

## ORIGINAL ARTICLE

# Spotted-throat individuals of the Rufous Vanga *Schetba rufa* are yearling males and presumably sterile

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**Abstract** The Rufous Vanga *Schetba rufa* is endemic to Madagascar and lives in one-female groups. During the 1994–1999 breeding seasons, a total of 294 nestlings were banded. Among these nestlings, 51 stayed within the study area as spotted-throat individuals. In the next breeding seasons, 35 of 45 spotted-throat individuals were subsequently observed as black-throated males, and once they became black-throated males, these individuals never reverted to the previous spotted-throat pattern. In contrast, 30 banded nestlings were recovered as yearling females with white throats, and the female's color pattern never changed thereafter. All the spotted-throat males were helpers or floaters. All the males of one group consisting of an adult male with a black throat and two males with spotted throats were captured and sacrificed humanely. The testes were dissected from each specimen and were histologically examined. The testes of the spotted-throat males contained only spermatogonia, and no spermatids or spermatozoa were present. In contrast, the testes of the black-throated male were well-developed and contained enlarged seminiferous tubules with lumen, where numerous spermatozoa were evident. Considering these facts, spotted-throat males of this species are assumed to be sterile. We suggest that, due to their underdeveloped testes, the spotted-throat males (one-year-old males) of the Rufous Vanga are physically incapable of breeding.

**Key words** Cooperative breeding, Delayed maturation, Madagascar, Plumage, *Schetba rufa*

The family Vangidae is monophyletic and underwent extensive *in situ* radiation in Madagascar (Yamagishi et al. 2001). The Rufous Vanga *Schetba rufa* is a member of this family. In a previous paper (Yamagishi et al. 1995) we reported that this endemic species lives in groups of two to four individuals and that the groups contain one adult female, one or two adult males and sometimes also an individual with a spotted throat. We described how those birds with spotted throats helped the pairs with brood care during part of the breeding cycle, and suggested that these individuals were immature males. In the present study we confirmed that individuals with spotted throats were yearling males.

Furthermore, we report that the spotted-throat males never attempted to copulate nor became breed-

ers. These observations implied that they had not reached sexual maturity. Was this absence of breeding in one-year-old males due to an inability of reproduction or to ecological constraints? The alternatives would lead us to different interpretations of delayed dispersal of yearling males. To answer the question of sexual maturity of yearling males, we here provide evidence concerning the change in plumage pattern of males and also provide anatomical evidence of spermatozoa maturation. From this viewpoint we then discuss the reproductive ability of helper males of this species.

## STUDY AREA AND METHODS

A study of Rufous Vanga ecology and behavior was conducted at Botanical Garden A in the Ampijoroa Forest Reserve (16°15'S, 46°48'E, c. 200 m asl) about 110 km southeast of Mahajanga in Mada-

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gascar. We marked nestlings with individually distinct combinations of color bands during 1994–1999. Then, every breeding season from 1995 to 2000 we recorded which groups each individual joined, its status in the groups, and the color patterns of its throat.

On 15 October 1998, we captured all the males of a group consisting of an adult male with a black throat and two males with spotted throats (spotted-throat males 1 and 2). At that time of year, the captured group was at the late stage of nest-building, at which time we considered that the testes of adult males had achieved full functional maturity. After capture, birds were sacrificed humanely, body mass was measured with an electric balance to the nearest 0.1 g and wing length was measured with a ruler to the nearest 0.1 mm. At the field station the testes were dissected from each specimen, and fixed in 10% formalin solution until histological examination. Right and left testes from each bird were weighed to the nearest 0.1 mg with an electric balance. Each testis was subjected to standard histological procedures for light microscopy; the testis was embedded in paraffin, and sectioned at 4  $\mu$ m, the sections then stained with hematoxylin and eosin.

