

Effects of Population Bottlenecks on the South Island Robin,

Petroica australis australis

A thesis

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Seeing the Animals

*Their eyes are not our eyes
yet we can see ourselves in them.*

*We do not walk the ways they walk,
yet we follow their footprints in sand.*

*Sometimes they come to us,
when we hold their silence they understand.*

*When they live with us we must give them respect,
though most stay apart like the bird which is hidden yet touches us with its song.*

*Sometimes we think that we humans can live without them,
but we are wrong.*

—Joseph Bruchac

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Abstract

In New Zealand, birds and other endangered animals are routinely transferred to offshore islands for conservation purposes. Such transfers typically involve only a small number of individuals and thus the effects of a population bottleneck on the 'fitness' of these organisms is of great interest to conservation biologists. In 1973, two populations of the South Island robin, *Petroica australis australis*, were established on Motuara and Allports Islands from outbred populations on Nukuwaiata Island and Kaikoura, respectively. The effect of these population bottlenecks on fitness related traits in the South Island robin is the subject of this thesis.

Reproductive success is an important measure of individual fitness. I measured hatch rate, number of fledged young, and in some instances, number of young that reach independence. The inbred robin population on Motuara Island was found to have lower clutch size, fewer clutches per season, and lower hatching success compared to mainland outbred populations.

The study of fluctuating asymmetry has generated increased enthusiasm over the last few decades as a potential tool for examining the overall stability of a population. Numerous studies have found that individuals exhibiting a higher level of heterozygosity usually have lower fluctuating asymmetry. The results of my study provide no evidence to support this association. Thus, the application of fluctuating asymmetry measurements as an easily interpretable conservation tool may not be useful in all situations.

There are two main theories on how bird song might evolve in island populations. First, founder effects may constrain song structure and lead to a reduction in song variation. Second, weaker selective pressures for species-specific signals may lead to an increase in song variation. Song variation in the inbred robin population on Motuara Island seems to support the predictions of the second hypothesis. Since the initial transfer, robins on Motuara Island have increased their song variability.

Overall, the low hatching success obtained from the South Island robin population on Motuara Island shows that population bottlenecks have a detrimental effect on individual fitness in the robin. However, fluctuating asymmetry measures, which might provide a quick estimate of the 'health' of a population, offered no evidence of detrimental effects. Consequently, there is a need to examine more than one population parameter when drawing conclusions about the effects of population bottlenecks and inbreeding.

Chapter 1

General Introduction

Population genetic theory predicts that inbreeding and a loss of genetic variation are likely to occur in small populations (Nei *et al.* 1975; Wright 1978). The potentially negative effects of inbreeding in small populations have been of major concern in conservation biology (Franklin 1980; Frankel & Soulé 1981). Keller *et al.* (1994) suggest that environmental and genetic effects on survival may interact and that, in fact, inbreeding depression may be most pronounced when individuals are environmentally stressed. Negative effects of inbreeding have been shown in the song sparrow, *Melospiza melodia*, (Keller 1998) and blue tit, *Parus caeruleus*, (Kempnaers *et al.* 1996) and initial studies of inbreeding in *Petroica* robins in New Zealand have provided evidence for reduced genetic diversity. For example, the black robin (*Petroica traversi*) population on the Chatham Islands is descended from a single female, and not surprisingly, it lacks significant genetic variation (Holmes 1994; Ardern & Lambert 1997). Two populations of New Zealand robins (*P. australis*), originally derived from one or two breeding pairs, retained greater diversity than black robins, but they also show reduced variation compared to outbred populations (Ardern *et al.* 1997).

Whether such reduced diversity has had any deleterious consequences on the fitness of individuals is not well known. Ardern & Lambert (1997) argue that there is little clear evidence of the deleterious consequences of inbreeding associated with low genetic variation in the black robin. In their study, however, only a hatchability of 67.5% was observed. This is much less than the mean hatchability rate of approximately 90% calculated by Koenig (1982) for a number of outbred species; therefore it would seem that reduced genetic variation may have affected the fitness of black robins. Similar information is not yet available for the South Island robins. Thus the purpose of this study is to examine the association between genetic variation and some fitness related traits in the South Island robin populations on Motuara, Allports and Nukuwaiata Islands (Marlborough Sounds), St Arnaud (Nelson Lakes National Park) and Kowhai Bush (Kaikoura). I used measures of reproductive success, fluctuating asymmetry, and song diversity to determine whether small island populations of robins are exhibiting any deleterious effects of inbreeding.

NEW ZEALAND ROBINS

Classification and distribution

The robins of New Zealand are not closely related to either of their Northern Hemisphere namesakes, the English robin (*Erithacus rubecula*), or the American robin (*Turdus migratorius*). To denote this, they have recently been placed into a new family (Eopsaltriidae) which includes the Australo-Papuan robins and flycatchers (Sibley & Ahlquist 1990). New Zealand robins, together with the tomtits, form the genus *Petroica*.

Two species of robin are found in New Zealand – the well known and endangered black robin, *Petroica traversi* Buller 1872 from the Chatham Islands, and the more common New Zealand robin, *P. australis*. The New Zealand robin, also known as “toutouwai” or “pītoitoi”, is split into three subspecies: one from the North Island (*P. a. longipes* Lesson 1828), another from the South Island (*P. a. australis* Sparman 1788), and a third from Stewart Island (*P. a. rakiura* Fleming 1950). Small morphological differences occur between these three subspecies.

