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NOTE

Multiple within-year breeding bouts during early colony establishment of Great Cormorants *Phalacrocorax carbo* at an inland reservoir in Taiwan

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ABSTRACT: Great Cormorants *Phalacrocorax carbo* have long been treated as winter visitors in Taiwan, with no established breeding population historically reported. Since 2021, individuals have remained year-round at Hushan Reservoir (Yunlin County, Taiwan). In 2023, we documented the first confirmed colonial breeding of the species in Taiwan. Using monthly boat-based surveys supplemented by drone verification (2023–2025), we quantified breeding phenology and productivity during the early stage of colony establishment. The colony showed multiple breeding bouts per year, increasing from two bouts in 2023 (April, September) to three in 2024 (February, May, October) and four in 2025 (February, May, August, November). Annual nest attempts increased from 6 in 2023 to 33 in 2025. Nest success to ≥4 weeks was 83.3% in 2023, 57.9% in 2024, and 100.0% in 2025, and the annual number of chicks reaching ≥4 weeks was 15, 27, and 83, respectively. Mixed-age pairs involving subadults were recorded across all years, and nest placement varied among bouts in relation to reservoir water-level conditions and available nesting substrates. These observations document increased breeding activity during the early establishment of an inland colony and suggest that reservoir systems may provide suitable conditions for Great Cormorant breeding in Taiwan.

KEY WORDS: Breeding phenology, colony establishment, Great Cormorant, *Phalacrocorax carbo*, reservoir, Taiwan.

INTRODUCTION

Great Cormorants *Phalacrocorax carbo* are widespread piscivorous waterbirds whose breeding phenology and productivity vary geographically and in response to local environmental conditions, including inland versus coastal breeding environments, food availability, and population structure (Frederiksen *et al*., 2001; Newson *et al*., 2005; Bregnballe, 2006; Liordos and Goutner, 2008). In Taiwan, the species has long been treated as a winter visitor, although a photographic breeding record from Aogu was reported in 2021. This observation has not been formally documented in the scientific literature and appears to have been non-colonial. No established breeding population has historically been reported in Taiwan (Ding *et al*., 2023). Since 2021, individuals have been observed year-round at Hushan Reservoir (Yunlin County, Taiwan), suggesting a potential shift in residency status. In 2023, we documented the first confirmed case of colonial breeding of Great Cormorants in Taiwan.

The establishment of a breeding colony provides a valuable opportunity to examine breeding phenology and productivity during its early stage, particularly in subtropical environments where environmental constraints may differ from those in temperate regions. In addition, repeated breeding within a single year has rarely been documented at the colony level in this species and may provide insight into patterns of population growth under favourable conditions. Here, we document breeding phenology and productivity during the early establishment phase of this inland colony. Specifically, we describe (i) changes in the annual number and timing of breeding bouts, (ii) nest success to ≥4 weeks and chick production, and (iii) the occurrence of subadults among breeding pairs during the early stage of colony establishment.

MATERIALS AND METHODS

Study area

Hushan Reservoir (23.687682°N, 120.630647°E) is an inland impoundment in Yunlin County, central Taiwan, with a full-supply surface area of approximately 200 ha and a full-supply level (FSL) elevation of 211 m above sea level. The reservoir has restricted public access, and recreational use is not permitted under local management practice; functionally, this creates conditions similar to a protected area with very low human disturbance.

Cormorants nested mainly in emergent or shoreline trees within the inundation zone. Available nesting substrates included Teak (*Tectona grandis*), Bamboo (*Dendrocalamus latiflorus*), and standing dead trees of India-charcoal (*Trema orientalis*). Depending on reservoir water level, nests were placed either in shoreline trees close to the water's edge or in emergent trees standing within the reservoir basin. Some nests were therefore located over water, whereas others were on trees along the inundated shoreline. Nest height relative to the full-supply level was recorded to evaluate changes in nest placement in relation to reservoir water level.

Colony surveys and definition of breeding bouts

We conducted monthly boat-based surveys around the inundation zone to detect nesting activity. When active breeding was detected, drone surveys were used to verify nest numbers, breeding stage, and nest contents. Drone surveys were conducted with authorisation from the Hushan Reservoir Management Center. To minimise disturbance, the survey boat remained at least 50 m from nesting trees, and nest contents were assessed primarily from drone imagery.

