Aspects of the breeding biology of Black Shags (*Phalacrocorax carbo*) near Lake Kohangatera, Wellington

R.G. POWLESLAND[1] and P.J. REESE[2]

[1]*64 Roseneath Terrace, Roseneath, Wellington 6001, New Zealand;* [2]*69 Hornsey Road, Melrose, Wellington, New Zealand*

ABSTRACT

The nesting activities and breeding success of Black Shags (*Phalacrocorax carbo*) near Lake Kohangatera, Wellington, were studied from 1993 to 1998. The colony was used during November-July by a mean of 67 birds per night, but in August-October numbers increased to a mean of 98 birds when fledglings were present. Courtship and nest-building began in March, and nesting continued until October-November when the last chicks fledged. Most clutches (85% of 185) were laid in April-May (early nests), the remainder being laid in June-September (late nests). The mean estimated laying date of early nests varied from 14 April in 1998 to 3 May in 1995, the overall mean (1993-98) being 24 April. During the day typically the male took two incubation stints, including the first, and the female one or two. The mean length of incubation stints by females was 3 h 46 min, over an hour longer than that of males. However, the mean time females and males were absent from the colony to forage, 2 h 39 mins and 2 h 21 mins respectively, did not differ significantly. Three types of changeovers seen during incubation are described, as are the activities of adults and chicks during nestling rearing. Fledglings took their first flights when 49-60 days old, but continued to be fed by their parents for 40 to 80 days afterwards, the oldest fledged young seen fed being about 140 days old. Of 185 breeding attempts during 1993-98, 83% were successful, the majority resulting in one or two fledglings per nest. Mean brood size at fledging varied with year, from 1.1 in 1997 to 1.7 in 1998. Overall, the mean brood size was 1.4 fledged young per nest, and 1.7 for successful attempts. Early clutches were more productive than late ones. We conclude that a pair of Black Shags would be unable to successfully rear two broods and complete their moult within a year, and that late nestings were replacement clutches.

KEYWORDS: Black Shag, *Phalacrocorax carbo*, Wellington, colony history, nesting activities, fledgling dependence, breeding success.

INTRODUCTION

The Black Shag (*Phalacrocorax carbo*) is "almost cosmopolitan", being present in Eurasia, Africa, Australasia and the northeast coast of North America, and consists of seven subspecies (Marchant & Higgins 1990). The subspecies *novaehollandiae* is widespread in Australia, Tasmania, parts of New Guinea, and New Zealand (Bull *et al.* 1985, Turbott 1990). There have been many studies of breeding by Black Shags, particularly in Britain, Europe and southern Africa, the findings from which are summarised in Cramp & Simmons (1977), Brown *et al.* (1982), Marchant & Higgins (1990), and Johnsgard (1993). Even so, little quantitative information is

Notornis 46: 484-497 (1999) © *1999 Ornithological Society of New Zealand*

available on some aspects of breeding, such as the interval of egg laying, duration of incubation stints by each sex, and age of fledgling independence.

In New Zealand, colonies of the Black Shag occur at coastal and inland sites from Northland to Southland. Foraging in a variety of habitats, it appears to favour coastal waters, harbours, estuaries, lakes and major rivers, but also feeds in ponds and streams (Marchant & Higgins 1990). However, despite being relatively common and widespread in New Zealand, the Black Shag has been little studied. Its diet has received most attention, mainly during 1920-1945 when there was much debate about the shag's impact on stocks of the introduced Brown Trout (*Salmo trutta*) and Rainbow Trout (*Oncorhynchus mykiss*)(Stead 1932, Falla and Stokell 1945, Williams 1945, Dickinson 1951, Lalas 1983). Stonehouse (1967) and Stidolph (1971) reported on the Black Shag's foraging behaviour, and Sim and Powlesland (1995) on the mortality and dispersal of birds banded in Wairarapa.