The North Island robin is now restricted predominantly to areas around the middle of the North Island from north of Wanganui to the Taupo-Rotorua region. It is also found on Kapiti and Little Barrier Islands and recently a population has been established on Tiritiri Matangi Island (Holmes 1994; Edwards 1997). The Stewart Island robin occurs in disconnected populations on the mainland and is abundant on surrounding islets such as Green, Motonui, Jacky Lee, Poutama and Tamitemioka Islands (Oliver 1955; Flack 1985; Holmes 1994). Information about the population trends and distribution of South Island robins is at least 20 years old and need to be updated. The current mainland distribution of the South Island robin is puzzling, as they appear to be common or locally abundant in forest areas north of Arthur’s Pass and west of the main divide, and yet are generally rare and patchily distributed elsewhere despite the presence of apparently suitable habitat (Edwards 1997). They also occur on several islands in the Marlborough Sounds which support moderately high densities (Oliver 1955; Hay 1975).

Robins seem to be in decline on the mainland due to extensive loss of lowland forest and predation by introduced mammals (Flack 1976, 1979; Powlesland 1980). In addition, introduced avian diseases and competition for resources with introduced birds may have contributed to this decline (Hay 1975).

General biology

New Zealand robins are a medium-sized passerine of 32-40 g and about 185 mm in length (Powlesland 1980). The South Island robin is recognised by its sooty grey head, neck and sides of body, distinctive yellowish-white breast, white frontal spot, long legs, and characteristic stance (Oliver 1930; Fleming 1950; Flack 1985). A slight dimorphism exists between the sexes. Males tend to be larger, a darker colour and they show a clear line of demarcation between the dark neck plumage and the yellowish-white breast plumage. In contrast, females have less yellow on their breast and the line separating the neck and breast plumage is more jagged. Juveniles are similar to adult females however, they have few white breast feathers and their sex cannot be determined by plumage characteristics.

As a consequence of its confiding nature and sedentariness, the robin has received more attention than most New Zealand passerines. A number of early ornithological texts record information on the biology of the New Zealand robin (e.g. Buller 1882; Oliver 1930; Fleming 1950; Soper 1972) and detailed studies of the South Island robin were undertaken by Flack (1973, 1974, 1976, 1979) and Powlesland (1980, 1981a, b, c, 1983a, b). Recent studies of New Zealand robins include learned predator recognition (Maloney & McLean 1995), the effects of possum control operations on robins (Spurr 1991; Edwards 1997), and parentage and molecular studies of robins (Holmes 1994).

Robins inhabit a variety of forest types including manuku, kanuka, coastal broadleaf, beech, and podocarp. In the North Island, robins can also be found in pine plantations (Oliver 1955; Powlesland 1980). The majority of their foraging time is spent on or near the ground (Powlesland 1980, 1981c). They feed on a variety of invertebrates and occasionally supplement their diet with small fruit (Oliver 1930; Soper 1972; Flack 1979; Powlesland 1981c). Major food items include worms, spiders, grubs, moths, caterpillars, wetas, stick insects and winged insects, including large cicadas (Flack 1973). Foraging often includes the use of a characteristic behaviour of trembling one foot in the litter. This may be a mechanism to get potential prey to move in response to the vibrations.

Robins are highly territorial and both adults will aggressively drive out intruders, although the male tends to play a more prominent role. Territory size varies from as little as 0.2 ha on densely populated islands to over 5 ha in some mainland locations. During the post-breeding moult adults are less able to defend their territory from young of the year and can be partially or totally displaced by invading young (Flack 1979).

Nests are situated 0.1-15 m above ground level, typically in tree forks, fern crowns, and large tree-trunk cavities. New Zealand robins are considered to be monogamous, forming stable long-term pair bonds (Holmes 1994). The duration of the breeding season, age at first breeding, and productivity vary between populations. On the mainland, robins usually breed between August and February, however, egg laying has been recorded as early as mid-May at Kaikoura (Flack 1979). In contrast, the breeding season on islands is shorter, beginning in August and finishing by late December (Powlesland 1981b). Age of first breeding is usually 8-12 months, but for some males and females on islands it may be two years. Only the female builds the nest and incubates the two to four cream-coloured, brown-spotted eggs. The female spends about 18 days incubating the eggs and relies on the male for most of her food. The chicks take 19-21 days to develop before they are ready to leave the nest and a further 4-7 weeks of parental care before becoming completely independent. On the mainland, females will often renest soon after the chicks fledge, leaving parental care predominately to the male. Mainland pairs commonly produce 2 or 3 broods in a season and if predation occurs, they can renest six times or more in a single season (Oliver 1930; Fleming 1950; Flack 1973, 1979, 1985; Soper 1972; Hay 1975; Powlesland 1983a). In contrast, robin pairs on islands typically raise one or two young and produce only one brood per season. Parental care of the fledglings is shared between the two parents, with the male taking the single offspring if only one fledges.

Early observers described the robin as a “songster” and were impressed by its loud vocalisations and its ability to sustain song for long periods at a time (Moncrieff 1932; Potts, cited in Oliver 1955). Hay (1975) performed a detailed study of robin song, which included a description of the types of songs and calls given by robins. A time budget study looking at the seasonal and diurnal variation of robin vocalisations was carried out by Powlesland (1980,1983b). Robin song is composed of a continuous series of phrases taken from a total repertoire of approximately 200 different syllable types (Hay 1975; pers. obs.).

