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THE BREEDING BIOLOGY OF THE ASIAN PARADISE FLYCATCHER *TERPSIPHONE PARADISI* IN KHAO PRA-BANG KHRAM WILDLIFE SANCTUARY, SOUTHERN THAILAND

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ABSTRACT

The breeding biology of the Asian Paradise Flycatcher *Terpsiphone paradisi* was studied at Bang Tieo area, in Khao Pra-Bang Khram Wildlife Sanctuary, Krabi Province, southern Thailand, from March–July of 1993 and 1994. Three types of male were observed in this study area: white-plumaged males with long tails (WL), rufous-plumaged males with long tails (RL), and rufous-plumaged males with short tails (RS). Each male type was found breeding. They started their breeding attempts in mid-March. Both males and females incubated eggs and fed the young. Various parts of nests were measured and there were no differences in characteristics among nests of these three male types. RS males started their breeding attempts later than both long-tailed males. The clutch size of females paired with RS males was smaller than that of females paired with long-tailed males. When the brood size was three, the body weight of nestlings of long-tailed males was found to be heavier than that of RS males. RS males had significantly smaller wing and tail length, and lighter body weight, than long-tailed males. These findings indicate that RS males were younger than long-tailed males. The elongated central tail feathers of RL males were significantly shorter than those of WL males. It was thought that WL males are older than RL males, but the reason for colour dimorphism in this species is still unknown.

INTRODUCTION

The genus *Terpsiphone* (Monarchinae) is widespread in Asia and Africa. There are 12 species in this genus, and in most species males have longtail feathers and plumage dimorphism (PETERS, 1986).

The Asian Paradise Flycatcher *Terpsiphone paradisi* is distributed from Russian Turkestan east through India, Sri Lanka, north-central and eastern China, Korea, and Indochina, south and east through the Malay archipelago to Sumba and Alor islands (MAYR & COTTRELL, 1986). It inhabits evergreen and mixed deciduous forests, secondary growth, from the plains to 1,500 m (LEKAGUL & ROUND, 1991). These flycatchers feed mainly by hawking insects in the air, and they are common residents in southern Thailand. There are 16 subspecies in these geographical areas (OWEN, 1963; PETERS, 1986). OWEN (1963) determined the geographical trends by examining relative frequency of occurrence of rufous and white males by examining the specimen occurrence in several museums. The ratio of occurrence of rufous and white long-tailed male specimens appears to vary geographically.

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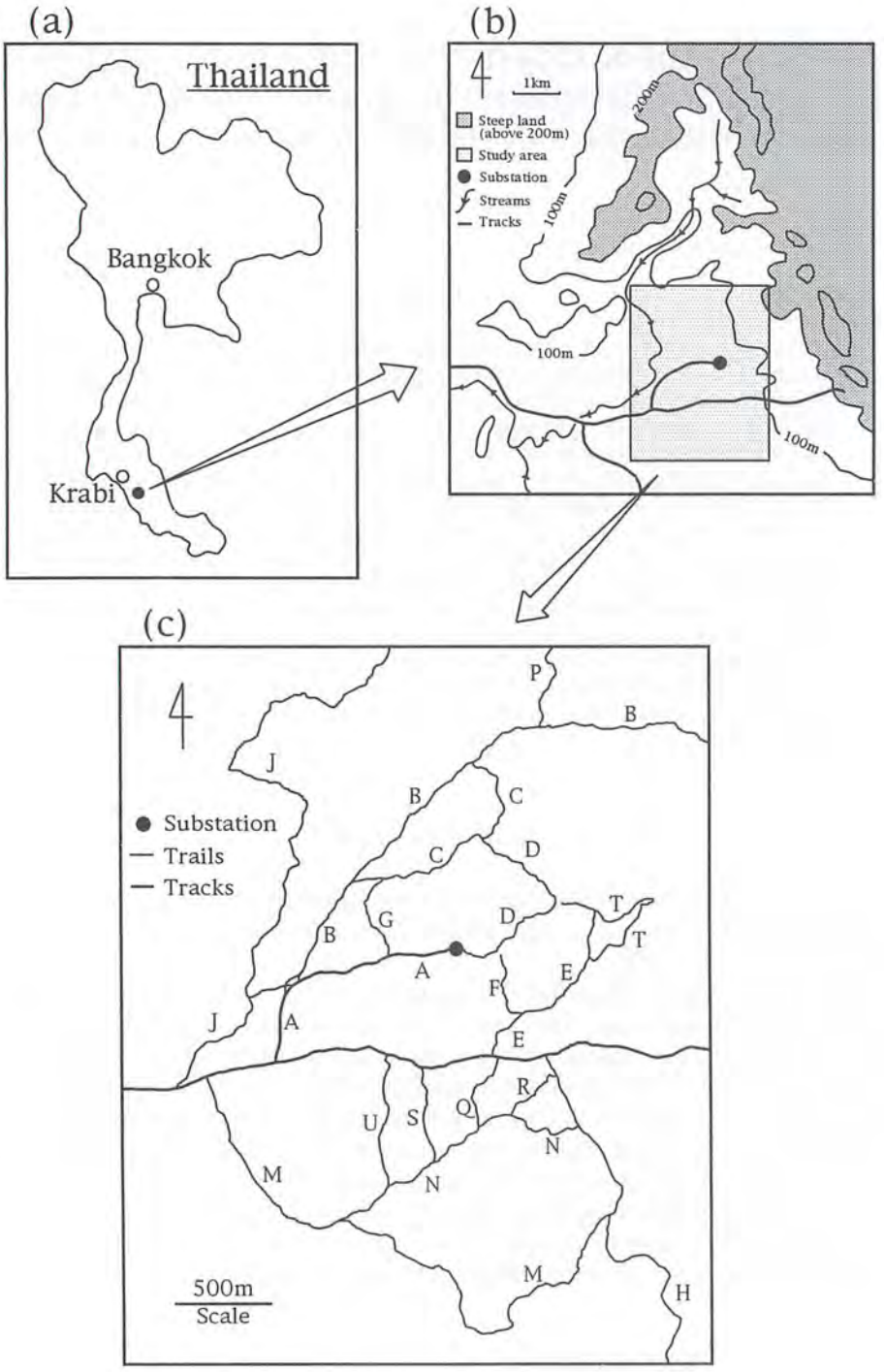

Figure 1. Maps of the study area. (a) Thailand. (b) Khao Pra Bang Khram Wildlife Sanctuary. (c) Bang Tieo study area.

