# Breeding ecology of Snares Island Snipe (Coenocorypha aucklandica buegeli) and Chatham Island Snipe (C. pusilla)

### COLIN M. MISKELLY<sup>1,2</sup>

<sup>1</sup>Zoology Department, University of Canterbury, Private Bag, Christchurch; <sup>2</sup>Present address: Wellington Conservancy, Department of Conservation, P.O. Box 5086, Wellington, New Zealand

#### ABSTRACT

Snares Island Snipe (*Coenocorypha aucklandica buegeli*) were studied on the Snares Islands during parts of six breeding seasons between 1982 and 1987. Laying was between 4 November and 19 February; the breeding season (including chick-rearing) spanned the months November to May. Nests were well concealed among dense vegetation with solid overhead cover. Most birds were monogamous, with shared incubation of the two-egg clutch. Males incubated for 51% of the time, mainly at night and during late afternoon; females incubated 49% of the time, mainly during the morning and early afternoon. The eggs hatched synchronously and the chicks stayed in the nest for less than 13 h. The male cared for the first chick to leave the nest. Growth of chicks is described using Gompertz equations. Full juvenile plumage took c. 54 days to attain, and adult size in all growth parameters was attained soon after independence (c. 65 days).

Chatham Island Snipe (*C. pusilla*) were studied on Rangatira Island during the 1983-84 breeding season. Laying was estimated to extend from late September to the end of December. Most nests found (86%) were under *Carex* sedges. Incubation of the two-egg clutch was shared; incubation patterns were not determined. The eggs were 19% smaller in relation to predicted egg-weight than those of Snares Island Snipe. The eggs hatched synchronously and the chicks stayed in the nest for less than 11.5 h. The male cared for the first chick to leave the nest. Full juvenile plumage took c. 47 days to attain. The bill grew much more rapidly than for Snares Island Snipe and chicks became independent much earlier (c. 41 days old).

KEYWORDS: New Zealand Snipe, *Coenocorypha aucklandica*, Chatham Island Snipe, *Coenocorypha pusilla*, breeding ecology, growth rates, Snares Islands, Chatham Islands.

### INTRODUCTION

New Zealand snipes (*Coenocorypha* spp.) are among the least studied of New Zealand's endemic birds. Local extinctions have confined these snipes to islands that do not have introduced predators (Miskelly 1987, 1988). On these islands, snipe live at high densities in the absence of effective predators or foraging competitors (Miskelly 1990a, 1999), occupying tussock grasslands, megaherb gardens, scrub, forest and areas of sedge. Our limited knowledge of the life histories of *Coenocorypha* snipes is due to the remoteness of the islands, their dense vegetation, and the secretive behaviour of snipe (Stead 1948, Warham & Bell 1979, Miskelly 1987). Only the Snares Island Snipe (*C. aucklandica huegeli*) and Chatham

Island Snipe (*C. pusilla*) have been studied enough for their behaviour and ecology to be compared (e.g. Miskelly 1987, 1990a, 1990b).

Chatham Island Snipe are about 30% smaller than Snares Island Snipe (Miskelly 1990a) and have lower wing-loadings and greater flying ability (Miskelly 1990b). Features of the breeding systems of Snares Island and Chatham Island Snipes considered to have arisen due to severe food limitation during the breeding season were summarised by Miskelly (1990a). Compared with Common Snipe (*Gallinago gallinago*), *Coenocorypha* snipes live at high densities and have courtship feeding, large eggs, a long laying interval, a small clutch and shared incubation. Hatching success is high, but chick growth rates are slow and there is a long period of chick dependence.

In this paper I describe breeding seasons, nests, eggs and chick development of Snares Island and Chatham Island Snipes, and the roles of the sexes during nest site selection, incubation and hatching. This information should be of use in designing captive-rearing programmes for snipe and as a baseline for comparative studies with other taxa of *Coenocorypha* snipes.

### **STUDY AREAS & METHODS**

Snares Island Snipe were studied during seven expeditions to the Snares Islands (48°02´S, 166°36´E) between December 1982 and December 1987. Field-work of 477 days, spanning September to March, included parts of six breeding seasons. The 7.5 ha study area of *Olearia lyalli* forest held about 20 pairs of snipe, all of which I individually colour-banded. I found nests by tracing the source of calls (n = 20), systematic searching (n = 19), chance disturbance of incubating adults (n = 4), or following returning adults (n = 2). Detailed descriptions were made of 36 nests. Eggs were measured to 0.1 mm with vernier calipers.