Less well studied has been the breeding biology of Black Shags in New Zealand (Marchant & Higgins 1990). Falla (1932) stated that the species bred twice a year, laying eggs in May and September but gave no other details. Gales (1984) made at least monthly visits to a small colony at Stony Creek, Dunedin, in 1982. Two clutches were laid in May, neither hatching. In September, clutches were laid in the same two nests, and in a third nest a clutch was laid in November. By comparison, eggs were laid at colonies near Lake Wairarapa during August-October (Sim & Powlesland 1995). Our aim in carrying out a study of nesting Black Shags at a colony near Lake Kohangatera, Wellington, was to determine the timing of the nesting season, and to quantify various aspects of breeding, dispersal and mortality. In this paper we describe the history, timing of breeding, and breeding activities and success of Black Shags at this colony.

STUDY AREA AND METHODS

Lake Kohangatera is a coastal lake near Pencarrow Head, on the eastern side of the entrance to Wellington Harbour. The lake occupies the lower portion of Gollans Valley, and merges into a swamp dominated by raupo (*Typha orientalis*) that extends several kilometres inland (Stephenson 1977). The shag colony (41^{0}23'S, 174^{0}52'E) is in a steep, forested gully at about 80 m a.s.l., about two kilometres from the coast, beyond the head of the lake, and on the eastern side of the valley.

Using binoculars (8x30) and telescope (x20), observations from a blind situated part way up the ridge on one side of the gully enabled counts of roosting shags, and the breeding activities and success of most pairs to be monitored. For most months between December 1993 and March 1996, one count per month of shags at the colony at sunset was made. The general location of each occupied nest that was not visible from the blind was evident from the flights of birds to and from it. While observations at the colony started in 1988, detailed records of shag breeding biology were recorded during only six nesting seasons, beginning in March 1993 and continuing until November 1998. Visits to the colony were at weekly or fortnightly intervals during the early portion of the nesting season (March-September) when most pairs nested, but were reduced to fortnightly or three-weekly afterwards when few nests were occupied. Details recorded during each visit for each nest were location, predominant activity of the occupants (mate attraction, courtship, nest-building, incubation, nestling rearing or fledgling rearing), and number of nestlings and their estimated age. During June and July 1993 and May 1994 observations were made from dawn till dusk on six days for a total of 45 nests to determine the incubation attentiveness of each sex.

A small proportion of nesting shags was banded, but for most pairs both birds were unbanded and in these instances members were distinguishable from one another by the incidence of nuptial plumes over the crown and upper neck. Males were distinguished from females by position during copulation, and during nest building and incubation, the male brought material to the nest which the female accepted and incorporated into the structure (Cramp & Simmons 1977, Marchant & Higgins 1990, Johnsgard 1993).

From the blind we were unable to determine the number of eggs or chicks that hatched in each nest, and we did not climb to nests before the chicks were large enough to band. Therefore, laying dates were estimated by subtracting the estimated age of nestlings (±1 week) when first seen, or when being banded, plus 29 days for incubation (Marchant & Higgins 1990).

As changeovers at nests could not be seen before sunrise, in determining the length of the first incubation stint of the day it has been assumed that the female incubates during the night and that the male takes over a quarter of an hour before sunrise (see Table 2).

The hatching of chicks was determined by hearing chick calls, seeing a parent feeding a chick, or seeing a chick. Thus, in determining the timing of nest failure, because our observations were made from a distance, we assumed that if we had not heard or seen evidence of chick hatching then the nesting attempt had failed during incubation. An attempt was considered to have failed during chick rearing if no chick 6-8 weeks of age was seen at the nest.

Some nestlings were banded when two to three weeks old. At this age their legs and feet were sufficiently well developed to retain bands, their bodies covered in down, the primary quills were beginning to appear, and they remained on the nest when approached. During the 1992 season, we marked nestlings with a red band on the left leg and a numbered size O metal band (from Banding Office, Department of Conservation) on the right. The combination for the 1993 nestlings was yellow on the left, and metal on the right. During the 1994, 1995, and 1996 seasons, each nestling banded received an individual combination of a metal band and three colour bands. Colour bands were made from UV-stable Darvic PVC as wrap-around bands 10 mm high. The outer flap of each colour band was fastened