Adult males have either predominantly bright rufous upper parts or predominantly white. In both colour types of adult males, the two central tail feathers are greatly elongated and form streamers. Long-tailed rufous males are generally devoid of shaft streaks on the wing and tail feathers, which in white males are black. Young males are rufous and have short tails. Females also have rufous upper parts and short tails (OWEN, 1963). Some authors (e.g. SALOMONSEN, 1933) consider rufous and white males as distinct colour forms or çcolour phasesé, while others (e.g. RILEY, 1938) consider the rufous males to be young adults and the white males full adults. With respect to this problem, OWEN (1963) suggested some explanations. First, two types of plumage colour of long-tailed males could be a genetic polymorphism; second, rufous and white males could be different ages, the long-tailed rufous males moulting into white plumage when they grow older; third, each of the above explanations could be true for some species; and fourth, the two differently coloured males could in fact be two sibling species. No one has ever studied the plumage dimorphism of this paradise flycatcher in the wild, so reasons for this dimorphism are not yet exactly known.

In this study, I conducted field research in a forest in southern Thailand, and report some basic information about the breeding biology of the Asian Paradise Flycatcher, particularly with respect to the colour dimorphism in males.

STUDY AREA

The field work was conducted at Bang Tieo, in Khao Pra-Bang Khram Wildlife Sanctuary, Krabi Province, southern Thailand (8°10"N and 98°80"E, maximum elevation of 650 m) (ROUND & TREESUCON, 1992) (Fig. 1) from March–July in 1993 and 1994. The vegetation is mainly constituted by small remnant patches of lowland rain forest. More than 290 species of birds have been recorded in the area. Most of the plant species are pioneer or secondary growth species due to the practice of wood cutting 30 or 40 years ago (ROUND & TREESUCON, 1992). There is a network of nature trails in this study area (Fig. 1), so it is rather easy to walk around the forest. There are many small streams in the forest, but some of them are dry when rain stops. In this area, the rainy season starts in April and ends in October or November. However, it does not rain every day, but once it does, it rains very hard. The dry season is the rest of the year. The breeding season of most birds here is synchronised with the rainy season.

METHODS

Identification of males and females.— Males were classified by their plumage colour and tail length. White and rufous-plumaged males with long tails were referred to as "WL male" and "RL male" respectively, whereas rufous-plumaged males with short tails were referred as "RS male" (Fig. 2). In some cases, WL males and RL males were lumped together and are called "Long-tailed males". All types of males had bright-blue eye-rings. Females resembled RS males, but their eye-rings were not as bright as of males and were used to distinguish between RS males and females.

Nest searching.—I hiked in the forest from 0600–1200 hours and from 1600–1800 hours almost every day, from early March to mid-July. I walked along the nature trails in the study area searching for nests of the birds or if I heard a call of the flycatcher, I follow the bird. If it was a male, I identified the type (mentioned above). When I found a nest, I inspected its contents. Once nests were found, I observed each one every day.

Measurements of a nest.—Various parts of nests and nest trees were measured after the chicks fledged or disappeared before fledging. Measurements included the nest height above the ground, diameters of nest (inner and outer), depth of nest, nest tree height, trunk diameters of nest tree (at the base, breast height, and at the nest), number of forks at the nest, number of trees around the nest (within 10 x 10 m). These trees were classified by three categories of diameters at breast height (DBH). The species of nest tree were identified.

Breeding stages.—I checked the morph of the male at each nest. All nests were inspected every day to certify the dates of laying, hatching and fledging. The breeding stages of the nest were divided into three periods: nest building, incubation and brooding. The nest building period is defined as when the nest was obviously under construction, and incubation and brooding periods are defined as the times when there were eggs or chicks in the nest, respectively. The incubation period is determined from the day on which the first egg was laid until one day before hatching. The brooding period is determined from the day on which the first egg hatched until fledging. When I found a nest with no egg and/or chick, and eggs did not appear after more than two weeks, I considered the nest as being predated and abandoned. I also recorded the number of eggs and/or chicks in the nest. Chicks were weighed when they were 9 days old, one day before fledging (see below).

Nest observation.— To minimise disturbances to the birds' activities during the brooding period, all nests were observed from an observation hide 10–20 m from the nest using a spotting scope (30x) or a pair of binoculars (7x). I divided the brooding period into two parts: early brooding period (from hatching to 5 days old) and late brooding period (from 6 days old to fledgling). To observe late brooding periods, I spent 90 minutes at each nest during the mornings of 1994. Total observation time for 14 nests was 1,260 minutes. Frequency of feeding behaviour was recorded during the 90 minute periods. Data of all three male types were pooled due to insignificant differences of feeding rates. I then classified the data on feeding rates by brood sizes.

Capture, linear measurement and marking of birds.— Adults: Adult birds were captured in front of the nest using mist nets. This was performed during the late brooding period, otherwise it was too risky for nest abandonment. For individual identification, a captured bird was marked with an aluminium ring on the right leg and four colour rings (two rings on each leg). Then the following measurements were taken: length of wing, tail, tarsus and bill and body weight. Tail length was taken as the length of the longest of the two central feathers. **Chicks:** Chicks were marked at the nest with an aluminium ring and four colour rings in the same way as adults when they were 9 days old. The criterion used in selection of chicks at this age was tarsus length, as the leg must be long enough to carry all the rings. Body weights of chicks were also taken at this age. To prevent parent birds from being disturbed, marking and weighing were done during their absence.

