

**Breeding systems of New Zealand Snipe
Coenocorypha aucklandica and Chatham Island Snipe
C. pusilla; are they food limited?**

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New Zealand Snipe *Coenocorypha aucklandica* were studied over six breeding seasons on the Snares Islands. The study area (7.5 ha) held about 20 pairs at a density of 3.2 ± 0.5 pairs/ha, plus 5 to 25 nonterritorial birds. Most matings were monogamous but simultaneous polygyny was recorded in one territory (by two different males) in four consecutive seasons. Males courtship fed females before egg-laying. The typical clutch was two eggs, laid three days apart. Incubation was shared equally by the sexes in monogamous pairs and took 22 days. Some females with polygynous mates attempted to incubate unaided, which took about 38 days. Broods were split at hatching, with the male caring for the first chick to leave the nest. Chicks were fed by adults for at least 41 days, and did not become independent until about 65 days old. Growth rates were slow compared to Common Snipe *Gallinago gallinago* and full plumage took about 54 days to attain. No pairs were double-brooded but 43% of pairs that failed during incubation or early chick-rearing renested together. Some breeders of both sexes who had lost their dependent chick bred a second time with a new mate while their first mate continued rearing the surviving chick (sequential polygyny and polyandry). Hatching success was 80%, and fledging success was 48%. Each pair produced, on average, 0.6 fledglings per year.

Chatham Island Snipe *C. pusilla* were studied on Rangatira Island during the 1983–84 breeding season. Breeding density was about 5.6 pairs/ha. The breeding system was very similar to that for *C. aucklandica* but chicks became independent at about 41 days old. Hatching success was 89%.

Compared to Common Snipe, *Coenocorypha* snipes occurred at high densities, had courtship feeding, large eggs, a long inter-egg interval, a small clutch, shared incubation and a long incubation period. Nest desertion rates were high, but overall hatching success was also high, chick growth rates were slow, there was a long period of chick dependence and a long relaying interval following nest failure or chick loss. Survival rates of both adults and chicks were high. These differences are attributed to the absence of predation, and to intense intraspecific competition for food in a stable environment.

Most shorebirds in the family Scolopacidae typically lay clutches of four eggs. Of the 72 species breeding in the holarctic, only two dowitchers *Limnodromus* spp. usually lay smaller clutches (Maclean 1972, Walters 1984, Sæther *et al.* 1986). In contrast, at least ten of the 13 species breeding in the southern hemisphere lay modal clutches of between one and three eggs (clutch sizes of three species unknown; Maclean 1972, Walters 1984); nine of the scolopacid species that breed in the southern hemisphere are snipe (Hayman *et al.* 1986). Breeding systems of scolopacids that lay small clutches are poorly known (Maclean 1972, Jehl & Murray 1986, Sæther *et al.* 1986). Furthermore, it is not clear why reduced clutches are a feature of shorebirds breeding in the southern hemisphere (Maclean 1972, Winkler & Walters 1983, Walters 1984).

The snipe genus *Coenocorypha* comprises two extant species found on outlying islands of New Zealand (Miskelly 1987). New Zealand Snipe *C. aucklandica* and Chatham Island Snipe *C. pusilla* are non-migratory and are considered the most

morphologically primitive snipes (Lowe 1915, Strauch 1978). As *Coenocorypha* snipes occur at high densities in environments free of effective predators or foraging competitors (McLean & Miskelly 1988, Miskelly 1990), populations may be limited by intraspecific competition for food. In this study I investigate parameters of the breeding systems of New Zealand and Chatham Island Snipes that could potentially be constrained by food availability. Their breeding systems are compared with that for Common Snipe *Gallinago gallinago*, the only other snipe species that has been studied in sufficient detail. An hypothesis for the reduced clutch size and other *K*-selected traits of *Coenocorypha* snipes is outlined.

Study areas and methods

Snares Islands

New Zealand Snipe (race *huegeli*; Fig. 1) were studied on Main Island, Snares Islands Nature Reserve (48°02'S 166°36'E) in the New Zealand subantarctic during seven expeditions between December 1982 and December 1987. Observations spanned September to March (total 477 days and 134 nights in the field), and included parts of six breeding seasons.

