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SOCIAL BEHAVIOR OF THE VINOUS-THROATED PARROTBILL DURING THE NON-BREEDING SEASON

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Lucia Liu Severinghaus (1987) Social behavior of the vinous-throated parrotbill during the non-breeding season. *Bull. Inst. Zool., Academia Sinica* 26(3): 231-244. During the non-breeding season, vinous-throated parrotbills form large flocks, which are active from dawn to dusk with only brief rests during the day. Foraging occupies most of the daylight hours. Their level of activity remains stable throughout the day, even during light to medium rain. Individuals which forage together during the day usually roost together at night. Neighboring flocks may share the same roost.

Flock sizes are small just after the breeding season. They increase through November and then remain stable during winter months. Flock sizes decrease starting with the onset of the breeding season in March.

Very little aggression was seen within a flock, and none between flocks. No wintering territory is maintained and no territorial behavior was ever witnessed by flocks, pairs, or individuals. There is no apparent leader within a flock and no detectable social hierarchy among the individuals of the flock. Every month of the year some individuals of a flock change to neighboring flocks. This flock-changing phenomenon most likely influences flock social structure.

Social behavior has been a major focus in ornithological research in recent years. All species in the genus *Paradoxornis* are highly gregarious as far as is known, yet no studies of their social behavior have been previously carried out. This study examines closely the social behavior of the vinousthroated parrotbill (*P. webbianus*) which is common and widely distributed in Taiwan. This report covers the non-breeding season as a first step toward understanding the nature and the reasons of their sociality.

METHODS

This research began in July 1983 and con-

tinues to the present. My field assistants and I have spent 10-15 days each month making field observations on vinous-throated parrotbill flocks. About 175 parrotbills inhabited the acasia woods and adjacent grassy and sugarcane fields of Tunghai University in central Taiwan. Periodic netting kept 85-95% of the population color-marked for individual identification in this study area of about 35 ha.

Vinous-throated parrotbills are small active birds living in dense vegetation, which makes continuous observation of any individual for more than a few seconds impossible. However, bird flocks usually are slow moving and can be followed on foot. The longest

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stretch of time we were able to follow and observe a flock was 313 min, and the shortest was a few minutes.

This is the first detailed study of this species. We therefore paid attention to all aspects of its behavior. We observed flock movements and recorded flock size as well as flock membership. We also recorded the date and location of an individual's fledging, its affiliation with any flock, and all its aggressive encounters with other individuals.

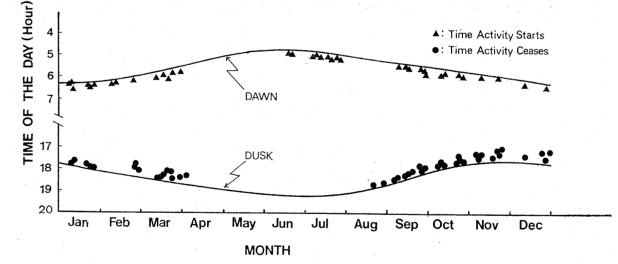
For interflock encounters, we recorded their duration, movement of the flocks subsequent to the encounters, and individual interactions during them. We determined flock sizes several times a day when the birds flew across gaps in the vegetation. In this study, non-breeding season refers to the period from September through March the following year.

RESULTS

1. Daily activity pattern

Vinous-throated parrotbills started their activities about 20 min after day break and continued throughout the day until about 40 min before dark (Fig. 1). The slight variations in this pattern reflect the reaction of the birds to the weather conditions of each specific day.

Vinous-throated parrotbills foraged almost continuously during the day, except for some short resting, bathing, or preening bouts. Even when it was raining or strong winds were blowing, they were still active in sheltered places. Their activities during heavy rain are unknown, because heavy rain made it impossible to observe birds through binoculars.