RESULTS

Breeding Biology

Types of breeding male

Three types of male Asian Paradise Flycatcher were observed in the study area, namely, WL, RL and RS males (Fig. 2). Each male type was found in breeding condition. No white male with a short tail was observed.

Characteristics of nests

A total of 31 and 57 nests, including abandoned or predated nests, were found in 1993 and 1994, respectively. Measurements of the nests and nest trees are shown in Table 1. Nests were built on a fork of the tree. The height of the nests was less than 2 m. Nests were open with a deep bowl-shape. The nest materials were finely interlaced twigs and dried grass blades, reinforced with mosses and spider webs. Fine fibre-like materials lined the inside of the nest, on which the eggs were laid. There were no differences in nest characteristics among nests of the three types of males (Kruskal-Wallis test: all n.s.) (Table 1). The nest trees were small with a mean height of less than 3 m (Table 1). In 1993, 25 out of 31 species of nest trees were identified (Table 2). Some trees were used more commonly than others: six nests were built on *Schima wallichii,* three on *Phyllanthus oxyphyllus* two each on *Vatica lowii* and *Mallotus subpeltatus;* 12 other species were used only once.

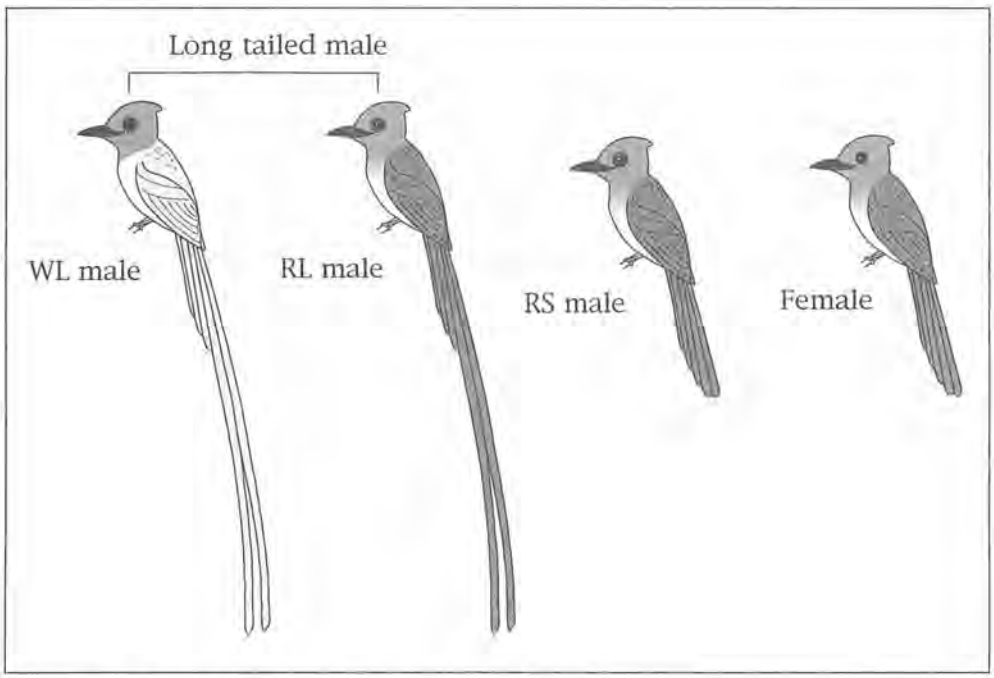

Figure 2. Three types of male and female Asian Paradise Flycatcher.

Table 1. Measurements of nests and nest trees obtained in two years' study. bh = breast height, DBH = diameter at breast height.

Male type		Nest characteristics						Nest tree characteristics				Number of forks at the nest	Number of trees in a plot (10x10m) around the nest, in size classes by DBH (cm)		
		height (cm)	diameter (cm)				depth (cm)	height (cm)	trunk diameter (cm)						
			Long diameter		Short diameter				at base	at bh	at nest		<5	5–30	>30
			Outer	Inner	Outer	Inner									
All males	Range	118–297	7.8–10.3	6.1–7.7	6.4–8.5	4.8–6.5	2.6–3.8	157–389	1.0–2.9	0.6–1.7	0.5–1.6	2–3	3–112	1–28	0–4
N=44	Mean	170.6	8.6	6.8	7.3	5.6	3.1	240.2	1.9	1.1	0.9	2.1	59.2	11.3	1.1
	S.D.	48.7	0.5	0.4	0.6	0.3	0.3	55.3	0.4	0.4	0.3	0.3	22.5	5.8	1.3
Long-tailed	Range	118–296	7.8–10.3	6.1–7.7	6.4–8.5	4.8–6.5	2.6–3.8	157–389	1.0–2.9	0.7–1.7	0.5–1.6	2–3	18–112	4–28	0–4
males	Mean	167	8.6	6.8	7.2	5.6	3.1	239.4	1.9	1.1	0.9	2.1	61.7	12.0	1
N=30	S.D.	50.4	0.5	0.5	0.5	0.4	0.4	59.7	0.4	0.4	0.3	0.3	20.7	6.0	1.3
WL male	Range	118–296	8.1–9.5	6.1–7.7	6.4–8.5	5.3–6.5	2.6–3.8	157–389	1.0–2.3	0.7–1.7	0.7–1.6	2–3	1889	4–18	0–3
N=12	Mean	168.9	8.6	6.7	7.3	5.5	3.3	244.6	1.9	1.1	1	2.1	57.1	10.6	0.9
	S.D.	46.3	0.5	0.6	0.7	0.3	0.4	55.4	0.3	0.3	0.3	0.3	19.9	4.5	1.1
RL male	Range	118–297	7.8–10.3	6.3–7.6	6.4–7.9	4.8–6.2	2.6–3.5	157–350	1.1–2.9	0.7–1.5	0.5–1.4	2–3	26–112	5–28	0–4
N=18	Mean	165.7	8.6	6.9	7.2	5.6	3.0	235.9	1.9	1.1	0.8	2.1	64.8	12.9	1.1
	S.D.	54.3	0.6	0.4	0.5	0.4	0.3	63.8	0.4	0.4	0.3	0.3	21.2	6.7	1.5
RS male	Range	125–274	8.1–8.9	6.1–7.0	6.9–8.4	5.4–6.3	2.6–3.5	178–342	1.1–2.5	0.6–1.7	0.6–1.3	2–3	3–96	1–22	0–4
N=14	Mean	178.4	8.6	6.6	7.7	5.7	3	241.9	1.9	1.1	1.0	2.1	53.7	9.9	1.3
	S.D.	45.6	0.3	0.3	0.4	0.3	0.3	46.5	0.5	0.3	0.2	0.3	26.0	5.6	1.3

