Original Article (原著論文)

Bigamous Trios in the Black-winged Stilt *Himantopus himantopus himantopus*: II. Contribution of Members of Trios toward Incubation and Chick-caring

Tamaki Kitagawa*

Abstract. The contribution of each member toward incubation and chick-caring was examined within six bigamous trios of the Black-winged Stilt *Himantopus himantopus himantopus*; three trios with joint-nests, two trios with two-simultaneous-nests, and one trio with three-successive-nests. The study extended over a ten-year period from 1997–2007. In the first joint-nesting trio, composed of two parents and a yearling daughter, only the parents incubated the eggs. In the second joint-nesting trio, composed of three adult birds, all members attended one nest, but the dominant female sometimes drove the subordinate female out of the nest when the latter was incubating. In the third joint-nesting trio, composed of two parents and a yearling daughter, all members participated in incubation cooperatively. In bigamous trios with two-simultaneous-nests, one was composed of two parents and a yearling daughter, and the other composed of a male and two females. All members of these two trios participated in incubation of eggs in both nests. In the bigamous trio with three-successive-nests, composed of a pair and an unrelated female, the male attended all three nests, the dominant female attended the first and third nests, and the subordinate female attended the second and third nests. In a joint-nest situation, it seems to be difficult physically for an individual to incubate all eggs of two clutches laid in a single nest. In two-simultaneous-nests and three-successive-nests, the males performed a greater proportion of incubation in the nests of dominant females than in those of the subordinates. In the Black-winged Stilt, the hatching success of bigamous trios did not differ significantly from that of monogamous pairs. One bigamous trio with a joint-nest, one trio with two-simultaneous-nests, and one trio with three-successive-nests were successful in hatching chicks. In the first two cases all members of the respective trios contributed to defending chick-caring territory. In the trio with two-simultaneous-nests, all members participated in brooding, guarding chicks and sentry activities. Bigamous trios are more successful than monogamous pairs in chick-caring activities.

Key words: A joint nest, Benefit, Bigamous trio, Three-successive-nests, Two-simultaneous-nests.

キーワード: 共同巣, 利益, 二雌トリオ, 継時的三巣, 同時的二巣.

Introduction

Joint nesting is a system of bird reproduction in which two or more females lay their eggs in a single nest (Brown 1987). In the Acorn Woodpecker *Melanerpes formicivorus* (Koenig *et al.* 1995), the Groove-billed Ani *Crotophaga sulcirostris* (Koford *et al.* 1990) and the Pukeko *Porphyrio porphyrio* (Craig & Jamieson 1990), the joint clutch is cared for by all members of the group consisting of females and their mates. Another nesting

Received 18 September 2008, Revised 27 January 2009, 2nd Revision 13 August 2010, Accepted 15 October 2010.

* Soya 2–20–3, Ichikawa, Chiba 272–0832, Japan. Email: tamaki.kitagawa@pure.ocn.ne.jp

system, in which two females lay their eggs in two simultaneous nests, is known as plural breeding (Brown 1987). In the Pukeko, the second nest is sometimes constructed adjacent to the first, and two birds incubate at the same time. These two types of nesting system are rare within cooperative breeders (Craig & Jamieson 1990).

Although the Black-winged Stilt *Himantopus himantopus* generally breeds in monogamous pairs, in which both sexes care for eggs and chicks (Cramp & Simmons 1983, Glutz von Blotzhaim *et al.* 1977, Kitagawa 2009), bigamous trios have been reported within the Japanese population (Kitagawa 2009). These arose when daughters of the previous year did not disperse from their parents, or when postbreeding groups composed of one male and two females had not dissolved prior to the onset of breeding activities during the next breeding season (Kitagawa 2009). In the six bigamous trios documented (trios I, II, III, IV, V and VI; trio III lasted for two breeding seasons), three types of nesting were observed: joint-nesting, two-simultaneous-nesting and three-successive-nesting. In all three types, every member of the trios participated cooperatively in incubating eggs.

In the Black-winged Stilt, 4.7% of total pairs were accompanied by a second female (Kitagawa 2009). This fact suggested that trio formation provides some benefit to the members. If more chicks hatch, or if chick-caring costs of breeding pairs are reduced, the trios may form, even though they occur rarely.

Here, I will describe variation of trios and the contribution of each individual forming the trios to breeding. The cost and benefit of forming trios is then considered in comparison to monogamous pairs.

Methods

I conducted the study at two breeding sites near the boundary of Tokyo Metropolis and Chiba Prefecture, facing Tokyo Bay, central Honshu, from 1985 to 2007 (cf. Kitagawa 2009).