## RESULTS

Among the 259 groups recorded during the seven years of study, 161 (62%) were pairs without male helpers, and 98 groups (38%) had one to four male helpers. Among the 98 groups containing helpers, 54 (55%) contained at least one male with a spotted throat. During the 1994–1999 breeding seasons, we banded a total of 294 nestlings, of which 51 stayed

within the study area as spotted-throat individuals (Fig. 1-a and Table 1). In the next breeding seasons, 35 of 45 spotted-throat individuals were subsequently observed as black-throated males (Fig. 1-b), and once they became black-throated males, they never reverted to the previous spotted-throat pattern (Table 1). In contrast, 30 individuals banded as nestlings were recovered as yearling females with white throats (Fig. 1-c) in the pre-breeding season or in the breeding season (some of them disappeared after the recovery). The female's color pattern never changed thereafter.

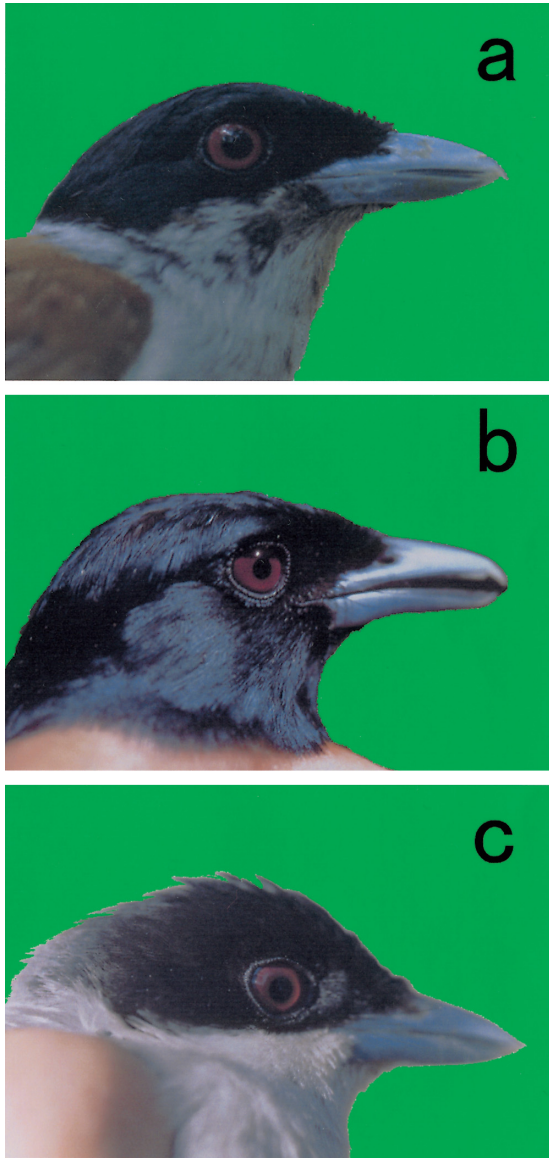
All the spotted-throat males were helpers or floaters. In general, after a male developed a black throat, he established a new territory and became a breeder. Of those 24 males whose age at first breeding was confirmed, 15 bred at two years old. During seven years of observations, we also noted seven instances where individually identifiable helper males with black throats attempted sneak copulations with breeding females. Of these incidents, in three cases the sneaking males were three years old, in two cases the same two-years-old male attempted mating, and in the remaining two cases the ages of the males were unknown. Furthermore, in the case of the two-years-old male, at least one nestling which the helping male cared for did not have an allele derived from the breeding male on a microsatellite locus developed as markers of paternity tests (Asai et al. 1999), but shared another allele with the helping male which attempted mating (Asai unpubl. data). We never observed males with spotted throats attempting to copulate with females, nor did we find them forming a pair. These observations suggest that the helper status