Table 2. Families and species of the nest trees of Asian Paradise Flycatchers studied in 1993 at Bang Tieo. ? = predated or abandoned nest. * RL male replaced WL male.

Nest No.	Type of male	Nest tree	
		Family	Scientific name
N1	WL-RL*	Pandaceae	*Galearia fulve*
N2	?	Euphorbiaceae	*Phyllanthus oxyphyllus*
N3	WL	Guttiferae	*Cratoxylon maingayi*
N4	WL	Rubiaceae	*Ixora cibdela*
N5	?	Theaceae	*Schima wallichii*
N6	WL	Dipterocarpaceae	*Vatica lowii*
N7	RL	Euphorbiaceae	*Phyllanthus oxyphyllus*
N8	WL	Theaceae	*Schima wallichii*
N9	WL	Papilionaceae	*Derris sp.*
N10	?	Violaceae	*Rinorea sp.*
N11	RL	Apocynaceae	*Wrightia dubia*
N12	RS	Theaceae	*Schima wallichii*
N13	RS	Rubiaceae	*Psychotria sp.*
N14	RL	Euphorbiaceae	*Glochidion sp.*
N15	RS	Euphorbiaceae	*Baccaurea parviflora*
N16	RS	Euphorbiaceae	*Phyllanthus oxyphyllus*
N17	?	Unknown	
N18	?	Dipterocarpaceae	*Vatica lowii*
N19	?	Unknown	
N20	RS	Myrtaceae	*Syzygium operculata*
N21	RL	Euphorbiaceae	*Mallotus subpeltatus*
N22	RS	Dilleniaceae	*Dillenia obovata*
N23	?	Verbenaceae	*Vitex pinnata*
N24	WL	Euphorbiaceae	*Aporosa aurea*
N25	?	Theaceae	*Schima wallichii*
N26	?	Theaceae	*Schima wallichii*
N27	?	Myrtaceae	*Syzygium oleina*
N28	?	Euphorbiaceae	*Mallotus subpeltatus*
N29	?	Theaceae	*Schima wallichii*
N30	?	Rutaceae	*Micromelum minutum*
N31	?	Theaceae	*Eurya acuminata*

* RL male replaced WL male

Egg laying and incubation

The breeding season of the Asian Paradise Flycatcher starts in early March and ends in mid-July. Dates of first egg laying and fledging of chicks are shown in Figs. 3a and 3b, respectively. The distribution of egg laying date and fledging date did not differ between the two years when nests of the three types of males were pooled (Mann-Whitney U-test: $Z = -0.52$, $n = 16,30$; n.s.). There was a significant difference among dates of first egg laying of the three types of male (Kruskal-Wallis test: $H = 14.67$, $n = 12, 21, 13$; $p = 0.0007$). WL male pairs laid first eggs earlier than did RS male pairs (Mann-Whitney U-test: $Z = -3.16$, $n = 12, 13$; $p = 0.0016$), and RL male pairs also laid first eggs earlier than RS male pairs (Mann-Whitney U-test: $Z = -3.35$, $n = 21, 13$; $p = 0.0008$). When the first egg-laying dates of long-tailed males were pooled, they proved to be significantly earlier than those of RS males (Mann-Whitney U-test: $Z = -3.72$, $n = 33, 13$; $p = 0.0002$). There was no significant difference in date of first egg laying between pairs of the two long-tailed male types (Mann-Whitney U-test: $Z = -1.16$, $n = 12, 21$; n.s.). There was also no difference in fledging date between pairs of the three male types. This might be affected by a too small sample size.

The incubation period lasted 14–16 days (mean 14.90 ± 0.74 s.d., $n = 10$) and nestling period lasted 9–12 days (mean 10.42 ± 1.00 s.d., $n = 12$). When I found a nest for which I was unable to confirm egg laying and hatching dates, I determined the laying date by counting 15 days backwards from hatching and the hatching date by counting 10 days backwards from fledging.

Clutch size and young

The numbers of eggs and young are shown in Table 3. The clutch size was usually three and sometimes two (mean 2.79 ± 0.41 s.d., $n = 39$). The eggs/chicks decreased in number as the breeding period proceeded due to cracking and/or crushing. The number of eggs and nestlings of long-tailed male pairs were significantly larger than those of RS male pairs (Mann-Whitney U-test: number of eggs: $Z = -2.15$, $n = 27, 12$; $p = 0.0313$; number of nestlings: $Z = -2.09$, $n = 28, 12$; $p = 0.0364$). There was no significant difference in the number of eggs and the young between WL and RL male pairs (Mann-Whitney U-test: number of eggs: $Z = -1.11$, $n = 10, 17$; $p = 0.0313$; number of nestlings: $Z = -0.57$, $n = 10,18$; $p = 0.0364$) (Table 3; Fig. 4). Body weight of the young differed with brood size. When the brood size was two, body weights of the young were slightly heavier than when the brood size was three, but the difference was not significant (Mann-Whitney U-test: $Z = -1.44$, $n = 20, 27$; n.s.). All types of male pairs could raise young with similar body weight when the brood size was two (Kruskal-Wallis test: $H = 1.49$, $n = 4, 10, 6$; n.s.) (Fig. 5). In contrast, when the brood size was three, body weights of the young differed with male type. Long-tailed male pairs raised significantly heavier young than RS male pairs (Mann-Whitney U-test: $Z = -2.16$, $n = 21, 6$; $p = 0.0306$) (Fig. 5). These results indicate that RS male pairs could not raise the young well if the brood size exceeded two. However, sample sizes were too small to make a definite conclusion.