A 7.5 ha study area of *Olearia lyalli* forest north of the Biological Station (Warham 1967) containing about 20 snipe territories was marked out in a 20 m grid. Snipe of all ages were captured with a handnet during the day, or with a spot-light and handnet at night. All adult snipe ($n = 93$) resident in the study area were individually colour-ringed for the duration of the study, and 73 chicks were given numbered metal rings or year colour-codes. Adult snipe were sexed by measurements and by sex-specific displays recorded after marking (unpubl. data). Pairs were identified by prolonged consorting, courtship feeding, mating, or attendance at the same nest, as observed during daily surveys of the study area.

All breeding attempts in 1985–86 and 1986–87 were detected by observing the behaviour of adults and by regular monitoring of female body-weight, cloacal swelling and brood patch condition. Forty-five



Figure 1. Adult female New Zealand Snipe, Snares Islands.

nests were located by tracing the source of calls ($n=20$), systematic searching ($n=19$), chance disturbance of incubating adults ($n=4$), or following returning adults ($n=2$). The 14 nests that were not found in 1985–86 and 1986–87 (11 successful, 3 unsuccessful) were included in overall analyses of breeding success but not in the analysis of hatching success. Eighty-one eggs were measured to 0.1 mm and weighed to 0.5 g when found. Forty eggs were weighed subsequently to determine rates of water loss during incubation. Fresh egg-weights were measured directly ($n=9$) or estimated by adding estimated water loss (0.18 g/day) to the weight when found ($n=68$). Weights for four eggs at two nests where incubation was not shared were estimated from linear measurements (Miskelly 1989), as water loss was less at nests with lower incubation constancy. Nests were checked daily, or more frequently during laying and hatching. Hides were erected at four nests (three with shared incubation and one with solo incubation). Five 24-h observations of incubation constancy (percent of time a bird was on the nest) were undertaken in the middle of the incubation period. A chart recorder, light beams and photo-electric cells were installed at two nests in addition to those above, and gave two 24-h tracings of incubation constancy.

Chicks were ringed in the nest or when first captured. Developmental data were obtained from 35 known-age chicks between hatching and 78 days old. As dependent young were always present when I left the island (February or March), fledging success and survival to independence could only be calculated for chicks that hatched at least 30 and 65 days respectively before my departure. However, survival from hatching to age one-year-old did not differ for chicks aged more or less than 30 days at my departure ($\chi^2_1=0.004$, n.s.). Breeding success was only determined in detail for 1985–86 and 1986–87, when observations spanned four months and covered the entire laying season (but see Miskelly 1990).

Chatham Islands

Chatham Island Snipe (Fig. 2) were studied on Rangatira (South East) Island Nature Reserve (44°21'S 176°10'W), Chatham Islands, from 25 November 1983 to 18 January 1984 and 7 to 15 July 1986 (61 days, 20 nights). The main study area was 4.3 ha of *Olearia traversi* and *Plagianthus regius* forest around the field hut, and contained about 24 snipe territories. Methods of capture and observation were similar to those for New Zealand Snipe.

Thirty-five adults were individually colour-ringed and 47 chicks were given numbered metal rings. Fourteen nests were found by systematic searching and 28 eggs were measured. Fresh egg weights were



Figure 2. Adult male Chatham Island Snipe, Rangatira Island.

estimated from linear measurements using the equation of Miskelly (1989). Developmental data were obtained from 28 known-age chicks between hatching and age 89 days.

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

Results

Breeding density

The density of New Zealand Snipe in the study area over six breeding seasons was 3.2 ± 0.5 territorial pairs per ha (2.6–3.8 pairs/ha). Total density (including nonterritorial birds) was 8.2 ± 2.2 birds per ha. (range over six years 5.4–11.5 birds/ha). Some nonterritorial birds attempted to breed during chick-rearing of territorial pairs (Miskelly in prep.).

The density of Chatham Island Snipe in the study area on Rangatira Island was about 5.6 pairs per ha, but I was not able to confirm the presence of nonterritorial birds due to my late arrival on the island.