Observations were made from approximately 14:00 to 18:00, every three to five days per week throughout the study years, as described in Kitagawa (2009). Individuals and their dominance status were identified as stated in Kitagawa (2009). Nests of a given trio were named consecutively in order of occurrence as N_A, N_B and N_C. Agonistic behaviors and copulations between individuals were recorded, along with reproductive output, measured as clutch size and number of hatchlings. In the cases of the joint-nest, I estimated how many clutches were contained in the nest by inspecting the number and color pattern of eggs, if possible.

In the Black-winged Stilt, chicks leave the nest within several hours after hatching and can pick up food by themselves (Kitagawa 2009). Therefore, provisioning of chicks is not a parental care activity in this species. To examine the relative contribution to breeding, I analyzed incubation time, brooding time, number of behaviors of guarding chicks or defending the chick-caring territory, and taking-charge time or being-on-sentry time of the chick-caring territory (henceforth 'sentry activity time'). Incubation time throughout the incubation period, brooding time and sentry activity time in the chick-

caring territory of each member of the trios were expressed as minutes per hour. The frequency of behaviors of guarding chicks or defending the chick-caring territory was expressed as number per hour. Incubation activities of trios *III* in 2001, *IV*, *V* and *VI* were recorded continuously with the aid of video cameras, but those of trios *I*, *II*, and *III* in 2000 were observed intermittently. For trio *III* in 2001, I separated data before (284.18 h, 18 days, 31 May–8 June and 10 June–19 July) and after (239.67 h, 16 days, 20 June–5 July) a snake preyed on the eggs of N_A . The latter data was excluded from comparison of statistical calculations, because after that time, all members of this trio showed a marked decrease in their attendance on N_A , and instead assigned almost all of their incubation efforts toward the eggs of N_B . Total observation hours on trios *IV*, *V* and *VI* were as follows: Trio *IV* at N_A , 319.85 h, 22 days, 24 May–14 June, 2002: at N_B , 305.92 h, 21 days, 25 May–14 June; trio *V*, 476.91 h, 32 days, 12 June–13 July, 2006; trio *VI* at N_A , 309.68 h, 24 days, 7–19 June and 21 June–1 July, 2003: at N_B , 156.44 h, 13 days, 7–19 June: at N_C , 155.45 h, 14 days, 2–15 July. The data for N_C of trio *VI* was also excluded from comparison of statistical calculations for the total incubation time at nests, because a chick had hatched out at N_A , and the male and the dominant female attended N_C while taking care of the chick.

Chick-caring activities of trio *IV* were recorded quantitatively, but those of trios *II* and *VI* were observed only intermittently. In trio *IV*, brooding was observed for a total of 26.37 h (9 days, 16 June–1 July, 2002), guarding chicks and defending the chick-caring territory for 49.59 h (18 observation days, 19 June–24 July), and sentry activity in the chick-caring territory for 49.86 h (18 observation days, 19 June–24 July).

I examined whether or not incubation time and chick-caring activities differed in relation to status based on breeding system, sex and social order, using *t*-test and one-way ANOVA. When significant interaction in the result was evident, Scheffe's *F*-test was used for *post hoc* analysis. Additionally, hatching success was examined between monogamy and bigamy (trio), using *t*-test.

Results

1. Reproductive output of monogamous pairs

The average clutch size was $3.36 \pm 0.05SD$ (Kitagawa 2005). Males and females took turns in incubating eggs. In all pairs combined (Table 1), there were no significant differences in the incubation time between males and females (male, $25.95 \pm 5.07SD$ min/h; female, $27.62 \pm 3.84SD$ min/h; *t*-test, $t=1.046$, $P=0.304$, $n=16$), and both sexes incubated for total of $53.57 \pm 4.88SD$ min/h. Of the 574 nests found during 1985–2006, the proportion of failed nests was 296 (51.6%). Flooding and nest predation were the main causes of failure of nests and eggs: 117 (39.5%) and 58 (19.6%), respectively. Desertion occurred in 20 (6.7%) nests and 101 nests disappeared by unknown causes. In 1985–2006 (excluding data of 1991 and 1993), monogamous pairs hatched, on average, $1.29 \pm 1.59SD$ chicks (Table 2).

Table 1. Incubation time among each status.

Breeding system	Sex	Status	Incubation time (Mean $\pm$ SD)	Numbers of observation days
Monogamy	Male	N/A	25.95 $\pm$ 5.07	16
	Female	N/A	27.62 $\pm$ 3.84	16
Bigamy ¹	Male	N/A	25.50 $\pm$ 5.47	4
	Female	Dominant	27.84 $\pm$ 3.56	4
	Female	Subordinate	18.15 $\pm$ 6.53	4

¹: Regarding trio *III* in 2001, data before a snake preyed on the eggs of N_A, are indicated.

