THE RAFFLES BULLETIN OF ZOOLOGY 1998 **46**(1): 101-112

BREEDING BIOLOGY OF MONOGAMOUS ASIAN PARADISE FLYCATCHER *TERPSIPHONE PARADISI* (AVES: MONARCHINAE): A SPECIAL REFERENCE TO COLOUR DIMORPHISM AND EXAGGERATED LONG TAILS IN MALE

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ABSTRACT. - The breeding biology of the Asian Paradise Flycatcher *Terpsiphone paradisi* was studied in southern Thailand in 1993 and 1994. Males were divided into three types, namely, white-coloured males with long tail feathers (WL), rufous-coloured males with long tail feathers (RL), and rufous-coloured males with short tail feathers (RS). WL males had significantly longer tail feathers, and wider growth-bars than RL males, and both had longer wing-lengths than RS males. No difference was found between WL males and RL males in the breeding activity. Females which paired with long-tailed males laid their first eggs earlier and had larger clutch-sizes than females which paired with RS males. These results suggest that RS males are probably younger than long-tailed males. Females paired with RS males also seemed to be younger than those paired with long-tailed males because of their small clutch-sizes. Old females with large clutch-sizes started their breeding attempts earlier than young females with small clutch-sizes. Therefore, old females may have the choice among many males. If females have a preference for male tail length, males with long tail feathers may have higher reproductive success than males with short tail feathers. The elongation of tail feathers in males may be maintained by female mate choice in this monogamous species.

KEYWORDS. - Asian Paradise Flycatcher, Colour dimorphism, Sexual ornaments, Monogamy, Sexual selection, Female choice

INTRODUCTION

The Asian Paradise Flycatcher *Terpsiphone paradisi* is a forest-living bird species that is widely distributed in Asia. Asian Paradise Flycatchers have twelve tail feathers of which the two central feathers of adult males are greatly elongated and form streamers. There are two colour types in males, rufous and white (Owen, 1963). Some rufous-coloured males do

Received 14 Aug 1997 Accepted 15 Sep 1997

not have long central tail feathers (Ali & Ripley, 1972; Lekagul & Round, 1991). Therefore three types of males (white-coloured male with long tail [WL], rufous-coloured male with long tail [RL], and rufous-coloured male with short tail [RS]) exist in the same population. Females are rufous-coloured and do not have elongated tail feathers. Females and RS males resemble each other in plumage colouration.

Usually it is said that the expression of sexually selected characteristics in males such as long tail feathers is limited in monogamous species because every male can acquire only one female. Males do not gain increased fitness by possessing exaggerated sexual ornaments in monogamous species. The mating system of the Asian Paradise Flycatcher is social monogamy (Mizuta, pers. obs.), despite the males' exaggerated long tail feathers. Therefore this characteristic appears to be one of the exceptions in the evolution of sexual selection (Møller, 1994).

In this study, we compared the body characteristics and breeding activity among these three types of males (WL, RL and RS), and discuss the adaptive significance of long tail feathers and colour dimorphism in males.

STUDY AREA AND METHODS

Study area. - Field work was conducted at Bang Tieo study area, in Khao Pra-Bang Khram Wildlife Sanctuary, Krabi Province, southern Thailand (8°10'N, 98°80'E) from March to July in 1993 and 1994. The vegetation in Khao Pra-Bang Khram mainly consists of small remnant patches of lowland rain forest. Many plant species in Bang Tieo study area are pioneer or secondary forest species due to logging 30 or 40 years ago (Round & Treesucon, 1992). There is a network of nature trails in this study area, so it is easy to make observations. In this area, the rainy season starts in April and ends in October or November.

Three types of males. - There were three types of plumage in males in the study area, namely, white-coloured males with long central tail feathers, rufous-coloured males with long central tail feathers and rufous-coloured males with short central tail feathers. Both WL male and RL male are collectively called "long-tailed males". All females were rufous-coloured, and the central tail feathers were short. Consequently, females resembled RS males. However, all types of males had bright-blue eye-rings, whereas eye-rings of females were not bright like males. Therefore, RS males and females could be distinguished from each other. We referred to the pair in which the male was WL as a "WL pair" for the sake of convenience. Similarly, pairs with RL and RS males were called "RL pair" and "RS pair", respectively. The pair in which the male was long-tailed was called "long-tailed pair", though the females did not have long tail feathers.

