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Breeding biology of kawau pāteketeke | New Zealand king shags (*Leucocarbo carunculatus*)

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Abstract: Kawau pāteketeke | New Zealand king shag (*Leucocarbo carunculatus*) nest occupancy, breeding, and offspring survival was studied for the first time at four colonies in 2018 and 2019, by analysing field camera still images. Nesting territories were retained year-round. Nest-building was underway by Mar and observed through much of the year. Successful pairs with stable nests were elevated and central to nest areas. Inter-colony asynchronous first clutches occurred over six months, with laying spanning 5–10+ weeks at single colonies (2019). Clutches of 2–3 eggs took ≤13 days to complete. Incubation commenced with first eggs; asynchronous hatching was 28–32 days later with brood reduction at early nestling stage and occasional replacement clutches observed. Chicks were unattended at 3–4 weeks, showing strong creche behaviour thereafter, and were fully feathered at 65 days, fledging soon after. Breeding outcome was most influenced by height above sea-level (waves), exposure (weather), and boat/landing disturbance. Most young disappeared from images at 4.5–5 months, their fate—dispersed or perished—unknown. Some resided at the colony into/beyond the subsequent breeding season, sometimes interacting with presumed parents. Any predation (by gulls) was seen as opportunistic during disturbances, or of eggs not in nests.

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INTRODUCTION

The kawau pāteketeke | New Zealand king shag (*Leucocarbo carunculatus*), hereafter NZKS, is a marine, pink-footed cormorant (Family: Phalacrocoracidae), one of three remaining endemic blue-eyed shags from the genus *Leucocarbo* remaining on the Aotearoa New Zealand mainland (Rawlence *et al*., 2017), and is currently restricted to Te Tauihu-o-te-Waka/Marlborough Sounds.

With low productivity and juvenile survival (Bell 2022) and <800 mature birds in a restricted and relictual range forecast to further decline with climate change, the species remains at a conservation status of Nationally Endangered (Robertson *et al*., 2021). The species is also highly vulnerable to human-induced threats (Nelson 1971; Taylor 2000). Recent annual estimates suggest 300 breeding NZKS pairs (2019–2021), spread across up to a

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dozen dynamic colonies in a total population of 784 individuals (Bell 2022), within the previous range of 645–839 birds counted between 1992 and 2015 (Schuckard *et al*., 2015). NZKS are sedentary and mostly breed in winter on small, exposed islands with 80% of the population breeding lower than 14 m above sea-level (Schuckard 2013, 2022). Pairs are monogamous, in territories just out of reach of neighbours, and produce altricial, nidicolous nestlings (Marchant & Higgins 1990).

In response to growing concerns on the potential impacts of regional aquaculture on NZKS, and to enable informed decision-making regarding resource consents, the Marine Farming Association (MFA) formed a King Shag Working Group, which included industry representatives, Ministry for Primary Industries (MPI), Ngāti Koata iwi, Marlborough District Council, and the Department of Conservation (DOC) (*marinefarming.co.nz/king-shag-project/*). Wildlife Management International (WMIL) and sibling company Toroa Consulting Ltd conducted a three-year project researching life history (sightings of marked chicks), and movement and foraging behaviour of NZKS at sea (Global Positioning System [GPS] tracking of adults) (Bell 2019, 2020, 2022).

Population dynamics and breeding biology were identified as research priorities for NZKS (Taylor 2000), yet few studies had been previously conducted due to the species' extreme sensitivity to disturbance. Knowledge of the breeding cycle is essential for predictive population modelling. A study on NZKS breeding was initiated by DOC in 2018, to run in parallel with the chick banding and adult tracking project, and was facilitated through advances in remote, field camera technology. The study also aimed to record disturbances and other events to further define threats at breeding sites, as well as banded bird observations. A detailed report on the results of image analysis was presented to the King Shag Working Group (Gummer 2021), and key findings are summarised in this paper.

METHODS

Images with data were successfully collected from ten static field/trail cameras across four different NZKS colonies—Duffers Reef, Kuru Pongi/North Trio (Trio Islands), Tawhitinui, and White Rocks—in Marlborough Sounds (refer to map and colony details in Schuckard *et al*., 2018), situated primarily on marine rock plateaus and steep rock faces. Duffers Reef, Kuru Pongi/North Trio (hereon referred to as Kuru Pongi), and White Rocks were chosen because they were the largest known breeding colonies—all have Wildlife Sanctuary status, but Kuru Pongi is privately owned. The main colony Duffers Reef, along with the only mainland colony Tawhitinui (part of Kenny Isle Scenic Reserve) were sites where the marking of birds could be achieved. Nesting areas at Kuru Pongi and Tawhitinui were more elevated at approximately 10–15 m above sea-level, while the White Rocks nesting site was estimated to be 5–10 m, and Duffers Reef the lowest lying at <5 m above sea-level.

Cameras were deployed at different periods from 10 Aug 2018 (DOC and WMIL/Toroa Consulting) with most image files collected by 26 Nov 2019 (Table 1). Files were stored on SD cards which had to be retrieved and replaced, influencing dates of deployment. With limited options for camera placement, personnel aimed for wide angles covering many nests at some locations, and close-up views of a smaller number of nests at others, while considering sun direction (sunstrike) and height above sea-level (storm surges). Use of multiple cameras at a single site aimed to cover different angles and views of each nesting area, although limited vantage points restricted coverage at some locations e.g., Duffers Reef. Cameras were mounted on metal posts hammered into the ground or glued into rock or tied to a tree (one site).

Mostly, cameras were set to take still images at set intervals throughout the day and turned off during the night to conserve battery power. However, image frequency varied between files (on the same camera) and/or cameras and in some cases was experimental. Different programming included: a) Daytime: half-hourly (most common) or quarter-hourly, from pre-dawn (dark) to mid-evening (dark); b) Nighttime: either no night shots; or shots taken less frequently through the night; or more night shots in winter; c) Some with multiple (eight) frames/every 30 mins; or d) Motion sensor settings (approx. 12 frames/min) which were unintentional and represented four days (Duffers Reef) and five days (Tawhitinui) of activity in Dec 2018 (17,472 of 104,477 usable images for these two colonies).

Trail camera properties considered important for this project were: durability in a hostile, marine environment; flexibility for mounting and positioning; image storing capacity and power output enabling longer periods between servicing, minimising colony disturbance; and internal software to suit project demands.

Methods were developed to manage viewing and analysing large numbers of images. Unusable images were eliminated as thumbnails and usable image viewing managed using a custom-made image library index. One or more master images was selected for each camera view for reference, usually when birds were incubating. Nests were assigned alphabetical labels in each master image, and nest label overlays applied to all relevant images in that file. Image data from every camera file were exported into data spreadsheets enabling

Table 1. Cameras deployed, and bird and nest numbers in still images at four New Zealand king shag colonies.