Vinous-throated parrotbills maintained a

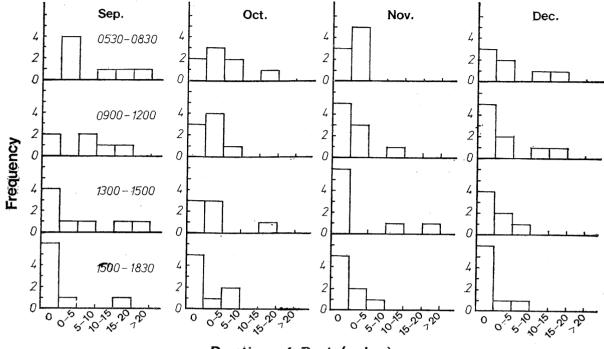
Fig. 1. Daily activity pattern of vinous-throated parrotbills during the non-breeding season.

Time	September	October	November	December
0530-0830	9.87*	4.75	1.21	5.99
0900-1200	7.30	2.77	2.37	3.14
1300-1500	8.40	3.24	4.80	1.89
1500-1830	2.74	2.59	1.19	1.43

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The	daily	resting	pattern	of	vinous-throated	parrotbills

a: Number is mean length (min) of rest per hour of observation. All the standard deviations are large. Values are often larger than the means.

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Duration of Rest (min.)

Fig. 2. The distribution of rest durations in the four time periods of the day. Data from each month are treated separately. The four time periods are divided the same way as noted for September. The height of each bar represents the frequency the specified length of rest occurred in that month.

stable level of activities throughout the day. Their activity levels were not higher in the early morning and late afternoon and lower in the middle of the day like many other passerines. They took short rests throughout the day, normally less than 20 min each time. There was very little difference in the mean amount of rest time during the day except in the late afternoon period when parrotbills rested less (Table 1). The distribution of rest durations showed the same pattern (Fig. 2). In fact vinous-throated parrotbills more frequently rested longer during the early morning hours than the rest of the day (Table 1).

2. Description of flock behavior, and leadership

Very little information exists in the literature concerning flock behavior of any of the parrotbills. Therefore, a general description of flock behavior of the vinous-throated parrotbill is given here, particularly those aspects that could not be easily quantified.

Parrotbills were rarely seen singly during the non-breeding season. We saw single birds less than five times in more than 420 field person-days during the non-breeding season. The single birds we observed flew around uttering a contact call until they joined a flock. Flocks responded to single birds with contact calls and were not seen to refuse any individual.

There was no apparent leader in a flock. Frequently birds in the middle or end of a moving flock assumed the lead when those up front stopped to feed, causing a shift in the sequence of individuals within the group. Also individual birds often doubled back and joined the birds behind. Individuals occasionally lingered in a spot until the entire flock had moved away before "rushing" to catch up with the flock. Sometimes, one or two birds of a flock moved to an area nearby to forage independently of the main flock,

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and then rejoined the flock later. It was very difficult to see whether one specific bird was the leader of the flock in its activities during a day. On some days it seemed obvious the flock followed the movement of a certain individual, but the next day or so the flock appeared to follow a different individual. Some individuals were seen to utter contact calls repeatedly from a short distance away but failed to attract the flock to it. These birds always returned to the flock subsequently.

Birds in a flock rarely flew long distances. When they moved forward in dense vegetation, they hopped rhythmically along a broad front, each bird landing on the branch just ahead of it or on the perch that the bird in front had just vacated. Occasionally one bird would move faster than the one ahead. causing a hurried departure of the latter. The distance between individuals was often the distance between perches, from 20 to 50 cm. Before they traversed a gap in vegetation larger then 5 m, the individuals in front of the flock tended to call and to wait until the ones behind had caught up. Then the whole flock quickly moved across together in a tight group. Usually the larger the gap the tighter the flock.

3. Roosting

Most parrotbill flocks roosted in specific areas at night. Normally a flock started moving towards its roosting site in the latter half of the afternoon. On a few occasions, a flock foraged until it was almost dark. Then its members noisily gathered on a high branch and flew in a tight flock at canopy level directly toward their roosting site, rarely stopping on route. Upon nearing their roosting site, they slowed down, moved to the lower vegetation level, and hopped slowly in the undergrowth toward their roost.

Roost sites were always fairly dense tangles of twigs, branches, vines, or clumps of miscanthus. Members of a flock separated into small clusters of individuals and spread out into suitable locations to spend the night. The size of the roosts differed, some as large as $5\times25 \text{ m}^2$, some only $1\times10 \text{ m}^2$. Each bird, or two to three birds sitting side by side, chose a spot just below a cluster of leaves. The distances between the heads of the birds and the leaves above were 3-5 cm in the two observable cases.