Nests were checked daily, or more frequently during laying and hatching. Hides were erected at four nests and five 24-h observations of incubation patterns were undertaken in the middle of the incubation period. A chart recorder, light beams and photo-electric cells installed at one nest gave a trace showing activity during laying of the second egg. If a bird sat on the nest the two light beams were broken, activating an ink pen on a revolving drum. The pen returned to base level when the bird left the nest and the light beams were uninterrupted. First-egg laying dates for 25 nests were calculated from hatching dates by subtracting 22 days for incubation and three days for laying interval (Miskelly 1990a).

Each of 35 known-age chicks was captured  $4.6 \pm 5.0$  times (range 1 - 18 times) between hatching and age 78 days (total = 160 handlings) and standard measurements taken. Linear measurements were recorded to 0.1 mm and weights to 0.1 g. Patterns of growth were found to conform most closely to the Gompertz equation, as in other Charadriiformes (Ricklefs 1973, Green 1985). Gompertz curves were fitted to chick growth parameters using the Maximum Likelihood Program (Ross 1980); the equations were of the form:

$$Y = A + C x \exp(-\exp(-D(T - M)))$$

where Y is the measured parameter, T is the age in days, and A, C, D and M are constants. The asymptote of the curve is equal to A + C. Growth constants ( $K_G = e \ge dY/dT$  at the point of inflection; Ricklefs 1967) for weight and bill length were obtained by preparing the data as proportions of the asymptote, and then solving Equation 2:

$$dY/dT = B \times C \times \exp(-\exp(-B(T - M) + B(M - T)))$$

at the point Y = 1/e. Growth rates of known-age chicks were used to calculate hatching dates for 38 chicks of unknown age. Thus, hatching and laying dates were calculated for all 58 breeding attempts recorded in the study area over five breeding seasons.

Chatham Island Snipe were studied on Rangatira (South East) Island (44°21´S, 176°10´W) from 25 November 1983 to 18 January 1984. The 4.3 ha study area of *Olearia traversi* and *Plagianthus regius* forest contained about 24 snipe territories. Observation techniques were similar to those outlined for Snares Island Snipe.

Fourteen nests were found by systematic searching, and 28 eggs measured. Laying dates were estimated from hatching dates by assuming that incubation length and laying interval were similar to those for Snares Island Snipe. Twenty-eight known-age chicks were captured  $2.4 \pm 1.4$  times (range 1 - 4) between hatching and age 89 days (total = 66 handlings). Gompertz curves were fitted to chick growth parameters, and growth constants for weight and bill length calculated using Equation 2. Hatching dates for 21 chicks of unknown age were estimated by comparing development with growth rates of known-age chicks, allowing hatching and laying dates to be estimated for all 40 breeding attempts recorded within and around the study area.

Measurements are given as mean  $\pm$  s.d., with range in parentheses, unless otherwise stated.

### **RESULTS & DISCUSSION**

### Breeding season

The date of the first egg laid for Snares Island Snipe over five breeding seasons ranged from 4 to 28 November (mean 16 November). The last egg in three breeding seasons was laid between 7 and 19 February (mean 12 February). Laying during these three breeding seasons extended over  $79 \pm 9$  days (71 - 89 days). As incubation and chick-rearing took about 87 days (Miskelly 1990a), the breeding season on the Snares Islands typically extended from mid-November to mid-May. Horning & Horning (1974) saw a small downy chick on 4 May 1972, which must have hatched from a clutch laid in early April. However, as no other small chicks had been seen for several months, this record was considered exceptional (D.S. Horning, pers. comm.).

Laying of Chatham Island Snipe in 1983 was estimated to have extended from 23 September to 29 December. Ignoring possible failed early nests, laying extended over 97 days, and was almost two months earlier than for Snares Island

Snipe. As incubation and chick-rearing took about 63 days (Miskelly 1990a), the 1983-84 breeding season was estimated to have extended from late September to the end of February. Laying occurred earlier in 1981; Mike Dennison (*in litt.*) saw a small chick on Mangere Island on 28 September that must have hatched from an egg laid in the first week of September. The latest breeding record is of a bird sitting on two eggs on 7 April 1990 on Rangatira Island (O'Donnell & West 1991); if these eggs were fertile, they must have been laid after 13 March.

Laying by snipe on the Snares Islands coincided with an annual peak in prey abundance between late November and early February (Miskelly 1989a). The much earlier laying season of Chatham Island Snipe suggests that peak prey abundance was two months earlier on the Chatham Islands.

### Mating system

About 95% of territory-holding male Snares Island Snipe were apparently monogamous early in the breeding season; the remaining 5% were simultaneously polygynous (Miskelly 1990a). The pair bond was broken following hatching, and either sex could breed with a new mate if they were not caring for a dependent chick (Miskelly 1999). Monogamous pairs shared incubation at the same nest (described below). Details of solo female incubation (associated with simultaneous polygyny) were given by Miskelly (1989b).