	Duffers Reef		Kuru Pongi/ North Trio	Tawhitinui		White Rocks	
Camera number and operating date range; date blocks in Gummer (2021)	3 cameras / 6 date blocks 13 Dec 2018–26 Nov 2019		2 cameras / 2 date blocks 04 Apr–26 Nov 2019	3 cameras / 6 date blocks 10 Aug 2018–26 Nov 2019		2 cameras / 4 date blocks 25 Aug 2018–31 Oct 2019	
Total images with data	1280		701	1191		821	
Breeding season	**2018**	**2019**	**2019**	**2018**	**2019**	**2018**	**2019**
Max head count (ads/ juvs)	50 (Dec)	See Dec 2018	n/a	-	56 (Mar)	-	80 (Jul)
2018 juvs as 1y birds in early 2019	-	4 (Jan) to 1 (Apr)	5 (Apr) to 10 (mid-May)	-	5 up to Apr	-	Few, no obs after Mar
(Total colony nest count)[1]	*(78)*	*(89)*	*(48)*	*(23)*[2]	*(26)*	*(31)*	*(30)*
Labelled nests in images	-	15	10	20	15	28	28
Nests followed (through season)	-	15	9	20	12	27	27
Breeding attempts	-	-	8	Min.10	Min.10	-	26
Non-breeding pairs	-	-	1	-	1	-	1
Nests with unknown status	-	3	-	10[3]	1	-	-
Nest failures egg/nestling	-	-	1	-	1	-	10
Nest failures downy, mobile chick	-	3	-	-	2	-	3
(Chicks with bands)[1]	-	*(23)*	-	*(11)*	*(13)*	-	-
Nest failures at fledging	-	-	-	-	-	-	1-3
Chicks in Jul	-	12	11	-	-	-	15
Juvs in Aug	-	-	≥8	11	14 (banded)[4]	-	12
Juvs in Sep	-	18 (banded)	≥8	9	12 (banded)[4]	10	11
Juvs in Oct	-	17 (banded)	≥7	10	10 (banded)[4]	7	8-10
Juvs in Nov	-	14 (banded)	-	10	9 (banded)[4]	5	-
Juvs in Dec	5-6	-	-	9	-	3	3

[1] Bell (2022) – boat-based surveys; chick banding operations.
[2] Bell (2019) – boat-based surveys.
[3] Contents of Tawhitinui nests in 2018 could not be seen; nests of unknown status include those belonging to non-breeders, or pairs that failed early on.
[4] Includes 2018 banded juvenile.

observations to be entered directly next to the relevant image number and date/time taken. Images were coded for data content and sorted after data collection, to facilitate analyses.

Data and observations were documented for each camera view at each colony on: 1) breeding biology; 2) banded birds—chicks banded at Tawhitinui (2018 & 2019) and Duffers Reef (2019), and adults fitted with back-mounted GPS devices at Duffers Reef (Bell 2019, 2020), 3) bird behaviours—including reactions to disturbance; and, 4) threats—all events impacting on NZKS. Gender roles are described in Gummer (2024) after sexually dimorphic plumage variation was identified.

Details on nest-building, egg-laying, incubation, hatching, and chick development were captured well in the more close-up images at Kuru Pongi, Duffers Reef and Tawhitinui, with images from the latter two sites producing good sightings of readable leg bands. Nests at Kuru Pongi provided the most accurate observations of clutch and brood size because camera angle allowed the best viewing of nest contents. While chick ages were known here, viewing was difficult closer to fledging time and ceased soon after due to obstruction by growing vegetation in spring.

Tawhitinui and Duffers Reef offered good viewing of downy, mobile chicks to fledglings/juveniles, but exact ages were unknown because of a break in camera operation mid-winter at both sites and lack of continuity between views during the incubation and downy chick-rearing phase.

Wide-angle views at White Rocks were ideal to monitor movements, breeding effort and productivity of the whole colony as well as nest site occupation throughout the year. A wide view here, and from some Tawhitinui cameras, gave better viewing of disturbances to the colonies.

RESULTS

A total of 131,946 usable images recorded from ten cameras were viewed—104,477 of these at Duffers Reef and Tawhitinui—; data were collected from 3995 images (Table 1). Camera deployment date ranges are summarised in Table 1; within these periods, cameras were serviced and not operating continually. Unusable images were discarded for the following reasons: loss of view caused by camera drop in severe weather conditions—Duffers Reef (one camera); nests obscured by spring vegetation—Kuru Pongi (both), Tawhitinui (one); and camera malfunction—White Rocks (one).

Number of nests seen during the breeding season in any one camera view ranged from nine at Kuru Pongi (less than a fifth of all nests counted there from boat-based surveys; Bell *et al*., 2022) to 28 at White Rocks (all but two of the total nests recorded by Bell *et al*., 2022), with up to 80 NZKS, including juveniles and non-breeders, counted at White Rocks when birds moved into camera view from loafing areas normally beyond it (Table 1). Between seven and 17 chicks could be followed through to independence at different sites in 2018 and 2019.

Courtship and nest building

Images taken over summer 2018/2019 revealed NZKS nest sites are retained through the off-season but not strongly defended by the end of the year (2018), a time when the 2018 juveniles were also disappearing. Old nests from the 2018 season in the form of muddy mounds (accumulated guano and vegetation) were obvious at Duffers Reef and Tawhitinui in early 2019. At Duffers Reef, these started to wash away with the onset of autumn weather, leaving bare rock, whereas some of the 2018 nest mounds at the more sheltered Tawhitinui remained through to the 2019 breeding season and were added to with fresh material. At the more exposed White Rocks, stained rock indicated the presence of nests at most territories in the 2018 season, but there were no mounds at all.

Nest site occupation and nest building in the 2019 season can be outlined as follows and includes inter-colony variation. In the late spring/summer (Dec–Jan), a pair might leave their site unoccupied during the day, but roost loosely there or nearby at night. By late summer/early autumn (Jan–Mar), distinct sites were occupied by birds and some nest material was present, although the pattern of nest occupation was sporadic; and, at some territories, first-year birds would be regularly seen with pairs (presumed parents). Shifts commenced by Mar–Apr when the nest site was occupied by at least one bird in the day; and, only during disturbances were nests left completely unattended.

Once the early stages of nest-building were underway (Feb–Apr, commonly Mar), adults began to sit during the day, probably as a way of anchoring the collected nest material—land vegetation and/or seaweed depending on location—; nests then increased in size and were more likely to withstand the elements. Prior to this, birds rarely sat down on land. Night images showed all birds standing on or next to nests when roosting, before eggs were laid.

While the disappearance of all nests at exposed sites was known to coincide with bad weather, often material would disappear soon after adults had positioned it. Where wind was not suspected (interpreting bird postures), and where conditions were dry (no rain to wash material away), it was suspected nest material was stolen by other birds, a behaviour only captured on two images. Pairs were only occasionally seen in aggressive postures

with neighbours during nest-building, e.g. when re-establishing territories after a bad weather event.