Mating system

Of 83 territory-holding male New Zealand Snipe from six breeding seasons, 79 (95.2%) had a single mate at the start of the breeding season. In each of four breeding seasons, one male had two or three mates simultaneously (see Miskelly 1989). Two different males on the same territory were involved; both held the territory for two consecutive years each. This territory was on a peninsula and had only a small defended boundary at its base, allowing the territory holders to defend a large area of high quality habitat. Both males had been monogamous for at least two breeding seasons before being polygynous. These simultaneously polygynous males assisted in incubation at one nest only, leaving the supernumerary females to incubate by themselves (Miskelly 1989).

The other 19 territories occupied each season had 3–7 adjoining territories, and all held monogamous pairs. Although 2–7 unpaired females were present in these 19 territories between 1985 and 1987, none attempted to breed with a male that was already paired. Two males were observed to court additional females around the date that their mates were laying; neither attempt at polygyny was successful and the males shared incubation at their first mates' nests.

Some breeders of both sexes which had lost their dependent chick paired with new mates and attempted to breed again while their original mate continued to rear the surviving chick from the first brood (sequential polygyny and polyandry; see Renesting).

Incubation was shared at all ten nests of Chatham Island Snipe for which incubation patterns were determined, suggesting that all females observed were in monogamous relationships (though it is possible that the males had other mates).

Courtship and copulation

New Zealand Snipe pairs consorted for up to 108 days before laying but it is not known if pairs stayed together during autumn and winter.

Courtship feeding was observed for eight different pairs on eight days (total number of food passes = 41, 1–22 per bout). All food passes were from male to female. Courtship feeding occurred from 62 days before the first egg of the pair was laid to the day before the second (final) egg was laid. Excluding the one outlier, courtship feeding was seen only in the three weeks before laying. Copulation was

observed on ten days, ranging from 62 to four days before the first egg of the pair was laid. Ignoring the one outlier (a different pair to the record of early courtship feeding), copulation occurred 14.4 ± 6.3 days (4–21 days, $n = 9$) before the first egg was laid. Courtship feeding was not required to solicit copulation; only one pair was seen to courtship feed and copulate on the same day but in this case courtship feeding immediately preceded copulation.

No pairs of Chatham Island Snipe were seen together during nine days on Rangatira Island in July 1986 (austral winter). Courtship feeding was observed on two days in 1983–84: on 28 November a male fed his mate nine times immediately after they had mated (the only copulation seen for Chatham Island Snipe); on 4 December a pair with recently independent young was seen courtship feeding (this pair was not observed to breed again during the ensuing 45 days).

Laying

Intervals between successive eggs of a clutch were determined to within 16 h for five nests of New Zealand Snipe. The mean egg interval was 72 h 24 min (range 67 h 40 min \pm 3 h 15 min to 76 h 23 min \pm 1 h 13 min). The shortest and longest egg intervals (also the most accurate) were for the same female in consecutive breeding seasons.

No information on laying was obtained for Chatham Island Snipe.

Eggs

Of the 42 New Zealand Snipe nests with complete clutches found during this study, 41 had two eggs and one had three eggs. Fourteen snipe nests with complete clutches have been found by previous workers on the Snares Is; all had two eggs (Stead 1948, B. R. Keeley *in litt.*, P. M. Sagar *in litt.*, P. E. N. Wright *in litt.*). Thus, of 56 complete clutches, 55 (98.2%) had two eggs and one (1.8%) had three eggs.

Fresh weight for nine New Zealand Snipe eggs was 24.0 ± 1.0 g (22.3–25.5 g). Estimated fresh weight for all 81 eggs was 23.7 ± 1.1 g (21.1–26.7 g). Thus, each egg was about 20.4% of the mean adult female body-weight (i.e. 116.0 g, $n = 62$).

Between 1971 and 1985 at least 51 nests of Chatham Island Snipe were found on Rangatira and Mangere Islands; 49 nests (96.1%) contained two eggs (pers. obs., Gaze 1986, M. D. Dennison *in litt.*, C. H. Hay *in litt.*, D. V. Merton *in litt.*, R. B. Morris pers. comm.). Forbes (1893) reported the clutch size of Chatham Island Snipe to be three eggs but did not state the number of nests on which this was based; his figure has been repeated often (e.g. Oliver 1955, Maclean 1972, Falla *et al.* 1979). A three-egg nest was found on Rangatira Island on 27 December 1971 (L. B. McPherson pers. comm.) and a pair with three recently hatched chicks was seen c.5 December 1979 (H. A. Robertson *in litt.*). A four-egg nest on Mangere Island on 15 October 1976 (R. B. Morris pers. comm.) was possibly laid by two females.