In trio *I*, one female disappeared before egg laying and the remaining male and female reproduced monogamously, but data of their incubation time was not included under monogamy.

Table 2. Hatching success.

Breeding system	Trio, Nesting type		Hatchling (Mean $\pm$ SD)	Number of pairs
Monogamy	—		1.29 $\pm$ 1.59	178
Bigamy ¹	—		1.33 $\pm$ 1.75	6
	<i>I</i>	N/A ²	0	1
	<i>II</i>	j	3	1
	<i>III</i> in 2000	j	0	1
	<i>III</i> in 2001	si	0	1
	<i>IV</i>	si	4	1
	<i>V</i>	j	0	1
	<i>VI</i>	su	1	1

¹: the Trio *I* was excluded.

²: Actually, the pair bred monogamously.

j: Joint nest

si: Simultaneous nests

su: Successive nests

2. Description of reproductive behavior in the trios

2-1. The bigamous trio which dissolved after establishing the nesting territory

Trio *I* consisted of a male *A*, and two females *a*₁ and *a*₂. The relatedness of the two females was unknown (Kitagawa 2009). All members engaged in defense of the nesting territory. Female *a*₂ was dominant over female *a*₁, and attacked the latter frequently. Male *A* did not perform agonistic behavior toward *a*₁ or *a*₂. Copulation between *A* and *a*₂ was observed twice, on 11 and 26 April, 1998. At those times *a*₁ was foraging several meters apart from copulating birds and did not respond with any behavior toward the copulating *a*₂. Female *a*₁ was twice observed to induce *A* to copulate by “*splashing water*” (one kind of copulation behavior of females) on 16 and 26 April, but *A* did not respond to her. Female *a*₂ disappeared from the nesting territory and the breeding site on 30 April. On the same day, copulation between *A* and *a*₁ was observed once. Thereafter, *A* and *a*₁ reproduced monogamously.

2-2. Bigamous trios with joint-nests

In three trios (trio *II*, trio *III* in 2000 and trio *V*), each of two females laid a clutch in one joint-nest, respectively. Trio *II* consisted of parents *B* and *b_I*, and a daughter *b_{III}* (Kitagawa 2009). Between 4–7 May, 1999, *b_I* laid four eggs. The parents shared incubation, but incubation by *b_{III}* was not observed until three chicks had hatched on 31 May. On that day, five eggs remained in the nest. Those five unhatched eggs and the nest were deserted by the trio after the three chicks left the nest. The parents defended the nesting territory vigorously against conspecific intruders, and during the incubation period no conspecifics other than *b_{III}* were able to approach the nest. One of five unhatched eggs had a markedly different spot pattern than the other four eggs. From these two observations it was surmised that one egg was the unhatched egg of *b_I*, and the other four eggs were those of *b_{III}*, although the laying date of *b_{III}* could not be ascertained. After the chicks hatched, *b_I* showed a “running toward” attacking behavior directed at *b_{III}* several times, but *B* did not attack *b_{III}* at all.

Trio *III* consisted of one male *C*, and two females *c_I* and *c₂*, but the relatedness of these females was unclear (Kitagawa 2009). On 17 May, 2000, *C* copulated with subordinate female *c₂*, only 15 min after copulating with the dominant female *c_I*. Each female did not disturb the other’s copulation activity. A nest of the trio, containing three eggs, was found on 8 June. It was not known which female of the trio had laid the eggs. Incubation activity was not observed. The nest and eggs were washed away by heavy rain on 12 June. On 25 June, the second nest of the trio was found, tens of meters apart from the first nest and containing five eggs. On the same day, *c_I* was observed to drive *c₂* out of the nest while the latter was incubating, and *c_I* then incubated eggs on behalf of the latter. On 2 July, seven eggs were found in the nest. Two females were presumed to have laid those eggs. On the same day, *c_I* approached the nest and attacked *c₂* while she was incubating eggs. The latter stood up and left the nest. Several eggs were always exposed beyond the belly feathers of the incubating bird, although it was not certain whether those eggs were always the same ones. On 5 July, the nest and eggs were again washed away by heavy rain in the early incubation period.

