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EGG-COLOR DIMORPHISM AND BREEDING SUCCESS IN THE CROW TIT (*PARADOXORNIS WEBBIANA*)

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ABSTRACT.—This study was conducted during the 1988-1989 breeding seasons in Dongguk University Forests (area A) at Namyangju-gun, and during the 1993–1994 breeding seasons in Puyong-ri (area B) at Yangpyong-gun, in Kyonggi-do, South Korea. The eggs of the Crow Tit (*Paradoxornis webbiana*) had two color types (blue and white) in both areas, but no nests had mixed blue and white eggs. In area A (n = 53), blue clutches (75.5%) were more frequent than white ones (24.5%). In area B (n = 62), the ratio of blue clutches (59.7%) to white ones (40.3%) was not skewed significantly from 1:1. In each area, neither the egg-laying period nor clutch size varied with egg color. Twenty females having two or more successive nests had the same egg color, irrespective of their male mates. However, of seven males that mated with different females, eggs in the nests of two males changed from white to blue. In each area, blue and white clutches tended to be widely distributed throughout the study area. Breeding success was related to nest height above ground, but not to egg color or species of nest tree. Nest predation seems to have been caused mostly by Eurasian Jays (*Garrulus glandarius*) in high nests, by Common Cuckoos (*Cuculus canorus*) in midlevel nests, and by snakes (*Natrix*) in low nests. *Received 14 November 1994, accepted 19 April 1995.*

LACK (1958, 1968) FOUND some correlations between nest site and egg coloration in passerines: white eggs were found in hole nests; and brown, gray or olive eggs were found in ground nests, amid vegetation or on ledges. Blue or blue-green eggs were common in thick bushes.

Crow Tits (*Paradoxornis webbiana*) have cupped nests, and nest sites usually are in dense shrubs (Yamashina 1933:420–423). Crow Tit eggs in Taiwan (*P. w. bulomachus*; Yamashina 1933) and in eastern Manchuria (*P. w. manschurica*; Dement'ev et al. 1954:943–944) are only blue in color, but in Korea (*P. w. fulvicauda*; Park et al. 1993) two color types, blue and white, occur. Few studies on the ecological significance of egg-color dimorphism exist for the Crow Tit.

Nest predation is thought to be one of the most important factors affecting breeding success in birds (Skutch 1949, 1966, Nice 1957, Ricklefs 1969, Nilsson 1984). Several experimental studies have shown that egg color enhances an egg's chance of escaping predation (Tinbergen et al. 1962, Montevecchi 1976). In the Song Thrush (*Turdus philomelos*), experimental studies have shown that blue eggs do not reduce nest predation (Götmark 1992).

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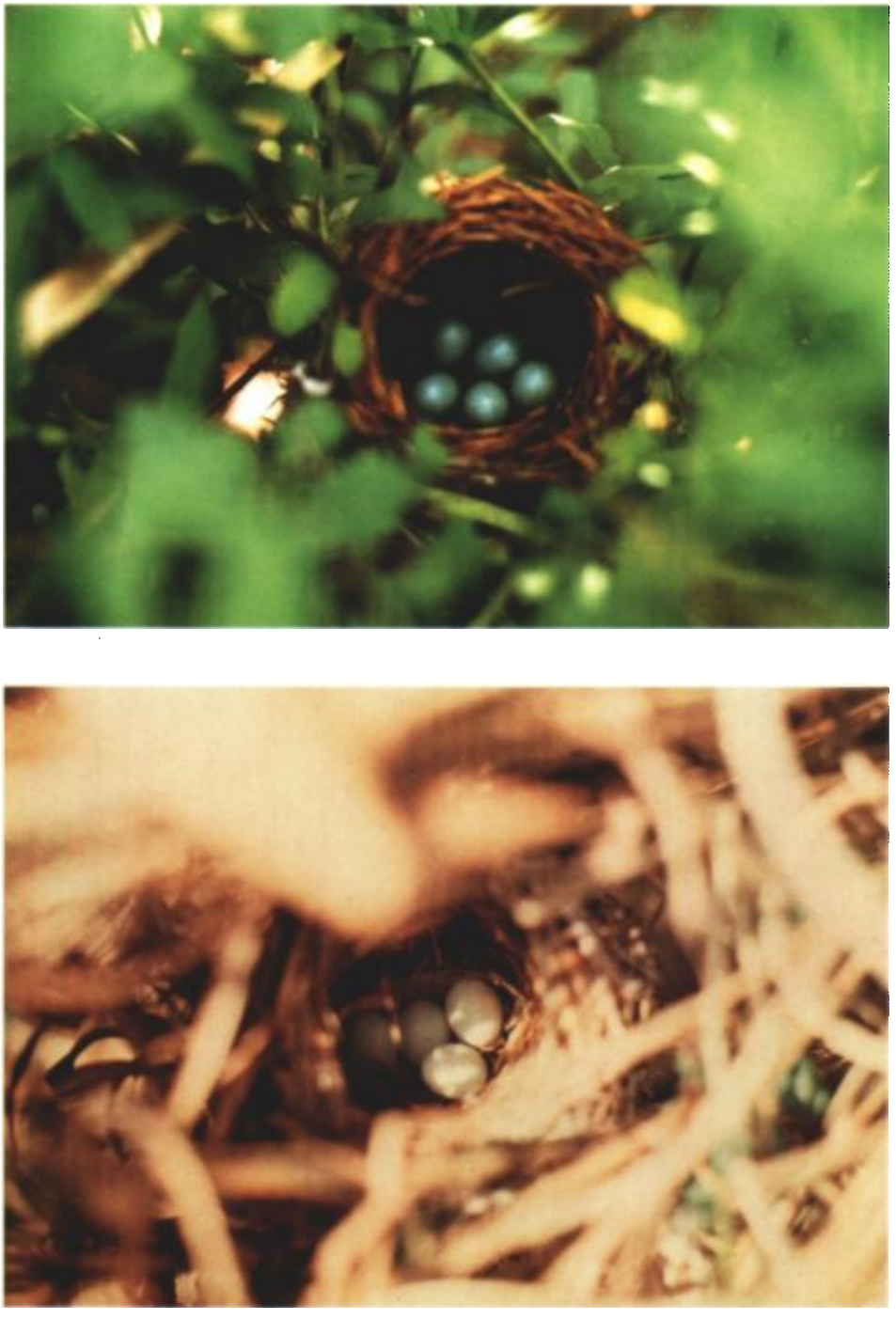