Nest observations. - We walked along the nature trails in the forest from 06:00 to 12:00 and from 16:00 to 18:00 almost every day in search of nests. Once we sighted a bird or heard a song, we followed it and tried to find a nest. When a nest was detected, its contents were inspected and the breeding stage of the nest was recorded. After finding the nest it was checked every day to certify the dates of egg-laying, hatching and fledging and to determine whether it was successful. The breeding stages of the nest was divided into three periods; nest-building, incubation, and nestling period. When a nest was found with no eggs and nestlings, and eggs did not appear within two weeks, we considered the nest to be abandoned or predated. We also checked the number of eggs or nestlings in the nest. The number of eggs was at most three, and only one egg was laid in one day, so the clutch size was determined two days after the first egg was laid. The number of nestlings was counted after all live eggs hatched. The number of fledglings was counted one day before fledging. When all eggs or nestlings disappeared at the same time, the nest was considered predated. When only some eggs or nestlings disappeared and the rest remained in the nest, we considered that they were broken or died because of some accident.

Capture, marking and measurements of birds. - Adult birds were captured in front of the nest by using mist nets. Birds were captured in the late nestling period to minimize the risk of nest abandonment. Captured individuals were colour-ringed for individual identification. The following parts were measured to the second decimal place; length of the unflattened wing, tail, tarsus, and body-mass. Tail-length means the length of the longest central feather. One rectrix (second outermost one from the right) was plucked out to measure the width of growth-bars. Growth-bars show up as striped patterns on the rectrix. The width of the growth-bar indicates the nutritional status when the feather grows (Grubb, 1989). Individuals that have wider growth-bars were considered to have been in better nutritional status than individuals that have narrower ones. The method of measurement of the width of growth-bars follows Grubb (1989). Total length of the rectrix and average width of six growth-bars were measured by using a slide caliper to the nearest 0.05 mm.

Nestlings were also colour-ringed when they were 9 days old. Nestlings at this age have legs long enough to accept rings, but they do not fledge until one or two days later. Each nestling was also weighed. To prevent the disturbance to the parent birds, marking and weighing of nestlings were done when they were absent from the nesting area.

Statistical analysis. - Differences in body characteristics, clutch-size, brood-size and nestling body-mass among three types of males or females were compared by Kruskal-Wallis tests. Mann-Whitney *U*-tests were used for each comparison between two of the three types of males or females following the sequential Bonferroni method (Sokal & Rohlf, 1995). We set the familywise error rate at $P = 0.10$ for the comparisons of clutch-size, brood-size and nestling body-mass because of the small sample sizes and conservativeness of the sequential Bonferroni method (Sokal & Rohlf, 1995). In other cases, we used the significance level of $P = 0.05$.

RESULTS

General breeding information. - Three types of males (WL, RL and RS) bred in the study area. White-coloured males with short tail feathers were not observed. The breeding season started in early March and ended in mid July (The first pair laid the first egg on 2 April in 1993 and 25 March in 1994, and last pair did so on 28 May in 1993 and 13 June in 1994). The mating system of this species was social monogamy, and we observed both male and female taking part in nest-building, incubation, brooding and feeding of the young. The incubation periods lasted 14-16 days (mean 14.90 ± 0.74 s.d., $n = 10$) and nestling periods lasted 9-12 days (mean 10.42 ± 1.00 s.d., $n = 12$). The clutch-size was either 2 or 3 (mean 2.79 ± 0.41 s.d., $n = 39$). The nest was open, deep bowl-shaped, and was built on a fork of a small sapling at a height of 118-297 cm (mean 170.61 ± 48.71 s.d., $n = 44$). Nest materials were finely interlaced twigs and dried grasses reinforced with mosses and spider's web. Fine fiber-like materials lined the inside of the nest. We examined the plumage colour of 103 nestlings from 39 broods (10 broods with WL male parents, 19 broods with RL male parents and 10 broods with RS male parents). All these nestlings were rufous regardless of father's plumage colour.

Body characteristics of males and females. - There were significant differences among the three types of males for wing-length and tail-length (Kruskal-Wallis test: wing-length: H = 13.33, df = 2, $P < 0.005$; tail-length: H = 17.98, df = 2, $P < 0.0001$; Table 1). However, differences in tarsus-length and body-mass were not significant among the males (Kruskal-Wallis test: tarsus-length: H = 0.65, df = 2, n.s.; body-mass: H = 4.34, df = 2, n.s.; Table 1). The tail-length of WL males was significantly longer than that of RL males (Mann-Whitney U-test: U = 4.0, $P < 0.005$; Table 1). Long-tailed males (WL and RL pooled) had significantly longer wing-length and tail-length than RS males (Mann-Whitney U-test: wing-length: U = 0.0, $P < 0.0005$; tail-length: U = 0.0, $P < 0.0005$; Table 1).