Because the colony was surveyed approximately monthly before breeding activity was detected, the exact date of laying or nest initiation could not always be determined. We therefore defined the onset of a breeding bout operationally as the first survey date on which active nesting was confirmed, including nest attendance, incubation, eggs visible in the nest, or chicks present. This date should be interpreted as the date of first detection rather than the exact laying date. Incubation in Great Cormorants has been reported to last approximately one month (Fukuda, 2002). After breeding was confirmed, follow-up surveys were conducted more frequently to monitor nesting results. During the first breeding bout in 2023, nests were checked every 3–5 days to document early colony development; in subsequent bouts, follow-up surveys were typically conducted at 4–7-day intervals after breeding had been detected.

We classified breeding into three stages: incubation, chick-rearing, and post-nesting stage. Incubation was recorded when adults were sitting tightly on nests or eggs were visible. Chick-rearing was recorded when chicks were visible in the nest. The post-nesting stage was recorded when chicks had left the nest structure but remained near the nest tree, shoreline, or adjacent water surface and were still attended or provisioned by adults. Nest-building behaviour was recorded when adults carried sticks or arranged nest material before incubation. We defined a breeding bout as a discrete, colony-level pulse of nesting activity involving one or more active nests that progressed through incubation and chick-rearing. Consecutive bouts were separated by an interval during which no active nests were detected during follow-up surveys.

Nesting results and productivity

A nest attempt was counted when an active nest was confirmed. We defined nest success as a nest in which at least one chick reached approximately four weeks of age. This criterion was used as a field-based measure of advanced nestling survival rather than confirmed fledging. Chick age was estimated from body size, plumage development, primary feather length, tail growth, and behaviour observed in field images. These assessments were supported by comparison with the hand-rearing records of two chicks rescued from the Hushan colony in 2023, which documented age-related changes in body size, wing and tail growth, and behaviour (Lin *et al*., 2025). At approximately four weeks of age, chicks usually stood at the nest rim or moved short distances from the nest structure and could be reliably counted from drone imagery. Because Great Cormorant chicks generally become fully volant later, our success metric should not be interpreted as confirmed fledging or independence. We therefore refer to this measure as "nest success to ≥4 weeks" throughout the manuscript. Breeding failure during incubation was recorded when eggs disappeared or incubation ceased with no subsequent hatching. Nestling failure was recorded when chicks disappeared before reaching approximately four weeks of age. Productivity was summarised by year as (i) nest success to ≥4 weeks, calculated as successful nests divided by total nest attempts, and (ii) mean number of chicks reaching ≥4 weeks per successful nest. Means are reported with standard deviation and sample size where appropriate.

Age composition of breeding pairs

We classified breeding birds into two plumage-based age categories: adults and subadults. Adults were identified by uniformly dark plumage, whereas subadults were identified by conspicuous white on the neck and/or body (Bregnballe and Carss, 2012). These classifications were made from field photographs and drone images. For each breeding bout, we recorded the number of nests attended by mixed-age pairs, defined as pairs consisting of one adult and one subadult. To avoid misclassifying nearby non-breeding birds as pair members, pair status was assigned only when two individuals were repeatedly observed attending the same nest during incubation or early chick-rearing, particularly when both birds were involved in nest attendance, guarding, or incubation exchange. Mixed-age pairing frequency was then summarised across breeding bouts and years.

RESULTS

Breeding phenology and frequency

Breeding was confirmed in two bouts in 2023, three bouts in 2024, and four bouts in 2025 (Table 1). The confirmed breeding bouts occurred on 24 April and 18 September 2023; 12 February, 16 May, and 10 October 2024; and 18 February, 10 May, 14 August, and 17 November 2025. The first breeding bout in 2023 was assigned to 24 April because nest attendance was observed on that date, although eggs were later confirmed by drone imagery after temporarily unattended nests allowed direct observation of nest contents. Within-year inter-bout intervals were 147 days in 2023, 94 and 147 days in 2024, and 81, 96, and 95 days in 2025. When all consecutive breeding bouts across the 2023–2025 study period were included, including intervals between years, inter-bout intervals averaged 117.3 days, with a median

