencies, combined with a lack of aggressiveness toward other species, resulted in attracting the second species, *P. albogularis*. The observations (1) that *A. spinicauda* is found as frequently in monospecific as in mixed flocks, (2) that *A. spinicauda* gives indications of being socially indifferent to other species, and (3) that *P. albogularis* occurs most of the time in mixed flocks suggest that the initial mechanism of interspecies flocking is, as Moynihan (1962) supposed, a one-way social bond between two species. In the *A. spinicauda*-*P. albogularis* flock, the apparent "social indifference" between the two species will probably turn out to be, upon careful analysis, an already complex set of behavioral interactions where all, or most, hostile interspecific expressions have been diverted by natural selection into other behavioral channels. In the long run, this initial flocking was maintained and reinforced because of selective advantages awarded to both species through better food exploitation.

CONCLUSIONS

Whether or not an interspecies flock will form after the encounter of two species will depend not only on the high degree of gregariousness of one of the species but also on the presence of a minimum set of behavioral prerequisites possessed by the second species. In a way, one is dealing here with a behavioral preadaptation.

Each species could be considered as a "behavioral structure" that evolved primarily independently of the other, *i.e.*, in response to different sets of selection pressures. If the two structures meet, their harmonious fusion into essentially one behavioral complex (mixed flock) will occur only if a threshold is reached at the time when a selection force acts to make the complex a balanced functional unit. In this model, selection forces both before and after the threshold are mostly ecological. Once two species have formed a mixed flock, whatever behavioral and morphological changes may take place during the subsequent evolution of the flock will be primarily in response to selection pressures relevant to the flock as such.

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