No significant differences in body characteristics were found among females paired with each type of males (Kruskal-Wallis test: wing-length: H = 3.23, df = 2, n.s.; tail-length: H = 0.17, df = 2, n.s.; tarsus-length: H = 1.73, df = 2, n.s.; body-mass: H = 4.58, df = 2, n.s.; Table 1). Although it seemed that the body characteristics of females paired with RS males were smaller than those of females paired with long-tailed males, the difference was not significant at the significance level of P = 0.05 (Mann-Whitney U-test: wing-length: U = 25.5, P = 0.07; tail-length: U = 50.5, n.s.; tarsus-length: U = 43.5, n.s.; body-mass: U = 25.0, P = 0.09; Table 1). RS males resembled females except for the eye-rings, and there were no significant differences in body characteristics between RS males and females (Mann-Whitney U-test: wing-length: Z = 0.94, n.s.; tail-length: Z = 1.05, n.s.; tarsus-length: Z = 1.49, n.s.; body-mass: Z = 1.83, n.s.; Table 2).

The length of second rectrix from the right and the width of growth-bar on this rectrix of males and females are shown in Figs. 1 a and 1 b. The length of rectrix did not vary among the three types of males (Kruskal-Wallis test: H = 4.97, df = 2, n.s.; Fig. 1 a). The width of growth-bar on the rectrix was significantly different among the three male types (Kruskal-Wallis test: H = 8.05, df = 2, $P < 0.05$; Fig. 1 a). WL males had wider growth-bars than RL males (Mann-Whitney U-test: U = 2.5, $P < 0.005$; Fig. 1 a). The length of the rectrix, of which width of growth-bar was compared, between WL male and RL male, was not significantly different (Mann-Whitney U-test: U = 23.5, n.s.; Fig. 1 a). No difference was seen between long-tailed males and RS males in the length of rectrix and the width of growth-bar (Mann-Whitney U-test: length of rectrix: U = 15.0, n.s.; width of growth-bar: U = 41.0, n.s.; Fig. 1 a). No differences were observed in the length of rectrix and the width of growth-bar among females which paired with each type of male (Kruskal-Wallis test: length of rectrix: H = 1.42, df = 2, n.s.; width of growth-bar: H = 1.47, df = 2, n.s.; Fig. 1 b).

Breeding phenology. - The distribution of the first egg laying dates did not differ between 1993 and 1994 (Mann-Whitney U-test: Z = 0.52, n = 16,30, n.s., nests of three types of pairs were pooled), therefore, data from the two years were pooled (Fig. 2). There was a significant difference in first egg laying dates for females with different types of mate (Kruskal-Wallis test: H = 14.67, df = 2, n = 12,21,13, $P < 0.001$). First egg laying dates of females paired with WL males and those paired with RL males were significantly earlier than those paired with RS males (Mann-Whitney U-test: WL males vs. RS males: Z = 3.16, n = 12,13, $P < 0.005$; RL males vs. RS males: Z = 3.35, n = 21,13, $P < 0.001$). Therefore, females paired with long-tailed males laid their first eggs significantly earlier than those paired with RS males (Mann-Whitney U-test: Z = 3.72, n = 33,13, $P < 0.0005$). No significant difference was found between females paired with WL males and those paired with RL males for the

Table 1. Body measurements of each type of male and female Asian Paradise Flycatcher.

	n	Length (mean ± s.d.) Wing (mm)	Tail[a] (mm)	Tarsus (mm)	Body-mass (mean ± s.d.) (g)
Male body measurements					
WL male	5	92.80±1.44	280.00±25.85	19.20±0.55	21.40±1.17
RL male	14	93.00±1.45	229.36±19.49	19.51±0.54	21.07±1.10
RS male	6	88.00± 1.73	93.67±5.79	19.22±0.59	20.03±0.78
Long-tailed males	19	92.95±1.41	242.68±30.78	19.43±0.55	21.16±1.10
Statistics					
Three types[b]		H = 13.33**	H = 17.98***	H = 0.65	H = 4.34
WL vs. RL[c]		U = 33.0	U = 4.0**	U = 30.0	U = 29.0
WL vs. RS[c]		U = 0.0*	U = 0.0*	U = 14.5	U = 4.0
RL vs. RS[c]		U = 0.0***	U = 0.0***	U = 32.5	U = 19.5
Long-tailed vs. RS[c]		U = 0.0***	U = 0.0***	U = 48.0	U = 23.5
Femaled body measurements					
Feamle paired with					
WL male	4	89.00±3.49	94.75±9.26	18.43±0.60	19.87±0.42
RL male	13	89.31±2.32	100.08±16.67	18.78±0.57	19.38±0.55
RS male	6	87.50±1.52	95.50±9.46	18.77±0.51	18.95±0.68
Long-tailed males	17	89.24±2.52	98.82±15.16	18.69±0.58	19.47±0.55
Statistics					
Three types[b]		H = 3.23	H = 0.17	H = 1.73	H = 4.58
Long-tailed vs. RS[c]		U = 25.5	U = 50.5	U = 43.5	U = 25.0