Pairs occupying central and/or elevated sites, buffered by other pairs/nests—seemed to be more successful in building larger, longer-lasting nests, were less often seen carrying nest material or arranging nests and were rarely seen in courtship display postures during this time. They sat much more than some of the peripheral pairs, their nests started from scratch less than a handful of times in two months of early-season nest-building activity.

Pairs at peripheral nest sites, including those close to cameras, were presumed to be less established, often the slowest to start nest-building (White Rocks, Tawhitinui) and taking longer to coordinate nest attendance. Consequently, their nests were more prone to disappearing, and they appeared less experienced, building numerous nests from scratch—up to 15 times in two months from mid-Mar. These pairings showed more courtship behaviour (Duffers Reef), some not previously described for the species in Marchant & Higgins (1990), such as 'biting' (head or nape), 'neck-crossing' (often after 'biting') and mutual 'sky-pointing' (refer Fig. 1 [bottom left photo] in Gummer (2024) for latter two displays).

Nests of breeding pairs thickened up just before egg laying and throughout incubation. Nest building happened at clusters of nests simultaneously—multiple nests were added to, with the same type of material, on a particular day—as well as on an individual basis, though few images showed birds carrying material or arranging nests. Copulation events, not captured often, were seen over one month to one day before their first eggs were laid.

Nest-building was a behaviour that could be seen for many months, from late Jan (Tawhitinui) right through to Oct (Duffers Reef), the latter being very late second breeding attempts.

Egg laying, incubation, and hatching

Egg-laying periods for first clutches spanned a minimum of five weeks (Kuru Pongi) to more than ten weeks (White Rocks), laying from mid-Mar in 2019 (Table 2). Earliest eggs were laid in nests higher up slopes (Tawhitinui, Duffers Reef), and some of the latest clutches were laid in peripheral nests near to cameras and at lower elevations.

Observing the standing and sitting behaviour of birds at night—2–3 h after dark and the same before dawn—proved to be the fastest method of establishing when a pair was laying (Fig. 1). Both adults in a pair stood at night right up until the night or night before first egg laying. Birds tended to sit at nests continuously from the time the first egg was laid with limited standing, if any, at night only. The pale blue eggs (appearing white in images) were rarely captured being laid in images but suspected from behaviour as laid between midnight and dawn, although some were laid during daylight hours too.

Clutch sizes in 56 nests where data could be collected on egg laying—White Rocks (26 nests), Kuru Pongi (16), Duffers Reef (10), Tawhitinui (4)—ranged from 1–3 eggs, with at least 40 (71%) confirmed to have 2–3 eggs. A single egg was laid and abandoned on bare rock at a peripheral site at one colony (then opportunistically preyed on by a red-billed gull *Chroicocephalus novaehollandiae*). Four or more eggs were never seen in any one nest.

Females laid each egg within a first clutch at roughly 3–4-day intervals: three clutches of three eggs each took six, seven and eight days to be laid, although a fourth took 13 days from the latest lay date of the first egg to the earliest lay date of the third (Fig. 1).

Hatching outcome could be observed at 34 nests at three colonies (2019). Accurate hatch dates could not be recorded at most nests because parents were rarely standing in images. In addition, dark grey nestlings were hard to see in dark nests in the shadow of parents (particularly White Rocks). Hatches were usually first detected by observations of clear brooding behaviour (adult sitting, loosely held wings), when chicks might already be >1 day old. On occasion, hatches were ascertained when eggshell appeared on the nest rim.

Accurate first egg hatch dates as well as first egg lay dates were only known for two nests (Duffers Reef, Kuru Pongi); the period spanning laying and hatching was 31 and 33 days, respectively.

Table 2: First clutch laying periods at four New Zealand king shag colonies in 2019.

Colony	Earliest possible first egg lay date	Latest possible final egg lay date	Maximum laying period (days inclusive)	Comments
Duffers Reef	21 Apr	5 Jun	46	Replacement clutches also observed.
Kuru Pongi	2 May	9 or 14 Jun	39 or 44	9 Jun one pair; 8-14 Jun another pair.
Tawhitinui	19 Mar	>31 May	>74	Second egg laid by estimated 4 Jun.
White Rocks	30 Mar	26 May	58	Replacement clutches also observed.

Figure 1. New Zealand king shag (*Leucocarbo carunculatus*) breeding at White Rocks (left) and Kuru Pongi/North Trio (right) in 2019. Clockwise from top left: incubating adults sitting at night and adults yet to lay standing on or next to nests, with group of juveniles roosting on left edge of nest area (12 Apr); three-egg clutch, with mostly males with dorsal 'saddles' attending other nests (Gummer, 2024) (8 May); chicks outside front nest unguarded and mobile for first time, and three chicks from two nests in creche (top right) in warm temperatures (26 Jul); downy chicks and feathered juveniles in supervised creches, adult incubating second clutch, black-backed gull scavenging king shag chick corpse (likely already perished in recent wet weather), and red-billed gulls foraging amongst nests (20 Jul). (Photographs taken by static field cameras).

First hatch and lay dates, both to within one day were known for a single nest only (Kuru Pongi), also with 31–33 days between events. Six other pairs showed a maximum period of 29–39 days between accurate first egg lay and latest possible first hatch dates. Date ranges larger than this were disregarded in any analysis. Therefore, the incubation period for NZKS eggs is likely to be 28–32 days, excluding day of hatch.

Of the 29 viewed pairs confirmed hatching eggs, three were known to produce single chicks, 12 pairs clearly produced two or more, and the remainder were likely to have produced more than one chick, but initial brood sizes could not be confirmed. Some three-chick broods were probably produced but were never seen in nests on images. The only evidence was seen later in the season (Tawhitinui): one nest with two large, well-developed, banded siblings and a third smaller sibling that eventually perished.

Replacement clutches

NZKS pairs laid replacement (second) clutches but only after failure at either egg or young nestling stage and no later, despite some pairs showing further courtship and/or nest-building behaviour after loss of older chicks. None of the second attempts by seven pairs (Duffers Reef, White Rocks) were successful in 2019.

First clutches at the lower lying Duffers Reef nesting area, vulnerable to weather disruptions, were very late due to continual wave washouts Mar–May 2019, and only two breeding attempts were still underway in late Jul, both failing at nestling stage. The timing between failure of one pair's first attempt (Aug) and re-lay (Sep) was 32 days; the continual and consistent presence of two birds at the site indicated the same pairing but neither were identified by markings. Both second clutches contained two eggs laid six days apart; one clutch soon disappeared, and the other was incubated to mid-Oct but was depredated during a disturbance.

Replacement clutches at four of five nests at White Rocks were all likely to have been laid late May–late Jun, not much later than the last breeding pairs laying first clutches at Kuru Pongi. Time between first clutch failure (May) and re-lay (Jun) was 28–33 days for one pair and was indicated by standing/sitting behaviour at night.