Table 1. Breeding chronology and breeding results of Great Cormorants at Hushan Reservoir, central Taiwan, 2023–2025

Year	Bout	Date of nesting confirmed	Nest substrate (dominant)	Nest attempts	Successful nests	Chicks ≥4 weeks	Mixed-age pairs (A+SA)	Min. nest height rel. to FSL (m)
2023	1	24 Apr	*Trema orientalis**	4	3	9	2/4	-8
2023	2	18 Sep	*Tectona grandis*	2	2	6	0/2	+8
2024	1	12 Feb	*Trema orientalis**	5	1	3	2/5	-4
2024	2	16 May	*Dendrocalamus latiflorus*	7	3	7	3/7	+9
2024	3	10 Oct	*Tectona grandis*	7	7	17	4/7	+9
2025	1	18 Feb	*Tectona grandis*	6	6	15	1/6	-4
2025	2	10 May	*Tectona grandis*	12	12	30	4/12	+8
2025	3	14 Aug	*Tectona grandis*	10	10	25	4/10	+9
2025	4	17 Nov	*Tectona grandis*	5	5	13	2/5	+8

* Standing dead. Breeding bouts represent discrete colony-level pulses separated by periods with no active nests detected. “Date of nesting confirmed” indicates the first date on which active nesting was detected, including nest attendance, incubation, visible eggs, or chicks. A nest attempt was counted when an active nest was confirmed; a successful nest was defined as one in which ≥1 chick reached approximately four weeks of age. “Chicks ≥4 weeks” indicates the number of chicks reaching approximately four weeks of age (operational definition), not necessarily fully volant fledglings. FSL = full-supply level (211 m a.s.l.); negative values indicate nests below FSL. Mixed-age pairs are expressed as the number of nests attended by adult-subadult pairs / total nests assessed for age; A = adult, SA = subadult.

Table 2. Annual breeding performance of Great Cormorants Phalacrocorax carbo at Hushan Reservoir, central Taiwan, 2023–2025.

Year	Breeding bouts (no.)	Nest attempts	Successful nests	Nest success rate (%)	Chicks ≥4 weeks	Chicks ≥4 weeks per successful nest
2023	2	6	5	83.3	15	3.00 ± 0.00
2024	3	19	11	57.9	27	2.45 ± 0.52
2025	4	33	33	100.0	83	2.52 ± 0.51

Breeding bouts represent discrete colony-level pulses separated by periods with no active nests detected. A nest attempt was counted when an active nest was confirmed; a successful nest was defined as one in which ≥1 chick reached approximately four weeks of age. “Chicks ≥4 weeks” indicates the number of chicks reaching approximately four weeks of age (operational definition), not necessarily fully volant fledglings. Nest success rate = successful nests / nest attempts. Values in “Chicks ≥4 weeks per successful nest” are mean ± SD; sample sizes correspond to the number of successful nests shown in the table.

of 113.5 days and a range of 81–147 days. The shortest intervals were recorded in 2025, when successive breeding bouts occurred at approximately three-month intervals.

Nesting results and productivity

A total of 58 nest attempts was recorded during 2023–2025, including 6 in 2023, 19 in 2024, and 33 in 2025 (Table 2). Nest success to ≥4 weeks varied among years, with 83.3% in 2023, 57.9% in 2024, and 100.0% in 2025. The number of chicks reaching ≥4 weeks was 15 in 2023, 27 in 2024, and 83 in 2025. The mean numbers of chicks reaching ≥4 weeks per successful nest were 3.00 ± 0.00 (n = 5) in 2023, 2.45 ± 0.52 (n = 11) in 2024, and 2.52 ± 0.51 (n = 33) in 2025 (Table 2).

Breeding failures were recorded during both incubation and chick-rearing stages. In 2023, one nest failed during incubation. In 2024, failures were recorded in the February and May bouts, whereas all nests in the October bout produced chicks reaching ≥4 weeks. No nest failure was recorded in 2025. Details of nest attempts, successful nests, and chicks reaching ≥4 weeks by bout are provided in Table 1.