Trio *V* consisted of parents *E* and *d_{2I}*, and a daughter *d_{2II}* (Kitagawa 2009). Seven eggs were found in a joint-nest on 8 June, 2006, although it was not known when the first egg was laid. Both *d_{2I}* and *d_{2II}* were presumed to have laid those eggs. However, 1–4 eggs were always exposed beyond the belly feathers of the incubating bird, although it was not certain whether those eggs were always the same ones. During incubating activity one egg was frequently piled up above the other eggs like a pyramid, especially when shifting-egg activity was being done. One egg was lost from unknown causes on 13 June and 9 July, respectively. Following the onset of nearby industrial activities from 13 July, incubating activities were interrupted frequently, and eggs were lost on 17 July. After at least 39 incubation days, the trio disappeared from the breeding site. As a result, trio *V* was unable to hatch any eggs, although their incubation period was longer than the usual duration of 26–27 days (Kitagawa 2009).

2-3. Bigamous trios with two simultaneous nests

In two trios (trio *III* in 2001, and trio *IV*), each of two females laid eggs in two-simultaneous-nests. Members of trio *III* in 2001 were the same as those with a joint-nest in 2000 (Kitagawa 2009). On 29 May, 2001, each of two nests (N_A and N_B), which were just one meter apart, contained four eggs. It was not certain when the first egg was laid, nor how many eggs each female laid in each nest, respectively. All members of the trio participated in incubation of eggs in both nests. A Japanese rat snake *Elaphe climacophora* preyed upon three of four eggs in N_A on 19 June, at least 25 days after the first egg was laid. A Japanese rat snake also preyed upon all eggs of N_B on 5 July, at least 41 incubation days after the first egg was laid. That day, the trio abandoned the egg remaining in N_A and disappeared from the breeding site.

Trio *IV* consisted of parents D and d_I , and a daughter d_{II} (Kitagawa 2009). Copulation between D and the dominant female or the mother d_I was observed once, on 20 May, 2002, and that between D and d_{II} was observed three times, on 16, 20 and 23 May, respectively. The females did not disturb each other's copulation activities. Four eggs were laid in N_A during 22–25 May. Three eggs were laid in N_B , 30 cm apart from N_A , during 25–28 May: d_{II} was observed to lay one egg in N_B on 25 May. All members participated in the incubation of eggs in both nests. Four chicks hatched out in N_A on 15 June. On the next day the trio deserted the four unhatched eggs in N_B and brought chicks to the site, about 500 m apart from the nest, where they established the chick-caring territory. Brooding activities were observed until 15 days after hatching. All members attended to brooding and participated in guarding chicks and defending the chick-caring territory. They attacked con- and hetero-specific invaders, such as the Kentish Plover *Charadrius alexandrinus*, the Moorhen *Gallinula chloropus*, and potential predators of the chicks, such as the Carrion Crow *Corvus corone* and the Herring Gull *Larus argentatus*, etc., which invaded into or flew over the chick-caring territory. Members of the trio and chicks stayed within the chick-caring territory until the chicks acquired flight ability. However, although they performed most maintenance activities within the territory, each member of the trio occasionally flew out of the territory to forage, bathe or rest. Flying out of the territory was performed alternately, like changeover in incubation duties. In contrast, the members remaining at the territory undertook sentry activities and responded rapidly to intrusion by invaders and predators of the chicks.

2-4. The bigamous trio with three successive nests

Trio *VI* consisted of a pair F and f_I , and an unrelated female f_2 . Both F and f_I were dominant over f_2 (Kitagawa 2009). Several copulation attempts were observed between F and f_I (5 times), and between F and f_2 (15 times). In one case, on 20 May, 2003, each female disturbed each other's copulation activities. On 5 June, 2003, f_2 was observed to lay one egg in N_A . Immediately thereafter, F and f_I came to N_A , and f_2 walked out the nest. Afterward, f_2 performed incubation at N_A only once, on 8 June, otherwise incubation of the egg in N_A was undertaken solely by F and f_I . On 6 or 7 June f_2 also laid one egg in N_B , 6.8 m apart from N_A , while f_I was present in N_A . Male F disturbed 104 out of 156 incubation tasks of f_2 and drove the incubating f_2 out of N_B . Immediately thereafter, F

sometimes directed “*running toward*” behavior at f_2 , to which f_2 responded by walking away. Female f_2 then showed “*irrelevant splashing water*” or “*splashing water*” behaviors (one of irrelevant behavior or copulation behavior). Occasionally, F mounted f_2 : copulation was observed on 7, 8 and 11 July. After the egg at N_B was abandoned on 20 June, between 28 or 29 June–2 July f_2 laid four eggs in N_C , about 360 m apart from N_A . Only F and f_2 incubated these eggs until a chick hatched out at N_A which had been attended only by F and f_1 . However, after this chick hatched, f_1 accompanied by the chick also participated in incubation of the eggs at N_C . F and f_1 sometimes undertook incubation while brooding the chick at N_C . Male F disturbed 14 out of 24 incubation tasks of f_2 at N_C .