THESIS OUTLINE

The three main chapters forming the bulk of this thesis have been presented in the format of scientific papers. Although this arrangement necessitates some repetition, it allows each specific investigation to be viewed separately and assists with preparation for future publication.

Holmes (1994) found in a previous study that the inbred South Island robin populations on Motuara Island and Allports Island have a lower level of genetic diversity than their outbred counterparts on Nukuwaiata Island and at Kaikoura. Thus, my main aim was to show whether such reduced diversity has had any deleterious consequences on the fitness of individuals. To do this I examined a number of robin traits associated with fitness, namely reproductive success, fluctuating asymmetry and song diversity, in the above four robin populations and also from another mainland population at St Arnaud.

Reproductive success is one of the most important measures of population viability. Several studies have measured reproductive success when looking at inbreeding depression in wild populations (e.g. Bensch *et al.* 1994; Kempenaers *et al.* 1996). Reproductive success can be measured in a variety of ways, including: hatch rate, number of fledged young, number of young that reach independence from parental care, and number of young surviving to reproduce. In Chapter 2, I examine the reproductive success of a number of robin populations by measuring their hatch rate, number of fledged young and, in some cases, number of independent young.

The study of fluctuating asymmetry (FA) is a potentially valuable tool for conservation biologists concerned with understanding and preventing extinction (Leary & Allendorf 1989). Fluctuating asymmetry is defined as those random differences that occur between the sides of a bilaterally symmetrical organism due to developmental accidents (Van Valen 1962). The underlying assumption is that the development of the two sides of a bilaterally symmetrical organism are controlled by the same set of genes and therefore any variation between the two sides must be environmental in origin (Waddington 1942). Fluctuating asymmetry is a measure of developmental stability, that is, the capacity to develop properly in the face of genetic or environmental stresses that tend to upset development. (Watson & Thornhill 1994). A number of species from populations with reduced genetic variation because of bottlenecks or founder effects have been shown to exhibit increased asymmetry relative to individuals from other conspecific populations or similar species (Vrijenhoek & Lerman 1982; Leary *et al.* 1985; Wayne *et al.* 1986; Parsons 1992). In amphibians, population declines can be predicted based on patterns of fluctuating asymmetry (Waldman & Tocher 1998). In Chapter 3, I examine the potential of

using asymmetry as a means of assessing the “stressfulness” of inbreeding on the development of the robin.

Bird song is an easily measurable trait that may provide information about the level of genetic variation within a population (Waldman & Tocher 1998). Two different hypotheses predict how song might evolve in populations that have gone through bottlenecks (Naugler & Smith 1991; Catchpole & Slater 1995). First, island populations may have more variable songs because they are subject to weaker selection pressures for species-specific signals than are mainland populations (Marler & Boatman 1951; Marler 1957, 1960; Miller 1982). Second, founder effects may constrain song structure and lead to a reduction in song variation and/or complexity (Thielcke 1973; Mundinger 1975; Mirsky 1976; Lynch & Baker 1986; Baker & Jenkins; Naugler & Smith 1991). In Chapter 4, I investigate the cultural effects of population bottlenecks by examining song structure in island and mainland populations of the robin.

Finally, Chapter 5 summarises the major findings of this study and discusses ideas for future research.

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Chapter 2

The effects of reduced genetic diversity on the reproductive success of the South Island robin

INTRODUCTION

Knowledge of the effects of inbreeding within populations of wild animals and plants is of fundamental importance to conservation biology. Inbreeding depression (i.e. the detrimental effects of inbreeding; Wright 1977) is a potential threat to small, isolated or fragmented populations (Senner 1980; Gilpin & Soulé 1986; Meffe & Carroll 1994). While there is ample evidence for inbreeding depression in captivity (Ralls *et al.* 1979; Charlesworth & Charlesworth 1987), it has rarely been documented in natural populations (Ralls *et al.* 1986; Ralls *et al.* 1988). Many studies on animal and plant populations have shown a negative effect of inbreeding on fitness related traits such as viability, fecundity and fertility (for reviews see Thornhill 1993). Among birds, inbreeding has been reported to affect hatchability (Sittman *et al.* 1966; Bensch *et al.* 1994; Kempenaers *et al.* 1996), survival of chicks to fledging (Greenwood *et al.* 1978) and survival of young to the following year (Brown & Brown 1998; Keller 1998).

In New Zealand, the Chatham Island black robin (*Petroica traversi*) is known to be highly inbred following a severe bottleneck event in the 1970s which left only a single effective breeding pair. In the course of research aimed at designing a recovery plan for the black robin, two experimental transfers of the South Island robin (*P. australis australis*), a closely related species, were made to Motuara and Allports Islands (Marlborough Sounds). Both populations were established in 1973 by transfers of five birds from Nukuwaiata Island (Marlborough Sounds) and Kaikoura respectively (Flack 1974, 1978) (Figures 2.1 and 2.2).