Table 3: Ages and date ranges of key events during growth and development of New Zealand king shag chicks in camera view in 2019, summarised from Gummer (2021). (Number of chicks with data in parentheses.)

Key events: First visible in nest = Chick sitting next to (not under) sitting adult in nest (i.e., not brooded); chicks can be seen before this only if adult is standing / First out of nest = first time chick seen sitting outside nest scrape/bowl / First time creche = chick joined by or joining another chick from another nest / Fully feathered = no traces of down left / First flight = absence of fully feathered juveniles from camera view then preening on return / Last seen at natal nest = disappearances occurring more than 2 days before end of viewing, allowing for temporary absence of night or two.

Colony	Chick(s) first visible at nest	Chick(s) first seen unguarded	Chick(s) first out of nest	Chick(s) first time creche	Chick(s) near size of parent	Juv1 fully feathered	Juv2 fully feathered	Juv(s) estimated first flight	Juv(s) last seen at natal nest
Chick ages (Kuru Pongi)	12–15 days (n=4)	20–29 days (n=4)	24–25 days (n=2)	26–39 days (n=4)	No data	65 days (n=1)	65 days (n=1)	No data (vegetation)	No data
Kuru Pongi dates	20 Jun–23 Jul (n=6)	10 Jul–6 Aug (n=7)	7 Jul–1 Aug (n=6)	20 Jul–16 Aug (n=5)	12–15 Jul (n=2)	29 Jul–8 Sep (n=5)	15 Aug–8 Sep (n=2)	No data (vegetation)	No data
Tawhitinui dates[1]	No data	18 Jul–8 Aug (n=6)	18 Jul (n=1)	19 Jul (n=2)	19–27 Jul (n=5)	7 Aug–20 Sep (n=6)	11 Aug–20 Sep (n=6)	20 Aug–3 Sep (n=3)	-
White Rocks dates	31 May–11 Jul (n=10)	16 Jun–23 Jul (n=14)	18 Jun–23 Jul (n=13)	21 Jun–24 Jul (n=12)	30 Jun–25 Jul (n=5)	15 Jul–23 Aug (n=7)	n/a	23 Jul–26 Aug (n=5)	6–28 Oct (n=4)
Duffers Reef dates[1]	No data	No data	2 Aug (n=1, youngest)	No data	No data	8 Aug–21 Sep (n=2, oldest, youngest)	No data	No data	6–22 Nov (n=9)

[1] Images only available from 18 Jul at Tawhitinui and 24 Jul at Duffers Reef.

Chick data

Dates for one or more key events during growth and development were recorded for chicks in 33 nests mainly at three colonies—White Rocks (17 nests); Tawhitinui (nine); Kuru Pongi (seven)—and are summarised in Table 3. Initial brood sizes could not be established because of limited opportunities to view nest contents around hatching and early nestling stage. Commonly just one or two chicks were followed per nest.

Juvenile alphanumeric plastic bands were read clearly in images and provided valuable data for about 18 chicks/juveniles at Tawhitinui in 2018 and 2019 (200 sightings), and 18 at Duffers Reef in 2019 (119 sightings) at and away from natal nests, although exact ages of these chicks were unknown — there were no images from either site during the early breeding season.

With so few accurate hatching dates, it was difficult to ascertain precise chick age at key development stages; most were estimated. Accurate hatch dates (within 1–2 days) were captured at some colonies, but data could not be collected from these known-aged chicks for reasons associated with camera operation or positioning. However, at Kuru Pongi, there were two nests with reliable hatch dates to within 1–3 days, and ages could be calculated at events up to feather completion in juveniles, mainly in one nest.

Nestlings and downy, mobile chicks

Brooded chicks' heads were visible from approx. one week of age. Chicks were around two weeks old before they were no longer brooded by day and adults stood next to the nest, brooding only at night.

Two known-age chicks (Kuru Pongi nest) were 20–21 days old when first left alone by parents (Fig. 1). Most other chicks were unguarded for the first time at roughly one month old. Chicks might only be left alone by parents up to 2 hrs at most to begin with but were unguarded for several hours at a time by mid-Jul 2019 (Kuru Pongi).

Occasionally, chicks left their nest bowl before being unguarded, i.e., could be seen sitting next to the nest with an adult, but this was uncommon. Robust data at White Rocks showed that chicks left the nest for the first time either on the same day or within four days after the day they were first left unattended, the same as one of the known-age two-chick broods at Kuru Pongi. Increased chick mobility—moving away from natal nest and beyond adjacent nest(s)—was apparent from around five weeks.

Creche behaviour was prevalent at White Rocks, especially when most adults vacated the colony (Fig. 1). All chicks showed this behaviour, either before they had left their nest (other chicks joining them in their natal nest) or within a week of leaving their nest (joining up with other groups of chicks). It was also commonly observed at Duffers Reef where single downy chicks were often with a neighbouring chick at night, rather than with parents. Adults seemed very tolerant of other pairs' chicks. Little obvious aggression between adjacent pairs at this time was captured on images, just occasional threat postures. Creche behaviour appeared less common at Tawhitinui.

The strong creche behaviour shown by NZKS young from an early age made it hard to keep track of individuals without bands. To add confusion, mobile chicks, leaving the vicinity of the natal and adjacent nests, appeared to roam sporadically by day, often not seen back at the natal nest until nightfall. Some chicks roosted away from natal nests at night—during viewing hours—but would be back at their nests with parents the next day. The odd chick would have a spell (days and nights) rarely seen back at the nest. It is not known if parents called chicks back to feed them, or if chicks were occasionally fed away from the nest by parents or other adults. All downy, mobile chicks would roost standing up at night by mid-Aug 2019 at Tawhitinui.

At all sites, chicks reached the size of their parents at around 5–6 weeks and were downy with feathers emerging. Most broods successfully reared to this stage were single chicks in 2019, and so any known second (and even third) nestlings that hatched had perished early on during brooding. However, at least two broods of two chicks were raised to juvenile stage at Kuru Pongi (2019), with others likely but obscured by vegetation. At least one brood of two chicks was closely followed at Tawhitinui (2019) after a third (smaller) sibling in the nest died. Two juveniles were usually seen together at one White Rocks nest in 2018, but there were no two-chick broods in 2019. It required many consistent observations to determine two-chick broods at sites where creche behaviour was prevalent, especially if the camera started mid-season.

Plumage development and fledging

At any one time in the breeding season, chick ages were spread across 5–6 weeks at each site (Table 3), e.g., youngest chicks immobile in the nest while others were nearly fully feathered. Very occasionally, within a brood, there may have been slightly staggered chick sizes or plumage development.

Chicks were fully feathered by around two months of age (oldest and youngest chicks) at White Rocks. Two known-age siblings showed no traces of down at 65 days (Kuru Pongi). Plumage development was only loosely followed at Duffers Reef as the focus was recording banded chicks.

Juveniles were distinguishable from first-year birds by their immaculate plumage.

