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History of Group Composition of the Rufous Vanga *Schetba rufa* at Ampijoroa in Northwestern Madagascar

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Abstract The rufous vanga *Schetba rufa* is a cooperatively breeding bird. In the western deciduous dry forest at Ampijoroa, Madagascar, studies have been conducted on the society of the rufous vanga under the leadership of Dr. Yamagishi since 1991. However, the lineage or the genealogy of the studied rufous vanga population has never been presented before in diagrammatic format. From our study we were able to draw the genealogy on the data from 1994 to 2000, and could discuss the details based on that. Here, we describe the histories of individuals, as basic information underpinning our seven years of continuous research on rufous vanga society.

Key words *Schetba rufa*, Cooperative breeder, Group composition, Genealogy, Madagascar

Introduction

Cooperative breeding has been reported in 3% of birds. The cooperative breeding species provide an excellent arena for testing emerging ideas concerning conflicts of interest among members of social groups (Emlen 1991). Yamagishi et al. (1995) reported that the rufous vanga *Schetba rufa* is one such cooperative breeder. The rufous vanga is a member of the family Vangidae, endemic to Madagascar (except for the blue vanga *Leptopterus madagascarinus*), and inhabits rain forest (eastern and northern parts of Madagascar) and deciduous dry forest (western part of Madagascar) (Langrand 1990). In the western deciduous dry forest, studies have been conducted on the society of the rufous vanga under the leadership of Dr. Yamagishi since 1991. This continuous and long-term research project has revealed the ecological traits of the cooperatively breeding rufous vanga (Asai *et al.* 1999, Eguchi *et al.* 2001, Eguchi *et al.* 2002, Yamagishi *et al.* 2002).

In order to reveal the benefits of the individuals that acted as the specific status within the society, we need pursue the history of the individual within that society. In a recent compilation of publications on cooperatively breeding birds (Stacey & Koenig 1990), half of the contributors adopt a similar genealogical presentation as a mean to explain clearly the transition of group members as the informative resource for the detailed analyses.

We also have discussed the benefit of each individual based on their history (Asai *et al.* 1999, Eguchi *et al.* 2002). However, the lineage or the genealogy in the rufous vanga

has not yet been presented in diagrammatic format. From our detailed results we were able to draw the genealogy of our studied population from 1994 to 2000. Here, we describe the histories of individuals as the basic information of the details on the continuous research for seven years.

Materials and Methods

Study area

The field study was conducted at the Ampijoroa forest station (16°15'S, 46°48'E, c. 200 m a.s.l.) in each breeding season from 1994 to 2000. The breeding season of this species ranges from late September to early January. This station is a part of Ankarafantsika Strict Nature Reserve, about 450 km northwest of Antananarivo, the capital of Madagascar. The study area is a deciduous broadleaved forest around 550 m × 450 m area (Botanical Garden A). About 40 individuals of the rufous vangas lived in this site in 1994. Since 1995, the study area has been expanded into an area of about 1 km × 1 km including Botanical Garden A, where about 100 individuals lived.

Methods

We marked each individual with distinct combination of color bands. The sex of the rufous vangas is easily identified, because they have sexual dimorphism of plumage. The sex and age of one-year-old males was also easily identified without capturing, because one-year-old males have distinct black spots on the white throat (Yamagishi *et al.* 2002). Furthermore, because one-year-old individuals have buff tips on the greater coverts, one-year-old females could be discriminated from older females if they were in hand. Because the rufous vanga is territorial and the bonds of group members (breeding pairs and auxiliaries) are very tight, we could confirm the group composition at censuses. Every breeding season from 1994-2000, we recorded which groups each individual joined in, and its status in each group.

At the beginning of the breeding season, the nest of each group was located. The number of eggs, nestlings and fledglings of each group was checked throughout the breeding season. The nestlings were measured and marked with color bands at about seven days of age. The sex of nestlings that were not observed as yearlings in the next season was determined by the method of analysis of the CHD gene on the sex chromosome (Fridolfsson & Ellegren 1999).