Although five individuals were transferred in each case, the Allports Island population appears to have been founded by two pairs, as one male disappeared soon after release. Both remaining pairs were productive in the breeding season subsequent to the transfer, producing a total of seven juveniles from five nests (Flack 1974). It is possible that a single pair founded

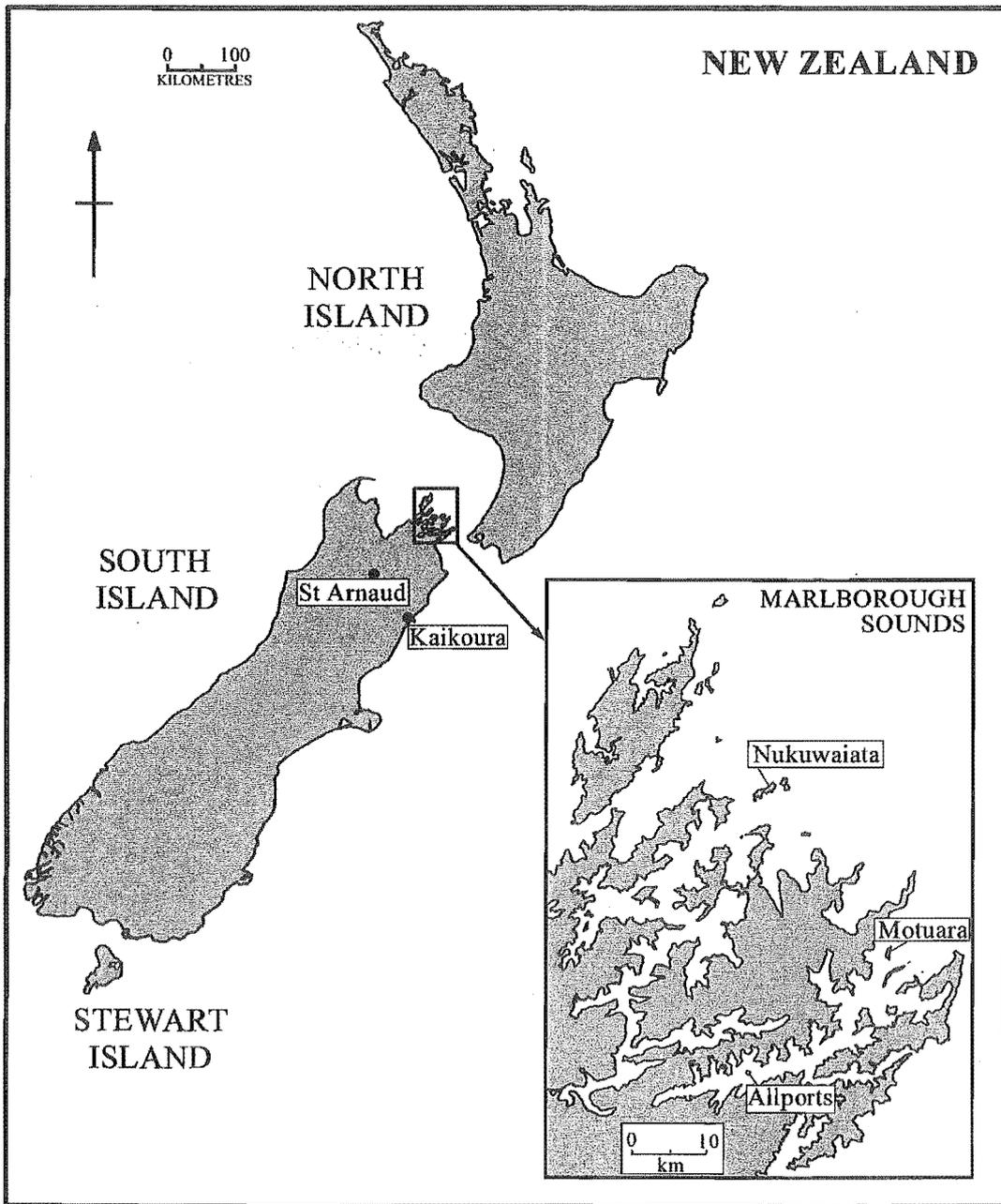


Figure 2.1 Location of the South Island robin populations examined in this thesis.