a Tail-length means the length of the longest central feather.
b Kruskal-Wallis tests were used for the comparisons among three types of males or females. Statistics were represented by H.
c Mann-Whitney U-test were used for the comparisons between two types of males or females following the sequential Bonferroni method. Statistics were represented by U.
* P <0.01, ** P < 0.005, *** P < 0.001.

Table 2. The comparison of body measurements between RS male and female Asian Paradise Flycatcher.

	n	Length (mean ± s.d.) Wing (mm)	Tail[a] (mm)	Tarsus (mm)	Body-mass (mean ± s.d.) (g)
RS male	6	88.00±1.73	93.67±5.79	19.22±0.59	20.03±0.78
Female[b]	23	88.78±2.40	97.96±13.78	18.71±0.55	19.33±0.62
Statistics[c]		Z = 0.94	Z = 1.05	Z = 1.49	Z = 1.83

a Tail-length means the length of the longest central feather.
b Females which paired with all types of males were pooled.
c Mann-Whitney U-test were used for the comparisons. Statistics were represented by Z.

first egg laying dates (Mann-Whitney U-test: Z = 1.16, n.s.).

Clutch size, brood size, and body-mass of nestlings. - There was a difference in the clutch-sizes and number of nestlings among females paired with each type of male (Kruskal-Wallis test: clutch-size: H = 5.39, df = 2, P < 0.10; number of nestling: H = 4.68, df = 2, P < 0.10; Table 3). No significant differences were found among the number of fledglings of pairs in relation to type of male parent (Kruskal-Wallis test: H = 1.95, df = 2, n.s.; Table 3). There