Fledging was best observed at Tawhitinui and White Rocks where there were wider fields of view, although fledglings were never really seen taking off, in flight, or landing in images. Fledging occurred in winter and spring, e.g., late Jul (earliest at White Rocks 2019), early Oct (latest at Tawhitinui 2018).

The first (oldest) birds were suspected to have fledged based on observations of their nests, around the time they had shed all down. The youngest chick at White Rocks (2019) fledged three days after the last traces of down were gone. A typical first sign was the absence of a chick for short periods, e.g., an hour mid-morning to noon, and preening activity (sometimes over an hour) immediately on return, after likely contact with water.

Fledging behaviour of two of the younger siblings at a nest closer to a camera (Tawhitinui) showed parents away much of the day in late Aug, leaving their fully feathered chicks at the nest site alone, potentially attempting to force the young to fledge. Two days later, both chicks left the nest for around an hour in the middle of the day, most likely flying by this stage. In early Sep, often the entire nest area was deserted in the middle of the day for an hour or so, suggesting that all adults and juveniles were out at sea, and that all young had fledged. In 2018, most Tawhitinui young were considered to have fledged by the end of Sep, later than in 2019, with the youngest two fledging in Oct after being left alone at the site.

When both fledglings and downy chicks were present at White Rocks, movements to/from sea were typically noted in the following order in late Jul 2019: females departed (early morning) followed by males and all fledglings (mid-late morning); young chicks were in a creche with few or no attending adults (middle of day); adults and juveniles trickled in (afternoon/early evening); young chicks left creches and returned to natal nests (early evening). Adults and juvenile sometimes returned at the same time (early afternoon), indicating they had perhaps been to sea together, although this could never be confirmed. In total, 11 juveniles fledged from 11 nests before Sep at White Rocks in 2019.

Juvenile movement and disappearance

Adults began to abandon their young in Aug (White Rocks) and Sep (Kuru Pongi) in 2019, likely forcing independence. Sometimes creches of juveniles were left roosting alone at White Rocks at night (good or bad weather); parents were back at the site by morning, but not always. By Oct, adults were occasionally seen back at the Kuru Pongi nest site but not interacting with juveniles.

On land, juveniles started to wander much farther away from natal nests after fledging. Most of the sightings of banded 2019 juveniles at Duffers Reef were made from Sep onwards; they were only passing through camera views briefly and did not socialise with any birds from monitored nests.

Groups of adults and juveniles appeared to move to and from sea independently by early Sep (White Rocks 2018), late Sep/early Oct (Tawhitinui 2019), and Oct (Duffers Reef, White Rocks 2019), with juveniles typically departing in the morning, often earlier than adults, and arriving back late morning to early afternoon (immediately preening) before the adults began to return. Two pairs, each with one offspring, were followed closely to confirm this. In one family, the juvenile departed 2–3 hrs after the first parent, just before the second and was back at the colony more in sync with the second adult; while in the other family, an older juvenile departed before both parents and returned in between parents by mid-afternoon.

At White Rocks, a few adults were commonly present with juveniles at the site in the middle of the day, when most other adults were away (Fig. 1). The most common time for a colony to be empty during Sep and Oct was around late morning and/or early afternoon. However, nesting areas at Tawhitinui and Duffers Reef were rarely completely deserted; if they were, a complete exodus was often around late morning and/or early afternoon and may have been due to disturbance (e.g., boats).

Occasionally, adults and juveniles appeared to be separated at night. For example, when all birds vacated the White Rocks nesting site during a night of bad weather in Sep 2018, around nine juveniles, unaccompanied by adults, were the first birds to arrive back at the site the following late morning. After a similar event in Nov, adults were back at the site by dawn without young.

The timing of observed declines in juvenile numbers at each colony is summarised in Table 1. Presumed independence did not occur before 2.5 months after fledging at White Rocks (two juveniles 2019); occasional feathered young disappearing earlier than this did not fit the common pattern and were thought to have perished. More commonly, juvenile sightings decreased as they reached 4.5–5 months of age, through Oct–Dec in 2018. Juvenile land movements away from natal nest sites peaked in Nov 2019 when many previously unseen banded juveniles entered one Duffers Reef camera view for the first time. Most juveniles still visited natal sites, mainly only at night and sometimes sporadically, until they permanently disappeared.

It was impossible to determine actual fate—dispersed or perished—of any juveniles that were no longer seen with parents or at natal nest sites, in this study. Dates of last sightings of 2019 juveniles at their natal nests are summarised in Table 3 but data are limited due to obscuring vegetation and camera retrieval in late Nov. Young from nests in camera

view present just before cameras were removed in 2019 were as follows: one at Duffers Reef (24 Nov), seven at Tawhitinui (24–26 Nov), and six at White Rocks (29–31 Oct).

For remaining juveniles, begging behaviour, and parent-juvenile feeding events were so rarely caught on any of the cameras taking one image per half-hour at any of the colony sites, e.g., only two images from one Tawhitinui camera showed young begging, and no images showed any juveniles being fed by parents. Begging behaviour by fully feathered juveniles at White Rocks was only noticed in a handful of images, and actual feeding of juveniles by adults was only seen twice.

Contrastingly, on cameras set to motion sensor in Dec 2018 (multiple frames per minute) there were numerous events captured of different juveniles at Tawhitinui and Duffers Reef harassing adults, and getting fed. Some interactions looked almost aggressive, with the juvenile ambushing the adult as soon as it landed, and the adult fleeing afterwards, sometimes pursued by the juvenile. Each interaction ranged from 2–5 mins (juvenile fed), or 1–8 mins (no feed). Ten harassments were counted on one day, half of these resulting in parental feeds. Some of the less aggressive interactions lasted for over an hour (following presumed parent and begging). Actual feeding events (juveniles head inside parent's bill) lasted up to 30 seconds.

A proportion of 2018 juveniles (at least 16 at three sites) remained at their natal colony into 2019. They were often observed allopreening, presumably with parents, but also with other immature birds suspected as being either siblings or other same-age birds they 'creched' with as chicks/juveniles. Most of the six banded juveniles at Tawhitinui left natal nests to loaf and roost at the edge of the nesting area by Apr 2019. Four of five juveniles at Duffers Reef dispersed from natal sites Jan–Apr. Five juveniles at Kuru Pongi were seen loafing at the edge of the nesting area to May when they were joined nightly by more first-year birds—most likely from other nests outside camera view. (White Rocks had no camera operating Jan to mid-Mar 2019.)

First-year birds

First-year birds (2018 juveniles) were distinguishable from the immaculate 2019 juveniles by their scruffier feathers, and more defined white alar (wing) markings. At Duffers Reef, juveniles seemed to have greyish feet Aug–Oct, while first-year birds had pinkish feet. After this, some first-year birds started to look more like adults in certain light, with dark chocolate-coloured feathers instead of black (one with dull blue eyes).