Results

In each breeding season from 1994 to 2000, 75% - 94% of individuals in the study site were marked with color bands. In principle, each breeding male with a mate was regarded as a group, and was given a unique name. The assignment of group names was arbitrary. Non-marked males that held a territory at the same place in subsequent breeding seasons (AX, BX, DX, KX, LX, SX2 and BY groups) were given the same group

Table 1. Numbers of each categorized group. The bottom row shows mean numbers of auxiliaries per group. We counted the number of groups present at the end of each breeding season. Solitary males are not included in the numbers of groups

	Group composition				
	Pair only	Pair and			
Year		One-year old males	≧ 2 years old males	One-year old and ≧ 2 years old males	Total
1994	8	3	2	1	14
1995	23	6	8	1	38
1996	25	7	5	1	38
1997	24	11	3	5	43
1998	35	4	7	1	47
1999	26	6	9	2	43
2000	17	2	7	2	28
Total	158	39	41	13	251
%	63	16	16	5	100
Mean ± SD		1.31 ± 0.57	1.32 ± 0.65	1.38 ± 0.65 + 1.31 ± 0.63	

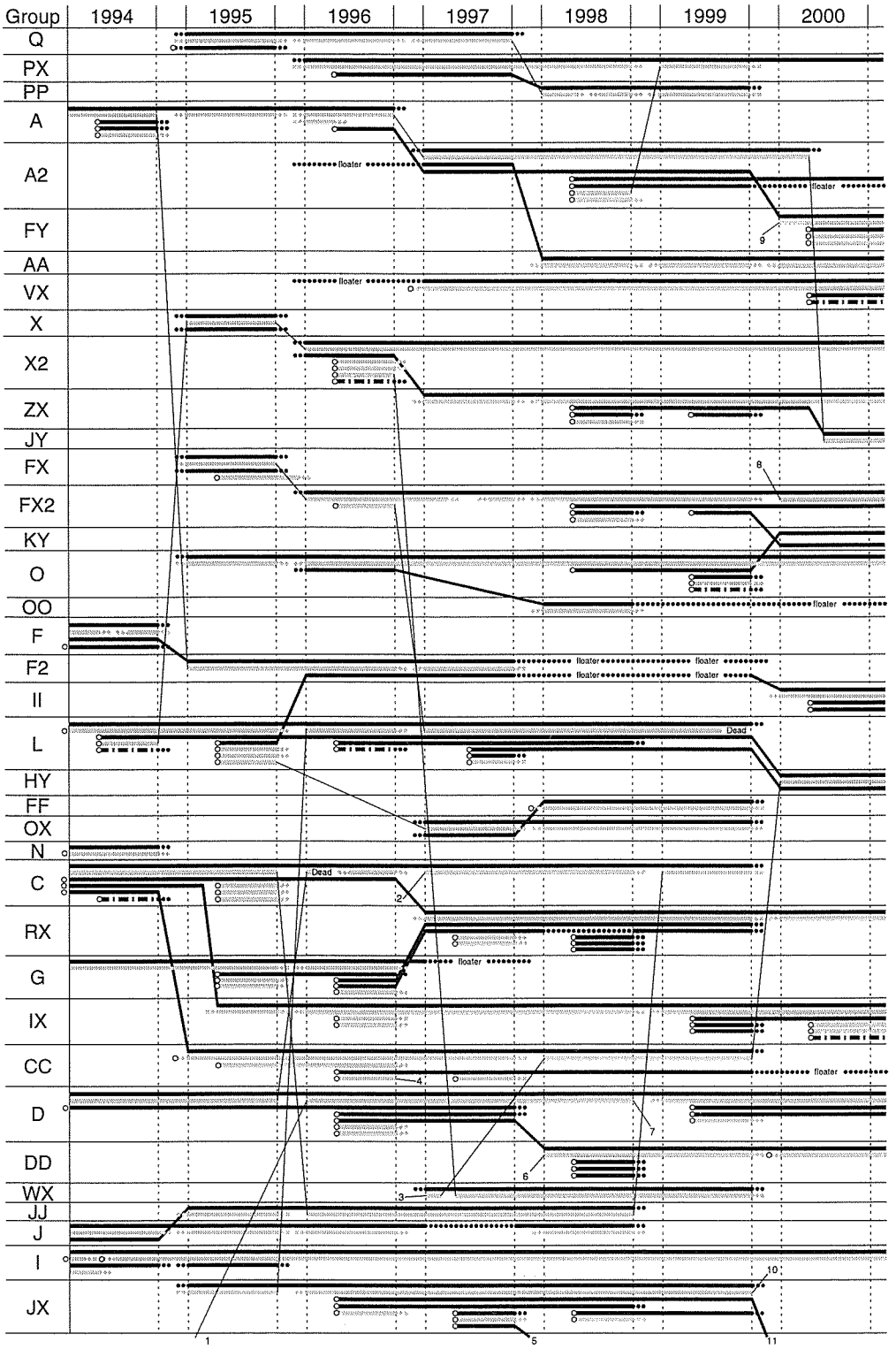
name in both years.