Behaviours during late brooding period

The total feeding rate by both parents increased with brood size (Fig. 6). Males contributed significantly to the increases of feeding rate in accordance with the brood size

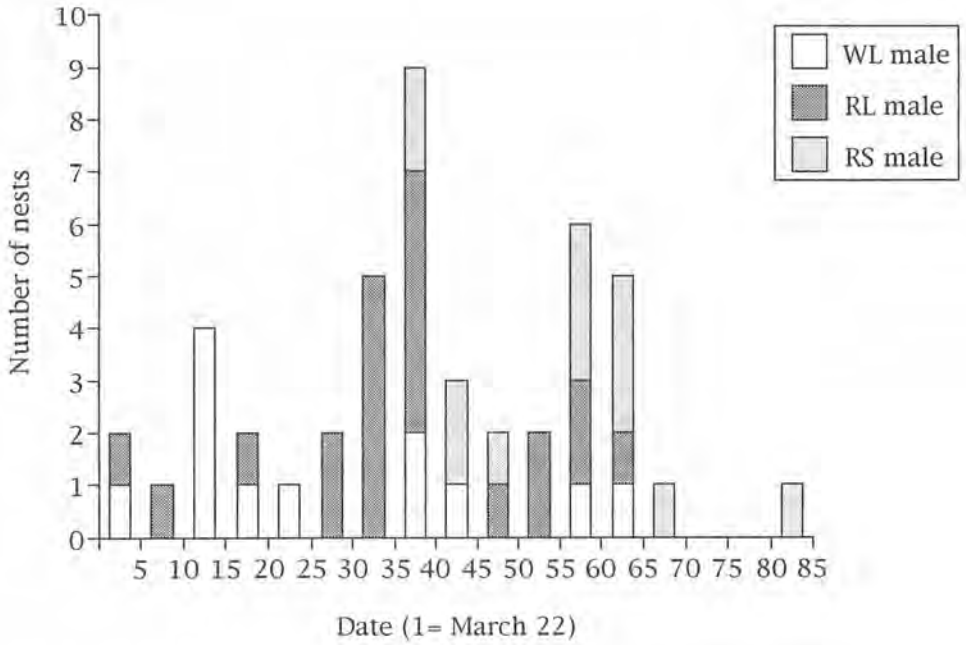

Figure 3a. Two year pooled data of first egg laying dates of three male types (1993 and 1994).

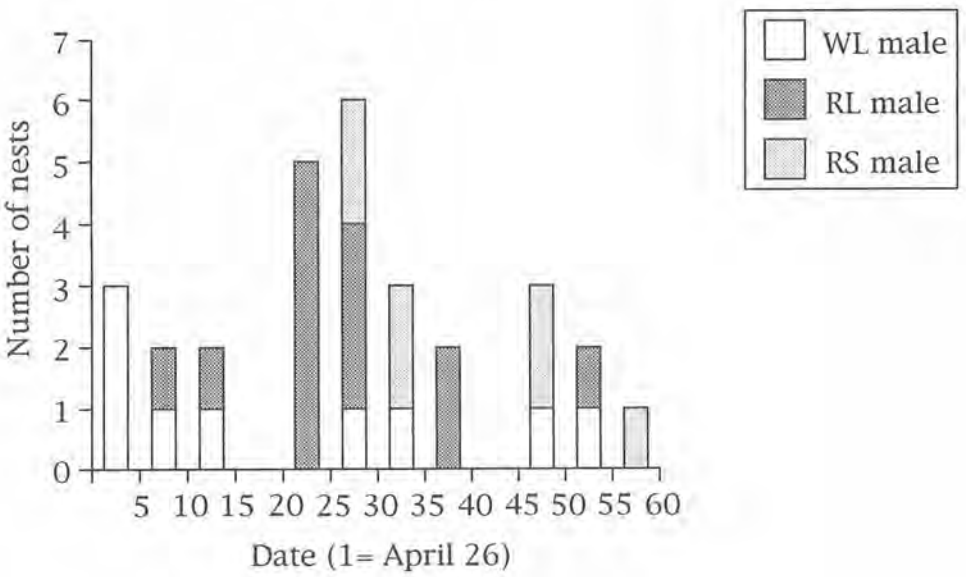

Figure 3b. Two year pooled data of fledging dates of three male types (1993 and 1994).

Table 3. Number of eggs, nestlings and fledglings of three male types. Data pooled from two years' study (1993–1994).

Male type		Number of		
		eggs	nestlings	fledglings
All males	Range	2–3	0–3	0–3
	Mean	2.79	2.50	1.67
	S.D.	0.41	0.85	1.28
	N	39	40	42
Long-tailed males	Range	2–3	0–3	0–3
	Mean	2.89	2.68	1.83
	S.D.	0.32	0.67	1.23
	N	27	28	30
WL male	Range	2–3	0–3	0–3
	Mean	2.80	2.50	2.00
	S.D.	0.42	0.97	1.18
	N	10	10	11
RL male	Range	2–3	2–3	0–3
	Mean	2.94	2.78	1.74
	S.D.	0.24	0.43	1.28
	N	17	18	19
RS male	Range	2–3	0–3	0–3
	Mean	2.58	2.08	1.25
	S.D.	0.51	1.08	1.36
	N	12	12	12

(Kruskal-Wallis test: $H = 7.33$, $n = 3, 5, 6$; $p = 0.0256$), whereas feeding rate by females did not increase significantly with brood size (Kruskal-Wallis test: $H = 1.42$, $n = 3, 5, 6$; n.s.) (Fig. 6). So the total feeding rate per nestling did not differ among different brood sizes. Increases in total feeding rate depended on the male feeding rate.