3. Relative contribution toward incubation within trios

Incubation time of each member in each trio type is indicated in Table 3. Among the three members in trio V with a joint-nest, the dominant female d_{21} spent the most time incubating (24.89 min/h), and the subordinate female d_{211} , the least time (13.46 min/h).

In trio III in 2001 with two-simultaneous-nests, male C and the dominant female c_1 incubated more at N_A (C , 19.58 min/h; c_1 , 17.85 min/h) than at N_B (C , 9.37 min/h; c_1 , 8.97 min/h), and the subordinate female c_2 did more at N_B (18.32 min/h) than at N_A (9.22 min/h). In trio IV with two-simultaneous-nests, the parents D and d_1 incubated more at N_A (D , 27.00 min/h; d_1 , 26.18 min/h) than at N_B (D , 0.06 min/h; d_1 , 0.46 min/h), but the subordinate female or the yearling daughter d_{11} did more at N_B (15.28 min/h) than at N_A (2.38 min/h).

In trio VI with three successive nests, the dominant female f_1 (33.01 min/h) incubated at N_A more than F (21.61 min/h). At N_B , the subordinate female f_2 (13.92 min/h)

Table 3. Incubation time of each individual.

Trio	Individual	Sex	Status	Incubation time (min/n)		
				N_A	N_B	N_C
III in 2001 ¹	C	M	—	19.58	9.37	—
	c_1	F	D	17.85	8.97	—
	c_2	F	S	9.22	18.32	—
III in 2001 ²	C	M	—	0.30	24.63	—
	c_1	F	D	2.89	18.84	—
	c_2	F	S	3.28	11.67	—
IV	D	M	—	27.00	0.06	—
	d_1	F	D	26.18	0.46	—
	d_{11}	F	S	2.38	15.28	—
V	E	M	—	17.38	—	—
	d_{21}	F	D	24.89	—	—
	d_{211}	F	S	13.46	—	—
VI	F	M	—	21.61	6.99	10.88
	f_1	F	D	33.01	0	18.22
	f_2	F	S	0.03	13.92	2.42

¹: Data before a snake preyed on the eggs of N_A .

²: Data after a snake preyed on the eggs of N_A .

h) did more than F (6.99 min/h), and f_1 did not incubate at all. At N_C , f_1 incubated the longest (18.22 min/h) among the three, and f_2 did the shortest (2.42 min/h). As described above, F and f_1 performed chick-caring activities, such as brooding and guarding chicks, simultaneously during incubation periods at N_C .

The average total incubation time that males in each trio spent at both N_A and N_B , including the male of the trio V with a joint-nest at N_A , was not significantly different from that by monogamous males (males in the trios, 25.50 ± 5.47 min/h; monogamous males, 25.95 ± 5.17 min/h; Table 1, $t=0.159$, $P=0.876$). However, total incubation time by females was different in relation to status: dominant females, 27.84 ± 3.56 min/h; subordinate females, 18.15 ± 6.53 min/h; one-way ANOVA, $F=8.179$, $P=0.0024$. The average total incubation time by dominant females at both N_A and N_B did not differ significantly from that by monogamous females, but that by subordinate females was significantly lower than that by monogamous and dominant females (Scheffe's F -test between monogamous females and dominant females: $P=0.996$; comparison between monogamous females and subordinate females: $P=0.003$; comparison between dominant females and subordinate females: $P=0.016$). This tendency is partly a consequence of some dominant females driving subordinate females from their joint-nests.

Concerning the trios with two-simultaneous-nests and three-successive-nests, the average total incubation time at N_A by the three members of those trios (53.29 ± 4.90 SD min/h) in which dominant females actively contributed to incubation was comparable to that by both sexes of monogamous pairs (53.57 ± 4.88 SD min/h, $t=0.418$, $P=0.681$). However, at N_B , where males and dominant females did not contribute to incubation so much, the average total incubation time by the three members of the trios (24.46 ± 10.87 SD min/h) was lower than that by both sexes of monogamous pairs ($t=7.833$, $P<0.0001$). In the case of the trios with a joint-nest, total incubation time by the three members did not differ significantly from that shown by monogamous pairs ($t=-0.429$, $P=0.674$, Table 3). Corresponding to these values, all hatchlings were derived from N_A of two-simultaneous-nests and also from a joint-nest.