Eggs of Chatham Island Snipe were about 32% smaller than those of New Zealand Snipe. Mean estimated fresh egg-weight was 16.1 g, i.e. about 18.9% of the mean adult female weight of 85.4 g ($n = 24$).

Incubation

Incubation began when the second egg was laid (observed at five nests). Incubation was shared equally by the sexes at 95% of nests (unpubl. data) but was undertaken solely by the female at two nests (where the male was simultaneously polygynous; see Mating system, and Miskelly 1989). Incubation constancy was 100% at five nests

with shared incubation, but was 60–83% at the two nests with female single-sex incubation (Miskelly 1989).

The incubation period (from laying of the last egg to hatching of either egg) was determined to within eight hours for three nests with shared incubation. The mean incubation period was 22 days 2 h (range 21 days 11 h \pm 8 h to 22 days 13 h \pm 6 h). One female incubating by herself successfully hatched an egg after 37–39 days of incubation (Miskelly 1989).

Incubation period was not determined for Chatham Island Snipe.

Care of young

Broods were always split as soon as the young left the nest; the two chicks were never seen together and no adult was seen with more than one chick ($n=26$ two-chick broods for New Zealand Snipe; $n=7$ two-chick broods for Chatham Island Snipe). The male cared for the first chick to leave the nest in both New Zealand ($n=10$) and Chatham Island ($n=5$) Snipes. An adult that lost its chick (or never had one) did not assist its mate to rear the other chick.

Chicks were not seen probing for themselves during the first 12 days. After this, they continued to be fed partly by their parents until at least 41 days old, and consorted with their parents for a further 2–5 weeks. The youngest independent chick seen was 57 days old but another chick was still with its parent at 78 days old. The minimum estimate for age of independence for 15 chicks was 65 ± 6 days (57–79 days).

The energetic cost of chick-rearing by New Zealand Snipe was estimated by comparing body-weights of successful versus failed breeders during the 65 days after hatching (or nesting failure). Body-weight did not vary with time for any of the four groups considered (successful females $r_{19} = -0.19$, failed females $r_{15} = -0.27$, successful males $r_{27} = -0.36$, failed males $r_8 = 0.05$; all n.s.). Females that bred successfully weighed 111.4 ± 5.8 g (103.0–120.0 g, $n=21$), significantly less than females that failed (119.3 ± 6.8 g, range 109.3–133.0 g, $n=17$; Mann-Whitney U -test $P=0.001$). The difference in weight between successful and unsuccessful males was not significant, but showed the same trend; successful males weighed 100.8 ± 4.6 g (92.5–112.0 g, $n=29$), males that failed weighed 103.8 ± 5.0 g (95.0–110.0 g, $n=10$; Mann-Whitney U -test $P=0.08$). There was no significant difference between weights of successful and failed birds of either sex before hatching or nesting failure occurred. The lower body-weights of successfully breeding birds indicate that there was an energetic cost to chick-rearing.

Although I never saw more than one Chatham Island Snipe chick with an adult, H.A. Robertson (*in litt.*) recorded a pair with three recently hatched chicks (see Eggs).

The youngest Chatham Island Snipe chick seen to feed itself (probing) was 18 days old. Chicks continued to be fed by their parents until at least 29 days old and consorted with their parents for a further 1–3 weeks. The youngest independent chick was 33 days old, and the oldest accompanied chick was 46 days old. The minimum estimate for age of independence for 12 chicks was 41 ± 5 days (33–47 days).

Development of young

The mean weight of 28 New Zealand Snipe chicks just after hatching was 15.5 ± 0.9 g (14.0–18.0 g), which was about 65.4% of fresh egg-weight and 14.3% of mean adult weight. Plumage development and down loss took about 54 days, and flight was first recorded at 30 days.

Recently hatched Chatham Island Snipe chicks weighed 11.0 ± 0.7 g (10.0 – 12.0 g, $n = 12$), which was about 68.3% of fresh egg-weight, and 13.9% of mean adult weight. Plumage development and down loss took about 47 days, and flight was first recorded at about 21 days.