At dawn vinous-throated parrotbills began uttering contact calls and some individuals began flying around. Usually the whole flock left the roost together, but sometimes the flock split into two unequal subflocks and left in different directions. These subflocks usually rejoined each other later in the morning, but sometimes remained separate through the day.

4. Interflock relations

Flocks in the non-breeding season occupied large home ranges and home ranges overlapped (Fig. 3). No interflock aggression was seen in 3 years (Table 2). Sometimes two flocks foraged near each other without joining. At other times, the same two flocks joined and foraged together for a period of time (Table 3). As they approached each other, there was often great excitement and loud contact calling. The longest distance recorded that one flock flew to join another upon hearing the latter's vocalizations was more than 100 m. A large portion of that distance was open space. Characteristically, several individuals from one flock flew toward and met individuals of the other flock in advance of the main group of birds. When the two flocks merged a period of loud chorusing occurred. Two flocks might stay together as long as 135 min, feeding and calling, before eventually separating into two again. When two flocks moved apart, individual birds flew back and forth over the expanding distance and called loudly until the separation was finally complete. Then the flocks went their own ways.

The frequency of interflock encounters

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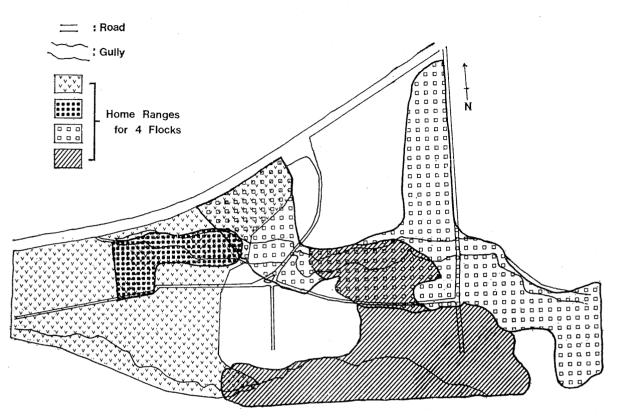


Fig. 3. The home ranges of four vinous-throated parrotbill flocks on Tunghai University campus. There is large overlap in area for all the adjacent flocks.

observed decreased in 1984-85 and 1985-86 as a result of habitat destruction. In 1983-84, all the home ranges overlapped (Fig. 3). By July 1986, two of the flocks were isolated while the overlapping areas of the other flocks also decreased. Several locations where two flocks used to roost together were also destroyed, and the frequency they were found

TABLE	2
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Vinous-throated parrotbill interflock encounters during the non-breeding season

Year	Flock	Encounters (n)	Times Roosting Together	Aggression $(n)^*$
83-84	A and B	8	1	0
	A and D	1	0	0
	C and D	11	5	0
	D and E	1	0	0
84-85	A and B	6	1	0
	C and D	1	1	0
85-86	A and B	1	0	0
	A and D_1	1	0	0
	C and D_2	1	0	0
	D_1 and D_2	2	2	0

a: This refers to any aggression seen between members of two flocks during the time the two flocks were together.

		Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
1.	Frequency observed:				•			
	Sept. 83-March 84	0	3	4	2	8	2	2
	Sept. 84-March 85	0	2	2	0	0	2	1
	Sept. 85-March 86	0	2	0	1	2	0	0
2.	X duration/Encounte	r (min):						
	Sept. 83-March 84	0	25.3	39.5	10	63.5	16.5	8
	Sept. 84-March 85	0	5.5	15	0	0	19.5	9
	Sept. 85-March 86	0	8	0	60	7	0	0
3.	Times flocks roosting	together:				•		
	Sept. 83-March 84		0	1 .	1	3	0	1
	Sept. 84-March 85	0	0	1	0	0	1	0
	Sept. 85-March 86	0	1	0	1	0	0	0

			TABLE 3		
Interflock	encounters	for	vinous-throated	parrotbills	during
	the	nor	h-breeding season	L	

roosting together also decreased (Table 3).