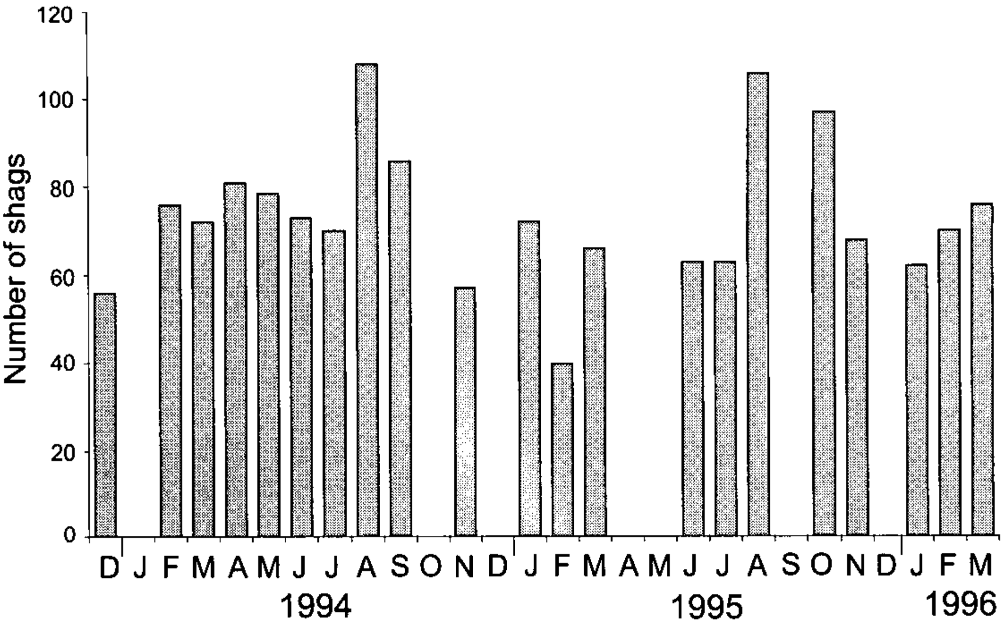

FIGURE 1 - Numbers of Black Shags counted at dusk roosting at the colony near Lake Kohangatera, Wellington, December 1993 - March 1996.

to the rest of the band with Selley's Supa Glue to prevent the band unravelling.

The computer package SigmaStat (Fox *et al.* 1994) was used for the statistical analyses. Where the *t*-test was inappropriate because the data were not normally distributed, the Mann-Whitney Rank Sum test was used to test for significant differences.

RESULTS

History of colony

A visit to the colony by Stidolph (1971) in June 1925 is the first published record of its existence. He mentioned seeing five nests in beech (*Nothofagus* sp.) trees. While the shags have not nested on this species since at least 1988, there are black beech (*N. solandri*) trees on a ridge beside the gully where the colony is situated now in the canopy of karaka (*Corynocarpus laevigatus*) trees. Falla and Stokell (1945) visited the colony several times and monitored its decline during the 1930s and 1940s when the Black Shag was persecuted by members of Acclimatisation Societies and angling clubs, a bounty being paid for each shag shot (Stead 1932, Williams 1945, Stidolph 1971). They counted 40 nests at the colony in 1930, 20 in 1932, 12 in 1934, and none in 1942. The next record of Black Shags again nesting in the area is that of P. Williams (pers. comm.) in 1965 when 11 nests were counted. We are not aware of other surveys at the colony before our counts. The number of occupied nests in April-May, at the start of the breeding season when the greatest number of nests were occupied, was 33 in 1994, 31 in 1995, 25 in 1996, 35 in 1997, and 30 in 1998.

Numbers roosting at the colony

The colony is used not only for nesting, but also for roosting at night throughout the year. Dusk counts of shags during 1993-96 yielded a mean of 67 birds (n=17, range=40-81, s.d.=10.7) roosting there in November-July (Fig. 1). However, during August-October, when fledglings were present, numbers increased to a mean of 98 (n=4, range=84-108, s.d.=9.9).