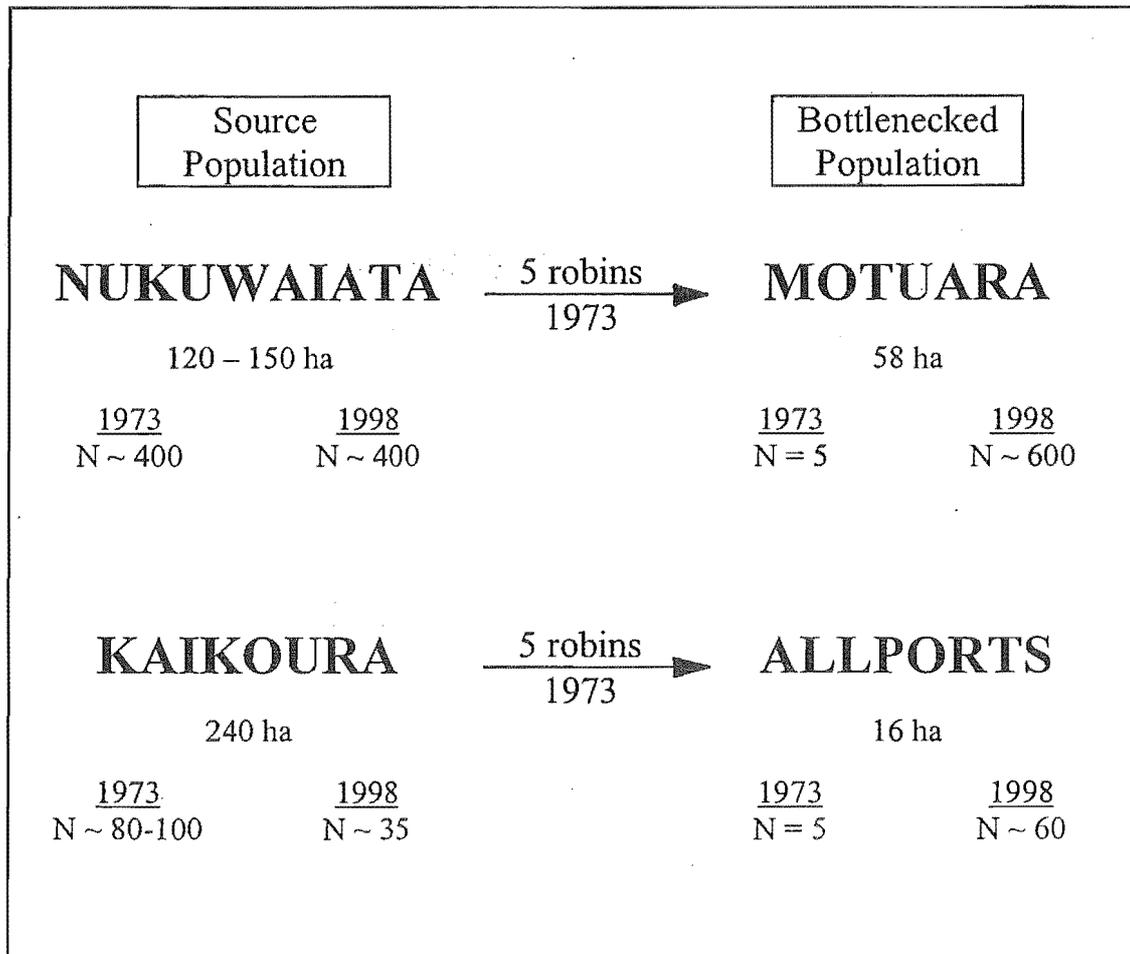


Figure 2.2 Details of the robin population bottleneck events showing changes in population sizes. N represents estimated population size. (All data are from Holmes 1994 except for the 1998 population estimates for Kaikoura (J. Briskie, pers. comm.) and for Motuara and Allports Islands (this study).

the robin population on Motuara Island. Although two pairs bred during the first season on the island, a high degree of infertility was recorded for one pair. The remaining female was not seen after the release. Five juveniles were produced from six nests in that season (Flack 1974). Island size has restricted the Allports population to a maximum of approximately 30 pairs (Maloney 1991), while the larger Motuara Island currently supports approximately 250-300 pairs (pers. obs.).

Despite the larger size of the Motuara population, both island populations have gone through a severe bottleneck and are now highly inbred. The parent population on Nukuwaiata Island is likely to have maintained a large population size since the time of transfer while the parent population at Kaikoura is smaller and fluctuations in population size appear to be more common here than in island populations (Flack 1979). However, there is a potential for immigration from adjacent populations to the mainland Kaikoura population whereas the Nukuwaiata population is presumably closed.

Holmes (1994) studied the effect of the population bottlenecks on genetic variation in robins on Motuara and Allports Islands relative to their respective source populations. It was found that the robin populations on Motuara and Allports had a lower level of genetic diversity compared to their source populations. The aim of this chapter is to show whether such reduced genetic diversity has any deleterious consequences on the reproductive success of individual robins. I do this by comparing the reproductive biology of robins from two inbred populations (Motuara and Allports Islands) with those from three outbred populations (Nukuwaiata Island, Kaikoura and St Arnaud).

METHODS

Study organism and study sites

The South Island robin is a medium-sized (30-44 g) insectivorous passerine, patchily distributed at moderate to low densities throughout the South Island but in higher densities (up to 5 pairs/ha) on a few offshore islands (Maloney 1991). Robins are highly territorial and form stable life-long pair bonds. Age of first breeding is usually between 8-12 months but for some males and females on islands it may be two years (Flack 1979). Breeding behaviour may be initiated as early as mid-July and extend until February. Nests are situated 0.1-15 m above ground level, typically in tree forks, fern crowns and large tree-trunk cavities (Maloney 1991).

Only the female builds the nest and incubates the eggs. The male feeds the female throughout the incubation period. Both birds feed chicks and fledglings (Oliver 1930; Fleming 1950; Powlesland 1980).

Reproductive success was measured for two populations of robins. Data were collected at St Arnaud, Nelson Lakes National Park, from 20 October 1997 to 20 March 1998 and on Motuara Island, Marlborough Sounds, from 7 September 1998 to 21 December 1998 and 25 January 1999 to 28 January 1999. There are a variety of predators present at St Arnaud including stoats, ferrets, possums, cats, hedgehogs, rats, mice, falcons, moreporks and wasps. Motuara Island is free from introduced predators following the eradication of kiore (*Rattus exulans*) in 1990 by the Department of Conservation (Cash 1997, cited in Renner 1998). An occasional morepork might fly over from the mainland but this occurs rarely as I never saw nor heard any in the four months I was there.