4. Contribution to chick-caring activities in the trio

Hatching success is indicated in Table 2. The number of hatchlings was not significantly different between monogamy and bigamy ($t=-0.07$, $P=0.9436$), exclusive of trio I .

In trio II with a joint-nest, the daughter of the previous year b_{III} remained continually within the chick-caring territory, even after three chicks had hatched. Chicks approached b_{III} and walked about near her. The daughter b_{III} was not observed to brood chicks, but did not attack chicks and defended the chick-caring territory.

In trio VI with three-successive-nests, the chick was attended solely by male F and dominant female f_1 . The subordinate female f_2 did not participate in chick-caring activity.

In trio IV , all members of the trio undertook chick-caring activities. The brooding time by each member is shown in Table 4. The dominant female or the female parent d_1 was observed to brood on every observation day (9 days), and she spent the longest brooding time (30.71 min) among the three birds. Male D brooded for 13.14 min (7 of 9

Table 4. Chick-caring activities of each individual in trio IV. *D*: male; *d_I*: dominant female; *d_{II}*: subordinate female or daughter of the pair (*D* and *d_I*).

Activity	Status			Observation hours
	<i>D</i>	<i>d_I</i>	<i>d_{II}</i>	
Brooding time (min/h)	13.14	30.71	12.67	26.37
Frequency of defending behaviors in chick-caring territory per hour	5.00	5.81	0.81	49.59
Sentry activity time (min/h)	34.78	49.15	46.88	49.86

Fig. 1. Frequency of attacking behaviors by members of the trio IV. In total, attacking behaviors of *D* (male), *d_I* (dominant female) and *d_{II}* (subordinate female) were observed 266,668 and 252 times, respectively. Vertical lines indicate attacks to the dead body of a duck. The attacking of a dead body was often observed. If the behaviors toward a dead body were excluded, attacking behaviors of *D*, *d_I* and *d_{II}* were observed 248,288 and 40 times, respectively. Attacking behaviors were categorized as follows: *walking nearby* (black), *mounting opponent* (white), *running toward* (slopes from left to right), *landing near* (gray), *alert flight* (slopes from right to left), and *offensive flight* (dots).

days) and a daughter *d_{II}* did so for 12.67 min (6 of 9 days).

The incidence of behaviors of guarding chicks and defending the chick-caring territory by each member of the trio is shown in Figure 1, in which vertical lines showed attacking behaviors toward the dead body of a duck (*Anas* sp.) placed within the chick-caring territory. The number of attacks by both females *d_I* and *d_{II}* toward the corpse were extraordinarily numerous, and this data was therefore excluded from analysis. The number of attacks against actual predators and invaders by *d_{II}* was remarkably low (0.81), but those by *D* (5.0) and *d_I* (5.81) were almost the same (Table 4).

Sentry activity time by each member of the trio is shown in Table 4. *d_{II}* spent the longest time (49.15 min) among the three, and *D* spent shortest time (34.78 min).

Discussion

The average rate of hatching success of bigamous trios does not differ significantly from that of monogamous pairs (Table 2). Therefore, bigamous breeding is not more beneficial than monogamous breeding for hatching eggs.

There are two main reasons for low hatching success in bigamous trios: (1) In joint-nesting, several eggs always remained exposed beyond the belly feathers of the incubating bird, and the number of eggs resulting from two clutches thus seem to be too many for one individual to incubate successfully. Therefore, development of embryos of those eggs may be hindered (trio *III* in 2000 and trio *V*, Table 3). In the Ring-billed Gull *Larus delawarensis* supernormal clutches receive less heat during incubation, and sub-optimal heating during incubation retards development (Hunter *et al.* 1976, Ryder & Somppi 1977). (2) In two cases of two-simultaneous-nesting, the males contributed incubation more toward one nest (N_A) than the other nest (N_B). Particularly, the dominant females performed a greater proportion of incubation effort at N_A than the subordinate females. The latter birds made a greater contribution to N_B than the former (trio *III* in 2001 and trio *IV*, Table 3). Accordingly, it is posited that the dominant females lay all or most of their eggs in N_A , and the subordinate females do so in N_B . Consequently, the total time spent on incubation at N_A by all members of the trios was not significantly different from monogamous pairs, but that at N_B is presumed to be insufficient for development of embryos (trio *III* in 2001, trio *IV* and trio *VI*, Table 3). Actually, hatching success of the male and the dominant female, which can hatch their own eggs in two-simultaneous-nests (2.0 ± 2.83), is not significantly different from that in monogamous pairs, although data is scarce ($t = -0.628$, $P = 0.531$, Table 2).