Courtship and nest building

The first evidence of the impending nesting season was the appearance of nuptial plumes on some adults in February. In March, shags were seen occasionally at day roosts about Wellington Harbour and at the colony performing the "gargling" display (Marchant & Higgins 1990) during pair formation. By mid-March, most mature males were actively defending nest sites for much of the day, collecting nest material and "wing-waving" (Marchant & Higgins 1990) to attract a mate. Any nests that remained reasonably intact from the previous season were refurbished, otherwise new nests were built. Once a male had a mate, the pair took turns to forage so that one was present to defend the nest site against other shags usurping it or robbing material. The male collected material and presented it to the female who incorporated it into the nest structure.

Observations of birds gathering material, and of nests when banding chicks, showed that much of the material was live or dead twigs and sprigs of foliage of kanuka (*Kunzea ericoides*) from trees within 200 m of the colony. Leaves and twigs of karaka from beside nests were often incorporated, as was material robbed from any unattended nests at the colony. Nests were lined with softer material, such as karaka leaves and occasionally dead, wet raupo leaves. Although branches about nests and those regularly roosted on were trimmed of foliage and tips by shags, the trees remained healthy despite the trimming and faeces coating portions of them, even overgrowing unused nest sites.

Egg-laying

The earliest clutches were laid during the first week of April and the latest in the second week of September. However, 157 (84.9%) of 185 clutches were "early" nests laid in April-May, and the remainder were laid during June-September ("late" nests). The mean estimated date of egg-laying at early nests varied by nearly three weeks between years, from 14 April in 1998 to 3 May in 1995 (Mann-Whitney Rank Sum test, $P<0.001$, Table 1).

Incubation

A few birds left the colony up to 30 minutes before sunrise, and most did so before sunrise, but it was too dark to identify from which nest an individual left. However, it was usually the male that took the first incubation stint (96.7%, n=30), and the female the last (76.5%, n=34). Table 2 shows two typical diurnal patterns

Table 1 - Estimated mean laying dates (±1 week) of early clutches (April-May) during 1994-98 of Black Shags at a colony near Lake Kohangatera, Wellington.

	1994	1995	1996	1997	1998
Mean date of laying	25 Apr	3 May	22 Apr	28 Apr	14 Apr
Range	11/4-19/5	10/4-31/5	2/4-9/5	16/4-21/5	1/4-13/5
Sample size	16	21	18	19	26
s.d.	12.5	13.2	9.9	9.5	9.9

Table 2 - *Three examples of diurnal patterns of incubation attentiveness of female (F) and male (M) Black Shags at a colony near Lake Kohangatera, Wellington, 1993-94.*

A Nest 21 -10 June 1993

1h 00m	c. 07:28[1]	Changeover, F left the colony
	07:43	*Sunrise*
5h 21min	08:30	F arrive at nest, changeover
	08:33	M go to abandoned nest
	08:37	M left the colony
	13:45	M arrive at nest
	13:46	M to roost
	13:51	F left the colony, M to nest
	16:11	F arrive at nest
	16:58	*Sunset*

B Nest 8 -25 May 1994

1h 10m	c. 07:17[1]	Changeover, F left the colony
	07:32	*Sunrise*
	08:10	F arrive at roost
4h 00min	08:25	F to nest, changeover
	08:29	M left the colony
	10:58	M arrive at nest
	10:59	M to roost
2h 41min	12:25	M to nest, changeover, F left the colony
	14:25	F arrive at roost
	14:49	F to nest
	15:06	changeover
	15:07	M left the colony
	16:34	M arrive at roost
	17:04	*Sunset*

C Nest 8 -19 June 1993

8h 06m	c. 07:31[1]	Changeover, F left the
	07:46	*Sunrise*
	15:36	F arrive at nest, change
	15:37	M made 8 trips with m from an abandoned nes partner
	15:57	M left the colony
	16:58	*Sunset*
	17:07	M arrive at roost

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[1] In determining the length of the first incubation stint of each day, it has been assumed that the female incubates at night and the male takes over 15 minutes before sunrise.