**Table 1.** Observed male nestlings within the study area and change of their throat color.

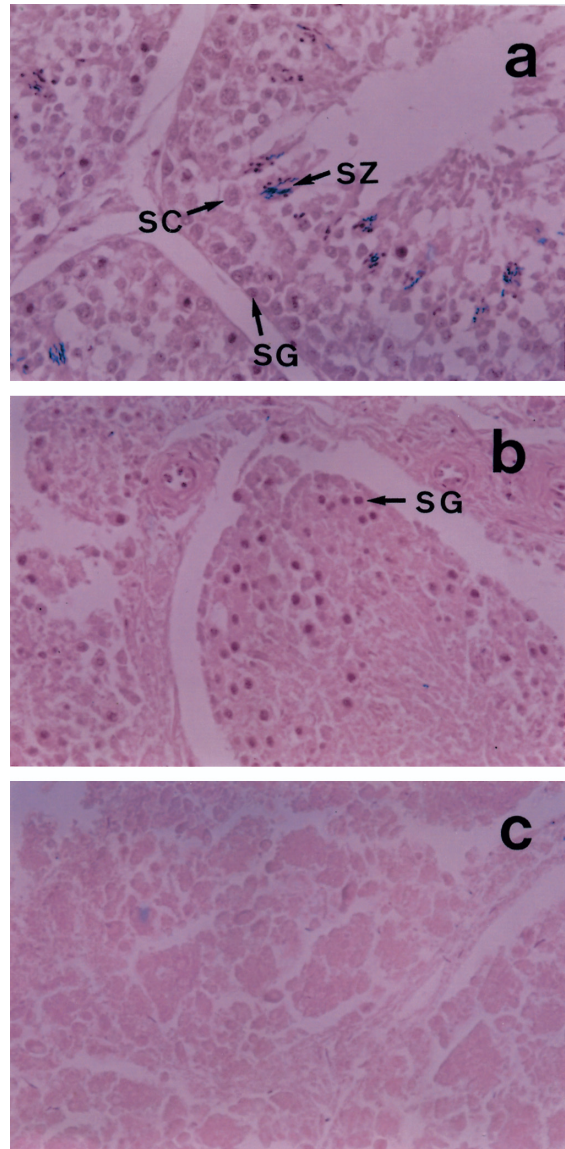
Year	No. nestlings banded	Observed individuals					
		1995	1996	1997	1998	1999	2000
1994	14	2	2	2	2	2	2
1995	38		8	7	7	6	3
1996	68			15	12	10	6
1997	53				10	7	7
1998	76					10	7
1999	45						6
Total	294						

Schadowed numbers indicate spotted-throat males.

of a black-throated male per se does not inhibit his reproductive activity. In comparison, among 21 yearling females observed in our study site during the



**Fig. 1.** The plumage of the head and throat in Rufous Vangas. a: a male with a spotted throat, b: a male with black throat, and c: a female.



**Fig. 2.** Testis showing seminiferous tubules of three Rufous Vangas from the same breeding group, captured at the study site at the late nest-building stage. a: Black-throated male, b: Spotted-throat male 1, and c: Spotted-throat male 2. Note that spermatozoa were only found in the black-throated male. SG: spermatogonium, SC: spermatocyte, SZ: spermatozoa.

**Table 2.** Combined testes mass and right testicular volume of each Rufous Vanga captured at the late nest-building stage.

	Body mass (g)	Wing length (mm)	Tarsus length (mm)	Combined tested mass (mg)	Right testicular volume (mm <sup>3</sup> )
Black-throated male	37.6	108.7	24.3	171.5	75.4
Spotted-throat male 1	39.4	103.9	24.4	60.8	38.5
Spotted-throat male 2	39.8	105.6	23.8	14.5	13.1

breeding season, 16 (76%) were breeders and 5 (24%) were auxiliary females.