New Zealand and Chatham Island Snipe chicks grew much slower in relation to their weight asymptotes than Common Snipe chicks (Fig. 3). Growth constants (K_G) for the three species are given in Table 1.

Renesting

Of 14 New Zealand Snipe pairs whose breeding attempts failed during incubation or when the chicks were less than five days old, six (43%) renested together. Pairs that failed after 8 January did not renest ($n = 5$). If a bird of either sex lost its chick (or one of the eggs had not hatched) while its original mate was still caring for a chick, it would attempt to obtain a new mate. Of seven emancipated males whose mates still had chicks, three obtained new mates and one of these pairs laid (sequential polygyny). Of 12 emancipated females whose mates still had chicks, six obtained new mates and three laid a second clutch (sequential polyandry).

Seven females relaid 36 ± 13 days (19–53 days) after failure of their first breeding attempt. The length of the relaying interval was not correlated with the date or year of failure. No female laid more than two clutches in a season but two polygynous males sired three and four clutches respectively in a season. None of the pairs was double-brooded but one male commenced incubating at a nest with a different female after raising his first chick for eight weeks (see Miskelly 1989). Of the three sequentially polyandrous females that laid a clutch with their second mate, only one female successfully hatched an egg from the second clutch. This female raised one chick from the second clutch, and her first mate raised one chick from the first clutch.

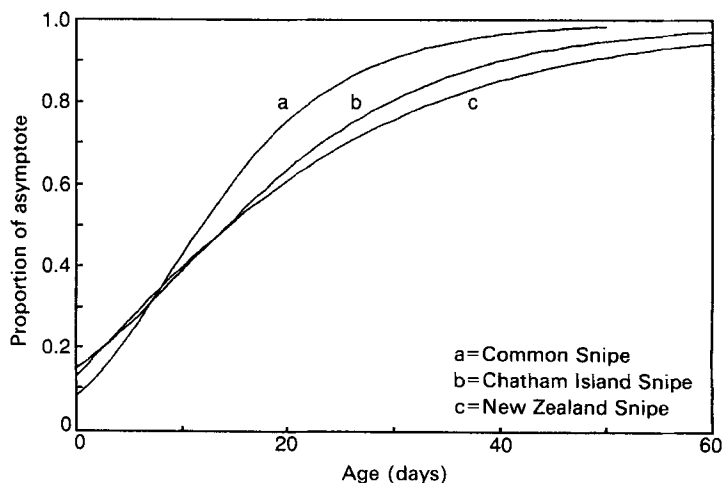


Figure 3. Weight growth rates of three species of snipe as a proportion of their growth asymptotes. Common Snipe (*Gallinago*) chicks were about 25% smaller in relation to adult body-weight at hatching compared with Chatham Island Snipe and New Zealand Snipe (*Coenocorypha* spp.). However, Common Snipe chicks grew much faster, reaching 95% of the asymptote after only 35.4 days (cf. 48.7 days for Chatham Island Snipe and 59.6 days for New Zealand Snipe). Gompertz growth equation for Common Snipe obtained from Green (1985a).

Table 1. Comparison of the breeding systems of New Zealand Snipe, Chatham Island Snipe and Common Snipe. Data on incubation for New Zealand Snipe do not include the two nests with female single-sex incubation (see text). Data for Common Snipe from Tuck 1972, Cramp & Simmons 1983, Green 1985a, 1985b & 1988, Sæther et al. 1986, Green et al. 1990.

	New Zealand Snipe	Chatham Island Snipe	Common Snipe
Breeding density (pairs/ha)	3.2	5.6	0.4
Mating system	95% monogamy	monogamy	monogamy
Courtship feeding	yes	yes	no
Egg interval (days)	3	—	1
Clutch-size	2	2	4
Egg-size as % of ♀ weight	20.4	18.9	16.5
Incubation	shared	shared	female only
Incubation constancy (%)	100	100	78.2
Incubation length (days)	22	—	18–20
Hatching success by nest (%)	80	89	36
Brood splitting	male takes first chick	male takes first chick	male takes first 2 chicks
Neonate weight as % of adult weight	14.3	13.9	10.6
Weight growth constant (K_G)	0.070	0.074	0.111
Fledging (days)	30	21	20
Independence (days)	c. 65	c. 41	c. 21

One female Chatham Island Snipe laid a second clutch about nine days after the artificial termination of her first breeding attempt.