of incubation between dawn and dusk; either three (Table 2A) or four (Table 2B) diurnal incubation stints. There were nine instances (20%, n=45) of only two stints (Table 2C). Often, after being relieved by their partner in the morning, a male would bring one or more items of material to the nest before leaving the colony (Table 2C). The mean time that females spent incubating per stint (3 h 46 min, n=29, range=1:03-7:12, s.d.=83.2) was significantly longer than that spent by males (2 h 30 min, n=45, range=0:54-5:31, s.d.=66.9; *t*-test, t=4.32, d.f.=72, P<0.001). *However, males and females spent the same time away from the colony* (females mean 2 h 39 min per stint, n=31, range=0:38-8:16, s.d.=107.1; males mean 2 h 21 min , n=27, range=0:38-5:15, s.d.=77.3; Mann-Whitney Rank Sum test, P=0.64).

Three types of changeover were seen. Type 1 involved the returning bird landing on the nest or a roost site close by, followed within two minutes by its partner backing off the clutch (during incubation by shags and cormorants the eggs are placed between the upper surface of the feet and the breast feathers (Johnsgard 1993)) and flying away, whereupon the returning bird took over incubation. In all 18 instances of Type 1 changeover, it was the male that vacated the nest promptly on his mate's arrival.

During Type 2 changeovers, the incoming bird remained roosting for some time after it arrived at the nest or roost site before the incubating bird vacated the clutch. There was no significant difference in the mean time females (16.4 min, n=9, range=4-41, s.d.= 14.0) spent roosting before their partners left the nest compared to males (33.1 min, n=12, range=5-107, s.d.=33.1; Mann-Whitney Rank Sum test, P=0.166).

Type 3 (n=11 observations) involved the incubating bird being forced off the eggs by the incoming bird crouching at its chest and pushing it back off the eggs. On six occasions the female was the incoming bird and on five it was the male. Males roosted significantly shorter (18.8 min, range=2-74, s.d.=28.2) than females (93.4 min, range=27-166, s.d.=51.5) before forcing their mates off the nest (*t*-test, d.f.=9, P=0.014).

Chick-rearing

For about the first week chicks were brooded constantly so the first indications that a chick had hatched was a distinctive, high-pitched, begging call and the occasional glimpse of a chick's head. When the parents changed over at the nest young chicks could sometimes be seen stretching up and begging for food. Usually, such chicks were fed by the sitting parent lowering and turning its head along its flank to allow a chick to take food from the open beak.

At about two weeks of age, chicks were covered in a short black down, except on the head and legs. From two until about five weeks old, a parent was invariably at the nest, standing on the rim rather than brooding the chicks. The chicks begged vigorously, standing and jostling each other to be closest to the front of the parent. After feeding one or more chicks, the guarding parent would often stand with its chest towards the brood but its head partially hidden on its back, which apparently stopped the chicks begging constantly.

From about six weeks of age, chicks in broods of two or three were usually left unattended, whereas single chicks were often attended by a parent. Chicks of this age greeted their parents by begging vigorously and often clambered off the nest to a parent a metre or two away. As soon as a chick had been fed, which was usually within a minute of the parent's arrival, the parent would move to a nearby roost. If followed, it would fly to another part of the colony.

Broods of two or three chicks six weeks of age or older could usually successfully defend their nests against other shags. However, occasionally an intruder was seen at the nest; the chicks would then either escape by scrambling over the side to nearby branches, or would be vigorously pecked by the intruder while crouching low in the nest. Such intruders were either paired males that took nest material or bachelors keen to usurp the nest. They left immediately a parent arrived.

Fledged young

Three broods fledged at 56 (1 chick), 49-54 (2), and 49-60 (2) days of age (±1 week), respectively. Once able to fly, fledglings were seen less often at their respective nests, and roosted elsewhere in the colony. When a parent flew in it would be mobbed by its brood, one of which would be fed within a minute or two. If the food transfer was unsuccessful or a chick was unfed, often the adult would be harrassed into flight and followed if it remained at the colony. Our observations were too infrequent to determine at what age fledglings first left the colony, attempted to forage, or became independent. However, three banded fledglings were fed when 110, 130 and 140 days old (±1 week), twice at the colony and once at a coastal site 3 km away.