At least two first-year birds (one each at Tawhitinui and Duffers Reef) were known to stay at natal nest sites to late Nov 2019, when cameras stopped operating. The bird staying with parents at Tawhitinui was not the last chick to be reared at this site in 2018. From mid-Jul 2019, the pair was assumed to be non-breeding based on behaviour and the presence of their 2018 offspring; however, Bell (2019) recorded them as failed breeders in Jun. The feeding of this bird by parents was never captured on images. The immature bird would commonly loaf alone at the nest by day. The first-year bird seen regularly at Duffers Reef at an unlabelled nest site was sometimes with an apparently non-breeding adult, their last interaction noted in Aug 2019. First-year birds were not seen associating with any of the current season breeding pairs or young at any of the colonies.

Breeding failures

At 34 monitored nests with eggs—White Rocks (26 nests), Kuru Pongi (seven), Duffers Reef (one)—in 2019, around one-third (first clutches, all at White Rocks) were thought to have failed before, during or very shortly after hatch. Two nests failed at egg stage, four nests at early nestling stage (dead chicks visible in two nests, a chick missing in another, and clear brooding behaviour ceasing at the fourth nest), and five nests failed at unknown stage as adults were rarely seen standing. It was impossible to deduce causes of failure at most nests, but staggered hatching was suspected as being a contributing factor to the loss of young nestlings. Two early losses coincided with bad weather. Four pairs here went on to lay replacement clutches.

The death of one of the two youngest nestlings at Tawhitinui was likely associated with researcher disturbance (capture of chicks for banding, Jul 2019). The other perished soon after this event but was the smallest chick in a three-chick brood. A young nestling corpse was seen at Duffers Reef on in Jul 2019 when the camera was reset following a similar chick banding event but may have been already deceased when the team arrived on the island.

Failures at downy, mobile chick stage were far fewer than those at early nestling stage and while some were to unknown causes (one each at Duffers Reef and White Rocks), others were mainly attributed to bad weather (one each at Duffers Reef and White Rocks) and/or chicks going missing—i.e., wandering away from nests and potentially suffering misadventure or predation—particularly following researcher disturbance. The event of accessing the colony to capture and band chicks was likely to have caused the premature displacement and loss of three mobile chicks at Tawhitinui and one at Duffers Reef; the youngest was unlikely to have been unguarded or to have ventured away from the nest prior to this disturbance. A black-

backed gull was seen scavenging one chick corpse at White Rocks, and so predation was a possibility although never seen.

Potential failures at juvenile post-fledging stage could only be investigated at White Rocks (2019) by observing roosting behaviour of known-aged (unbanded) fledglings with parents at natal nests and comparing with other pairs rearing young of the same age. Just one fledgling disappeared mid-Sep, 3 weeks before any other young and was thought to have perished.

All failed breeding pairs at all colonies were still regularly occupying their nesting sites right through to the end of the breeding season (e.g., 31 Oct at White Rocks). There was evidence that at least one White Rocks pair had divorced following breeding failure. One failed breeding pair was seen in courtship postures in late Aug, where breeding pairs rearing chicks Jul–Nov were never spotted in such postures. A failed breeding pair was the first to be suspected of commencing moult in early Oct 2019 (Duffers Reef)—white feathers in the nest bowl.

Non-breeding birds

'Floating' non-breeding adults and first-year birds were the hardest demographic to count in the breeding season because they were usually only seen sporadically on the edges of or beyond the main nesting area at all sites.

There was usually at least one nest site in most camera views (all colonies) where there was limited or no nest-building at the start of the breeding season but where through the rest of season one or two adults sporadically visited, sometimes nest-building (nest not always present) but not breeding. Pairs with failed early breeding attempts could be interpreted as non-breeders if there were no images of the early breeding season.

At one peripheral White Rocks nest, an unpaired bird roosting alone in Mar acquired a mate in late Apr (two birds roosting together), and nest-building commenced in May. The site was not always occupied, and a nest not always present. This newly established pairing continued to occupy the nest site right through to end of Oct (end of camera operation).

Potential threats to New Zealand king shag breeding

Major disturbances at colonies usually caused all birds to leave the site. There were a few occasions (e.g., Tawhitinui) where it was hard to distinguish between a potential morning disturbance or mass exodus of birds to sea to feed. It was also unclear during some disturbances whether birds had fled the colony or if they had just moved out of camera view until it was safe to return.

Bad weather events were not seen to affect nesting behaviour at Tawhitinui (two seasons), and none was reported for Kuru Pongi (2019) during the time of camera operation. In contrast, many bad weather events were recorded at White Rocks and Duffers Reef, with impacts on breeding. In the off-season, sites might be vacated by all birds during extreme weather. At the start of the breeding season, heavy winds and rain overnight often resulted in many birds leaving their nests if there were no eggs/chicks present, to roost relatively tightly together, sometimes close to the camera where perhaps it was more sheltered. Birds resiliently started rebuilding immediately after a nest was lost. During the incubation and rearing phase, it was more likely that one adult remained at the nest while the partner roosted elsewhere out of camera view. Juveniles would form creches and shelter together through a rough night, even if parents failed to return until the following day.

Bad weather had a significant negative impact on the NZKS breeding cycle at the low-lying nesting area on Duffers Reef where nesting attempts were thwarted (nests/eggs/chicks lost) and delayed by multiple wave washout events, pushing repeat nesting attempts late into the season. Sometimes even adults would vacate the site for a night/day. Contrastingly, at the apparently more sheltered, elevated nesting area on Duffers Reef, birds did not move away from nests in response to any bad weather, nest material never seemed to be blown away, and birds were rarely forced to roost away from the site.

Camera setting/servicing/removal and the capture of chicks for marking were clearly the most disturbing events. Cameras were serviced by day at times when the most NZKS were out feeding, minimising disturbance. Adults returned to the nesting area 3 hrs after research personnel departed Tawhitinui in Dec 2018 (off-season), and 2 hrs at White Rocks in Mar 2019 (pre-breeding). On the chick banding day (Jul 2019), adults took 15–30 mins to return to their nests after personnel left Tawhitinui, but chicks took 1–3.5 hrs to return; it was then 24 and 48 hrs before two more chicks were reunited with parents, and three chicks remained missing. Single adults and mobile chicks at Duffers Reef had returned to most nests within approx. 1 hr of people leaving after banding chicks.

Presence of cameras may have affected NZKS behaviour to a small degree at night only but did not directly disrupt any breeding. Birds nesting nearest to cameras at all sites were deduced to be less established pairs on the edge of the main nesting area, behaving like other peripheral pairs.

Boats were seen near or approaching three sites on several occasions with no major impact. If birds were displaced from the site, they were usually back

Table 4. Comparison of clutch size and incubation period in *Leucocarbo* shags in the New Zealand region.