Size of Males and Females

Body size

Males: Wing, tail, tarsus and bill lengths, and body weight of three types of male are shown in Table 4. The tail of WL male was significantly longer than that of RL male (Mann-Whitney U-test: $Z = -2.87$; $p = 0.0041$) (Table 4). Long-tailed males had significantly longer wings and tails, and heavier bodies, than RS males (Mann-Whitney U-test: wing length: $Z = -3.65$, $p = 0.0003$; tail length: $Z = -3.63$, $p = 0.0003$; body weight: $Z = -2.04$, $p = 0.0418$, $n = 19, 6$) (Table 4).

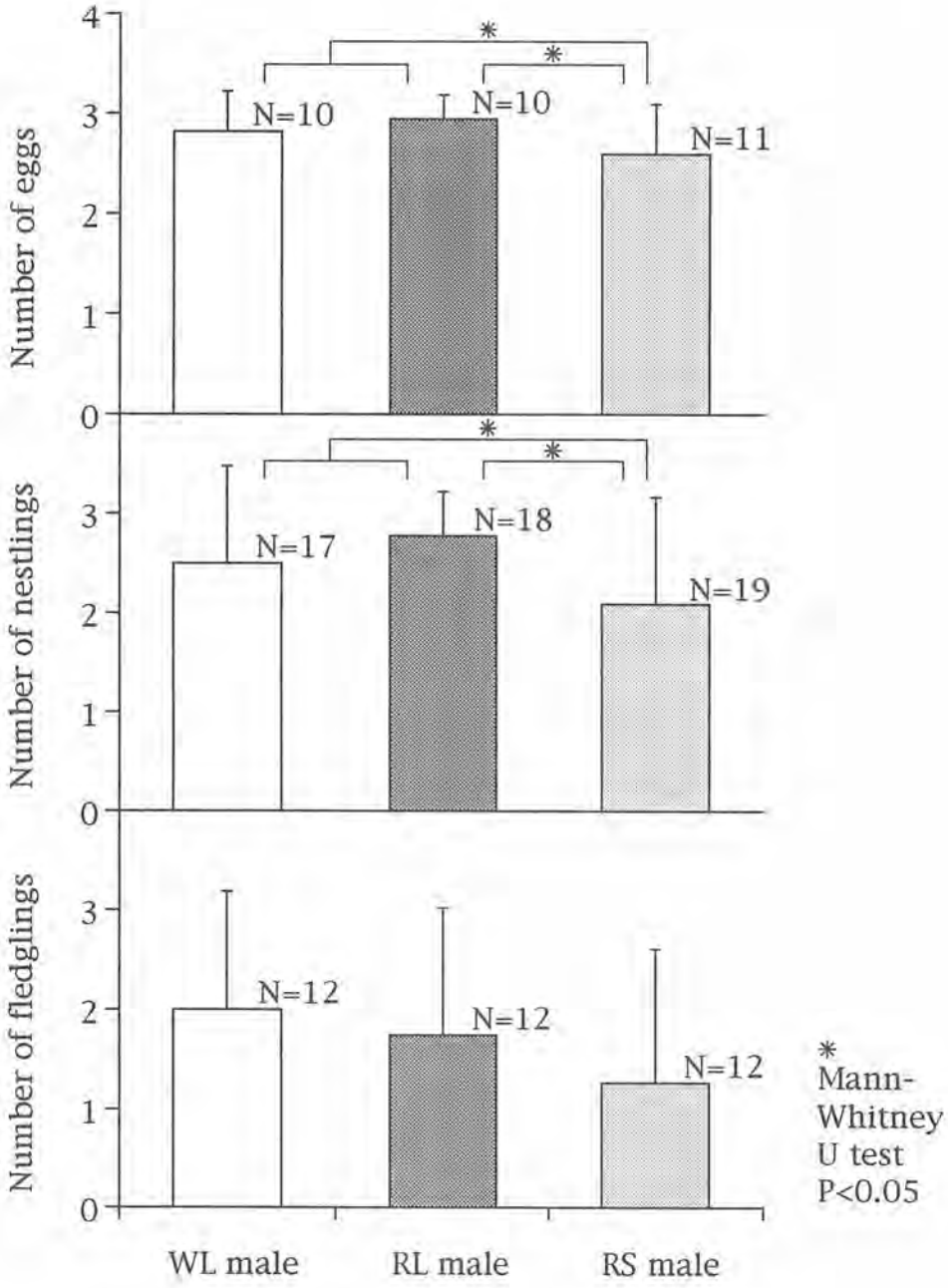

Figure 4. Number of eggs and young in nests of three male types.