All Chatham Island Snipe seen were apparently monogamous, but the sample (10 nests) was too small for rare mating behaviours to be detectable.

### Nest sites

Nest sites were chosen by courting pairs, but only females were seen to construct nests (although incubating males rearranged nest materials). Nests were constructed from materials within reach of the nest, except for two Snares Island Snipe nests where *Poa* leaves had been carried at least 1 - 1.5 m.

Snares Island Snipe made two types of nests depending on the site chosen. Type I (Fig. 1a) nests were in fern clumps (n = 33, 73% of nests found). Most (n = 24) were on the downhill side of clumps of prickly shield fern (*Polystichum vestitum*), with the nest sheltered above by a solid *Polystichum* trunk and at the sides by the skirt of dead fronds. The remaining nine Type I nests were in clumps of shore spleenwort (*Asplenium obtusatum*) and/or coastal hard fern (*Blechnum durum*). Type I nests were formed from plant detritus that had gathered under the skirt - generally fern fragments but also tree leaves and fragments of bark. The eggs were laid in a shallow natural depression if there was little detritus, or in a bowl up to 6 cm deep. Bowl depth for 24 Type I nests was  $1.8 \pm 1.8$  cm. The internal diameter of 23 nests was  $10.0 \pm 1.4$  cm (8.5 - 13 cm). Of the 33 Type I nests, 32 had solid wood or matted stipes  $18.6 \pm 5.4$  cm (10 - 30 cm) above the bowl.

Type II nests for Snares Island Snipe (Fig. 1b) were found in the heart of *Carex trifida* sedges (n = 9) or *Poa tennantiana* tussocks (n = 3). A Type II nest has also

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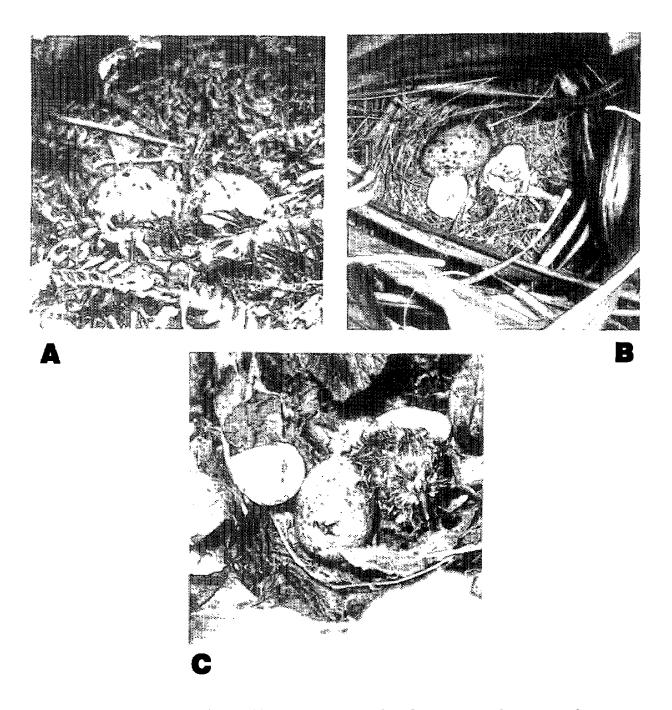


FIGURE 1 – a - Snares Island Snipe Type I nest under *Polysticbum vestitum* fern. A simple scrape in detritus, surrounded by fern fronds.

b - Snares Island Snipe Type II nest under Carex trifida sedge. A well formed cup of Poa astonii and Carex leaves.

c - Hatching Chatham Island Snipe in nest under blackberry. This nest was unlined, but 86% of nests were lined with sedge or grass leaves.

been found in a *Poa astonii* tussock (P.M. Sagar, *in litt.*). Nests were well-formed cups constructed of substantial amounts of *Carex* or *Poa* leaves. Mean bowl depth of 10 nests was  $4.0 \pm 2.4$  cm (1 - 10 cm). The internal diameter of the bowl was  $11.1 \pm 1.3$  cm (9 - 13 cm). Of the 12 Type II nests, eight had solid wood  $18.6 \pm 8.9$  cm (7 - 30 cm) above the bowl. The remaining four nests were protected from above by a dense crown of sedge or tussock leaves.