Length of breeding season

As courtship and nest-building takes about 14 days (this study), the incubation stage 27-31days (Marchant & Higgins 1990) and chick dependence lasts at least 100 days (this study), a successful nesting cycle would take at least 143 days. With a mean date of egg laying at early nests during 1994-98 of 24 April, the nesting cycle of successful pairs would extend from early April until early September. By comparison, pairs that re-nest after a failed attempt may be involved in nesting activites for as long as seven months. For example, a banded male (the only male among the three shags from the 1992 cohort seen at the colony in 1995) was seen copulating with an unbanded female on 23 April 1995. Their brood died during 1-9 July when about two weeks old. The banded male and an unbanded female were refurbishing the same nest on 30 July. Their subsequent three chicks were banded on 18 September and all had fledged by 2 November, when about 65 days old.

Breeding success

Breeding success was determined from the number of fully-feathered chicks at each nest just before nest leaving. Of 185 nesting attempts during the six seasons 1993 to 1998 that were sufficiently visible for their outcomes to be determined, 32 (17.3%) failed (Table 3). The proportion per season that failed varied from 3.3% in 1998 to 23.7% in 1997. Of the failed nesting attempts, 21 (65.6%) did so during incubation, and the rest during nestling rearing. Brood size at fledging varied from one to four nestlings, most successful pairs reared either one (37.9%) or two (49.7%) nestlings (Table 3).

In total, early clutches resulted in significantly more fledged young per brood (1.51, n=157) than late ones (1.07, n=28; Mann-Whitney Rank Sum test,

Table 3 - Number of Black Shag broods (combined early and late clutches) of various sizes at fledging and failed nesting attempts, and breeding success (mean number of fledglings per nest) during 1993-98 at the colony near Lake Kohangatera, Wellington

Season	Failed	---------Brood size---------				Mean no. of fledglings per nest		
	0	1	2	3	4	Early[1]	Late[2]	Total
1993	3	9	8	3	1	1.8 (21)[3]	1.0 (3)	1.6
1994	9	7	14	5	0	1.5 (30)	1.2 (5)	1.5
1995	6	9	14	4	0	1.4 (27)	1.7 (6)	1.5
1996	5	7	10	3	0	1.6 (22)	0.3 (3)	1.4
1997	9	17	11	1	0	1.2 (30)	0.9 (8)	1.1
1998	1	9	18	2	0	1.8 (27)	1.0 (3)	1.7
Total	32	58	76	18	1	1.5 (157)	1.1 (28)	1.4

[1] Early = clutches laid during April-May

[2] Late = clutches laid during June-September

P=0.0054)(Table 3). Overall (early+late clutches), 1.44 fledged young per brood were reared from the 185 clutches, and 1.75 fledged young per brood from the 153 successful nesting attempts. Although productivity varied with the season (range=1.1-1.7, Table 3), the difference was not significant (Kruskal-Wallis one-way analysis of variance = 8.53, d.f. = 5, P = 0.129).

DISCUSSION

History of the colony

During 1994-98, usually 30-35 pairs of Black Shags nested at the colony early in each season compared with 40 pairs in 1930 (Falla & Stokell 1945). Whether the slightly fewer pairs evident in recent years at the Lake Kohangatera colony is related to increased human-induced mortality (the occasional shag is shot during the duck-shooting season; each year a few shags are found dead around Wellington Harbour after suffering internal injuries from swallowing hooked fish on broken-off or snagged portions of fishing line), reduced prey resources, or some other factor is unknown.