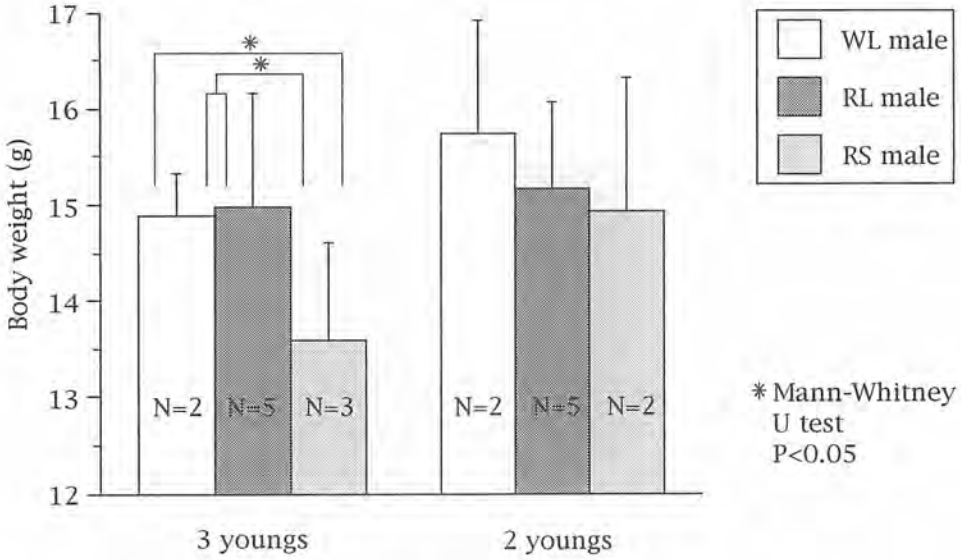

Figure 5. Body weight of nestlings of three male types.

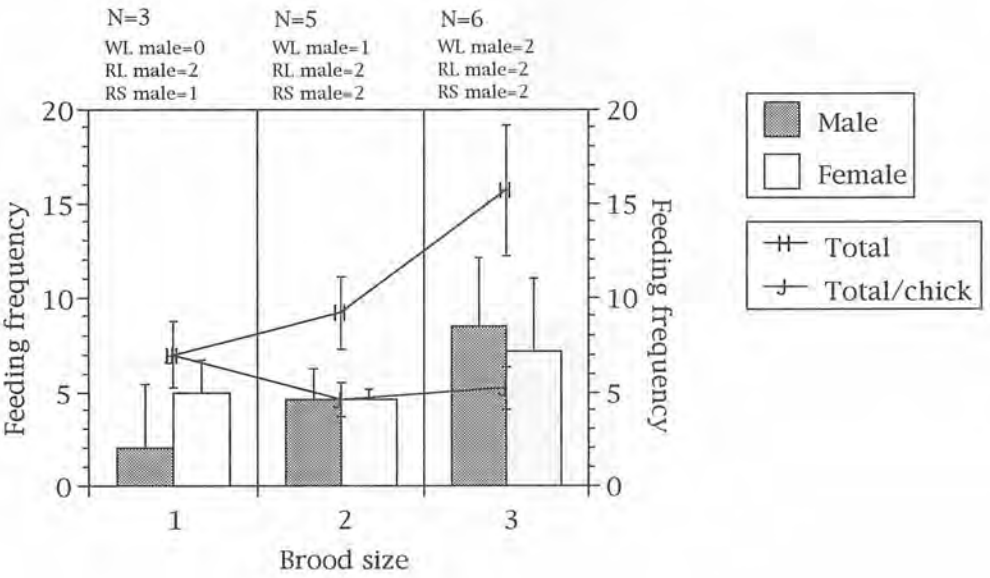

Figure 6. Two year pooled data of frequency of feeding by male and female, with different brood sizes (1993 to 1994).

Table 4. Body measurements of the three male types. Data is pooled from two years' study (1993–1994).

Male type		Wing (mm)	Tail (mm)	Tarsus (mm)	Bill (mm)	Body weight(g)
All males	Range	86.0–95.0	90.5–310.0	18.3–20.8	19.2–23.3	19.1–22.9
(N = 25)	Mean	91.76	206.92	19.38	21.88	20.88
	S.D.	2.6	70.26	0.55	1	1.13
Long-tailed	Range	91.0–95.0	197–310	18.3–20.8	19.2–23.3	19.6–22.9
males	Mean	92.95	242.68	19.43	21.89	21.16
(N = 19)	S.D.	1.41	30.78	0.55	1.07	1.1
WL male	Range	91.5–95.0	240–310	18.3–19.8	21.3–22.4	19.6–22.5
(N = 5)	Mean	92.8	280	19.2	21.62	21.4
	S.D.	1.44	25.85	0.55	0.79	1.17
RL male	Range	91.0–95.0	197–266	18.8–20.8	19.2–23.3	19.7–22.9
(N = 14)	Mean	93	229.36	19.51	21.99	21.07
	S.D.	1.45	19.49	0.54	1.17	1.1
RS male	Range	86.0–90.5	90.5–104.0	18.3–20.0	20.9–22.7	19.1–20.9
(N = 6)	Mean	88	93.67	19.22	21.83	20.03
	S.D.	1.73	5.79	0.59	0.79	0.78

Females: Wing, tail, tarsus and bill lengths, and body weight of females which paired with the three types of males were measured. There were no differences among these females. Although wing length and body weight of females paired with RS males were slightly shorter and lighter than those of females paired with long-tailed males, the differences were not significant.

Changing of plumage colouration and pairing

Two RL males ringed in 1993 were recovered in 1994. Although one retained the RL plumage to breed in 1994, the other was found to have changed to the white plumage between seasons.

One female was seen to change mates between the two breeding seasons, pairing with a WL male in 1993 and a RL male in 1994.

DISCUSSION

The breeding biology of the Asian Paradise Flycatcher had not been well studied. This study revealed some differences between long-tailed males and RS males in body

characteristics and in breeding. RS males had smaller body size (wing length and body weight) than long-tailed males. RS males started their breeding attempts later, and the clutch sizes of their mates were smaller than those of the long-tailed males. This is similar to the younger Great Tits *Parus major,* which lay eggs a little later, lay smaller clutches or are less successful in raising their young (KLUIJVER, 1951; PERRINS, 1965). Thus, I am convinced that the RS male Asian Paradise Flycatchers are a younger age group than the long-tailed males. This is due to the fact that I have never seen any white-plumaged, short-tailed males. Moreover, the plumage of all nestlings was rufous, indicating that RS males are probably yearlings.