FRONTISPIECE. Nests of Crow Tits with blue and white eggs (photographs by Chang-Hoe Kim).

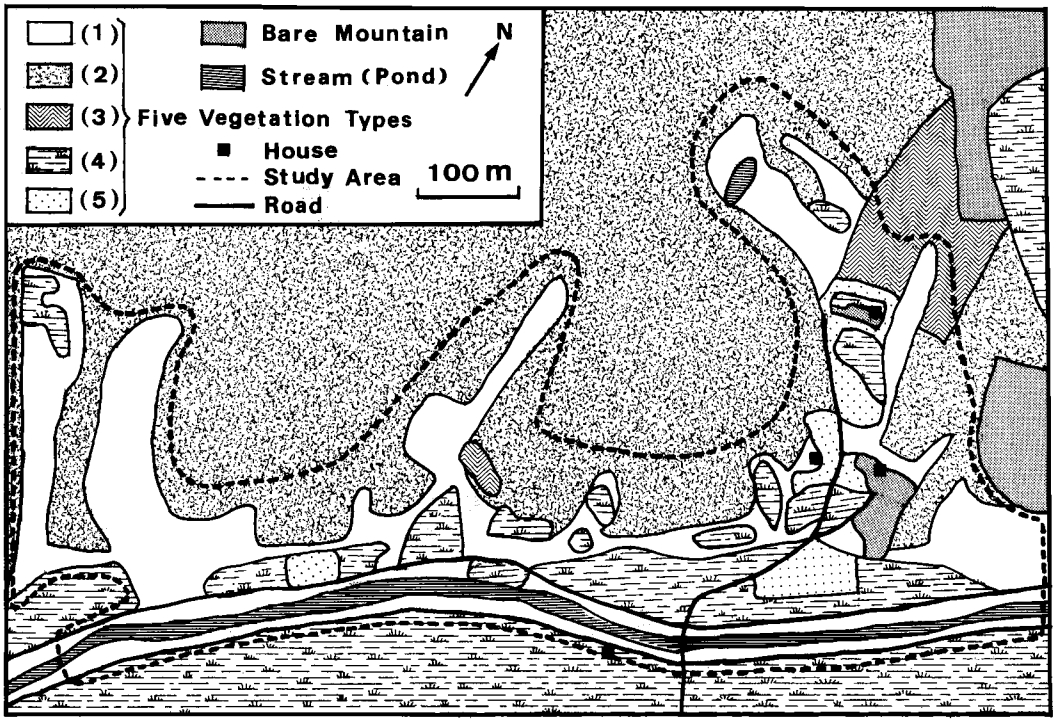

Fig. 1. Vegetation of Puyong-ri study area (area B). Stream flows from northeast to southwest. Vegetation types are: (1) bush; (2) mixed forest covered with scattered large trees and shrubs; (3) plantation; (4) agricultural field; and (5) nursery garden with young trees.

Our paper provides information on three topics concerning Crow Tit eggs: (1) the existence of color dimorphism; (2) a comparison of hatching success for two egg-color types; and (3) factors influencing hatching success.