Breeding success

Of 62 pair-years of New Zealand Snipe in the study area over four breeding seasons, 42 pairs (68%) attempted to breed. Of 40 nests studied, 26 (65%) hatched both eggs, 32 (80%) hatched at least one egg, and eight (20%) failed totally. Of the eight nests that failed, seven were deserted and one (the only three-egg nest found) was destroyed by a Sooty Shearwater *Puffinus griseus* attempting to scratch out a nest burrow.

Of the 79 eggs laid in these 40 nests, 58 (73.4%) hatched (a mean of 1.45 eggs per nest, and 1.81 eggs per successful nest). Six eggs that were incubated full term failed to hatch; one was infertile, three were slightly cracked and addled (cause of damage unknown) and two chicks died at hatching.

Some chicks came from nests that were not found, or were still dependent when I left the Snares Islands, hence sample sizes differ for each age class in the following summary.

Twelve out of 25 (48%) chicks ringed in the nest survived to fledging (age 30 days) and ten fledglings all survived to independence (age 65 days). Of 15 chicks that disappeared between hatching and fledging, nine were last seen on the day of hatching, and the others were last seen on days 2, 4, 10, 15, 16 & 30. [Note that living chicks were seen every 3.6 ± 5.0 days; $n = 384$, range 0–41 days.] No study chicks were found dead; however, a juvenile Red-billed Gull *Larus novaehollandiae* regurgitated a pair of legs of a small snipe chick on the edge of the study area on 6 February 1984. Gulls rarely used the same habitat as snipe on the Snares Is, and so were unlikely to have been significant predators of chicks.

Table 2. *Breeding success of New Zealand Snipe on the Snares Islands over two breeding seasons. Sample sizes are given in parentheses.*

	% pairs breeding	% eggs hatched	% chicks fledged	fledglings per pair	% survival to 1 year	1-year-olds per pair
1985-86	78.9 (19)	81.8 (22)	54.2 (24)	0.68 (19)	30.8 (13)	0.21 (19)
1986-87	85.0 (20)	75.6 (41)	42.3 (26)	0.55 (20)	36.4 (11)	0.20 (20)
TOTAL	82.1 (39)	77.8 (63)	48.0 (50)	0.62 (39)	33.3 (24)	0.21 (39)

Three of 29 chicks (10.3%) that were ringed in the nest survived to one year of age; 15 of 33 fledglings (45.5%) were found as one-year-olds. This compares with annual adult survival of about 83.3%.

In 1985-86 19 pairs produced 13 fledglings, of which four survived to age one year; in 1986-87 20 pairs produced 11 fledglings, of which four survived to age one year (Table 2).

Of nine two-egg nests of Chatham Island Snipe, seven (77.8%) hatched both eggs, eight (88.9%) hatched at least one egg, and one (11.1%) failed (deserted the day after an addled egg was ejected from the nest). The one egg incubated full term that failed to hatch was cracked and addled. Of the 18 eggs laid in nine nests, 15 (83.3%) hatched (a mean of 1.67 eggs per nest, and 1.88 eggs per successful nest).

Discussion

Snipe breeding systems

The breeding systems of New Zealand and Chatham Island Snipe were very similar (Table 1); both species occurred at high densities and laid small clutches of eggs that were large in relation to female body-weight. Incubation was shared and there was high hatching success. Chick weights increased at a similar rate but Chatham Island Snipe chicks became independent when about three weeks younger than New Zealand Snipe chicks (Table 1).

Common Snipe occur at much lower densities than New Zealand Snipe and Chatham Island Snipe (Table 1; mean density of 0.4 ± 0.7 pairs/ha for Common Snipe based on 21 estimates of density given by Tuck 1972 and references therein, and Green 1985b). The high density of New Zealand Snipe was associated with high annual survival of adults (83.3%). The highest estimate of survival for adult Common Snipe is 62.5% (Spence 1988).