5. Flock size

Flock size changed with season (Fig. 4). At the end of the breeding season, flocks typically consisted of 1-2 adults with 1-4 fledged young which they were still feeding. Flock size gradually increased as family groups came together with the passage of time. In 1983, flock sizes stablized around 40 birds per flock by November. The pattern was the same in 1984 and 1985, except flock sizes were smaller and averaged 35 and 30 birds respectively. These flocks remained together through February and then gradually decreased in size as they broke up in pairs with the onset of the breeding season.

6. Flock membership

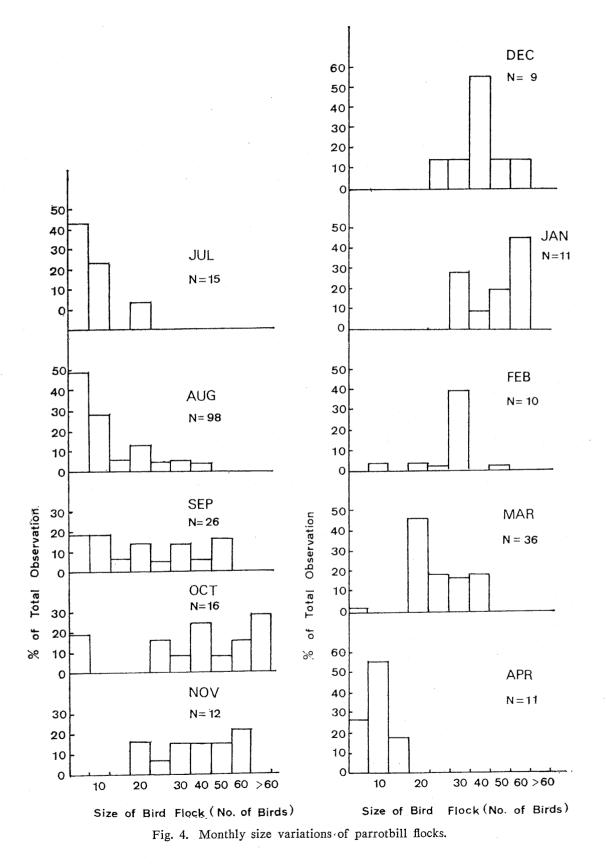
The membership of each flock was labile during late summer, when different family groups combined and remained together for a day or less. Flock size and membership stablized in November. Birds that appeared in one flock tended to appear together repeatedly.

In 1983-84 only three young shifted to neighboring flocks. The others (96.4% of total) remained with the parental flocks and four of them (14.3%) bred there (Table 4). In 1984-85 71% of the young remained with the parental flock and in 1985-86 66% remained. Seventy percent of the surviving 1983 birds, and 76.9% of the surviving 1984 birds were still breeding in their parental flocks in July 1986. Among the young that moved away, some also bred when they were one year old. Thus whether or not a young bird left its parental flock did not seem to influence its chances of breeding.

7. Flock changing phenomenon

We determined flock membership by identifying the colored band combinations observed on each field trip. It was easy to determine the size of each flock, but it was impossible to identify every banded bird in a flock each time. Consequently the number of birds identified in each flock varied from month to month. We could only be certain of the status of the birds we identified. Those not seen might also be in the flock. Therefore, flock composition was viewed on a long term basis. Individuals not seen for two months or more were considered dead. All living ones were considered to be with their original flock unless seen otherwise.

Some birds changed flocks every month



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	1983	1984	1985
Size of cohort	28	31	47
By July 1985:			
% stayed in parental flock	96.4	71	
% bred by Aug. 1985	14.3	25.8	
% bred in parental flock	14.3	12.9	
Alive in August 1985	10	26	47
1985 survivors by Oct. 1986:			
% stayed in parental flock	70	76.9	66
% alive by Oct. 1986	40	30.8	29.8
% bred by Oct. 1986	10	15.4	4.3
% original cohort surviving	14.3	25.8	29.8