Species	Clutch size (eggs)	Incubation (days)	Reference
Auckland Island shag *L. colensoi*	3	28–32	Marchant & Higgins, 1990
Bounty Island shag *L. ranfurlyi*	2–3	No data	Marchant & Higgins, 1990
Campbell Island shag *L. campbelli*	2	No data	Heather & Robertson, 2005
Chatham Island shag *L. onslowi*	2–4	c.30	Heather & Robertson, 2005; Bell, 2022
King shag *L. carunculatus*	2–3	28–32	This study
Macquarie Island shag *L. purpurascens*	1–3	No data	Marchant & Higgins, 1990
Foveaux shag *L. stewarti*	1–3	No data	McKinlay & Rawlence, 2022a
Otago shag *L. chalconotus*	1–3	No data	McKinlay & Rawlence, 2022b

in the next image or two. The longest times birds were kept away from the site by an approaching boat was 1–2 hours in Mar 2019 before egg-lay (White Rocks), and up to an hour in Oct 2019 (Duffers Reef). There were no such apparent events during incubation or young nestling stage and so there were no consequences on breeding efforts. Boat sightings at Tawhitinui were more common, but most were passing and there was no discernible impact on the shags, particularly during the off-season when many birds were normally absent from the colony in the middle part of the day.

Only two fur seals (*Arctocephalus forsteri*) entering colony nesting areas were captured on camera (White Rocks and the low-lying area on Duffers Reef) with a third incident suspected, outside the NZKS breeding season. One seal displaced the shags from their territories for up to 4 hrs. A sheep (*Ovis aries*) caused all shags to leave Tawhitinui one Sep day for at least an hour. Here, a common brush-tailed possum (*Trichosurus vulpecula*) was captured on camera on four nights Mar–Aug 2019 but not entering the nesting area (cameras were not operating all night). Predators such as rats and mustelids were not noted in any images at this mainland site.

There was no single incident where the death of a chick could be directly attributed to predation by southern black-backed gulls (*Larus dominicanus*) or red-billed gulls. Black-backed gulls were only seen at White Rocks scavenging one chick (2019). Only two images featured this species in Jul–Nov 2019 at Duffers Reef. Any eggs known or suspected as being consumed by either gull species were opportunistic when eggs were left exposed in nests due to another disturbance or were already lying on bare rock outside nests.

Western weka (*Gallirallus australis australis*) was not identified as a threat to king shag productivity on Tawhitinui in this analysis, despite appearing in the nesting area on six nights Mar–Apr 2019.

DISCUSSION

For the first time, details on nest occupancy, breeding, and survival of young have been captured for a sample of the NZKS population, by analysing data collected from still images. Field camera technology is now commonly used for the remote monitoring of threatened seabirds in New Zealand (e.g., Bell *et al*., 2013; Fischer *et al*., 2017; Black 2018) and facilitated sampling from four different colonies in this study in 2018 and 2019.

NZKS nesting territories were retained year-round but were not strongly defended by Dec. Bell (2022) confirmed high mate fidelity; this, along with defence of nest sites throughout the year seen in this study, enabled birds to retain prime nesting locations across seasons. This study shows prime sites to be the most elevated, and central to each colony with larger, more stable nests and more established pairings. Nest-building commonly began in Mar as seen by Schuckard (1994) and extended over many months, particularly at exposed, low-lying nesting areas vulnerable to wave surges. Peripheral and low-lying nest sites at all locations were sporadically occupied by less experienced pairings, with uncoordinated nest attendance, later and more frequent nest-building, and more courtship postures, some described for the first time—'sky-pointing', 'biting', and 'neck-crossing' (or entwining)—the latter occurring in other cormorants/shags for pair-bond maintenance (Marchant & Higgins 1990). Limited images suggested NZKS steal nest material from others, a behaviour also reported for Foveaux (*Leucocarbo stewarti*) and Otago shags (*L. chalconotus*) (McKinlay & Rawlence 2022a, b).

There was both inter- and intra-colony asynchronous egg laying with first eggs laid across all colonies between mid-Mar and early Jun 2019, and over periods ranging 5–10+ weeks at a single colony. A 5- to 6-week laying period is reported for similar species (e.g., Bernstein and Maxson 1984).

With occasional replacement clutches laid around one month following failure at either egg or young nestling stage, incubation of second clutches was still underway in mid-Oct 2019 (Duffers Reef) extending the NZKS egg period to seven months. McKinlay & Rawlence (2022a, b) report a laying period May–Sep in Foveaux and Otago shags. Asynchronous laying occurred in European shags (*Phalacrocorax aristotelis*) because older birds at better nesting sites laid five weeks earlier than younger birds at poor sites (Potts *et al*., 1980). While ages were unknown, NZKS reflected this with apparently more experienced central pairs laying earlier than less-stable pairings at peripheral sites. Sapoznikow & Quintana (2009) suggest the extended and asynchronous egg laying period (3–4 months) and high re-nesting rate in rock shags (*Leucocarbo magellanicus*) indicates a stable and predictable food source. An asynchronous laying strategy in NZKS colonies is likely to be linked to food supply but has yet to be investigated for this species.

Clutches of 2–3 eggs were commonly laid. Three-egg clutches were observed to take 6–13 days to complete for different females, similar to egg-laying intervals of 48–96 h recorded for Auckland Island shag (*Leucocarbo colensoi*) (Marchant & Higgins 1990). Incubation was 28–32 days, excluding hatch date, commencing after the first egg was laid. Data are compared with other New Zealand *Leucocarbo* shags in Table 4. Clutch size and lay-to-hatch intervals were very similar for the Antarctic shag (*L. bransfieldensis*), where staggered hatches accounted for the loss of many nestlings (Shaw 1984). Hatching asynchrony is commonly seen in Pelecaniformes (Nelson 2005). The facultative brood reduction strategy promotes early death (within the first week) of the smallest Phalacrocoracidae chick(s) in a nest due to starvation through unequal distribution of food by parents, probably representing an adaption to variability in food availability, individual foraging proficiency, and hatching failure (Drummond 1987) and is likely to explain the high rate of nestling loss in NZKS nests. All second clutches were unsuccessful. Replacement clutches are known to be laid in other similar species, e.g., Macquarie Island shag (*L. purpurascens*), Marchant & Higgins (1990); rock shag, Sapoznikow & Quintana 2009.

A brooding period of around two weeks fits with similar species, e.g., South Georgia shag (*L. georgianus*) 12–15 days (Bouglouan, n.d.).

Chicks were unguarded from 3–4 weeks, left the nest soon after (usually within four days), and showed strong creche behaviour from then onwards, with nestlings grouping in, or later between nests, and then anywhere in the nesting area including on the periphery. Creche behaviour in downy chicks was suspected to be for warmth, particularly at exposed sites, as noted for other cormorants (Carter & Hobson 1988), as there was no observed pressure from predators or perceived adult (conspecific) aggression at any of the colonies—other hypotheses for creche formation in shags (Velando 2001). However, it was also strongly suspected to be for socialisation—temperatures recorded on images were sometimes not cold enough to warrant such thermoregulatory behaviour, e.g., during daytime (Fig. 1). Shag creches are thought to facilitate the development of social skills (Velando 2001) and the learning of fledging behaviours in groups (Carter & Hobson 1988).