Courtship feeding has not been recorded previously for any scolopacid (Lack 1940, Tuck 1972, Johnsgard 1981, Sutton 1981, Cramp & Simmons 1983). Although New Zealand Snipe pairs consorted together for up to 15 weeks before laying, courtship feeding was only seen in the last three weeks and was not directly associated with mating attempts. These observations suggest that courtship feeding of females by male *Coenocorypha* snipes evolved to decrease energy demands on the female during egg formation, rather than simply to maintain the pair-bond (see Cullen & Ashmole 1963, Royama 1966, Lack 1968, Nisbet 1973, Tasker & Mills

1981). The long interval between successive clutches laid by New Zealand Snipe that failed during their first breeding attempt also suggests that nutrient availability during egg formation was limiting. Common Snipe females that failed during their first breeding attempt relaid after 14 days ($n=5$, range 11–19 days; Green 1988), compared with a mean of 36 days for New Zealand Snipe.

A small clutch size is characteristic of birds in environments with low food availability (Lack 1954, Stearns 1976). As New Zealand Snipe feed their young for up to 6 weeks, clutch size may be limited by the ability of parents to rear young (Winkler & Walters 1983), as well as by the cost of egg formation (Lack 1954, 1968, Stearns 1976).

Common Snipe lay eggs that are only slightly smaller than expected for a 112 g charadriiform (Table 1; Rahn *et al.* 1975, Sæther *et al.* 1986) and these are laid only one day apart (Cramp & Simmons 1983). New Zealand Snipe eggs are 22.8% larger than expected for a 116 g charadriiform (Rahn *et al.* 1975). Large eggs are considered to be an adaptation 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 consumption following hatching (Martin 1987 and references therein). Large egg-size and low food availability may have been the cause of the long (3 day) inter-egg interval of New Zealand Snipe. The long egg intervals of passerines in Tasmania and south-east Australia have been attributed to low food availability during egg formation (Thomas 1974, Woinarski 1985).

Large eggs take longer to hatch than small eggs (Rahn & Ar 1974, Sæther *et al.* 1986). Under the same incubation regime, New Zealand Snipe eggs would be expected to take 5.5% longer to hatch than Common Snipe eggs (equation 1 in Rahn & Ar 1974). However, New Zealand Snipe had an incubation period 15.8% longer than Common Snipe, even though incubation was shared (100% constancy). A female New Zealand Snipe incubating by herself (analogous to incubation by Common Snipe) took about 38 days to hatch an egg, twice as long as Common Snipe.

Single-sex incubation is associated with lower incubation constancy, as the incubating parent must leave the nest to feed (Løfaldli 1985, Miskelly 1989). The low incubation constancy (*c.* 70%) and long incubation period of female New Zealand Snipe incubating by themselves suggests that food availability on the Snares Islands was insufficient for the short foraging excursions required to keep eggs above physiological zero temperature (Løfaldli 1985, Kålås 1986). Shared incubation by New Zealand Snipe (95% of pairs) may be interpreted as an adaptation to low food availability, as the eggs were maintained above physiological zero temperature, yet both parents had up to 50% of the day in which to forage (*cf.* *c.* 22% for an incubating female Common Snipe; Green *et al.* 1990).

Although New Zealand Snipe chicks were about 37% heavier than Common Snipe chicks on hatching, their rate of growth was 37% slower (Fig. 3; Table 1). New Zealand Snipe chicks took about 1.5 times longer to fledge and about three times longer to reach independence as Common Snipe chicks (Table 1). Lack (1968), Case (1978) and Ricklefs (1968, 1983) argued that growth rates are adjusted to the amount of food that is available. Low body-weights of adult New Zealand Snipe during the prolonged period of parental care provide direct evidence of energy limitation during chick-rearing.

The durations of incubation and fledging periods are positively correlated (Lack 1968, Drent 1975); chicks that take longer to develop before hatching also take longer to fledge. The growth rates (K_G) of *Coenocorypha* snipes are exceptionally low for birds with an incubation period of 22 days (Fig. 2 in Drent 1975). The rate of development determines the period during which young are vulnerable to predation (Lack 1968). As predation of snipe chicks is rare on the Snares or Rangatira Islands,

growth rates may be lowered to an energetic optimum. However, Ricklefs (1969, 1973) has argued that growth rate and mortality are not correlated and that in most species growth rates are driven to a physiological maximum.