TABLE 4 Fate and dispersal of young

during the non-breeding season. There was no apparent pattern in the rate of change over in 1983–1984, but from 1984 to 1986 the change was more frequent just after the breeding season than during the winter and spring periods (Fig. 5). Flock change was not expected at the beginning of the study. Therefore, data on flock change for the first few months were treated as errors in observation; thus the change-over rates for the fall and winter of 1983 were no doubt too low. The number of birds changing flocks per month never exceeded 15% of the total population in 1983-84. It was high in the fall of 1984 and spring of 1985 while low in the intervening winter. It was very high

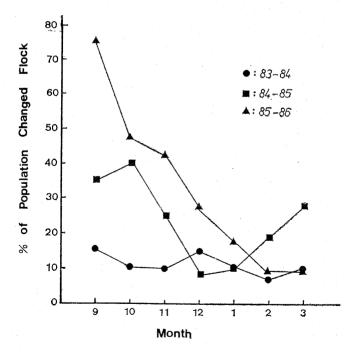


Fig. 5. Proportion of the color marked birds identified per month that changed flocks during the non-breeding season. Number of birds identified each month differed.

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		Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Total
1.	Frequency:								
	1983-84	16	11	9	14	11	7	11	79
	1984-85	40	42	24	8	10	21	31	176
	1985-86	70	53	49	21	19	. 9	9	230
2.	% of Popula	ation Change	d:						
	1983-84	15	10	9	14	11	7	9	45
	1984-85	35	40	24	8	10	18	28	47
	1985-86	76	48	43	28	18	9	9	48
3.	Total Numb	er of Birds	Changed Fl	ocks:					
	1983-84		70 birds				· .		
	1984-85		87 birds						
	1985-86		109 birds						

IABLE D							
Frequency	of	vinous-throated	parrotbill	flock	change	in	the
Tunghai population [*]							

a: Only banded birds are included in this analysis. Total frequency of flock change is higher than total number of birds changed flocks because some individuals changed more than once. Population refers to color marked birds identified each month.

again in the fall of 1985 and decrease through the subsequent winter and spring (Table 5).

Flock changes probably took place after the encounter of two flocks or after roosting together. I witnessed one marked bird moving along with one flock as the flock was separating from another. The bird then seemed to "realize" it was with the "wrong" flock, and flew directly to rejoin its original flock still audible in the distance. Apparently some individuals remained with the new flock. Birds that follow the "wrong" flock may realize so late that their own flocks are no longer in the vicinity. Or, when several birds change at the same time they are more likely to remain with the new flock.

During the non-breeding season, 70 birds changed flocks 78 times in 1983-84, 87 birds changed 176 times in 1984-85, and 109 birds changed 230 times in 1985-1986 (Table 5). Some individuals changed back to their original flock at a later date. The number of individuals changing flocks was 45%, 47%, and 48% of the total population each year for the three consecutive years respectively (Table 5). The increase in the three years was not satistically significant ($\chi^2=0.37$, df=2).

TABLE 6						
The number of times individua	al birds					
changed flocks from August						
1984 to March 1986						

Adu	lts	Ýou	Young			
Freq. of Change	No. of Birds	Freq. of Change	No. of Birds			
1984-1985:						
1	38	1	4			
2	29	2	6			
3	15	3	5			
4	10	- 4	5			
5	3	5	1			
6	3	6	2			
9	1	:				
Total	99	Total	23			
1985-1986:						
. 1	51	1	15			
2	23	2	1			
3	9	3	2			
4	8	4	<u> </u>			
5	1	6	1			
7	2					
Tota1	94	Total	19			

TABLE 7		
Sexual differences i	in	flock
changing freque	nc	v

	Males	Females	Total
No. of birds known	12	5	17
No. of changes made	29	18	47

Chi square=0.428 df=1 n.s.

Flock changing apparently is not related to juvenal dispersal, sexual differences, or aggression. In both 1984–85 and 1985–86, some adults and juvenals changed flocks while some did not. The highest number of flock changes an adult made per year was nine times, while that of a juvenal was six (Table 6). The frequency that males and females changed flocks did not differ significantly either (Table 7).