STUDY AREA AND METHODS

Our study was conducted during the 1988–1989 breeding seasons in Dongguk University Forests (area A; 37°3'N, 127°1'E) at Namyangju-gun and during the 1993–1994 breeding seasons in Puyong-ri (area B) at Yangpyong-gun, in Kyonggi-do, South Korea. The study sites are located about 4 km apart. A river about 1 km in width separates the two sites. Area A (ca. 80 ha) is mostly surrounded by mountains rising to between 610 and 680 m above sea level, and divided by Chokok Stream (Kim et al. 1992). Area B (ca. 30 ha) straddles Puyong Stream, which flows from northeast to southwest, and is situated adjacent to a hill of about 200 m above sea level, which extends to the northwest (Fig. 1). Elevations ranges from 20 to 140 m in area A, and 15 to 130 m in area B. The widths of the two streams are 30 to 40 m, except for a narrow part of the Chokok, which is only 5 to 15 m in width. In area A, a large part of the foot of the mountain borders the banks of Chokok Stream, but area B is relatively far from the banks of Puyong Stream.

In the previous study, Kim et al. (1992) distinguished four vegetation types in area A: (1) bush, made up dense shrubs and perennial plants; (2) mixed forests covered with scattered large trees and shrubs; (3) plantations; and (4) agricultural fields. The habitats in area B include the four types listed for area A and (5) a nursery garden with young trees. In area B, the area to the southeast of the stream is cultivated.

Crow Tits were individually banded with three colored plastic leg bands. Nestlings were banded seven to eight days after hatching. Male and female were distinguished by the shapes of their cloacae in the early breeding stages (nest building, egg laying, and early incubation). Males have a cloacal protuberance and female cloacae were dilated (Lake 1981). Nest height was measured from the bottom of the nest to the ground.

The study areas were surveyed one (area B) or two times (area A) daily along a regular route to find nests. Nests (63 in area A and 68 in area B) were plotted on a 1:2,500 scale map and were visited daily. In data analyses, nests containing eggs of unknown color (10 in area A, including one that was parasitized by a Common Cuckoo [*Cuculus canorus*], and six in area B) were excluded.

TABLE 1. Number of nests with clutches of blue or white eggs in Dongguk University Forests (area A) and Puyong-ri (area B).

	No. nests		Binomial test
	Blue	White	(*P*)
Area A			
1988	11	3	ns
1989	29	10	<0.01
Subtotal	40	13	<0.01
Area B			
1993	16	16	ns
1994	21	9	<0.05
Subtotal	37	25	ns
Total	77	38	<0.01

RESULTS

Egg-color dimorphism.—The eggs of Crow Tits were of two color types: blue (color 65, turquoise blue; Smithes 1975) and white (see Frontispiece). Both color types were found in both areas (Table 1). No clutch had mixed blue and white eggs. The ratio of blue to white clutches was different between the two areas. The ratio was biased to blue in area A (40 blue and 13 white clutches; binomial test, $P < 0.01$), although no significant difference occurred in 1988. The ratio was not skewed in area B (37 blue and 25 white clutches; $P > 0.05$), although a significant difference occurred in 1994 ($P < 0.05$).

The laying period of first eggs for Crow Tits was from mid-April to mid-July (Fig. 2). In each year, the laying period of the first eggs of blue clutches or white clutches were not different. In each year, differences in the laying dates of the first eggs between the two color types were only a few days (Mann-Whitney *U*-test; for 1988, $U = 9.5$, $n = 11$ and 13; for 1989, $U = 120.5$, $n = 29$ and 10; for 1993, $U = 78.0$, $n = 16$ and 16; for 1994, $U = 75.5$, $n = 21$ and 9; $P > 0.05$ in each year).

Of 115 nests of known egg color, the eggs of three nests (area A) disappeared during the egg-laying period, and the owners of seven nests (four nests in area A, and three nests [including one parasitized by a Common Cuckoo] in area B) abandoned their eggs before they started incubation. All nests with egg loss or egg abandonment had one- to three-egg clutches (i.e. incomplete clutches). With these 10 nests excluded, clutch size ranged from four to six in area A, and four to seven in area B. Only one clutch had seven (blue) eggs. In each area, no statistically significant difference in clutch size was detected between the egg-color types (Table 2).

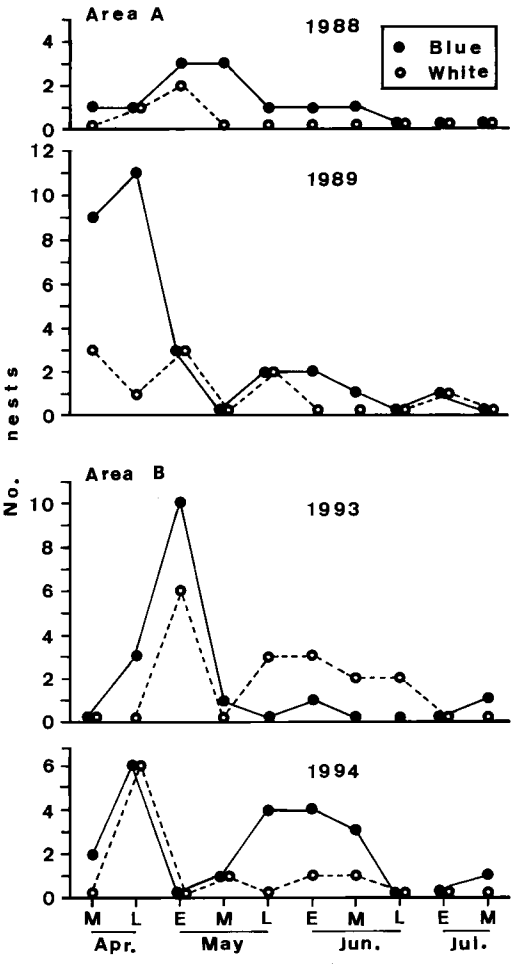

Fig. 2. Laying period of first eggs of blue and white clutches in Dongguk University Forests (area A) and Puyong-ri (area B; early [E], middle [M], and late [L] for each month).