Chicks were adult size by six weeks and fully feathered at nine weeks, fledging shortly after this in groups from late Jul (2019) to mid-Oct (2018) across all colonies. Fledging period (around 65 days) is 1–2 weeks longer than for the pied shag (*Phalacrocorax varius*) (Marchant & Higgins 1990), but the same as similar species (Shaw 1984; Bouglouan, n.d.). Once flying, young birds generally departed the nesting area daily in loose groups with other juveniles, although there was some indication that fledglings may have departed with males in the morning and possibly even returned with some adults. With the spacing of images over time, it was hard to ascertain if young took off or landed at the same time as adults. Otherwise, juveniles were seen returning together by early afternoon before adults; Bernstein & Maxson (1985) also reported recently fledged blue-eyed shags returned to their nests in all-juvenile groups approximately one hour before adults and were then fed by parents in the afternoon. Juvenile NZKS also moved independently from adults during bad weather events.

Productivity could only be calculated for White Rocks (2019) up to fledging in this study: 37% of nests produced single fledglings (not yet independents) from 30 nests—26 pairs in camera view and an additional four pairs from boat-based counts (Bell 2022). Marchant & Higgins (1990) state that Auckland Island shags usually raise two chicks, and while this may have occurred at the other NZKS colonies, this species commonly reared just one fledgling at White Rocks. Loss of downy, mobile chicks was mainly attributed to bad weather; no chick disappearances resulted from human disturbance—banding was not undertaken at White Rocks.

Young ventured farther from natal nests on land by Nov (banded chicks at Duffers Reef) and sightings then gradually decreased, reflected by a gradual rate of juvenile mortality (up to 25% of young perishing) seen up to Dec by Bell (2022). Many young disappeared at 4.5–5 months, their actual fate—dispersed or perished—unknown in this study. Bell (2022) found an average period of 4.9 months of parental care before young disappeared from boat-based observations, and that juvenile

mortality was highest in Jan–Feb when young were 5–7 months old—presumably when young birds were learning to forage— stabilising by Mar. NZKS appear to have a period of at least three months of post-fledging parental care, 1–2 weeks longer than for pied shags (Marchant & Higgins 1990). Burger (1980) attributed prolonged aftercare in shags to be necessary in order to develop specific skills for the difficult activity of catching fish. The vigorous, persistent begging observed in NZKS juveniles is known in other cormorants, peaking during the transition to independence (Drummond 1987).

A proportion of 2018 juveniles resided at each colony site until they permanently left natal nests by Apr–May 2019, and were either never seen again, or observed loafing with other young birds at the edge of the nesting area, also observed by Bell (2022). As first-year birds, two offspring at different colonies stayed with parents through the 2019 breeding season, with one directly observed by Bell (2019) being fed by parents every month Jan–Jun 2019. These birds were still associating with parents after attaining full adult plumage by 18 months, and Bell (2022) established that 28.3 months was the longest period of parental association.

The more productive nesting areas in 2019 appeared to be the sheltered Tawhitinui colony (inner-Sounds), and elevated Kuru Pongi where most of the two-chick broods were successfully reared (to near fledging stage when viewing ceased) and where there were relatively fewer disturbances noted. Bell (2022) also found adverse weather was the key influence on NZKS productivity and reported the best output at these two sites in 2019—0.83 and 0.85 fledglings/pair for Kuru Pongi and Tawhitinui respectively. Chick losses caused by disruption during chick banding events (Duffers Reef, Tawhitinui) was almost unavoidable given the staggered breeding season and range of chick ages on the colony but was considered an acceptable risk for the significant gain in knowledge from having marked known-aged birds in the population. This was the first ever banding of nestlings attempted for this species.

White Rocks generally received less overall disturbance than other sites—alert birds were rarely seen over two seasons—but appeared more exposed to the elements (outer-Sounds) which may be why creche behaviour was prevalent here and pairs reared only single chicks in 2019.

The most vulnerable nesting area, subject to most disruption—rough seas, seal intrusion, and unexplained disturbances causing temporary exodus from camera view or alerted/alarmed postures—was the low-lying area at Duffers Reef. With no breeding output at nests in this camera view, and some disruption caused by the chick banding operation, breeding output (0.51 fledglings/pair, Bell 2022) would have been attributed to pairs in the slightly more elevated nesting area at this colony in 2019. Nest site quality proved critical to breeding success, as seen in other shags (Potts *et al*., 1980).

Estimating productivity in NZKS colonies proved to be difficult from fixed cameras, with views obscured by vegetation growth or cameras failing at critical times, and because of chick mobility. Shaw (1984) found that mean clutch size varied little from year to year in the Antarctic shag whereas annual chick survivorship fluctuated substantially, and this may also be the case for NZKS, being characteristic of the facultative brood reduction strategy, where third, and sometimes second chicks serve an insurance function as well as providing an additional chick when feeding circumstances are favourable.

Causes of disturbance could not always be ascertained at colonies with close-up camera views (Duffers Reef, Tawhitinui) but were likely to be passing boats (fishing or recreational). Bell (2022) found tracked (GPS) individuals were disturbed (birds left land, flying or swimming, but not to forage) on average 0.6 times/day, for 4–44 mins with most (84%) less than 20 mins, at four colonies including Duffers Reef, Kuru Pongi and Tawhitinui over several seasons. Boat disturbance remains a high risk to breeding NZKS from Mar (first clutches) to at least Aug (most replacement clutches).

Large mammals (seals, sheep) did not access NZKS nesting areas during the vulnerable early breeding season during this study, but images capturing these events provided an insight into the negative impact of such appearances at three colony locations. Fur seals are increasing in numbers (main colonies) and range in New Zealand (Ministry for Primary Industries 2017), and so increased disturbance by this species is likely. NZKS sit tightly through the night during egg and small nestling stage, so possums or weka at mainland sites are unlikely to have an opportunity to take eggs and young. Black-backed gulls were seen more as scavengers in this study. Red-billed gulls were opportunistic predators of eggs laid or displaced outside established nests—they were regularly present foraging in and around nests and could even play a beneficial role in removing parasites from nests (Fig. 1). Either species was suspected to have taken eggs in at least one exposed nest. The degree of impact of gulls on NZKS will be influenced by colony disturbance and potentially by proximity and size of nearest gull roosts/colonies.

This study corroborates the assumption that NZKS sitting in horizontal positions on nests during winter aerial surveys are highly likely to be breeding (incubating or brooding) or intending to breed (first or replacement clutch), confirming that these birds can be included as breeders in the annual

census. The study also suggests that empty nests attended by birds in premium nesting locations at a colony nesting area (e.g., elevated, central) are also likely to be of breeding status—pairs about to lay, already failed, or rearing mobile chicks that are temporarily absent from the natal nest—solving a query regarding empty nest status by Schuckard *et al*. (2018).

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