Nest placement relative to full-supply level

Nest placement relative to the full-supply level differed among breeding bouts (Table 1, Fig. 1A). During the first confirmed breeding bout in 2023, nests were placed below the full-supply level. In later bouts, nests were placed at or above the full-supply level in several nesting areas, although nest height still varied among bouts and nest sites. Nest positions included shoreline trees and emergent trees within the inundation zone.

Age composition of breeding pairs and chick movements

Mixed-age pairs were recorded in all three years, accounting for 2/6 nest attempts in 2023, 9/19 in 2024, and 11/33 in 2025 (Table 1). Mixed-age pairs occurred in most breeding bouts (Fig. 1B), including 4/12 nests in May 2025 and 4/10 nests in August 2025.

At approximately 4–5 weeks of age, chicks typically moved away from the nest tree and began using the shoreline and lake surface, where they mainly swam and dived rather than undertaking sustained flight; adults continued provisioning during this post-nesting stage (Fig. 1D).

DISCUSSION

This study documents the first confirmed colonial breeding of Great Cormorants in Taiwan and describes the early development of a newly established inland breeding colony at Hushan Reservoir. During 2023–2025, the colony showed an increase in the annual number of breeding bouts, from two in 2023 to four in 2025, and annual nest attempts increased from 6 to 33. Nest success to ≥4 weeks varied among years, but reached 100% in