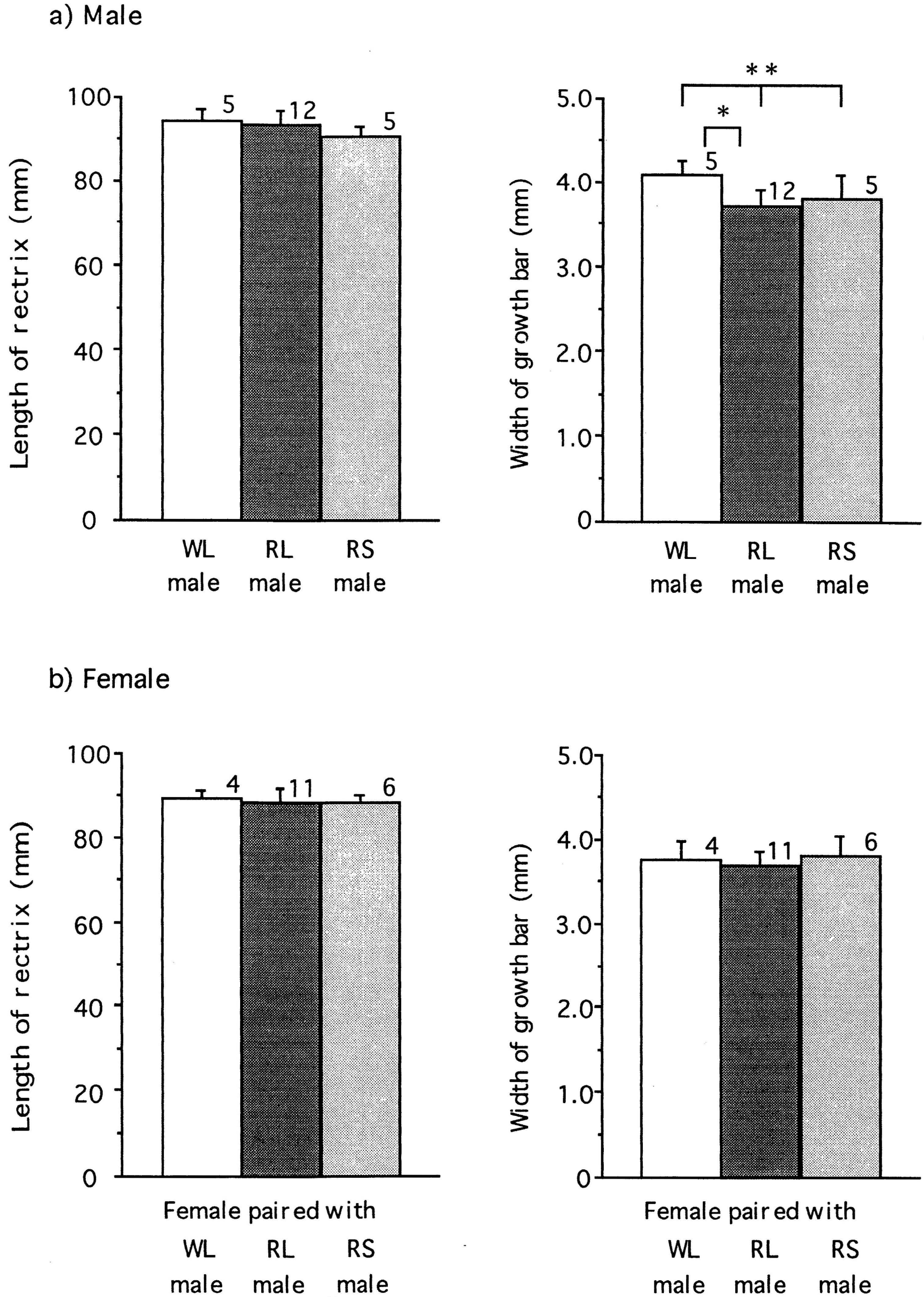

Fig. 1. Length of rectrix and width of growth-bar of WL males and their mates (white column), RL males and their mates (dark grey column) and RS males and their mates (light grey column). Figures above each bar show sample sizes. Vertical bars indicate standard deviation. No difference was found among three types of males in the length of rectrix. The width of growth-bar was different among three types of males (Kruskal-Wallis test: $H = 8.05$, df = 2, $P < 0.05$). WL males had wider growth-bar than RL males (Mann-Whitney U-test: $U = 2.5$, $P < 0.005$). No difference was found among females which paired with each type of males in the length of rectrix and the width of growth-bar.
*Mann-Whitney U-test, $P < 0.005$. **Kruskal-Wallis test, $P < 0.05$.