I could not find any differences in frequency of feeding among the three types of males, but it is possible that the difference in feeding rate between long-tailed males and RS males was a consequence of the larger clutch size. RS males may have had less ability in raising young than long-tailed males whose clutch sizes were larger. It seems that the increase in number of nestlings from two to three may not cost WL males and RL males much, but might considerably cost the RS males. Generally in birds, body weight of the young tends to decrease with increasing brood size (KLOMP, 1970). In the present study, the brood size of the Asian Paradise Flycatcher varied from one to three, and mean body weight of the young when the brood was three was only slightly lighter than when it was two.

I could not specifically determine whether the difference in feeding rate was really influenced by the number of nestlings or by the male type, because the data were pooled due to small sample size. It is possible that the low feeding rate for brood size of one was affected by RS males, and a high feeding rate in brood size of three was affected by WL and RL males. Another explanation is that when the number of nestlings is small, males skimp, but they are eager to feed when the number of nestlings is large, regardless of male type.

My explanation for the two different colour morphs in males of this species has not yet been proven. I could find a difference only in tail length between WL males and RL males, and I found one RL male that turned into a WL male. From these findings, I was convinced that WL males are older than RL males. According to my observations on change of plumage colouration, the sibling species hypothesis proposed by OWEN (1963) can be challenged. I would hypothesize as follows: yearling males possess rufous plumage with short tail feathers and resemble females. Then, by the second year of age the long tail feathers develop, although rufous plumage is retained. Later the rufous plumage may turn to white, although it is unknown at which age the plumage begins to change. Moreover, it is unknown whether the change of colour from rufous to white occurs in all males or only in some individuals genetically predisposed to change (Fig. 7). To investigate the adaptive significance of the plumage dimorphism, it is necessary to collect data with sufficient sample sizes of breeding behaviour, reproductive success, feeding rate and foraging efficiency of individual males.

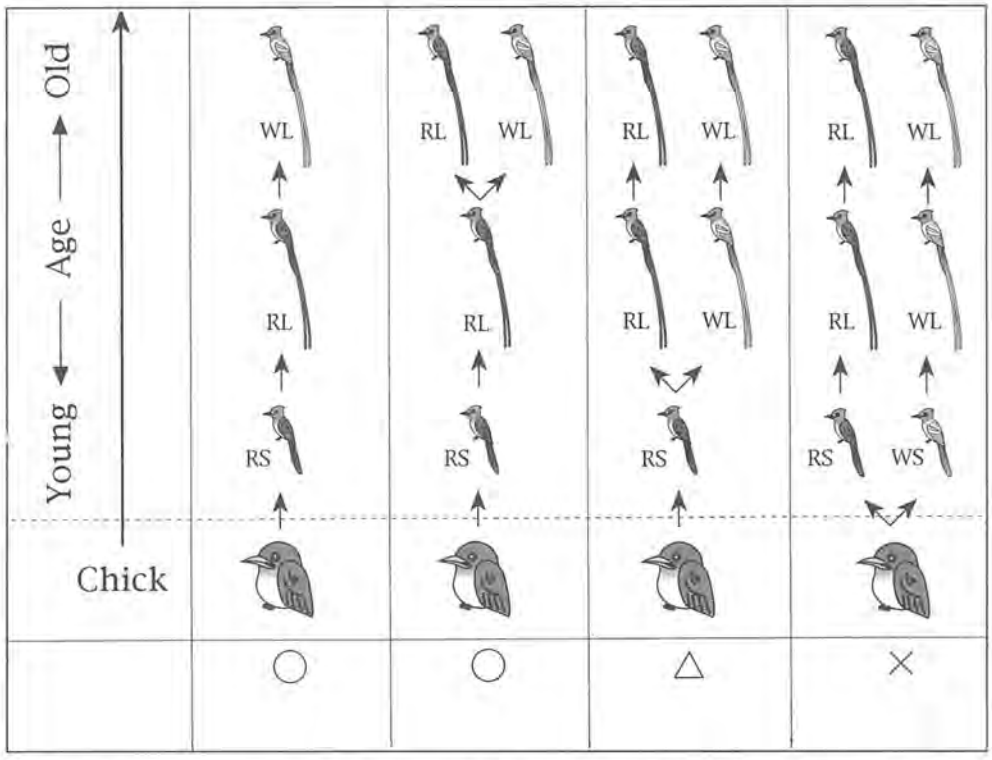

Figure 7. Four possible hypotheses of development of plumage in male Asian Paradise Flycatchers.

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REFERENCES

KLOMP, H. 1970. The Determination of clutch-size in Birds. *Ardea* 58: 1–124.

KLUIJVER, H. N. 1951. The population ecology of the Great Tit. *Ardea* 39: 1–135.

LEKAGUL, B. AND P.D. ROUND 1991. *A Guide to the Birds of Thailand.* Saha Karn Bhaet Co., Ltd., Thailand.

MAYR, E AND G.W. COTTRELL (eds.). 1986. *Check-List of birds of the world: A Continuation of the Work of James L. Peters.* Volume XI. Museum of Comparative Zoology, Cambridge, Massachusetts, U.S.A.

OWEN, D. F. 1963. The rufous and white forms of an Asiatic Paradise Flycatcher, *Terpsiphone paradisi. Ardea* 51: 230–236.

PERRINS, C. M. 1965. Population fluctuations and clutch size in the Great Tit *Parus major. J. Anim. Ecol.* 34: 601–647.

RILEY, J. H. 1938. Birds from Siam and the Malay peninsula in the United States National Museum collected by Drs. Hugh M. Smith and William L. Abbott. *Bull. U.S. Nat. Mus.* 172.

ROUND, P. D. AND U. TREESUCON. 1992. Thung Tieo Nature Trail. Khao Pra Bang Khram Non-Hunting Area. Khao Nor Chuchi Lowland Forest Project, Thailand.

SALOMONSEN, F. 1933. Revision of the group *Tchitrea affinis* Blyth. *Ibis*: 730–745.