Blue and white clutches were widely distributed throughout each study area (Fig. 3). In area A, nests were concentrated near the banks of Chokok Stream. In area B, nests were less concentrated near the banks of Puyong Stream.

Six females that bred both in 1988–1989 (area A) and in 1993–1994 (area B; Fig. 4; females 612, 544, 435, 634, 712 and 644) had only blue clutches, even though four of them mated with different males in successive years (Fig. 4). Pairs

TABLE 2. Clutch sizes ($\bar{x} \pm$ SD, with n in parentheses) of blue and white eggs in Dongguk University Forests (area A) and Puyong-ri (area B). None of the comparisons between blue and white eggs were statistically significant ($P > 0.05$; t-test).

	Blue	White
	Area A	
1988	5.0 ± 0.77 (10)	4.50 ± 0.50 (2)
1989	5.15 ± 0.70 (27)	5.0 ± 0.76 (7)
Subtotal	5.11 ± 0.73 (37)	4.89 ± 0.74 (9)
	Area B	
1993	5.44 ± 0.50 (16)	5.38 ± 0.48 (16)
1994	5.16 ± 0.67 (19)	5.38 ± 0.48 (8)
Subtotal	5.29 ± 0.74 (35)	5.38 ± 0.48 (24)
Total	5.19 ± 0.68 (72)	5.24 ± 0.60 (33)

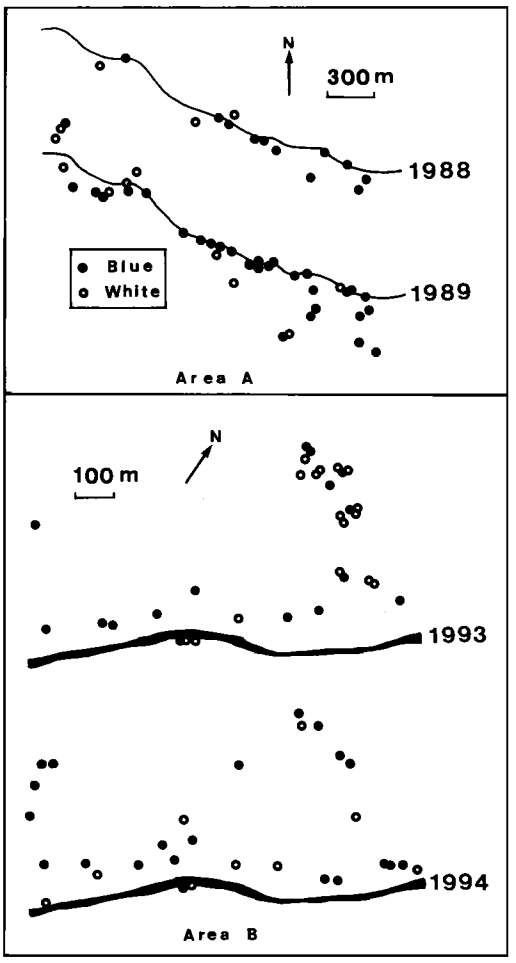

Fig. 3. Locations of nests with blue and white clutches in Dongguk University Forests (area A) and in Puyong-ri (area B). Thin (area A) and thick lines (area B) indicate streams.

with two clutches in the same year (1989, 1993 and 1994) also had eggs of the same color. Of 18 females, including 4 that bred in successive years, 10 always had blue eggs and the others always had white eggs. In contrast, one male (no. 638) with two white clutches in 1993 had two blue clutches in 1994 when paired with a different female. Another male (no. 761) had a white clutch with the first female and a blue clutch with a second in 1994.

Abandoned nests (1 during incubation stage and 4 during nestling stage), nests of incomplete clutches (10 including 1 parasitized nest), and nests parasitized by cuckoos (5) were excluded from the analyses of nesting success. If any eggs hatched or any nestlings fledged in a nest, it was considered a success for that stage in the nesting cycle. Depredated nests always lost all eggs or young.

When comparing blue or white clutches (Table 3), no differences were found in the proportions of nests where eggs hatched or where young fledged (Fisher's exact test, $P > 0.05$ in all combinations). This was true for all data combined, for data separated by area, and for data separated by area and year.

The species of nest trees and shrubs used by Crow Tits varied in each area (A and B; Table 4), and there was no relationship between the species of the nest tree and egg color, nor between the species of the nest tree and the success of the nest.