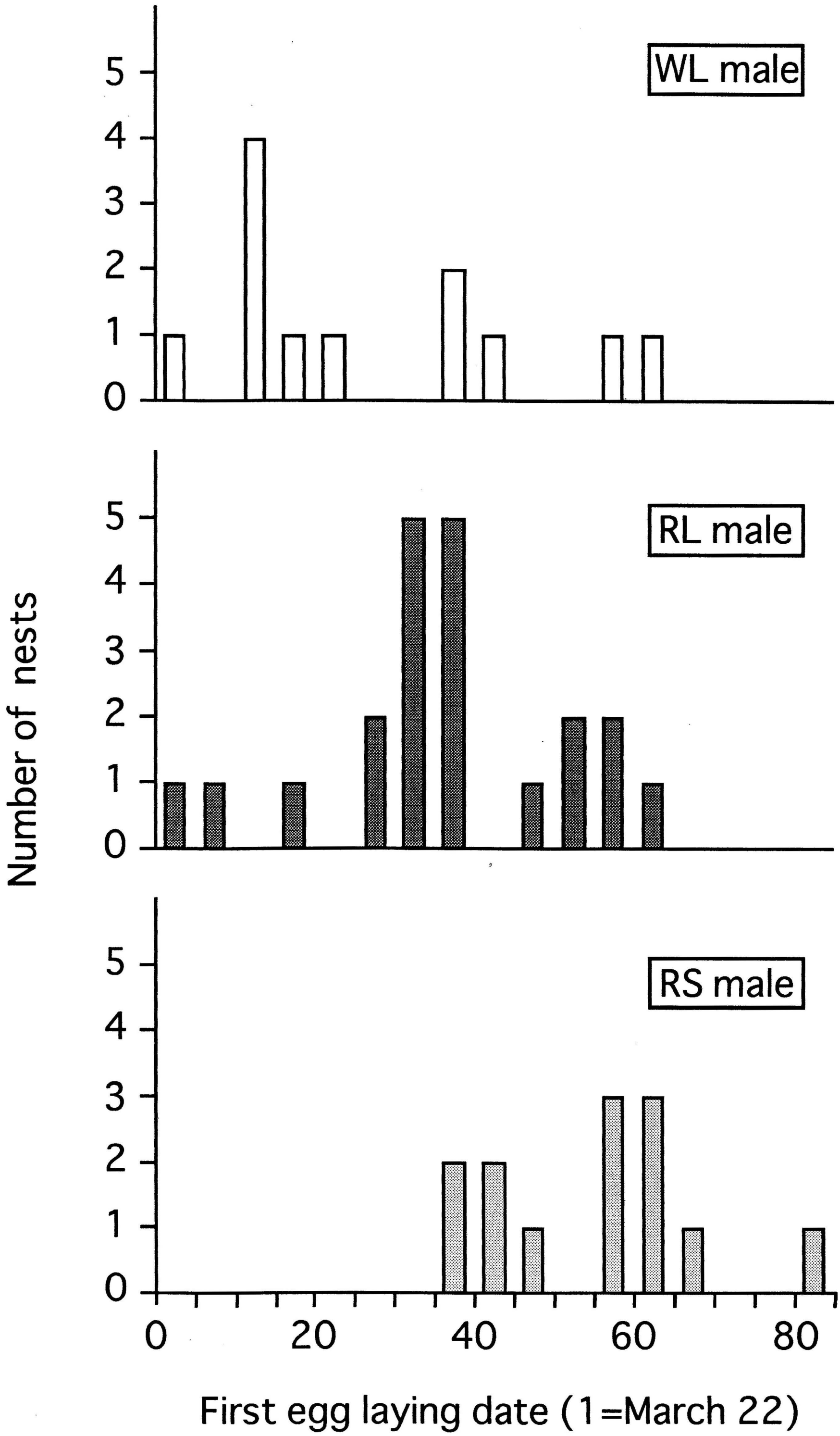

Fig. 2. Distribution of the first egg laying dates of females in relation to type of male mate. Data of two years were pooled. Significant difference was seen among pairs of each type of males (Kruskal-Wallis test: $H = 14.67$, $df = 2$, $P < 0.001$). Pairs of long-tailed males laid their first egg earlier than pairs of RS males (Mann-Whitney U-test: $Z = -3.72$, $P < 0.0005$).

Table 3. Clutch-size, brood-size and nestling body-mass in relation to type of male parent of the Asian Paradise Flycatcher.

	Clutch size mean ± s.d.(*n*)	Brood-size: nestlings[a] mean ± s.d. (*n*)	Brood-size: fledglings[b] mean ± s.d. (*n*)	Nestling body-mass (g): brood size 2[c] mean ± s.d. (*n*)	Nestling body-mass (g): brood size 3[c] mean ± s.d. (*n*)
Type of male parent					
WL male	2.80±0.42 (10)	2.50±0.97 (10)	2.00±1.18 (11)	15.75±1.17 (4)	14.88±0.44 (6)
RL male	2.94±0.24 (17)	2.78±0.43 (18)	1.74±1.28 (19)	15.16±0.90 (10)	14.97±1.19 (15)
RS male	2.58±0.51 (12)	2.08±1.08 (12)	1.25±1.36 (12)	14.92±1.40 (6)	13.60±1.01 (6)
Long-tailed males	2.89±0.32 (27)	2.68±0.67 (28)	1.83±1.23 (30)	15.33±0.98 (14)	14.94±1.02 (21)
Statistics					
Three types[b]	$H = 5.39$*	$H = 4.68$*	$H = 1.95$	$H = 1.70$	$H = 4.85$*
WL vs. RL[c]	$U = 73.0$	$U = 81.0$	$U = 92.5$	$U = 13.5$	$U = 41.5$
WL vs. RS[c]	$U = 47.0$	$U = 43.5$	$U = 45.0$	$U = 7.0$	$U = 4.0$*
RL vs. RS[c]	$U = 65.5$*	$U = 65.0$*	$U = 91.5$	$U = 22.5$	$U = 22.0$
Long-tailed vs. RS[c]	$Z = 2.15$*	$Z = 2.09$*	$Z = 1.28$	$U = 29.5$	$Z = 2.16$*

a The number of nestlings was counted when nestlings were hatched.
b The number of fledglings was counted one day before the nestlings fledged.
c The number of nestlings which had not decreased from 5 days to 9 days was used as brood-sized when the body-mass measured.
d Kruskal-Wallis tests were used for the comparisons among pairs of three types of males. Statistics were represented by *H*.
e Mann-Whitney *U*-tests were used for the comparisons between two following the sequential Bonferroni method. Statistics were represented by U (n_1<20, n_2<20) and Z (n_1>20, n_2<20).
* P < 0.10.

were no significant differences in the clutch-sizes, number of nestlings and fledglings between females which paired with WL males and those paired with RL males (Mann-Whitney *U*-test: clutch size: $U = 73.0$, n.s.; number of nestlings: $U = 81.0$, n.s.; number of fledglings: $U = 92.5$, n.s.; Table 3). However, the clutch-sizes and the number of nestlings of females paired with long-tailed males were larger than those of females paired with RS males (Mann-Whitney *U*-test: clutch size: $Z = 2.15$, $P < 0.10$; number of nestlings: $Z = 2.09$, $P < 0.10$; Table 3). No significant difference was found in the number of fledglings between long-tailed pairs and RS pairs (Mann-Whitney *U*-test: $Z = 1.28$, n.s.; Table 3).