Roosting numbers

The reduction in numbers roosting at the colony after August (Fig. 1) is probably related to two main factors. First, some shags disperse to roosts elsewhere in the region after nesting. For instance, adults and juveniles banded at the colony have been seen at several roosts about Wellington Harbour, including Matiu/Somes Island, Melling on the Hutt River, Karori Wildlife Sanctuary and along the coastline south and west of Wellington as far north as Porirua (RGP, PJR, R. Empson, A. Munro unpubl. data). High mortality of juveniles is a second factor affecting the colony. Preliminary results indicate that about 80% of banded fledged young disappear during their first year (RGP unpubl. data). Similarly, Stuart (*in* Cramp & Simmons 1977) determined that 70% of *P. carbo* young fledged from a Scottish colony died in their first year.

Nesting activities

Courtship and nest-building activities observed at the Lake Kohangatera colony were the same as those described elsewhere (Cramp & Simmons 1977, Marchant & Higgins 1990, Johnsgard 1993). Also, most incubation activities (including the addition of further material to the nest) were as described previously (Cramp & Simmons 1977, Johnsgard 1993). There were usually three or four incubation stints at each nest during daylight, involving two or three changeovers, the same number of diurnal changeovers as noted in other studies (Cramp & Simmons 1977, Marchant & Higgins 1990, Johnsgard 1993). However, the three types of changeover we describe have not been reported previously in Black Shags, although observations that male Black Shags took the first incubation stint of the day, and then, once relieved by their partners, sometimes collected material before foraging, has been reported for male New Zealand King Shags (*Leucocarbo carunculatus*) (Schuckard 1994).

With the following exception, the activities of adults and chicks during the nestling-rearing stage at the Kohangatera colony were as described from studies at other sites (Cramp & Simmons 1977, Marchant & Higgins 1990, Johnsgard 1993). We noted that nestlings were about five weeks old when first left unattended, whereas Brown *et al.* (1982) and Johnsgard (1993) stated that this occurred when the chicks were only two weeks old.

Fledging

The age at which nestlings took their first flight during this study (49-60 days, n=3) was similar to that reported in other studies; 53 days (range=49-56 days) (Olver & Kuyper 1978), 56 days (Brown *et al.* 1982), and c. 50 days (Kortlandt 1942, Cramp & Simmons 1977, Marchant & Higgins 1990). However, there is some disparity as to the age of independence, with van Dobben (1952) and Urban (1979) giving it as c. 56 days, Marchant & Higgins (1990) as c. 80 days, Kortlandt (1942) as 84-91 days, and Cramp & Simmons (1977) as 90-100 days. Our observations of three fledglings being fed when about 110-140 days old suggest that they may not become independent until they are at least 100 days of age. Similarly, although both Pied Shags (*Phalacrocorax varius*) and Shags (*P. aristotelis*) fledged, on average, when 53 days old, fledglings were seen being fed up to a maximum of 130 days old (Millener 1972) and up to 96 days old (Snow 1960), respectively. These records from studies of individually banded young suggest that the age of independence for many shag species is probably much older than "shortly after fledging" (Johnsgard 1993).

Shags are specialised underwater pursuit-divers and they presumably take some time to learn to forage efficiently (Wunderle 1991). Foraging involves learning a variety of skills: finding profitable areas in which to forage; selecting species suitable as prey, manoeuvring quickly and precisely underwater to capture fish, and seizing and handling prey deftly to swallow them without escape. Although there are no data on causes of death in juvenile shags, they may have some difficulty learning the skills needed to capture sufficient food to meet their requirements, because juveniles often have a high mortality in their first year. Skead (1980) found that 73% of banded Whitebreasted Cormorants (*P. carbo lucidus*) died within a year of banding. Preliminary data from our study of banded fledged young indicate a similarly high mortality in the first year (c. 80%, RGP unpubl. data). While detailed observations are required to verify it, it seems likely that young Black Shags continue to receive food from the parents until 3-4 months old to allow them to survive the long period it takes to become sufficiently skilled at finding and capturing enough prey.