The total incubation time at both N_A and N_B by each of the males and the dominant females is not significantly different from that of monogamous males and females, respectively (Tables 1 & 3). Therefore, breeding by bigamous trios does not appear to be beneficial for lightening the incubation burden of males and dominant females, compared with that by each sex in monogamous pairs.

In contrast, the total incubation time at both N_A and N_B by the subordinate females is significantly shorter than that of the monogamous females. Therefore, if the subordinate females could hatch their own eggs, the mating system of the bigamous trios would be beneficial for them (Table 1). However, as noted above, insufficient incubation heat in the case of the joint-nesting, and the male's lower incubation efforts at N_B in the case of two-simultaneous-nests together mean that there is little possibility for hatching of the subordinate female's eggs. Furthermore, the males and dominant females sometimes disturb the incubating activities of subordinate females (trio *III* in 2000 and trio *VI*).

However, if the nest N_A and eggs of dominant females were lost through predation or other accidents, all members of the trio then focus their incubation efforts exclusively on eggs of the subordinate females at N_B (trio *III* in 2001, Table 3). At that time, there is a possibility that the eggs of the subordinate females would hatch.

In some joint-nesting species, egg removal from the nest occurs frequently: rolling

eggs out of the nest in the Greater Rhea *Rhea americana* (Bruning 1974), the Ostrich *Struthio camelus* (Bertram 1992) and the Magpie Goose *Anseranas semipalmata* (Frith & Davies 1961); destruction of eggs in the Acorn Woodpecker (Koenig *et al.* 1995); and tossing eggs out of the nest in the Groove-billed Ani (Vehrencamp 1977). In the Black-winged Stilt, removal or destruction of eggs did not occur. On 3 July, 2001, one egg was rolled out accidentally from N_B in trio *III* with two-simultaneous-nests. Although the egg in N_B was presumed to be that of the subordinate female, all members of the trio tried repeatedly to pull it back into the nest. Finally, after many trials over two days, it was the dominant female c_I which succeeded in returning the egg to the nest (Kitagawa unpublished data). This example indicates that both females of the trio attend all eggs cooperatively, and suggests strongly that each female does not remove the other's eggs, unlike in some other cooperative species, or that females of the trio cannot recognize their own eggs. In communally breeding trios of the Moorhen also, females do not favor their own eggs and show no evidence of recognizing their own eggs (MacRae 1996).

Concerning the contribution toward chick-caring activities, in trio *IV* the eggs of the dominant female d_I were hatched successfully at N_A , and subordinate female d_{II} also contributed to brooding, guarding chicks, defending the chick-caring territory, and sentry activities at the territory even though the eggs of d_{II} did not hatch at N_B . In trio *II* also, the subordinate female b_{III} contributed to defending the chick-caring territory, although only relatively briefly (Kitagawa 2009).

In these instances, although data is scarce, the additional assistance of the subordinate female in chick-caring activities and defending the chick-caring territory might be beneficial to the male and the dominant female when compared with monogamous pairs.

In trio *IV* the subordinate female, which could not hatch her own eggs, switched to helping the chick-caring activities of the breeding pair. Therefore, further study of the formation and behavior of trios in the Black-winged Stilt might provide important insights into the appearance of cooperative breeding or helping behavior in birds.

Acknowledgements

I wish to express my sincere gratitude to Dr. S. Yamagishi, Director General, Yamashina Institute for Ornithology, and Dr. S. Asai for their critical reading of the manuscript and valuable suggestions. I also thank Professor H. Katakura, the Faculty of Science of Hokkaido University, and to Professor S. Mawatari, for their invaluable suggestion and encouragement during the study; further to Dr. I. Nishiumi and two anonymous referees for their valuable comments. I also express my cordial thanks to all the staff of Gyotoku Bird Observatory, and all the staff of the Tokyo Metropolitan Government Bureau of Environment at Chubo (Chuo Breakwater), for their help which facilitated this study. This study was partly funded by the Grant-in-Aid for Scientific Research (Encouragement of Scientists) in 1999 and the Takara Harmonist Fund in 2000.