Nest failure.—Nest failures were due to: abandonment (6 nests with blue eggs, including 1 parasitized by a cuckoo, and 6 with white eggs); egg loss (19 with blue and 12 with white); nestling loss (5 with blue and 2 with white); or brood parasitism (4 with blue, excluding 1 in which a cuckoo egg was removed; Fig. 5). During the incubation stage, one nest was abandoned in area B that was built in an unsuitable bush, the biennial plant (*Erigeron canadensis*). During the nestling stage, four nests (all in area B) were abandoned: one had an active bee nest under a branch of the nest tree; another had many ants above the nest in dry grass that covered the tree and concealed the nest; and two probably because the males disappeared. The two pairs that abandoned their nests because of disturbance by insects renested.

Eurasian Jays (*Garrulus glandarius*), snakes

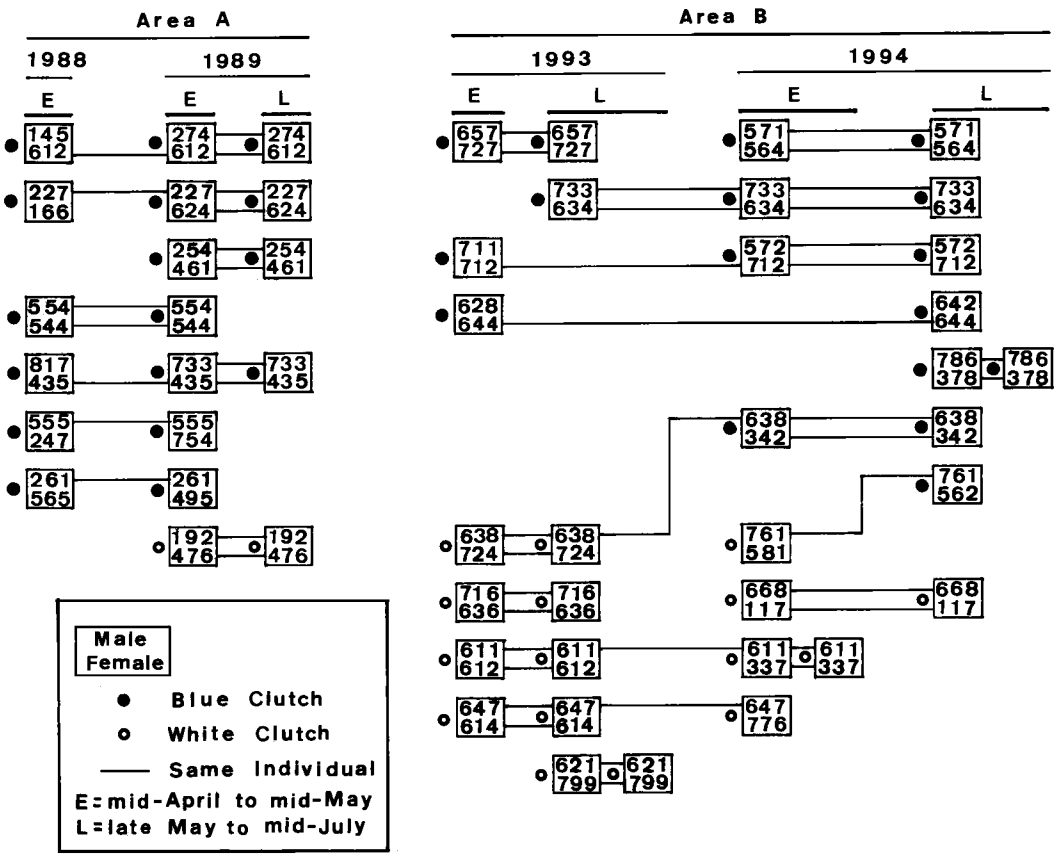

Fig. 4. Egg color produced by individual females and males: with same or different mates with two or more clutches; within one breeding season; or in successive years. No individual occurred in both study areas; therefore, identical numbers in different areas pertain to different birds.

(*Natrix tigrina* and *Elaphe rufodorsata*), and Common Cuckoos probably were the main nest predators. We often saw Eurasian Jays and Common Cuckoos (especially in 1989 and 1994) close to nests, and we observed snakes near the nest site during all four breeding seasons. In all nests with egg loss, we found no broken eggs or disturbed nests.

TABLE 3. Number of successful nests between two egg-color types of Crow Tit in Korea.

	Blue			White		
	n^a	Hatched	Fledged	n^a	Hatched	Fledged
			Area A			
1988	9	6	5	2	2	1
1989	28	24	22	7	4	4
Subtotal	37	30	27	9	6	5
			Area B			
1993	15	9	9	14	11	10
1994	12	8	6	8	3	3
Subtotal	27	17	15	22	14	13
Total	64	47	42	31	20	18

[a] Number of nests.

TABLE 4. Species of nest tree or shrub for nests with blue or white clutches, and number of nests and of successful nests (in parentheses) in relation to species of nest tree in Dongguk University Forests (area A) and Puyong-ri (area B).