Forest composition and structure in the two study sites are somewhat different. St Arnaud is predominately a mixed red (*Nothofagus fusca*) and silver (*N. menziesii*) beech forest with occasional mountain beeches (*N. solandri*). There are also patches of swampy vegetation on poorly drained sites containing mountain beech, kanuka (*Kunzea ericoides*), Hall's totara (*Podocarpus hallii*) and cedars (*Libocedrus bidwillii*). It is of interest that all the robin nests found were located very near to these swampy areas. In contrast, Motuara Island is almost completely covered with regenerating forest. The dominant tree species are kanuka (*K. ericoides*), manuka (*L. scoparium*), great pepper (*Macropiper excelsum*), pate (*Schefflera digitata*), mahoe (*Melicytus ramiflorus*) and tree fuchsia (*Fuchsia excorticata*).

Reproductive success data collected at St Arnaud and Motuara Island were also compared to data found in the literature. South Island robins have been most extensively studied at the mainland location of Kaikoura (e.g. Flack 1979; Powlesland 1983), although some data are available for offshore island populations (e.g. Flack 1974; Maloney 1991). Two studies of significance are those by Maloney (1991) and Powlesland (1983). Maloney collected reproductive success data from Motuara and Allports Islands while Powlesland worked largely on the mainland at Kowhai Bush, Kaikoura. Motuara Island, Allports Island and Kowhai Bush are all influenced by approximately the same environmental conditions (i.e. similar vegetation, temperature and altitude). Mice (*Mus musculus*) and kiore (*Rattus exulans*) were eradicated from Allports Island and Motuara island in 1989 and 1990 respectively, leaving no mammalian predators present. The same variety of predators described previously for St Arnaud are also present at Kowhai Bush.

Examination of nests

Robin nests were found using three methods: (1) by searching in likely places, e.g. tree forks, tree fern crowns; (2) by listening for the begging calls of chicks in the nest; and (3) by feeding meal worm larvae (*Tenebrio* sp.) to the male or female and watching where they took it. If the female was incubating, the male would collect the larvae in his beak and fly off in the approximate direction of the nest while giving a feeding call. The female would then usually fly to a perch nearby and emit a series of juvenile-like begging calls (Hay 1975). After the male has fed the female she either goes directly back to the nest or forages nearby before returning to the nest via an indirect route. If there are chicks in the nest then either the male or the female will feed them but not at the same time. Both parents usually use an indirect route to the nest, probably so that predators may lose track of them, however, the chicks can be very noisy at times.

I used a mirror attached to a branch to examine nests. At St Arnaud only one nest was low enough to examine. It would have been very difficult to carry an extension ladder to the other nest sites at St Arnaud; therefore, the contents of these are unknown and data for hatchability are limited for this population. However, I was able to observe the success of these nests through binoculars. Nests were checked approximately every three days. I found that if the nests were checked every day then the female would be more likely to abandon her nest.

Definitions

I identified pairs either by observing the male robin feeding the female robin or from seeing both the male and female feeding the same offspring.

Hatchability is defined here as the percentage of eggs that hatch out of the total number surviving to the time of hatching. Thus, eggs lost to predation, abandonment, accidental breakage, or any other unknown factor are excluded. The exact cause of hatching failure (e.g. infertility, embryo mortality or death during hatching) was not determined in most cases; thus, such losses were lumped together in determining hatchability.

Fledging success is defined as the percentage of chicks that hatched and survived to the time of fledging. It does not include those chicks that were lost to predation, unknown factors or had not left the nest by the end of the observation period. Chicks were known to have fledged when parents collected mealworms and flew away from the nest to feed the fledglings. Fledglings could usually be heard begging before they were seen. If the parents repeatedly ate

the mealworms and never flew away giving the feeding call, then the fledglings were presumed dead. On a number of occasions this occurred near to the time of fledging and it was not known whether the chicks died just before or just after they had left the nest. Hence, I was not sure of the fate of the chicks (i.e. if they died in the nest or fledged). Thus I placed these ambiguities into the unknown category.

For the purpose of this study I have defined: **chicks** as robins still in the nest; **fledglings** as robins out of the nest but still dependent on their parents; **juveniles** as robins independent of their parents but not old enough to breed; and **adults** as those robins old enough to breed.

Statistical analyses

Clutch number, number of fledglings per nest and number of fledglings per pair per season for the Motuara and St Arnaud populations were compared using two-sample *t*-tests. Clutch size was also compared between Motuara and Kaikoura populations using a two-sample *t*-test. The fates of robin eggs, chicks and nests were compared using the log-likelihood ratio or *G*-test. This test is an alternative to the chi-squared test and commonly results in the same conclusions (Zar 1996). Its use is recommended when expected values are less than 5.0, which was the case with my data. Calculations on hatching and fledging success included only those eggs and chicks that survived until time of hatching or fledging.

RESULTS

The breeding season was already underway when I arrived at my two study sites. In the St Arnaud population, nesting was asynchronous with some pairs having fledglings when I arrived while others were still in the pre-nesting courtship phases. On Motuara Island, nesting was slightly more synchronised with most pairs having just laid their first clutch when I arrived. Given an average time of 18 days for incubation and 20.8 days for chick rearing (Powlesland 1983) the first clutches were laid at St Arnaud about mid-September and on Motuara Island about 23 August.