References

- Bertram, B. C. R. 1992. *The Ostrich Communal Nesting System*. Princeton University Press, Princeton.
- Brown, J. L. 1987. *Helping and Communal Breeding in Birds: Ecology and Evolution*. Princeton University Press, Princeton, New Jersey.
- Bruning, D. F. 1974. Social structure and reproductive behavior of the Greater Rhea. *Living Bird* **13**: 251–294.
- Craig, J. L. & Jamieson, I. G. 1990. Pukeko: different approaches and some different answers. In *Cooperative Breeding in Birds* (eds. P. B. Stacey & W. D. Koenig), pp. 385–412. Cambridge University Press, Cambridge.
- Cramp, S. & Simmons, K. E. L. (eds.) 1983. *The Birds of the Western Palearctic*, Vol. 3. Oxford University Press, Oxford.
- Frith, H. J. & Davies, S. J. J. F. 1961. Ecology of the Magpie Goose *Anseranus semipalmata*. *CSIRO Wildlife Research* **113**: 555–557.
- Glutz von Blotzheim, U. N., Bauerl, K. M. & Bezzel, E. 1977. *Handbuch der Vögel Mitteleuropas 7. Charadriiformes*. Aula-Verlag, Wiesbaden. (in German)
- Hunter, R. A., Ross, H. A. & Ball, J. S. 1976. A laboratory simulation of predator-induced incubation interruption using Ring-billed Gull eggs. *Canadian Journal of Zoology* **54**: 628–633.
- Kitagawa, T. 2005. The clutch size of the Black-winged Stilt *Himantopus himantopus himantopus*. *Journal of the Yamashina Institute for Ornithology* **36**: 117–119.
- Kitagawa, T. 2009. Bigamous trios in the Black-winged Stilt *Himantopus himantopus himantopus*: I. Pathways to form bigamous trios. *Journal of the Yamashina Institute for Ornithology* **40**: 73–82.
- Koenig, W. D., Mumme, R. L., Stanback, M. T. & Pitelka, F. A. 1995. Patterns and consequences of egg destruction among joint-nesting Acorn Woodpeckers. *Animal Behaviour* **50**: 607–621.
- Koford, P. R., Bowen, B. S. & Vehrencamp, S. L. 1990. Groove-billed Anis; joint-nesting in a tropical cuckoo. In *Cooperative Breeding in Birds* (eds. P. B. Stacey & W. D. Koenig), pp. 335–355. Cambridge University Press, Cambridge.
- McRae, S. B. 1996. Family values: costs and benefits of communal nesting in the Moorhen. *Animal Behaviour* **52**: 225–245.
- Ryder, J. P. & Somppi, P. L. 1977. Growth and development of known-age Ring-billed Gull embryos. *Wilson Bulletin* **48**: 276–277.
- Vehrencamp, S. L. 1977. Relative fecundity and parental effort in communally nesting anis, *Crotophaga sulcirostris*. *Science* **197**: 403–405.

セイタカシギの二雌トリオの抱卵・育雛活動

1997–2007年にセイタカシギの一夫二妻（二雌トリオ）の抱卵活動について、共同巣に産卵した3例、同時的2巣に産卵した2例、そして継時的3巣に産卵した1例について調査を行った。共同巣を持った1例目の両親と娘からなるトリオは、両親のみが抱卵活動を行った。2例目の3羽の成鳥からなるトリオは、全ての成員が抱卵活動に参加したが、優位雌が抱卵中の劣位雌を巣から追い出す妨害をたびたび行った。3例目の両親と娘からなるトリオでは、すべての成員が抱卵活動に協同的に従事した。同時的2巣を持った2例のトリオでは、すべての成員が両巣の抱卵に関与したが、両巣への関わりの程度は個体により異なった。継時的3巣を持った1例のトリオでは雄は3巣すべての抱卵活動に参加し、優位雌は第1と第3の巣の抱卵に、劣位雌は第2と第3の巣の抱卵に参加した。共同巣では、各個体にとって1羽で二腹全ての卵を抱卵することは物理的に難しかった。同時的2巣と継時的3巣では雄が劣位雌の巣よりも優位雌の

巣でより多くの抱卵活動を行った。トリオでの孵化成功の割合は一夫一妻のつがいと比べ有意差はなかった。そのためセイタカシギのトリオ形成は雛の孵化に関しては一夫一妻の場合と比べて利益があるとは言えなかった。雛の孵化には共同巣を持った1例のトリオと同時的2巣を持った1例のトリオ、そして継時的3巣を持ったトリオが成功した。育雛活動に関しては、継時的3巣を除いた2つのトリオでは、全ての成員が育雛なわばりの防衛に貢献した。中でも同時的2巣のトリオでは全ての成員が抱雛活動、雛の防衛活動、育雛なわばりの見張り活動にも貢献した。トリオ形成は一夫一妻のつがいに比べ、つがいの育雛行動の負担が軽減される点で利益があると言える。

北川珠樹：〒272-0832 市川市曾谷 2-20-3.