The male of HH group obtained the reproductive opportunity artificially, and mated a female apart from the study area in 1998. The prior mate of the female had been captured and sacrificed for an analysis of testicular maturation (Yamagishi *et al.* 2002). Thereafter, in 2000 the male of HH group returned to the study area with another non-marked female.

The genealogy of the rufous vanga within the study area is shown in Fig. 1, and their territories are shown in Fig. 2. Once a male established a territory, he rarely moved to another place. In contrast, a breeding female occasionally moved to another place. Newborn males remained at their natal territory, whereas newborn females dispersed before the next breeding season. After spending at least one year as auxiliaries, whenever possible males established their own territories (n=25). Fig. 3 shows the total numbers of transitions of males from 1994 to 2000. Although males without females were categorized as 'solitary', male birds in this category were only rarely observed. No female was

Fig. 1. Histories of individuals (1994 - 2000). A series of linked lines shows the history of an individual. Black lines and gray lines represent males and females, respectively, but black thin lines show transitions of females. Dashed-and-dotted lines represent individuals of unknown sex. Broad lines between two narrow lines are members of a group; black top lines are breeding males; second gray lines are breeding females; and other lower lines are auxiliaries and nestlings that were fledged. Groups are named arbitrarily. In principle, we applied a group name to the male that settled as a breeder. This is why breeding males never move among groups in this diagram.

Although each research period is partitioned by vertical dots, the length of each historical line does not correspond to the period of staying in the group. When the information about an individual was unclear, the unknown period is represented by dots on the historical line. An open circle represents the birth of an individual. Dots added 'floater' represent floater males. We could confirm that four individuals were dead. One of them (a female of group C in 1996) died accidentally, caught in a folded mist net.Numbers in the diagram represent the connection to another page.


Group
1994
1995
1996
1997
1998
1999
2000
Q
PX
PP
A
A2
FY
AA
VX
X
X2
ZX
JY
FX
FX2
KY
O
OO
F
F2
II
L
HY
FF
OX
N
C
RX
G
IX
CC
D
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I
JX
floater
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2
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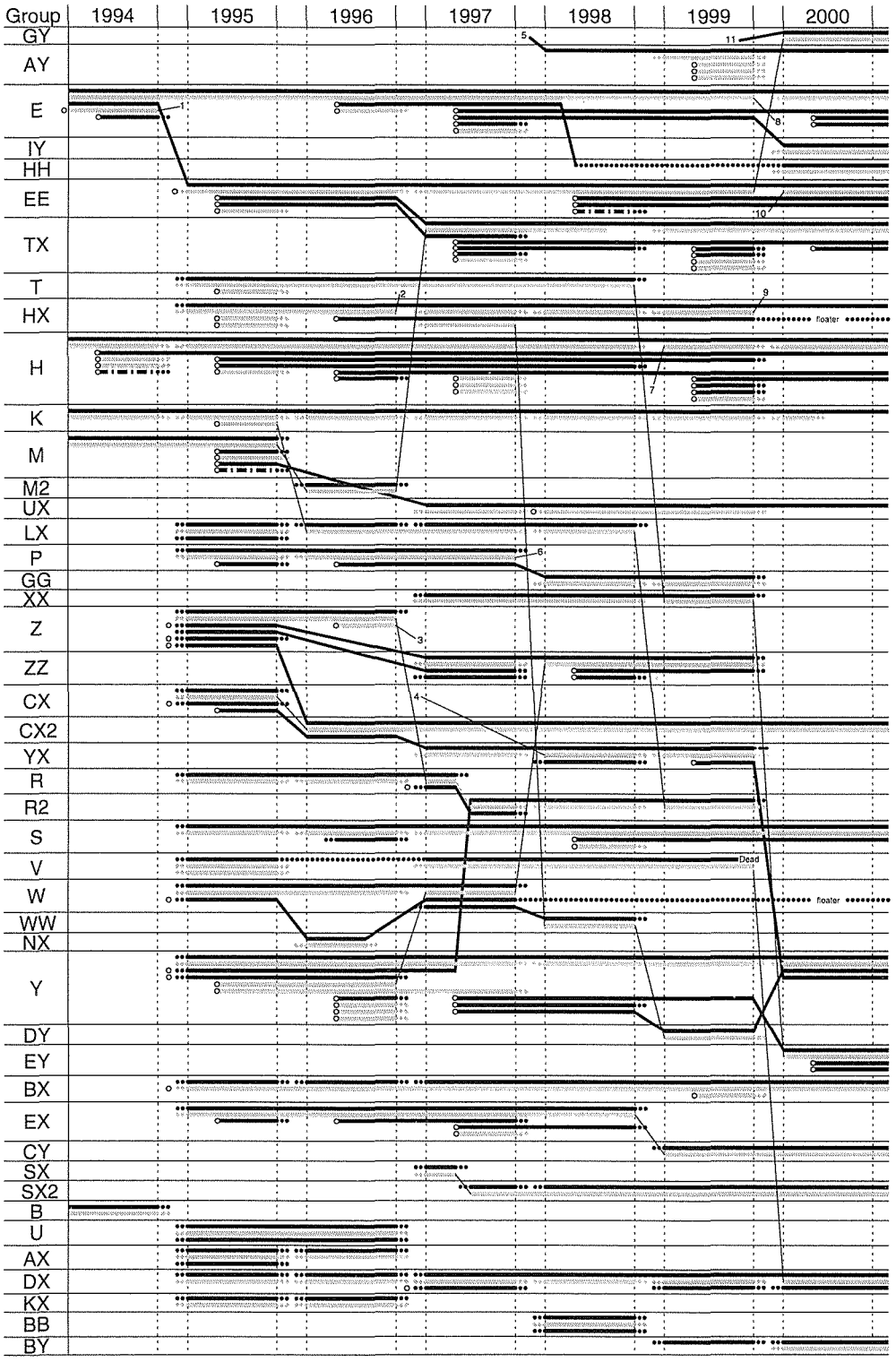
10
11