Of eight Snares Island Snipe females for which 2 - 5 nests each were found, four constructed only Type 1 nests (n = 14 nests) and four constructed both types of nest (6 x Type I, 7 x Type II). The choice of nest site (and type) seemed to depend on what sites were available - those females in territories which did not contain extensive areas of *Poa* or *Carex* constructed only Type I nests.

Empty scrapes were often found during systematic searches, and so Snares Island Snipe may make more than one nest before laying. This was confirmed in the following case. Two empty nests were found 2 m apart on 25 November 1987. The resident female was seen within 3 m of these nests four times over the next five days (the male was never seen near the nests). Small amounts of detritus placed daily in the nests were removed or incorporated into the nest. On 30 November, the female was sitting on Nest B at 0840 hrs, and on Nest A at 1450 hrs. An egg was laid in Nest A between 1450 and 1605 hrs.

Three nest sites were used more than once. One site was used in three different seasons by three different pairs. The second site was used in two consecutive seasons by the same male with different females. The third site was used in the same season by the same male with two consecutive mates (his first mate had used a second site before the male returned to the first site with his second mate). No female was found to re-use a nest site.

Twelve of the 14 Chatham Island Snipe nests found were under *C. trifida*, one was under blackberry (*Rubus fruticosus*; Fig. 1c) and one was under Yorkshire fog grass (*Holcus lanatus*) and bracken (*Pteridium esculentum*). Nests were shallow cups of *Carex* or *Holcus* leaves (n = 12) or simple unlined scrapes (n = 2; Fig. 1c).

A major cause of nest loss for passerines on the Snares Islands and Rangatira Island is damage by 'crash-landing' petrels (Cemmick & Veitch 1985, McLean & Miskelly 1988). Sooty Shearwaters (*Puffinus griseus*) have a mean adult bodyweight of 819 g and breed at an average density of 11,600 pairs/ha under Olearia forest on the Snares Islands (Warham & Wilson 1982). Snipe nests on the Snares Islands were all well protected from above by solid wood or matted vegetation or were in areas with a very dense Olearia canopy. Chatham Island Snipe nests on Rangatira Island were less well protected, often under small *Carex* sedges in clearings or at forest margins. The predominant petrel species breeding on Rangatira Island (White-faced Storm Petrel *Pelagodroma marina*, 45 g; Broad-billed Prion *Pachyptila vittata*, 202 g) are much lighter and land more gently than do Sooty Shearwaters. Thus, the weight and landing habits of locally abundant nesting petrels may influence nest sites chosen by *Coenocorypha* snipes.

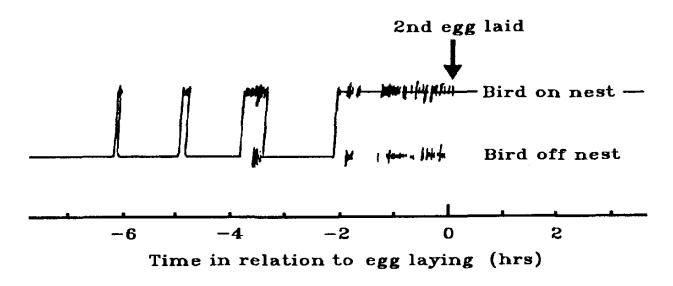


FIGURE 2 – Activity at a Snares Island Snipe nest during the 7.5 hours before laying of the second (final) egg. The tracing was obtained using an activity recorder (see Methods). A blurred trace is caused by frequent movement of a bird at the nest; a smooth trace indicates inactivity.

### Laying

I determined laying time within six hours for nine Snares Island Snipe eggs. Eight were laid between 0910 hrs and 2050 hrs (mean 1458 hrs  $\pm$  2 h 55 min), the ninth was laid during the night. The two eggs in each clutch were laid three days apart (n = 5; Miskelly 1990a).

Activity at one nest was followed in detail for 8 h 20 min until the second egg was laid (Fig. 2). A bird visited the nest briefly 6 h 07 min, 4 h 55 min and 3 h 50 min before the egg was laid. The female was on the nest continuously for 2 h 06 min until the egg was laid, with much vigorous movement during the last 1 h 18 min. Steady incubation began as soon as the second egg was laid.

I have no information on laying for Chatham Island Snipe.

## Eggs

Snares Island Snipe eggs were bluntly ovoid, light to very pale brown, and marked with dark brown, pale brown and mid-grey spots and blotches, especially around the larger end. Length was  $43.9 \pm 1.1 \text{ mm} (39.1 \cdot 46.4 \text{ mm}, \text{n} = 81)$  and width was  $31.9 \pm 0.6 \text{ mm} (30.4 \cdot 33.1 \text{ mm}, \text{n} = 81)$ . Fresh weight was estimated as  $23.7 \pm 1.1 \text{ g} (21.1 \cdot 26.7 \text{ g}, \text{n} = 81; \text{Miskelly 1990a})$ . Estimated egg-weight loss during incubation was  $15.9 \pm 2.3\%$  of fresh weight (n = 40).