At St Arnaud a total of 8 nests were found from 5 pairs. Five other pairs were known to successfully fledge chicks. Most nests were found during the incubation or chick rearing stages, however, occasionally I found robin pairs with fledglings (i.e. the chicks had already left the nest). Four of the pairs renested three times in one season, however, only one pair was

known to successfully fledge chicks on all three occasions. By the end of the breeding season there were numerous juvenile robins within the study area but they came from unknown origins.

On Motuara Island, a total of 35 nests were examined. Except for a single clutch of three, all had a clutch size of two. The nest with a clutch of three, however, had only two eggs in the nest and the other one was laid on the rim. Thus, only two were being incubated. Four pairs re-nested for a second time but no pairs had more than one successful clutch per season.

A comparison of robin populations at St Arnaud and Motuara Island shows that island robins produced a significantly lower number of clutches ($t=-2.48$, $d.f.=36$, $P<0.05$) and lower number of fledglings per nest ($t=-2.51$, $d.f.=43$, $P<0.05$; Table 2.1). Even though robin pairs on Motuara Island produced only 0.94 fledglings per season and robin pairs at St Arnaud produced 2.83 fledglings per season there was no significant difference found between them ($t=-1.70$, $d.f.=36$, $P=0.15$; Table 2.1). This is most probably due to the small sample size ($n=6$) and large variation (range 0-7) obtained for the St Arnaud population. Clutch size was found to be significantly lower for the Motuara Island population than the Kaikoura population ($t=13.44$, $d.f.=183$, $P<0.0001$; Table 2.1).

Fate of robin eggs

Two types of data were analysed. First, I examined the fate of *individual* robin eggs on Motuara Island and compared this to data collected at Kowhai Bush by Powlesland (1983) (Table 2.2). Hatching success was significantly better at Kowhai Bush (91.0%) than on Motuara Island (75.9%) ($G=8.48$, $d.f.=1$, $P<0.01$). The presence of predators had a significant effect on the overall nesting success of mainland robins ($G=28.31$, $d.f.=1$, $P<0.001$). This was obvious when I examined the fate of robin eggs at Kowhai Bush, where just about a quarter of the eggs laid (23.7%) were lost to predation. On Motuara Island there are no predators and no eggs were lost to predation. Nonetheless, a large number of eggs (18.3%) did not hatch on Motuara Island. The cause of hatching failure is unknown but this number is significantly higher compared to the number of unhatched eggs at Kowhai Bush (6.2%) ($G=9.72$, $d.f.=1$, $P<0.005$). The number of eggs lost to unknown factors was also significantly higher for Motuara Island (8.5%) compared to Kowhai Bush (2.2%) ($G=5.60$, $d.f.=1$, $P<0.001$). Twice as many eggs were abandoned on Motuara Island (8.5%) than at Kowhai Bush (4.0%), but this was not found to be significant ($G=2.35$, $d.f.=1$, $P>0.05$).

Table 2.1 Productivity of South Island robins at four locations, including two island populations and two mainland locations. Data for Kaikoura and Allports Island were found in the literature.

	Island populations		Mainland populations	
	Motuara	Allports*	St Arnaud	Kaikoura**
Mean number of clutches (\pm SE)	1.13 (0.07)	1.13	2.14 (0.40)	—
Mean clutch size (\pm SE)	2.03 (0.03)	2.0	—	2.7
Percentage of eggs hatched	75.9	—	—	91.0
Percentage of chicks fledged	96.9	—	—	84.9
Mean number of chicks fledged/nest (\pm SE)	0.91 (0.14)	—	1.70 (0.30)	—
Mean number of fledglings/pair/season (\pm SE)	0.94 (0.14)	—	2.83 (1.11)	2.5

* Data from a single season only (1989) (Maloney 1991)

** Data from 2 seasons (1977/78 – 1978/79) (Powlesland 1983)

Next I examined the fate of robin *nests* with eggs so that I could compare my data to those collected by Maloney (1991) from Allports and Motuara Islands. If we consider only those eggs that survived until hatching, then hatching success for those years measured was very good, with the lowest being 84.5% (Table 2.3). Kiore were present on Motuara Island in 1989; therefore, there was a significantly higher loss due to predation for this population ($G=11.46$, $d.f.=3$, $P<0.01$). There were no predators present on Allports Island in 1989 or on Motuara Island in 1990 and 1998/99. Quite a high proportion of eggs were abandoned on Motuara Island in 1989 and 1990 (13.0% and 13.9% respectively); however, this was not found to be significantly different from the other populations ($G=2.78$, $d.f.=3$, $P>0.05$).

Fate of robin chicks

Fate of chicks (i.e. individual and nest success) was analysed in the same way as the fate of eggs. Fledging success of individual chicks was good at both sites, although it was significantly better on Motuara Island (96.9%) than at Kowhai Bush (84.9%) ($G=36.56$, $d.f.=1$, $P<0.001$) (Table 2.4). On a number of occasions it was not known whether chicks died just before or just after they had left the nest, thus they were placed into the unknown category. This ambiguity lead to a significantly higher proportion of chicks lost to unknown factors on Motuara Island (22.0%) compared to Kowhai Bush (4.3%) ($G=12.57$, $d.f.=1$, $P<0.001$). Starvation is the most likely cause for this loss but inter- or intra-specific harassment could also be a possibility. Almost half the chicks at Kowhai Bush were lost to predation (46.3%). Perhaps they are more susceptible at this stage because of the noise they produce in the feeding process.