When the brood-size was two, body-masses of nestlings did not differ among pairs in relation to type of male parent (Kruskal-Wallis test: $H = 1.70$, df = 2, n.s.; Table 3). However, there were significant differences in nestling body-masses among pairs in relation to type of male parent when brood-size was three (Kruskal-Wallis test: $H = 4.85$, df = 2, $P < 0.10$; Table 3). Body-masses of nestlings did not differ between WL pairs and RL pairs in either brood-size (Mann-Whitney *U*-test: brood-size two: $U = 13.5$, n.s.; brood-size three: $U = 41.5$, n.s.; Table 3). However, long-tailed pairs had heavier nestlings than RS pairs when brood-size was three (Mann-Whitney *U*-test: $Z = 2.16$, $P < 0.10$) while there was no difference when brood-size was two (Mann-Whitney *U*-test: $U = 29.5$, n.s.) (Table 3). It seemed that RS pairs did not feed nestlings as well when there were three.

DISCUSSION

Ages in relation to male colour types. - In many bird species, the egg laying date and the clutch-size are affected by the age of the female (Kittiwake *Rissa tridactyla*: Coulson & White, 1958; Tree Swallow *Iridoprocne bicolor*: De Steven, 1978; Great Tit *Parus Major*: Harvey et al., 1979; Perrins & McCleery, 1985; Meadow Bunting *Emberiza cioides*:

Yamagishi, 1981; Song Sparrow *Melospiza melodia*: Nol & Smith, 1987; Klomp, 1970, for summary). Young females tend to start breeding later, and have smaller clutch-sizes, than older females. The age of their mate also affects breeding activity such as the egg-laying date and the number of fledglings (Harvey et al., 1979; Curio, 1983; Perrins & McCleery, 1985). This is thought to be associated with greater efficiency in finding food and courtship feeding of old males. However, in some species, the clutch-size is not affected by the age of the male (Yamagishi, 1981; Perrins & McCleery, 1985). Young females lay smaller clutches than old females regardless of the age of their mates. In short, clutch-size is influenced by the age of the female parent, not by the age of the male parent in those species. In the present study, we could not assess the age of the female Asian Paradise Flycatcher. However, we found that females paired with RS males laid their first egg later, and had smaller clutch-sizes, than females paired with long-tailed males. Males do not feed their mates before egg laying in this species, so the age of the male may not affect the clutch-size. As egg laying dates are influenced by the age of both parents, but clutch-size by the females' age only, this suggests that females paired with RS males may be young individuals.

In some field guides, it is said that the young male Asian Paradise Flycatcher is rufous-coloured, and has short tail feathers like female (Ali & Ripley, 1972; Glenister, 1971; Lekagul & Round, 1991). Ali & Ripley (1972) stated that rufous-coloured males often breed before acquiring long tail feathers. We found that RS males bred, had shorter wings than long-tailed males, as well as starting to breed later than long-tailed pairs. Nestlings of RS pairs in broods of three were lighter than those of long-tailed pairs. The body-mass of nestlings of young parents tends to be lower than that of old parents in some other birds (Red-winged Blackbird *Agelaius phoeniceus* and Yellow-headed Blackbird *Xanthocephalus xanthocephalus*: Crawford, 1977; Willow Ptarmigan *Lagopus lagopus*: Hannon et al., 1988). Thus our results support the suggestion in the field guides that RS males are young birds. The facts that white-coloured males with short tail feathers were not seen and that the plumage of all nestlings and fledglings was rufous, also support this conclusion.

In summary, both RS males and their mates seem to be younger individuals than WL males, RL males and their mates.

RS males resemble females, so it can be said that the plumage colouration of RS males is a kind of delayed plumage maturation though the adaptive significance of this colouration is not known.