Nest tree	No. nests	
	Blue	White
Area A		
Rosa multiflora	11 (9)	1 (0)
Ligustrum obtusifolium	4 (2)	1 (0)
Stephanandra incisa	4 (2)	1 (1)
Juniperus chinensis	3 (2)	—
Lespedeza maximowiczii	3 (2)	—
Rubus parvifolius	3 (2)	—
Corylus heterophylla	2 (2)	—
Rubus phoenicolasius	2 (0)	—
Juniperus rigida	1 (1)	—
Quercus serrata	1 (1)	—
Morus alba	2 (1)	1 (0)
Acer palmatum	1 (1)	1 (0)
Spiraea prunifolia	1 (0)	1 (0)
Zelkova serrata	—	1 (1)
Miscanthus sinensis	—	2 (0)
Salix gracilistyla	—	2 (1)
Euonymus alatus	2 (2)	2 (2)
Total	40 (27)	13 (5)
Area B		
Rosa multiflora	17 (5)	6 (2)
Euonymus alatus	3 (2)	—
Sambucus williamsii	2 (0)	—
Lonicera japonica	1 (0)	—
Erigeron canadensis	1 (0)	—
Ligustrum obtusifolium	1 (0)	—
Artemisia princeps	1 (1)	—
Salix gracilistyla	1 (1)	1 (0)
Lespedeza maximowiczii	1 (0)	1 (0)
Juniperus chinensis	—	1 (0)
Thuja orientalis	—	1 (1)
Cucculus trilobus	—	2 (2)
Abies holophylla	2 (1)	2 (0)
Zelkova serrata	2 (2)	3 (1)
Rubus parvifolius	5 (4)	8 (7)
Total	37 (16)	25 (13)

We saw Eurasian Jays eating nestlings from two nests in area A (white clutch in nest 76 cm above ground in 1988, and blue clutch in nest 119 cm high in 1989). A snake (*N. tigrina*) was observed eating nestlings in one nest in area B (blue clutch in nest 37 cm high in 1994). Six nests were parasitized by Common Cuckoos. Five of the parasitized nests (47–86 cm in height) failed, but in one (105 cm in height), from which the host removed the cuckoo egg, the nest was successful. The cuckoo eggs ($n = 4$) always hatched first and, soon after a cuckoo egg hatched, all eggs of the host were gone.

Success rates for nests with eggs of either color were higher in nests of midlocation (40–90 cm in height) in 1988, 1989 and 1993, than low nests (< 40 cm) or high nests (> 90 cm; Fig. 5; Fisher's exact test, both $P < 0.001$ for midheight vs. low, and midheight vs. high).

DISCUSSION

The egg color within many species of birds varies. In the Village Weaver (*Ploceus cucullatus*), for example, egg color varies extensively from white to colored (turquoise to emerald), and from faint to intense. Some eggs have brown spotting (Collias 1993). The Greater Redheaded Parrotbill (*Paradoxornis r. ruficeps*) also has two color types of eggs (Ali and Ripley 1971:207).

Female Crow Tits in our study, whether they laid blue or white clutches, laid their eggs during the same time period. The timing of breeding for this species is related to factors other than the color of eggs the females lay. The date of laying may be determined by the date at which the female for this species is able to find enough food to form eggs (Svärdson 1957, Bryant 1975, Nolan and Thompson 1975, Sealy 1978).

No significant difference in clutch size was detected between study areas when the two egg-color types are combined, although a significant difference in clutch size of white clutches existed between the two areas ($t = 2.24$, $P < 0.05$). We know of no reason for this difference. It is likely that vegetation types in the two areas are not different. Crow Tits of area A probably do not interact with those of area B, because we never saw them fly to a distance of 200 m or more without landing on the perch along the way.

When pairs remained together to renest, second clutches were always the same color as first clutches. These records suggest that an individual female had clutches of uniform egg-color type (blue or white). In contrast, when a male mated with a different female, the egg color of clutches differed from first clutches. It is evident that egg color was determined by the female alone. Collias (1993) reported that color and amount of spotting of the eggs of a given Village Weaver female were constant throughout her life, and the trait for type of egg color is passed from mother to daughter. One Crow Tit female known to have hatched from a white egg laid white eggs.