The events before and after a flock change were analyzed to explore whether aggression could be the cause or the result of flock change. Aggression occurrd in three varieties; fighting, chasing through the bushes, and supplanting. All three types of interactions were rare. with chasing slightly more frequent than the other two. The occurrence of both fighting and supplanting was unrelated to flock change. Only an insignificant number of chasings was prefaced by or followed by flock change. In 1984-85 only 2.27% of the total flock changes occurred after known chasing, and 4.55% occurred before chasing. Only 7.58% of all the chases were followed by flock change, and only 15.2% of all the chases took place before flock change.

Individuals which changed flocks were not limited to a certain age group. In September 1984, for example, there were a total of 40 changes. Among these, 15 were made by juvenals less than 1 month old, 4 by adults at least 13 months old, 2 by those 14 months old, 4 by those 18 months old, 7 by those 19 months old, 4 by those 2 years old and 4 by those 25 months old.

DISCUSSION

Body size vs activity pattern

Vinous-throated parrotbills are omnivor-

ous and have an abundant food supply in my study area (Severinghaus, unpublished data). Yet this study found them foraging almost continuously with very short rests interspersed throughout the day, as if they had to use all the available time feeding in order to meet their energy demands. Yangtze parrotbill (P. heudei) appear to focus an unusual amount of attention on foraging also (Lynes 1914). The food items of vinousthroated parrotbills are mainly seeds, flowers, fruits, and insects. The mean weight of 73 vinous-throated parrotbills was 10.9+1.5 gm. However, their small body size seems to provide only partial explanation for their high energy demand. The formula given by Calder (% of time feeding= $M^{-0.25}$, 1974) predicts birds as small as vinous-throated parrotbills need to spend approximately 55% of their time feeding. Vinous-throated parrotbills spent about 85% of their awaking time on activities related to foraging. Further research is necessary to understand their energy requirements.

Vinous-throated parrotbills are known to be difficult to keep in captivity. Pet stores report that they die more easily than other species of wild caught passerines. Perhaps there are special diseases that infect them more than other species, or perhaps there are tiems essential to their diet which are not easily available in ordinary pet store food items. Or perhaps these items can only be obtained through wide-ranging foraging activities.

Behavioral characteristics

Vinous-throated parrotbills have an unique combination of social characteristics. They maintain strongly social and fairly stable flocks during the non-breeding season, but defend no group feeding territories. They occupy large and overlapping home ranges, but there is very little inter- and intra-flock aggression. Even during the breeding season they maintain no territories (Severinghaus in preparation). Although the highly unaggressive white-fronted bee-eater (*Merops bullockoides*) does not maintain territories either, this species breeds colonially (Emlen 1984), while parrotbills breed in scattered pairs.

Many species of animals maintain territories. Species which live in rich habitats with superabundant resources or in poor habitats may not defend resource for exclusive use (Carpenter and MacMillen 1976). When the distribution of resources is unpredictable in time and in space, there is usually no territoriality (Crook 1965). Therefore animals utilizing patchily distributed resources tend to remain in groups. Ephemeral resources cannot be defended easily. The spotted hyena which uses ephemeral resources roams in large areas without defending any territory (Kruuk 1972). Wagtails utilizing patchily distributed resources also do not defend territories while those using more evenly distributed resources did (Davies 1976).

Vinous-throated parrotbills inhabit a wide variety of habitat but prefer early successional stages. Such habitat is usually rich in food. Plant food resources are predictable in location and in seasonality. When a plant species is flowering or seeding, usually such large quantities of the food are available that aggression would only take time away from feeding. The distribution of animal food items is probably unpredictable both in space and in time, and cannot be easily defended.

Thus it seems clear that territoriality is not necessary or always beneficial for the vinous-throated parrotbills. But the factors causing parrotbills to form flocks are complex, and are not simply a result of the distribution and quantity of food resources. Several species whose niches overlap with vinousthroated parrotbills are territorial, e.g. tawny wren-warbler (*Prinia subflava*) and yellow bellied wren-warbler (*P. flaviventris*). Further studies are necessary to learn the causes of the flocking behavior of the parrotbills.