Exaggerated ornaments. - It has been difficult to explain why males with exaggerated ornaments occur in monogamous bird species, because most males should be able to acquire a mate. Males would seem not to enhance their fitness substantially by possessing exaggerated sexual ornaments in socially monogamous species. Darwin (1871) proposed a theory for sexual selection in monogamous species based on the idea that the females in best condition will be the first to breed, and they will have the choice of many males. If females have a preference for certain male traits or characters, these conditions lead to higher reproductive success for preferred males. Thus male sexual ornaments may be maintained by female mate choice even in socially monogamous species. This theory was supported theoretically (e.g., Fisher, 1958; O'Donald, 1972; Price et al., 1988; Kirkpatrick et al., 1990). It seems that the breeding performance of the Asian Paradise Flycatcher support Darwin's theory, as the mates of long-tailed males lay eggs earlier, have larger clutches and rear heavier young than the mates of short-tailed males. If there is a preference for male tail-length among females, males' long tail feathers can evolve even in this monogamous species. The fittest females come into breeding condition first, and they can make the best choice among the males, and mate with the most attractive (namely long-tailed) males. When less fit females attain sexual maturity, only less attractive (namely RS) males are left unpaired, so they have to mate with these less attractive males.

There are some other explanations for the evolution of male sexual ornaments in monogamous species such as weak polygyny (Gowaty, 1985) and extra-pair fertilizations (Møller, 1988). From our observations, weak polygyny is not likely to occur because both male and female take part in nest building, incubation, brooding and feeding of the young earnestly. Extra-pair copulations could possibly occur though we did not find any evidence. In the Madagascar Paradise Flycatcher *Terpsiphone mutata*, some males were observed to intrude into the neighbouring territory just before and after the egg laying period of the neighbours (Mizuta, 1996). This is thought to be a circumstantial evidence for extra-pair copulations. Some flight techniques such as the high-speed dives or manoeuvrability for insect hawking may constrain the development of tail elongation (Evans & Thomas, 1992; Balmford et al., 1993; Winquist & Lemon, 1994). This manoeuvrability is very important for foraging in the Asian Paradise Flycatcher, so the elongated tail feathers could act as a handicap, or at least a good measure of male quality. Young birds are not skilled and cannot survive with this handicap. In some species there is an evidence that juvenile or inexperienced birds are less efficient at obtaining food than adults or more experienced individuals (e.g., Recher & Recher, 1969; Davies & Green, 1976; Gochfeld & Burger, 1984; Breitwisch et al., 1987). The Asian Paradise Flycatcher usually capture aerial insects by flycatching or hovering. Such foraging techniques require high skill as mentioned in the study of the Spotted Flycatcher *Muscicapa striata* (Davies, 1976).

Two colour types in males. **-** There were no differences in egg laying dates and clutch-sizes between WL pairs and RL pairs. Only the tail-length and the width of growth-bar on tail rectrix were different. WL males had longer tail feathers and wider growth-bar than RL males. The width of growth-bar indicates the nutritional status when the rectrix is growing (Grubb, 1989). Thus, WL males may have some nutritional advantages over RL males when the rectrices grow. One possible reason for this difference is that WL males are more skillful in foraging than RL males. If WL males are more skillful in foraging than RL males, WL males may be older than RL males. But this explanation is still uncertain.

Riley (1938) considered the long-tailed, rufous-coloured males as young adults and the white-coloured males as full adults. Ali & Ripley (1972) also mentioned that rufous males were young individuals (up to three years) and white males were old ones (four years or more) in the Indian subspecies. However, Salomonsen (1933) considered rufous and white males as genetically determined colour morphs. In male Madagascar Paradise Flycatcher *Terpsiphone mutata*, some individuals change colour from rufous to white when they are three years old, while others remain rufous (Mizuta, unpubl. data, but see also Yamagishi et al., 1992). In this study, we could not identify the cause of colour dimorphism in male Asian Paradise Flycatcher. Both age and genetic difference are possible to explain this colour dimorphism in males. More intensive study is needed to clarify the cause of colour dimorphism and its adaptive significance in Paradise Flycatchers.

ACKNOWLEDGEMENTS

We are very grateful to Dr. Pilai Poonswad and the staff of the Hornbill Project for their kind invitation to Thailand and support for the study. We thank Messrs. Philip D. Round, Uthai Treesucon and the members of Khao Nor Chuchi Lowland Forest Project, which is supported by the Birdlife International, for their cooperation in the field research. We also thank Mr. Tasanet Petkhong, the chief of Khao Pra-Bang Khram Wildlife Sanctuary, for the research permission. Many thanks are offered to Drs. Takeo Kawamichi, Masanori Kohda, Eiichiro Urano, Masanobu Hotta, Michio Imafuku, Akira Mori and the members of the Laboratory of Animal Sociology in Osaka City University and the Laboratory of Ethology in Kyoto University for their useful comments through many discussions. This study was partly supported by a grant-in-aid of Shimizu Foundation in the Ornithological Society of Japan.

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