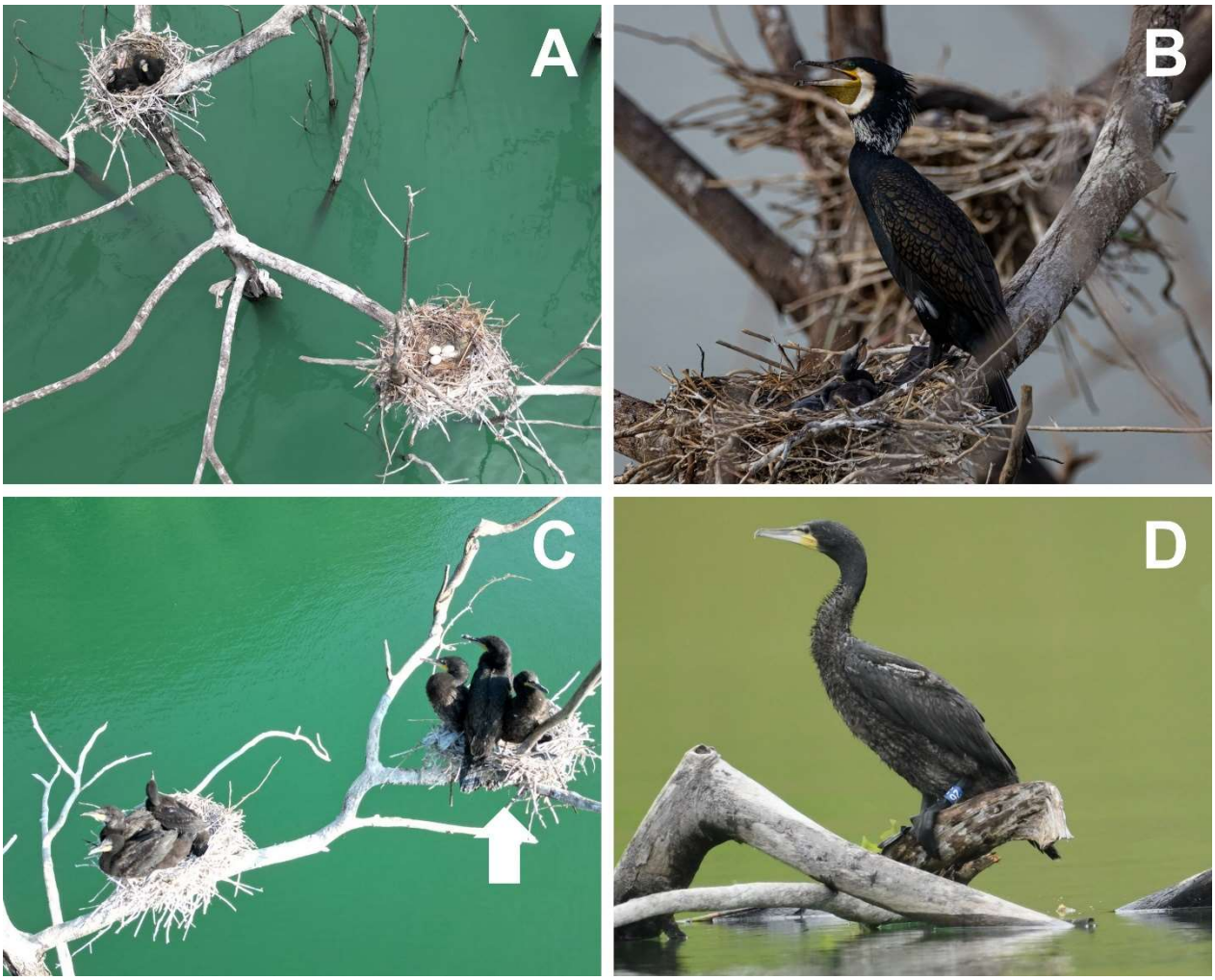

Fig. 1. Colony establishment and chick development of Great Cormorants ***Phalacrocorax carbo*** at Hushan Reservoir, central Taiwan. **A.** During the first confirmed breeding bout in April 2023, nests were placed below the full-supply level (FSL; 211 m a.s.l.) and were subsequently inundated as the water level rose. Nest placement relative to the FSL varied among subsequent breeding bouts. **B.** A subadult attending a nest with 3-day-old chicks, illustrating adult–subadult pairings in this newly established colony. **C.** An adult with 3-week-old chicks. The nest indicated by the arrow was located above the FSL. **D.** A 5-week-old chick that has moved away from the nest area and has begun swimming and diving but is not yet fully volant; the individual shown was banded in this study.

2025. These observations suggest that, once breeding was established, the Hushan colony was able to maintain repeated colony-level breeding activity within a single year under local reservoir conditions.

Repeated breeding activity within a year is noteworthy in the context of Great Cormorant breeding biology. Across much of the species' temperate range, Great Cormorants are generally regarded as seasonal and effectively single-brooded, although replacement clutches and occasional late breeding have been reported. Craik and Bregnballe (2008) found that new clutches initiated after fledging of a first brood were uncommon and that successful second broods represented only a small proportion of breeding attempts. However, a prolonged breeding season with a secondary summer peak has been documented in the Po Delta, Italy (Grieco, 1994). In Japan, Great Cormorants have been reported to breed year-round, although the timing and duration of breeding vary among colonies (Fukuda, 2002). In comparison, the Hushan colony showed repeated, discrete colony-level breeding bouts across most of the year, especially in 2025, when four bouts were recorded at intervals of approximately three months. Although our data do not identify whether the same pairs bred repeatedly, the colony-level pattern indicates an unusually prolonged and frequent breeding schedule for this species and suggests that breeding phenology may be more flexible in warmer regions. Thus, prolonged breeding activity is not restricted to the Hushan Reservoir colony; nevertheless, the regular occurrence of three to four discrete colony-level bouts per year at Hushan remains noteworthy.

The repeated breeding bouts observed at Hushan Reservoir may be partly related to the subtropical

environment and local reservoir conditions. Inland colonies can differ from coastal colonies in breeding timing and productivity, and Newson *et al*. (2005) showed that inland breeding Great Cormorants in England and Wales had higher breeding performance than coastal colonies, largely through higher survival during late chick development. The Hushan colony shares several features that may favour breeding persistence, including an inland freshwater environment, abundant nesting substrates within a restricted-access reservoir, and low direct human disturbance. These factors may allow breeding attempts to continue over a longer seasonal window than is typical in temperate colonies. However, because prey availability and weather effects were not formally quantified in this study, their roles should be regarded as hypotheses requiring further study.