Flock changing

It is unknown why young parrotbills change flocks. In many other species, juvenals disperse to other areas and leave parental territory. In other species, juvenals of one sex disperse. In the case of vinous-throated parrotbills, there is no definite dispersal pattern. Juvenals of both sexes may leave or stay to breed in parental flock. Even when they change to another flock, it is usually to the one adjacent to the parental flock. Sometimes the young birds then later change back to the parental flock. There is no ready explanation why adults change flocks, either. Perhaps they "make a mistake" when two flocks encounter.

Interestingly, flocks maintain relatively stable sizes given the high frequency of flock changes. The size of a flock is probably directly related to the condition of the habitat which it frequents, but the mechanism regulating the size of the flock needs further study. In Hsi-tou, Nan-tou County, vinousthroated parrotbill flocks often have 70 individuals (Chang Wan-fu, pers. comm.); in Fu-hsing Hsiang, Chang-hua County, flock size is around 50, slightly higher than my study population (pers. observ.); in Yang-ming-shan, Taipei County, flock size is only about 20 individuals (pers. observ.). Perhaps individual parrotbills have a way of sensing the size of the flock and avoid joining a flock with more individuals than the home range habitat can support.

Frequent flock changing necessarily puts limitations on the social structure of a flock. Given frequent membership change, it would be difficult to maintain a definite social hierarchy within a flock and for individuals to maintain stable leadership. Thus, a flock of parrotbills can be described as a community of individuals with a certain amount of family relationship, but it does not have linear or other types of social organization.

Inbreeding is a threat for populations whose young remain in or near the parental flock. Inter-flock encounters and changing of flocks could be mechinisms that have evolved to help decrease the potential danger of inbreeding. If the habitat is extensive and numerous flocks are free to encounter each other, gene flow should be substantial. Around Tunghai University campus, however, flocks are becoming fewer and more isolated. Therefore, even when individuals change flocks they are still in the vicinity of their original flocks. On Tunghai University campus, I have found 3 parrotbills with abnormal white tail feathers which could be a kind of albinism, and reflect a certain degree of inbreeding.

Similarity with other species

Babblers may be parrotbills' closest relatives, although there is disagreement on the classification of parrotbills. There are scientific publications on 12 species of babblers. Among these, winter flocking is the rule (Gaston 1977, Johnsingh *et al.* 1982, Zahavi 1974). Among the 16 species of babblers found in Taiwan, at least 11 of them form flocks in the non-breeding season (personal observations). All the babblers discussed in the available literature defend group territories during the non-breeding season (Gaston *op cit*, Johnsingh *et al. op cit*,). Parrotbills differ from them in this regard.

The birds most similar to vinous-throated parrotbills in general behavior are the bushtits (Psaltriparus minimus). Early descriptions of Grinnell (1903) and Miller (1921) read like descriptions of the vinous-throated parrotbills with regard to flock movement This is a good example of bepatterns. havioral convergence in two groups of unrelated birds found separately on two continents. The major difference between the two species is that bushtit flocks will defend their home range when they encounter an-Vinous-throated parrotbills do other flock. not and stand alone in this regard for their lack of territoriality. If there is any territorial defense, it is expressed so subtly that it has not been detected yet. Among higher vertebrates, only the coati (Kaufmann 1962) demonstrated a total lack of antagonism between members of different herds when they met each other in overlapping areas of their home ranges.

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粉紅鸚嘴於非生殖季節之社會行為

劉小如

於非生殖季,粉紅鸚嘴自天亮至天黑均形成大羣活動。 全天各時段活動量相似,主要活動是覓食, 即使有小雨或中雨,往往仍繼續覓食。白天一起活動的個體,通常一起過夜,兩羣鄰島也可能一起過夜。

生殖季結束後,鳥羣中個體隻數較少,入秋後數量漸增,到冬季各羣鳥之隻數相當穩定,但於生殖 季前又開始逐漸減少。

同羣的粉紅鸚嘴之間甚少有敵對行為。 鳥羣與鳥羣之間則從未見過敵對行為。 鳥羣及個體均不維持 領域,也從未見任何領域行為。一羣鳥中並無明顯的領袖,個體間也看不出優勢地位關係。 羣中個體常 會換到鄰羣活動,換羣現象全年各月均有出現,此種現象顯然會影響鳥羣之社會組織。 粉紅鸚粉應是鳥 類中甚具社會性的鳥種。

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