Chatham Island Snipe eggs were pale pinkish brown, marked with fine spots of dark brown and larger blotches of mid-grey around the widest part, but sparsely marked elsewhere. Length was  $38.7 \pm 1.5 \text{ mm} (35.9 - 41.9 \text{ mm}, n = 28)$  and width was  $28.1 \pm 0.6 \text{ mm} (27.1 - 28.9 \text{ mm}, n = 28)$ . Mean fresh weight was estimated as 16.1 g (Miskelly 1990a).

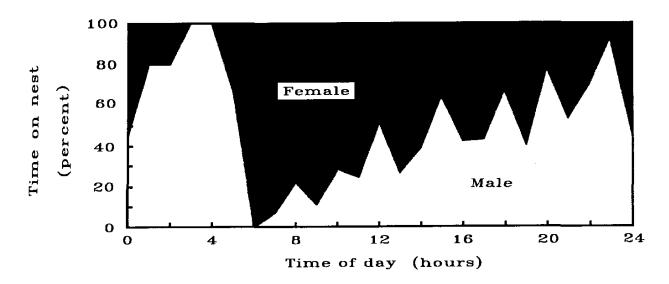


FIGURE 3 – Daily pattern of incubation sharing by male and female Snares Island Snipe based on 531 spot checks at 32 nests. Males were on nests 51.3% of the time, and females 48.7%.

Eggs of Snares Island and Chatham Island Snipes differed in their size, colour and markings (Fig. 1), but both species laid eggs that weighed 19 - 20% of mean female body-weight (Miskelly 1990a). Egg-weights of birds do not increase in direct proportion to body-weight; a regression equation for Charadriiformes was given by Rahn *et al.* (1975). Eggs of Snares Island Snipe (mean female bodyweight 116.0 g) were 22.8% larger than expected, whereas those of Chatham Island Snipe (85.4 g) were only 3.9% larger than expected. Large eggs are considered an adaption to a poor or unpredictable food supply, as the young hatch more fully developed and/or with a large yolk supply to compensate for the low rate of food intake after hatching (Martin 1987). The relatively (and absolutely) larger eggs of Snares Island Snipe may indicate that food is less available on the Snares Islands during the breeding season than on Rangatira Island.

### Incubation

Three 24-h watches at three Snares Island Snipe nests with shared incubation revealed that males incubated for 60.4 - 64.0% of the time, and females 36.0 - 39.6% (Miskelly 1989b). However, 531 spot checks at 32 nests throughout the day and night revealed almost equal sharing of incubation by the sexes (Fig. 3). Males tended to incubate from midnight to dawn (c. 0600 hrs) and females from dawn to noon or early afternoon. There were frequent changeovers during mid-afternoon through to dusk, with either bird sitting at nightfall (c. 2200 hrs).

As male Snares Island Snipe did most of the nocturnal incubation, females were able to forage at night. At night, snipe frequently were seen up to 120 m from the nearest cover (Miskelly 1990b), feeding in exposed swards of *Callitriche antarctica* and *Crassula moschata* that they did not use during the day. These swards contained huge numbers of amphipods (up to 12,000/m<sup>2</sup>; pers. obs.), a major snipe food (Miskelly 1989a). Nocturnal foraging by female snipe during

incubation may have evolved to allow rapid recovery from the energetic stress of egg production; the clutch represents about 41% of female body-weight for Snares Island Snipe.

The longest incubation shift recorded for male Snares Island Snipe at three nests was 12 h 48 min. For females, the longest incubation shifts recorded were 8 h 32 min (nests with shared incubation; three nests observed) and 10 h 27 min (at one nest with solo female incubation; Miskelly 1989b).

The well-concealed nests of Snares Island Snipe were very difficult to find. Recognising the incubation pattern (Fig. 3) greatly improved my nest-finding; the same technique may be useful for locating nests of other *Coenocorypha* snipes. Male Snares Island Snipe defended their territories with Loud Calls - a vibrant *chup* repeated 5 - 19 times at a rate of about twice per second, and/or a disyllabic *queeyoo* repeated 2 - 4 times (Warham 1967, Warham & Bell 1979, Miskelly 1987 & 1990b). Female snipe occasionally answered their mate's Loud Call with a softer *chur* repeated 2 - 4 times. Between 0600 hrs and 1200 hrs most male snipe were foraging (Fig. 3) but I could prompt them to call by playing back tape-recorded Loud Calls. If a male called within 20 m of the nest, his incubating mate often replied and then I could usually find the nest after a few minutes' searching. Pairs that were not incubating typically foraged together; I would start nest-searching whenever I made regular sightings of a solitary bird from a known pair.