Hatching success for New Zealand Snipe and Chatham Island Snipe was far higher than Green (1988) found for Common Snipe. The main causes of nest failure for Common Snipe in his study were egg predation, trampling of nests by livestock and flooding (Green 1988); none of these factors was present on the Snares Islands or Rangatira Island during this study. The main cause of nest failure for both New Zealand and Chatham Island Snipes was desertion. Of the seven New Zealand Snipe clutches deserted over five years (17.5% of nests), two were during the severe El Niño event of 1982–83 (Miskelly 1990), one was in a nest with female single-sex incubation (Miskelly 1989), one was laid and deserted before the annual summer increase in prey availability in early December 1986, and three were deserted following a decline in prey abundance in mid-February 1987 (Miskelly, unpubl.). Thus all seven desertions may have been due to inability of the incubating birds to obtain sufficient food. Desertion rates of Common Snipe were much lower (6.7%; data from Green 1988). The higher desertion rates of *Coenocorypha* snipes suggest that incubating birds were more subject to food shortages than Common Snipe.

There are no data available on the number of chicks reared per year by Common Snipe. Green (1988) used estimated chick mortalities of 6–12% per day to model relaying frequency of Common Snipe, and estimated that each female hatched between four and eight eggs. Using these figures, each breeding female would have produced between 0.3 and 2.2 fledglings per year. These figures encompass the 0.6 fledglings per year reared by New Zealand Snipe pairs on the Snares Islands. The low mortality of New Zealand Snipe chicks (c.1.6% per day until fledging) was presumably due to the almost total absence of predation.

Environmental constraints on breeding of *Coenocorypha* snipes

Ten features of the breeding system of New Zealand Snipe indicate that the population on the Snares Islands is severely limited by food availability during the breeding season. Several of these features have not been recorded for other scolopacids, suggesting that they arose as functional responses to recent environmental conditions, rather than being plesiomorphic traits. Compared with Common Snipe, New Zealand Snipe have courtship feeding, large eggs in relation to female body-weight, a long egg-interval, a small clutch, shared incubation, a long incubation period in relation to egg-size, slower chick growth rates, a long period of chick dependence, a higher nest desertion rate, and a long relaying interval following breeding failure. At least eight of these features are shared by the less studied Chatham Island Snipe. The only aspects of *Coenocorypha* life histories that appear, at first glance, to run counter to this argument are their high population densities, high hatching success and high survival rates; I suggest that these features are due to the absence of predation.

Other waders breeding in southern temperate latitudes lay small clutches (Maclean 1972, Winkler & Walters 1983) but it is not known whether their breeding systems share other features with *Coenocorypha* snipes. Why are the breeding systems of New Zealand snipes (and, presumably, other southern hemisphere waders) limited by food to a greater extent than holarctic waders?

A positive correlation between latitude and clutch size has long been recognized for northern hemisphere birds (Lack 1968, Klomp 1970, Ricklefs 1980). Small clutches of tropical birds are thought to be due to reduced seasonality in the tropics (Ashmole 1963, Ricklefs 1980, Winkler & Walters 1983). Species living in a stable

environment are expected to be at or near carrying capacity (Cody 1966) and hence to invest reproductive energy into producing fewer, more competitive offspring.

The correlation between latitude and clutch size does not apply to New Zealand birds (Oliver 1955, Cody 1966, Niethammer 1970). The New Zealand climate is highly moderated by the southern ocean, with mild winters and cool, protracted summers (Hurnard 1978). Most New Zealand plants have year-round leaf production (Dumbleton 1967, Wardle 1978) and insect diapause is rare (Roberts 1978). Reduced seasonality in food availability is likely to increase winter survival of non-migratory waders and create intense competition for food resources during the breeding season. Reduced climatic seasonality may be the driving force behind small clutch sizes of southern hemisphere waders (see also Ricklefs 1980, Woinarski 1985).

Small oceanic islands are very stable environments (Cody 1966, Stamps & Buechner 1985). Annual mean monthly temperature range on the Snares Islands is about 6.6°C (New Zealand Meteorological Service 1972) and is about 7.1°C on the Chatham Islands (Thompson 1983). The absence of predators of snipe on the Snares and Rangatira Islands has permitted snipe to occur at very high population densities; these high densities in a stable environment are likely to result in severe food limitation during the breeding season. I suggest that the breeding systems of New Zealand and Chatham Island Snipes have been constrained through intense intraspecific competition for a limited food supply.

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