Table 2 shows the combined testicular mass and measurements of body mass, wing length and tarsus length for each of the three dissected males. Histological pictures of testis sections are given in Fig. 2. When these pictures are considered together with the data of testicular mass, it is indisputable that the spotted-throat male 2 was an immature individual with completely regressed testes. The spotted-throat male 1 had heavier testes than spotted-throat male 2, but histological examination indicated that spermatogenesis in this individual had been arrested at the early stages. The testes contained only spermatogonia, and no spermatids or spermatozoa were present (Fig. 2-b). In contrast, the testes of the black-throated male were well-developed and contained enlarged seminiferous tubules with lumen, where numerous spermatozoa were evident (Fig. 2-a). This histological evidence indicates that the black-throated male was reproductively active, whereas the two spotted-throat males were not.

## DISCUSSION

The observations that spotted-throat males never attempted to copulate nor became breeders, and that helper males of age two years or more could potentially copulate with females suggest that sexual maturity of males is not dependent on social constraint with respect to the helper status, but is instead age related. However, observational field data cannot strictly identify whether it is physiological restraint of maturity or ecological constraint on chance of mating which resulted in the absence of mating by the yearling males. In this context, although the direct evidence is lacking in black throat helpers, our anatomical evidence is more informative.

Morphological characters of the three sacrificed males were identical (Table 2), indicating that all had achieved mature adult size. However, testicular masses were different; only the black-throated male had mature testes, whereas the two yearling males with spotted throats had small regressed testes.

The testicular masses were different between two yearling males (Table 2). Unfortunately, we have insufficient data to explain the individual difference of testicular masses between these two yearlings. Such a difference, considering that these were immature individuals, might fall within the range of individual variations related to physiological conditions, or

might result from ecological constraints that acted to either advance or inhibit the developmental process of testes. In the former case, the difference of testicular masses might not be functional. In the latter case, the development of testes might correlate with the extent of helping activity of yearling males (cf. Eguchi et al. in press). However, even if the difference of testicular masses affected helping behavior, the anatomical data indicated clearly that the yearling males had not reached sexual maturity (Fig. 2).

Related helper males of the cooperatively breeding African White-browed Sparrow Weaver also have smaller testes (around 100 mg) than breeding males (>300 mg) in January/February (Wingfield et al. 1991). In this species, plasma levels of luteinizing hormone and testosterone in the helpers are also lower than in breeding males, indicating that helpers are not fully mature. Similarly, in the cooperatively breeding Florida Scrub-jay, helpers are subordinate and nonbreeders, and have smaller testes than the breeding males, with whom they share a territory (Schoech et al. 1996).

Suppression of hormonal levels of helpers is known in several cooperative breeding species (Schoech et al. 1996; Wingfield et al. 1991; Poiani & Fletcher 1994; Mays et al. 1991). However, whereas those studies emphasized the role of spontaneous restraint by subordinates, we suggest that, due to their underdeveloped testes, the spotted-throat males (one-year-old males) of the Rufous Vanga are physically incapable of breeding.

In the cooperatively breeding Mexican Jay, yearling males also never breed, and have low reproductive steroid levels during the breeding season (Vleck & Brown 1999). Two-year-old males do regularly breed whether or not they are nest owners. Vleck and Brown (1999) consider that yearling males delay sexual maturity in order not to pay any physiological costs of high testosterone levels. Furthermore, yearling males of the Mexican Jay may be tolerated by other males to a greater extent than those males with high testosterone levels, because they are readily identifiable through their juvenile bill coloration (Vleck & Brown 1999). The spotted-throat coloration of the male Rufous Vanga might have a similar effect as the bill coloration of the Mexican Jay, and is assumed to be an example of delayed plumage maturation (Rohwer et al. 1980; Greene et al. 2000). Delayed maturation is expected to delay the dispersal of males, and therefore may be closely related to the maintenance of the cooperative breeding system of

the Rufous Vanga. Additionally, it is evident that females achieve sexual maturity at age one, and thus the delayed maturation of males affects the operational sex ratio. Although the population sex ratio containing yearling males was biased toward males (0.60 on average), the operational sex ratio was 0.55 on average (Asai et al. unpubl.).

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