Fifty-eight spot checks at 10 Chatham Island Snipe nests between 0600 hrs and 0200 hrs revealed no pattern in diurnal division of labour by the sexes. Between these hours, 67.2% of records were of females and 32.8% of records were of males. Observations were too few to show whether females spent more time on the nest than males; if males incubated more from 0200 to 0600 hrs, incubation could have been shared equally.

### Hatching

Snares Island Snipe eggs hatched at any time of the day or night (determined to  $\pm 5$  h for 28 eggs). The two eggs of the clutch hatched 5 h 3 min  $\pm 4$  h 32 min apart (0 - 12 h 40 min, n = 11). The time spent in the nest was determined to within 1 hour for five chicks, and ranged from 2 h 48 min to 12 h 43 min (mean 6 h 41 min). Chicks that hatched during the night were kept in the nest until dawn, and chicks stayed in the nest longer during wet or cold conditions. Egg shells were left in the nest (n = 28) or within 0.5 m of it (n = 2).

Male Snares Island Snipe led the first chick from the nest in all ten 2-chick broods observed during hatching. At four nests where only one egg hatched, the male took the chick in two cases and the female in two. In the first two cases the remaining egg was infertile or the second chick died while hatching. In the second two cases the second egg had been cracked and addled well before the eggs were due to hatch, and so when one egg hatched, the female did not continue to sit on the damaged second egg. The single infertile egg left in a nest was incubated for less than a day after the first egg hatched.

Two of 12 pairs of Snares Island Snipe swapped their chicks within the pair within a day of leaving the nest, but no other within-pair exchange was recorded. One between-pair chick-swap was observed; a male swapped his 2 - 3 week old chick for the 3 - 4 week old chick of a neighbouring female. Each adult cared for the 'fostered' chick for at least 20 days after the swap was first noticed.

The sex of Snares Island Snipe chicks was independent of the sex of the adults caring for them (n= 28,  $\chi^2 = 0.144$ , P = 0.71).

Brooding by Snares Island Snipe was observed only on the day of hatching. Chicks were fed entirely by adults for the first fortnight; the youngest chick seen to feed itself (probing) was 13 days old (bill length 28.3 mm).

The sexes were equally good as parents with respect to the growth rate and survival of Snares Island Snipe chicks. Increase in weight of chicks (g/day) reared by either sex was similar (Parallel curve analysis;  $F_{1,84} = 1.015$ , n.s.). Chick survival until my departure from the Snares Islands (83% for 41 cared for by males; 77% for 34 cared for females) and until age one-year-old (37% for male-parented; 32% for female-parented) did not differ between the sexes of parents ( $\chi^2 = 0.054$  and 0.072, n.s., respectively).

Chatham Island Snipe eggs hatched at any time of the day or night (n = 8). At four nests, the two eggs hatched 7 h 36 min  $\pm$  7 h 3 min apart (range 2 h 30 min - 18 h). Five chicks spent 1 h 15 min to 11 h 15 min in the nest (mean 7 h 09 min). At five nests where both eggs hatched, the male took the first chick to leave the nest.

Chatham Island Snipe were observed brooding young only on the day of hatching. The youngest chick seen probing was 18 days old (estimated bill length 27.9 mm).

# Development of young

### At hatching

Newly-hatched Snares Island Snipe chicks had uniformly dark grey down tipped with pale brown, slightly paler ventrally (Fig. 4a). A thin blackish line extended from the nostril to the eye, and another reached the top of the crown from the base of the bill. The overall appearance was of uniform charcoal grey with flecks of brown. The bill was black, and the legs and feet grey with black on the sole and the back of the tarsus. The egg tooth was lost within a day of hatching (n = 7). Measurements of 28 chicks at hatching were: bill length 15.8  $\pm$  0.7 mm (14.3 -16.6 mm); tarsus length 19.3  $\pm$  0.7 mm (18.0 - 20.5 mm); mid toe & claw length 26.8  $\pm$  0.9 mm (25.0 - 28.5 mm). Weight was 15.5  $\pm$  0.9 g (14.0 - 18.0 g).