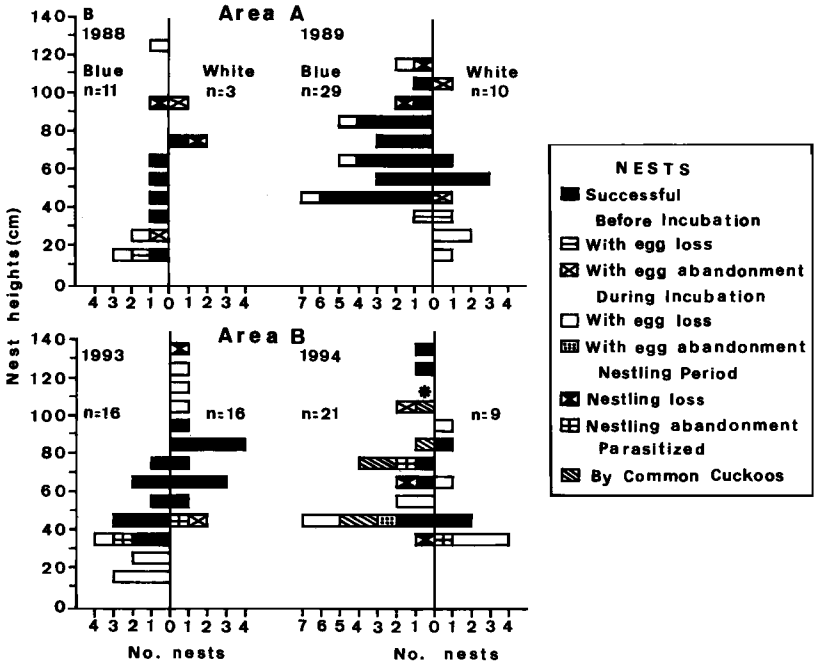

Fig. 5. Fate of nests in relation to their height above ground in Dongguk University Forests (area A) and Puyong-ri (area B). An asterisk (*) marks nest from which host removed cuckoo egg.

Many passerine birds with open cup-shaped nests lay blue or blue-green eggs (Lack 1958, 1968). It is generally believed that cryptic egg coloration reduces nest predation (Tinbergen et al. 1962, Montevecchi 1976). Redondo and Carranza (1989) reported that the predation risk often is greater during the egg stage than during the nestling stage. In our study, we were not able to conclude that blue eggs were more difficult to find by predators than white ones, because no significant difference existed in success between the two egg-color types. This suggests that egg coloration does not influence the probability of nest predation in Crow Tits, as Götmark (1992) showed in his experiment with the Song Thrush (*Turdus philomelos*).

Nests in area A were distributed along stream banks, but nests in area B were placed far from the banks. The surroundings of the banks of the stream in area B were more open than those in area A. The habitat characteristics that influence the probability of nest predation may be particularly important, because nest predation often is the primary source of nesting mortality for a wide range of bird species (Ricklefs 1969).

The eggs of Common Cuckoos often closely match those of the particular foster species in color and pattern; different hosts' eggs may even be mimicked by different cuckoos in the same locality (Davies and Brooke 1991). We found no evidence that Common Cuckoos laid an egg within a nest with white eggs, because during daily observations of nests there was no nest in which a white egg was eliminated. Of the six eggs of Common Cuckoos laid in nests with blue eggs, one was deserted by the host, two were successful, and one was eliminated by the host; nestlings of two nests disappeared. These constitute the first records of Common Cuckoo eggs in Crow Tit nests.

Eurasian Jays may find nests (eggs or nestlings). According to Møller's (1987) experimental study, the Eurasian Jay was a predator of branch and hole nests, but not ground nests. Most nest predation by Eurasian Jays probably occurred in high nests. Skutch (1966) noted that predators, especially snakes, usually detect the nest by seeing the parents approach and leave the nest, so it may be more important that the nests rather than the eggs be concealed. Most nest predation by snakes probably occurred in nests on or close to the ground. However, nest predation seems to have occurred independently of the species of nest tree.

For the Crow Tit in Taiwan, Severinghaus (1992) suggested that the within- and among-year variation in the breeding success was influenced by predation and weather conditions. Snakes in her study area were the most important nest predators. The Chinese Goshawk (*Accipiter soloensis*) is a predator of postnestling Crow Tits (Kwon and Won 1975), but not a nest predator.

In a study of the Hermit Thrush (*Catharus guttatus*), Martin and Roper (1988) found that concealed nests experienced lower predation than more exposed nests. In hole-nesting small passerines (Nilsson 1984), the predation risk decreased with increased nest height, but in a group of Jackdaws (*Corvus monedula*; Johnsson 1994) risk was not related to the nest height. Jackdaws defended their nests from their important predator, the pine marten (*Martes martes*). In our study, Crow Tits seemed unable to defend their nests from their common predators—Eurasian Jays, snakes, and Common Cuckoos.

In this study, breeding success in Crow Tits was related to nest height, but not to egg coloration or species of nest tree. In a coevolutionary arms race between the Crow Tit and the Common Cuckoo, both sides may evolve adaptations that will ensure the survival of their own offspring. If Common Cuckoos lay blue eggs among eggs in Crow Tit clutches that are white, the hosts may reject the eggs in direct proportion to number the parasites lay, whereas cuckoos laying blue eggs among blue Crow Tit eggs are likely to have their eggs accepted by their hosts in proportion to the number laid. White clutches, however, are more easily detected by other predators. Therefore, Crow Tits may have the capacity to lay eggs of two color types in order to decrease predation risk where there are several or many predators. Further studies on the ecological significance of egg-color dimorphism in this species are necessary to elucidate the mechanism involved.