Duration of breeding

Falla (1932) stated that "Black Shags breed twice a year, laying in May and September", but he did not indicate whether the same pairs bred twice a year or that pairs at different colonies had different nesting seasons. Brazil (*in* Johnsgard 1993) suggested that individual pairs of this species raised two broods per year in Japan. Although it is not known precisely how long fledged young depend on their parents for food, if our records for age of independence are representative (110-140 days), then the breeding cycle would last nearly five months. Wing and tail moult of Black Shags is continuous but is suspended for nesting (Ginn & Melville 1983, Alstrom 1985). Therefore, given the duration of a successful breeding cycle and the time needed to moult, it seems unlikely that an individual pair of Black Shags at the Kohangatera colony would be able to successfully rear two broods annually.

Our observation of a banded male rearing a brood after its first nesting failed is the first record of a Black Shag attempting a replacement nesting (Marchant & Higgins 1990). Whether the same female was involved in both nestings is unknown, but it does indicate that an individual can be involved in nesting activities for up to seven months.

Breeding success

We are unaware of results from other Black Shag studies to compare with the 83% of nests being successful (fledging at least one nestling) found during this study. Most researchers have quantified nesting success in terms of percentage of eggs or chicks that have resulted in fledged young. For example, Olver & Kuyper (1978) determined that 52% of Whitebreasted Cormorant eggs hatched and the resultant chicks survived to fledge.

Why late clutches (1.07 fledglings/nest) resulted in fewer fledged young per brood than early clutches (1.51) is unknown. Millener (1972) reported a similar result for the Pied Shag. As late clutches of the Black Shags seemed to be renestings, possibly these pairs included at least one member that was a first-time breeder or that less prey was available than earlier in the season.

The overall result of 1.44 fledglings per nest from the 185 nests monitored during 1993-98 is similar to the breeding productivity recorded for the species overseas. Of 60 nesting attempts over two seasons in Natal and Ethiopia, 1.6 fledglings per nest were reared (Brown *et al.* 1982), of 17 attempts in Nova Scotia, Canada, 1.2 fledglings per nest were reared (Lock & Ross *in* Johngard 1993), and in the Netherlands, Kortlandt (1942) estimated that 1.25 fledglings per nest were reared. Debout *et al.* (1995) reported that the productivity of successful attempts at some colonies in Britain and Norway was 1.8 to 3.1 fledglings per nest during 1985-91 when populations were increasing. In comparison, successful attempts during our study averaged 1.7 fledged young per nest, which suggests that the Wellington population is at or close to the carrying capacity of the habitat.

While stoats (*Mustela erminea*), brushtail possums (*Trichosurus vulpecula*), ship rats (*Rattus rattus*), and Australasian Harriers (*Circus approximans*) are predators of eggs and chicks of birds nesting in trees (Brown *et al.* 1996, Brown *et al.* 1998, Moors 1983) and were seen at or about the colony, we have no evidence that shag nesting failures were caused by any of these species. However, we had no means of observing activity at nests during the night when the mammalian predators would have been most active. One or two harriers were seen over the colony on most days we were there. Occasionally a harrier hovered 1-2 metres above a nesting shag; the latter responding with harsh alarm calls but never left the nest. Given the high nesting success of the shags (83% of nesting attempts being successful) and the presence of the four predatory species about the colony, it seems likely that few, if any, nesting attempts failed because of predation. Likewise, Millener (1972) did not see any cases of predation at Pied Shag nests during three years of intensive observations. The large size of the Black Shag and the constant presence of at least one adult at each nest until the chicks were large and wary enough to defend themselves probably meant that the eggs and chicks were relatively immune from attacks by stoats, rats, possums, and harriers.

ACKNOWLEDGEMENTS

We thank David, Michael and Richard Bell, June Bullock, David Cornick, Reg Cotter, Geoff de Lisle, Alan Munro, Kerry Oates, Jon Powell, Mary Powlesland, Neville Todd, Janice Woon and the late Gavin Woodward for assistance with banding nestlings and for reporting sightings of banded shags; Mike and Jane Curtis for access across their land to the colony; the Hutt City Council for allowing us vehicle access beyond Burdan's No. 2 gate; to Graeme Elliott for some statistical advice; and to Robin Fordham, Don Franklin, Richard Holdaway, Mike Imber, and two anonymous referees for improvements to drafts of this paper.

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Received 27 May 1999; accepted 20 October 1999