Chatham Island Snipe chicks (Fig. 4b) had dark grey down with brown and buff tips, more rufous on the nape, but the same head markings as Snares Island Snipe. The overall appearance was of pale rufous brown because of more brown on the tips of the down feathers. The bill was black, and the legs and feet lead grey, darker on the sole and the back of the tarsus. Measurements of 12 chicks at hatching were: bill length  $12.7 \pm 0.6 \text{ mm}$  (11.5 - 13.5 mm); tarsus length  $16.8 \pm$ 



FIGURE 4 – a - Newly hatched Snares Island Snipe chick. b - Newly hatched Chatham Island Snipe chick.

0.6 mm (16.0 - 17.7 mm); mid toe & claw length  $22.4 \pm 0.8$  mm (20.9 - 23.4 mm). Weight was  $11.0 \pm 0.7$  g (10.0 - 12.0 g).

#### Feather development

Feather development and down loss of Snares Island Snipe chicks took about 7.5 weeks (Table 1). Plumage development of Chatham Island Snipe chicks was similar to that outlined for Snares Island Snipe (based on 23 handlings of Chatham Island Snipe chicks 13 - 51 days old). However, after day 40, Chatham Island Snipe lost their down more rapidly and had shed the last traces by day 47 (n = 4). The youngest Chatham Island Snipe chick seen to fly was about 3 weeks old (Mike Dennison *in litt.*).

### Growth rates

The asymptotes for six growth parameters of Snares Island Snipe chicks fell between the mean adult male and mean adult female measurement for each parameter (Table 2), indicating that chicks reached full adult size in all parameters soon after independence. The asymptote for Chatham Island Snipe chick weight was only 96% of mean adult male weight, but the other three asymptotes (Table 2) all exceeded mean adult male dimensions. Snares Island Snipe chicks had exceeded 95% of the asymptote for all parameters by the time they reached independence (age c. 65 days; Miskelly 1990a). Chatham Island Snipe chicks did not attain 95% of the asymptote for weight and bill length until about a week after becoming independent (age c. 41 days; Miskelly 1990a).

Age (days)	N	Development					
0-6	40	Totally downy					
<b>7 · 1</b> 0	8	Scapular feathers starting to emerge from sheaths, belly feathers in sheath					
11 - 13	7	Scapular feathers 10 mm out of sheaths, primaries in sheath					
14 · 16	7	Back and part of belly and flanks well feathered; primaries 1 - 9 mm out of sheaths					
17 - 19	10	Extensive down, thinning on back and belly; primaries 6 - 14 mm out of sheaths					
20 - 23	12	Well feathered; dense down around head and rump, sparse elsewhere; primaries 12 · 32 mm out of sheaths					
24 - 27	12	Down on head and rump, sparse on upperwing coverts, traces elsewhere; primaries 27 - 53 mm out of sheaths					
28 - 35	21	Fully feathered; down on head and rump, traces on upperwing coverts; primaries 40+ mm out of sheaths; can flutter along ground from day 30					
36 - 44	17	Down on nape, chin and frons, trace on rump					
45 - 53	14	Trace of down on nape					
54+	12	Down-free					

TABLE 1 -Plumage development of Snares Island Snipe chicks, based on 160 handlings of known-age<br/>chicks between hatching and 78 days old. N = number of chicks handled per time interval.

TABLE 2 -Characteristics of the Gompertz growth equations determined for Snares Island Snipe and<br/>Chatham Island Snipe chicks. (See Methods for details). Growth equations for Snares Island<br/>Snipe could be used to estimate ages of chicks of the similar sized *Coenocorypha* snipes from<br/>Antipodes, Auckland and Campbell Islands. Asymp. = asymptote\*.

	Start time		Gompert	z consta	nts	r <sup>2</sup>	Asymp.	Time to 95% Asymp (days)
Parameter	(days)	A	C	D	M			
Snares Island Snij	pe							
Weight	1	-45.88	150.54	0.06	-1.17	0.95	104.7	59.6
Bill	0	-4.18	62.66	0.05	2.73	0.99	58.5	61.2
Tarsus	0	18.80	6.11	0.14	6.48	0.93	24.9	17.0
Mid toe & claw	0	6.27	27.61	0.08	-15.44	0.88	33.9	19.9
Wing	21	56.05	53.34	0.16	23.10	0.94	109.4	37.3
Tail 	28	20.30	20.29	0.17	35.06	0.90	40.6	48.3
Chatham Island S	nipe							
Weight	1	1.72	70.01	0.08	9.90	0.94	71.7	48.7
Bill	0	10.13	35.13	0.07	12.72	0.99	45.3	49.8
Tarsus	0	15.95	7.50	0.10	7.53	0.95	23.5	25.4
Mid toe & claw	0	-709.59	740.81	0.05	-83.62	0.96	31.2	32.6

\* Asymptote measurements in mm, except weight (g).