Group
1994
1995
1996
1997
1998
1999
2000
GY
AY
E
IY
HH
EE
TX
T
HX
H
K
M
M2
UX
LX
P
GG
XX
Z
ZZ
CX
CX2
YX
R
R2
S
V
W
WW
NX
Y
DY
EY
BX
EX
CY
SX
SX2
B
U
AX
DX
KX
BB
BY
floater
Dead
floater

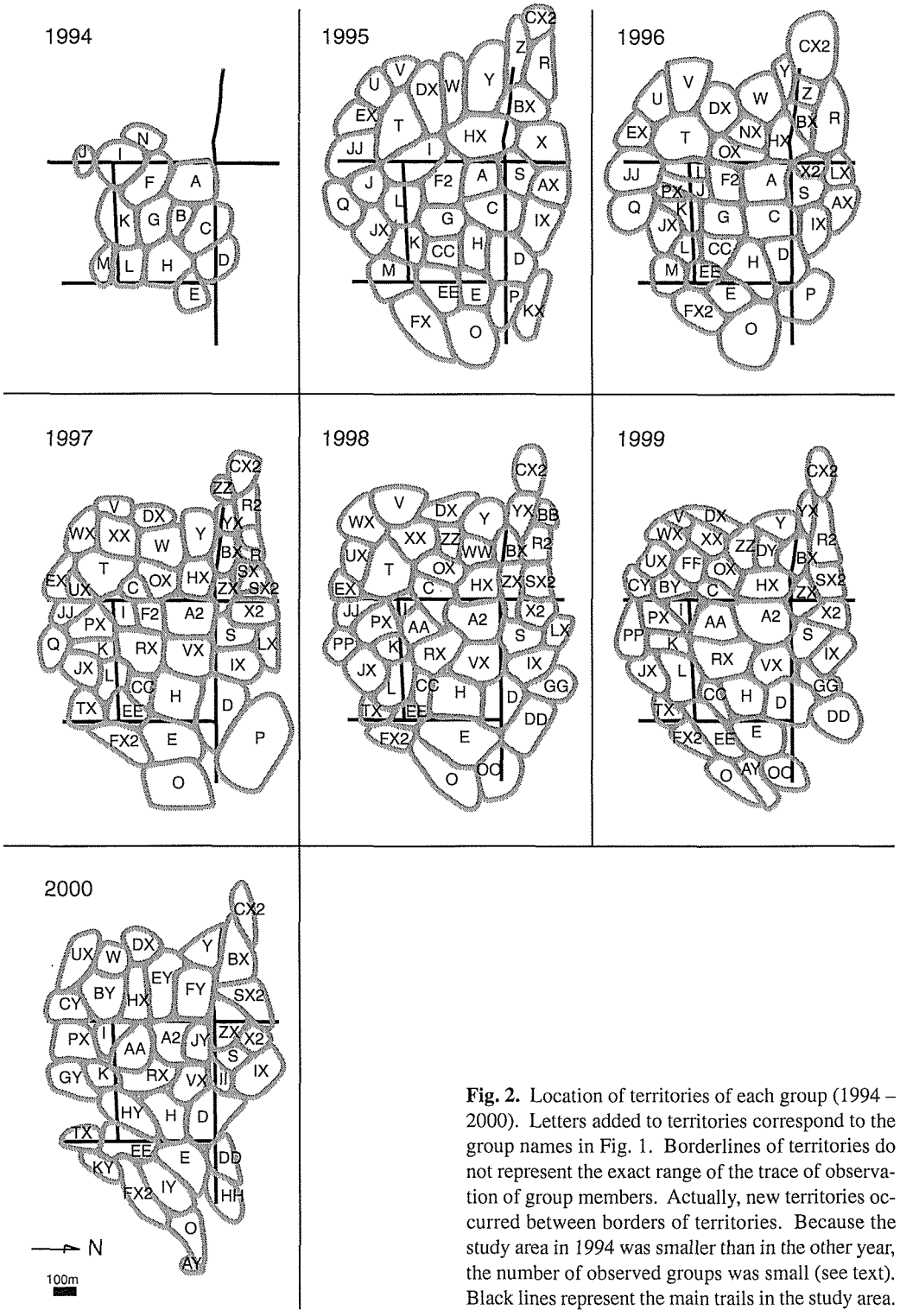


Fig. 2. Location of territories of each group (1994 – 2000). Letters added to territories correspond to the group names in Fig. 1. Borderlines of territories do not represent the exact range of the trace of observation of group members. Actually, new territories occurred between borders of territories. Because the study area in 1994 was smaller than in the other year, the number of observed groups was small (see text). Black lines represent the main trails in the study area.

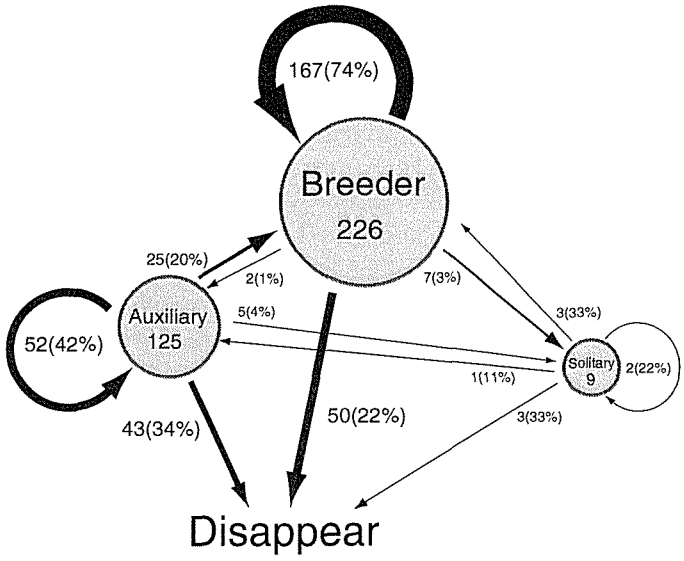


Fig. 3. Transition of males from 1994 to 2000. Arrows show transitions of status, and numbers added to the arrows show total of transitions from 1994 to 2000. 'Disappear' includes the numbers of disappearances by emigration, unknown status and death. Floater males were included in the category of 'solitary'.

categorized as 'solitary'.

Accordingly, our results show that members of a group circulated between a phase of a breeding pair and a phase of a one-female unit with plural males. Only one of the males in a group bred, whereas the other males were auxiliary males, most of which were sons of the breeding pair. As an overview of the group members in a breeding season, it can therefore be said that territories of breeding pairs and territories of one-female groups with plural males were intermingled within the study area (Table 1).

Discussion

In the most common form of cooperative breeding in birds, younger individuals delay dispersal and aid their parents in the rearing of a later brood at the natal territories (Emlen 1991). Auxiliaries of the rufous vanga also comprise young individuals that remain at their natal territories. Thus, the rufous vanga is a typical cooperative breeder.

The history of each individual, as presented in this paper, is essential to understand the interactions among individuals or the trend between the population and individuals. The trend of the population determines the selection pressure acting upon an individual. For example, the determinant that induces auxiliaries to desert the group and to disperse for their own reproduction could depend on the trend of the other individuals. Also, females could manipulate the sex ratio in their clutches depending on the extent of the bias of the population sex ratio. Thus, each study to examine the option of an individual act is founded on the data of the history of individuals.

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