Among other colonial waterbirds, repeated nesting within a year is better documented in some ardeids. For example, in a relatively new Little Egret *Egretta garzetta* colony in Pattani, southern Thailand, nesting was bimodal across a 12-month observation period, with two distinct nesting periods initiated in December and March, respectively (Buatip *et al*., 2013). For Cattle Egrets *Bubulcus ibis*, prolonged seasonal incubation peaks and renewed nesting activity later in the season have been interpreted as being consistent with second broods in several studies (e.g. Maxwell and Kale, 1977; Prosper and Hafner, 1996), and a detailed colony study in Italy reported strong evidence for a second clutch, while noting that the literature includes reports of second and even third broods in some contexts (Dragonetti and Giovacchini, 2009). These ardeid examples indicate that, under warm climates and favourable foraging conditions, repeated nesting within a year can occur in colonial waterbirds; however, the regularity and scale of the three to four colony-level bouts per year documented at Hushan Reservoir still appear striking for Great Cormorants.

The use of "nest success to ≥4 weeks" requires careful interpretation. Great Cormorant chicks generally become fully volant later than four weeks of age, and our metric therefore does not represent confirmed fledging or independence. Instead, it provides a repeatable field-based measure of advanced chick survival that could be assessed reliably from drone imagery. At approximately four weeks of age, chicks at Hushan were large, visible, and often stood at the nest rim or moved short distances from the nest structure. Some individuals subsequently used nearby branches, shoreline areas, or the water surface while still being attended or provisioned by adults. Thus, the high nest success to ≥4 weeks observed in 2025 should be interpreted as high survival through the early and middle chick-rearing period, rather than as confirmed post-fledging survival.

Nest placement varied in relation to reservoir water level and available substrates. During the first breeding bout in 2023, nests were located below the full-supply level and were later affected by rising water. In subsequent bouts, nests were often placed at or above the full-supply level, including on emergent or shoreline trees such as *Tectona grandis* and *Dendrocalamus latiflorus*. This pattern suggests that nest-site use changed after the initial inundation event, but the mechanism remains uncertain. The higher placement of later nests may reflect behavioural adjustment by breeding birds, seasonal water-level conditions, availability of exposed nesting substrates, or a combination of these factors, but this pattern should be interpreted cautiously because we did not experimentally test nest-site selection or quantify substrate availability through time.

The regular occurrence of mixed-age pairs is another notable feature of the Hushan colony. Mixed-age pairs were recorded in all three years, accounting for 2/6 nests in 2023, 9/19 in 2024, and 11/33 in 2025. In Great Cormorants, reproductive performance can vary with age, and older breeders may differ from younger individuals in breeding competence, timing, and productivity (Frederiksen *et al*., 2001; Bregnballe, 2006). The presence of subadults among breeding pairs at Hushan may therefore indicate that younger birds were able to enter reproduction during the early stage of colony establishment, possibly because competition for nest sites or mates was still relatively low. However, because individuals were not marked before breeding and exact ages were not known, we do not interpret mixed-age pairing as direct evidence of age-specific reproductive performance. Long-term marking of breeding adults and subadults will be needed to determine whether subadult participation contributes substantially to colony growth.

The Hushan record also has broader significance for the status of Great Cormorants in Taiwan. The species has historically been treated as a winter visitor, and previous breeding observations in Taiwan appear to have been isolated, non-colonial, and not formally documented in detail. The repeated breeding bouts, increasing nest attempts, and continued presence of breeding birds at Hushan Reservoir suggest that Taiwan may now support at least one established inland breeding colony. Reservoirs and other large inland water bodies may provide suitable nesting and foraging conditions, particularly where public access is restricted and disturbance is low. A notable regional comparison is provided by Lake Biwa, Japan. Following an apparent post-war interruption in breeding, only five Great Cormorant nests were confirmed on Chikubushima Island in 1982. The colony subsequently increased to 1,439 nests by 1996. A second colony established on the Isaki Peninsula in 1988 also increased rapidly, from 30–40 nests to 1,939 nests by 1996 (Ishida *et al*., 2000; Fukuda *et al*., 2002). Although Hushan Reservoir remains at a much earlier stage of colony establishment, the Lake Biwa case illustrates how a small initial breeding aggregation can grow rapidly under suitable inland

freshwater conditions. Nevertheless, the present study covers only the first three years of confirmed breeding, and continued monitoring will be necessary to determine whether the colony persists, whether annual nest attempts continue to increase, and whether breeding expands to other reservoirs or wetlands in Taiwan.

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