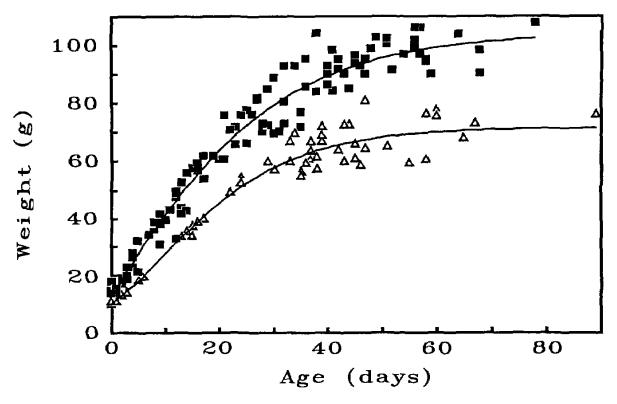


FIGURE 5 - Weight gain of Snares Island Snipe chicks (solid squares) and Chatham Island Snipe chicks (open triangles). Details of Gompertz growth equations given in Methods and Table 2.

Chicks of Chatham Island Snipe were about 30% smaller than Snares Island Snipe of the same age (Fig. 5; Table 2). The growth constant ( $K_{\rm c}$ ) for Snares Island Snipe weight was 0.070, compared with 0.074 for Chatham Island Snipe, indicating similar growth rates for the two species (see also Fig. 3 in Miskelly 1990a).

The bill of Snares Island Snipe chicks grew much more slowly in relation to their growth asymptote than those of Chatham Island Snipe chicks (Fig. 6; Table 2). The growth constant for Snares Island Snipe bill length was only 0.055, 38.3% of that for Chatham Island Snipe ( $K_c = 0.143$ ).

As snipe get all their food by probing in the soil, bill-length must be a major constraint on the foraging ability of developing chicks. Chicks of both species started to probe for themselves when the bill was about 28 mm long. With rapid bill growth, Chatham Island Snipe chicks may become independent sooner than Snares Island Snipe chicks (41 v. 65 days). However, bill length alone does not explain the longer period of dependence of Snares Island Snipe, as they had a mean bill length of 56 mm at fledging (96% of asymptote) compared to 41 mm for Chatham Island Snipe (91% of asymptote). Food may have been less available on the Snares Islands, prolonging the period of dependence on parental feeding.

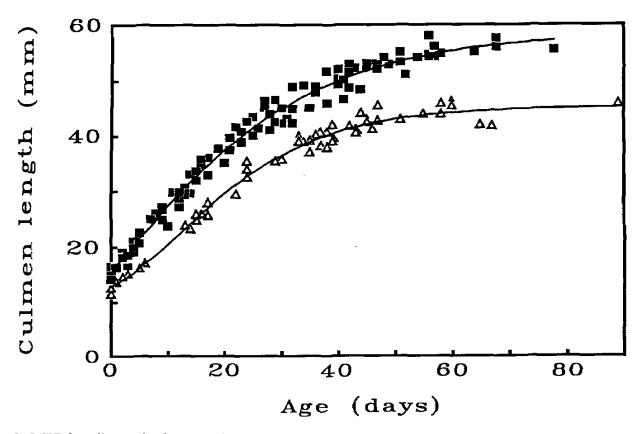


FIGURE 6 - Bill growth of Snares Island Snipe chicks (solid squares) and Chatham Island Snipe chicks (open triangles). Details of Gompertz growth equations given in Methods and Table 2.

### CONCLUSIONS

Snares Island Snipe and Chatham Island Snipe were similar in their breeding ecology, although data on laying and incubation by Chatham Island Snipe are incomplete. Both species had prolonged breeding seasons during the spring and summer. Most matings were monogamous, with courtship feeding of the female by the male during egg-formation (Miskelly 1990a) and shared incubation of the two-egg clutch. Nests were concealed under vegetation; solid overhead cover was a feature of Snares Island Snipe nests, probably as protection from crashlanding Sooty Shearwaters. Broods were split soon after hatching, the male caring for the first chick to leave the nest.

Chatham Island Snipe differed from Snares Island Snipe in breeding two months earlier and laying smaller eggs. The bill of Chatham Island Snipe chicks grew more rapidly and they attained independence three weeks sooner than Snares Island Snipe chicks. These differences in breeding ecology may have been due to differences between the two islands in the timing and size of annual peaks in prey abundance. This hypothesis could be tested by systematic sampling of soil invertebrates during spring and summer on Rangatira Island by techniques similar to those used on the Snares Islands (Miskelly 1989b).

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