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LITERATURE CITED

ALI, S., AND S. D. RIPLEY. 1971. Handbook of the birds of India and Pakistan, vol. 6. Oxford Univ. Press, London.

BRYANT, D. M. 1975. Breeding biology of House Martins *Delichon urbica* in relation to insect abundance. Ibis 117:180–216.

COLLIAS, E. C. 1993. Inheritance of egg-color polymorphism in the Village Weaver (*Ploceus cucullatus*). Auk 110:638–692.

DAVIES, N. B., AND M. DE L. BROOKE. 1991. Co-evolution of the cuckoo and its hosts. Sci. Am. 264(1): 92–98.

DEMENT'EV, G. P., N. A. GLADKOV, A. M. SUDILOVSKAYA, E. P. SPANGENBERG, L. V. BOEHME, I. B. VOLCHANETSKII, M. A. VOINSTVENSKII, N. N. GORCHAKOVSKAYA, M. N. KORELOV, AND A. K. RUSTAMOV. 1954. Birds of the Soviet Union, vol. 5. Sovetskaya Nauka, Gosudarstvennoe Izdatel'stvo, Moscow.

GÖTMARK, F. 1992. Blue eggs do not reduce nest predation in the Song Thrush, *Turdus philomelos*. Behav. Ecol. Sociobiol. 30:245–253.

JOHNSSON, K. 1994. Colonial breeding and nest predation in the Jackdaw *Corvus monedula* using old Black Woodpecker *Dryocopus martius* holes. Ibis 136:313–317.

KIM, C. H., S. YAMAGISHI, AND P. O. WON. 1992. Social organization of the Crow Tit *Paradoxornis webbiana* during the non-breeding season. Jpn. J. Ornithol. 40:93–107.

KWON, K. C., AND P. O. WON. 1975. Breeding biology of the Chinese Sparrow Hawk *Accipiter soloensis*. J. Yamashina Inst. Ornithol. 7:501–522.

LACK, D. 1958. The significance of the colour of turdine eggs. Ibis 100:145–166.

LACK, D. 1968. Ecological adaptations for breeding in birds. Methun and Co., London.

LAKE, P. E. 1981. Male genital organs. Pages 1–61 *in* Form and function in birds, vol. 2 (A. S. King and J. McLelland, Eds.). Academic Press, London.

MARTIN, T. E., AND J. J. ROPER. 1988. Nest predation and nest-site selection of a western population of the Hermit Thrush. Condor 90:51–57.

MØLLER, A. P. 1987. Egg predation as a selective factor for nest design: An experiment. Oikos 50: 91–94.

MONTEVECCHI, W. A. 1976. Field experiments on the adaptive significance of avian eggshell pigmentation. Behaviour 58:26–39.

NICE, M. M. 1957. Nesting success in altricial birds. Auk 74:305–321.

NILSSON, S. G. 1984. The evolution of nest-site selection among hole-nesting birds: The impor-

tance of nest predation and competition. Ornis Scand. 15:167–175.

NOLAN, V., AND C. F. THOMPSON. 1975. The occurrence and significance of *anomalous* reproductive activities in two North American nonparasitic cuckoos *Coccyzus* sp. Ibis 117:496–503.

PARK, E. M., C. H. KIM, S. YAMAGISHI, AND P. O. WON. 1993. Breeding biology of Crow Tit *Paradoxornis webbiana fulvicauda* (Campbell) in Korea. Bull. Inst. Ornithol. 4:47–61.

REDONDO, T., AND J. CARRANZA. 1989. Offspring reproductive value and nest defence. Behav. Ecol. Sociobiol. 25:369–378.

RICKLEFS, R. E. 1969. An analysis of nesting mortality in birds. Smithson. Contrib. Zool. 9.

SEALY, S. G. 1978. Possible influence of food on egg-laying and clutch-size on the Black-billed Cuckoo. Condor 80:103–104.

SEVERINGHAUS, L. L. 1992. Demographic patterns of the Vinous-throated Parrotbill (*Paradoxornis webbiana*). Pages 489–501 *in* Wildlife 2001: Population (D. R. McCullough, and R. H. Barrett, Eds.). Elsevier Science Publishers, London.

SKUTCH, A. F. 1949. Do tropical birds rear as many young as they can nourish? Ibis 91:430–435.

SKUTCH, A. F. 1966. A breeding bird census and nesting success in Central America. Ibis 108:159–169.

SMITHES, F. B. 1975. Naturalist's color guide, part 1 and 2. American Museum of Natural History, New York.

SVÄRDSON, G. 1957. The "invasion" type of bird migration. Br. Birds 50:314–343.

TINBERGEN, N., G. J. BROEKHUYSEN, F. FEEKES, J. C. W. HOUGHTON, H. KRUUNK, AND E. SZULC. 1962. Egg shell removal by the Black-headed Gull, *Larus ridibundus* L.: A behaviour component of camouflage. Behaviour 19:74–117.

YAMASHINA, Y. 1933. A natural history of Japanese birds, vol. 1. Azusa-Shobo, Tokyo [in Japanese].