There was a significant difference found in the percentage of nests that fledged at least one chick ($G=8.11$, $d.f.=3$, $P<0.05$) (Table 2.5). The 1989 season seemed to be the best, with 100% fledging success on both Allports and Motuara Islands.

DISCUSSION

My observations suggest that a reduced level of genetic diversity seems to affect reproductive success in the South Island robin. Although not all differences can be attributed to inbreeding, the robin population on Motuara Island was found to have lower clutch size, number of clutches per season and hatching success compared to mainland populations.

Table 2.2 A comparison of the fate of robin eggs (% of total) between an inbred population (Motuara Island) and an outbred population (Kowhai Bush). The values in parentheses were calculated using only eggs that survived until hatching (i.e. those lost to predation, abandonment, accidental breakage, or any other unknown factor are excluded).

	Motuara Island (this study)	Kowhai Bush (Powlesland 1983)
Total number of eggs laid	71	405
Preyed on	0	23.7
Fell from nest	7.0	1.5
Abandoned	8.5	4.0
Unhatched	18.3	6.2
Unknown	8.5	2.2
Hatched	57.7 (75.9)	62.5 (91.0)

Table 2.3 A comparison of the fate of robin nests with eggs (% of total). The values in parentheses were calculated using only the nests with eggs that survived until time of hatching (i.e. those lost to predation, abandonment, accidental breakage, or any other unknown factor are excluded).

	Allports 1989	Motuara 1989	Motuara 1990	Motuara (this study)
Number of nests	25	46	108	35
Preyed on	0	13.0	0	0
Fell from tree	8.0	0	3.7	5.7
Abandoned	4.0	13.0	13.9	8.6
Lost during incubation	0	0	7.4	0
Unhatched	4.0	0	8.3	2.9
Unknown	4.0	0	8.3	8.6
Not hatched by end of study period	0	0	13.0	0
Hatched	80.0 (95.2)	73.9 (100)	45.4 (84.5)	74.3 (96.3)

Table 2.4 A comparison of the fate of robin chicks (% of total hatched) between an inbred population (Motuara Island) and an outbred population (Kowhai Bush). The values in parentheses were calculated using only the chicks that were not lost to predation or unknown factors.

	Motuara Island (this study)	Kowhai Bush (Powlesland 1983)
Number of chicks	41	255
Preyed on	0	46.3
Fell from nest and died	2.4	3.5
Died in nest	0	3.9
Unknown	22.0	4.3
Fledged at least one chick	75.6 (96.9)	42.0 (84.9)

Table 2.5 A comparison of the fate of robin nests with chicks (% of total). The values in parentheses were calculated using only the nests with chicks that were not lost to predation, unknown factors or had not left the nest by the end of the study period.

	Allports 1989	Motuara 1989	Motuara 1990	Motuara (this study)
Total number of nests	20	34	90*	26
Preyed on	0	8.8	0	0
Fell from nest and died	0	0	0	3.8
Died in nest	0	0	8.9	0
Unknown	5.0	5.9	6.7	19.2
Not fledged by end of study period	0	8.8	36.7	0
Fledged at least one chick	95.0 (100)	76.5 (100)	47.8 (84.3)	76.9 (95.2)

* Of the 90 nests observed on Motuara Island in 1990, 49 were found at the incubation stage and 41 during the chick rearing stage. All the nests that had not fledged by the end of the study period were found during the incubation stage.

Variation in clutch size is common in bird populations at different sites (Lack 1968), and has been observed in New Zealand among species such as saddlebacks (*Philesturnus carunculatus*; Craig 1991). The lower clutch size and number of clutches found on Motuara Island is most probably due to the limited space and food availability associated with islands. My personal observation of robins on Motuara Island suggests that they were close to carrying capacity. Fledglings tended to stay in their parent's territory much longer than they would on the mainland and the parents, on average, produced only one clutch per season. Most robins that re-nested a second time did so only because their first nest had failed. This contrasts greatly with what I observed at St Arnaud. There most robin pairs re-nested three times and produced up to seven fledglings in the one season. Juvenile mortality was not measured for this population; thus, the proportion of fledglings that survive to adulthood is not known. Flack (1979) found that the survival to first breeding at Kaikoura was highly variable between years (10-90%). Territory size and distance between territories varied greatly at St Arnaud but could be quite large with some pairs occupying over 5 hectares. This should certainly provide ample food and space for recruitment.

Hatchability is defined here as the percentage of eggs that hatch out of the total number surviving to the time of hatching. An egg failing to hatch is a considerable energetic loss to the bird that laid it as well as to those that incubated it (Koenig 1982). There is considerable evidence that inbreeding reduces both fertility and the proportion of fertile eggs that hatch in domestic fowl (Romanoff 1972). Similar effects have been found in the Great Tit (*Parus major*) on the island of Vlieland in Holland (van Noordwijk & Scharloo 1981). The hatchability rate measured for Kowhai Bush of 91.0% was, in fact, nearly equal to the mean hatchability rate of 90.6% measured by Koenig (1982) for a number of outbred species. However, the significantly lower value for Motuara Island of 75.9% suggests that there may be a negative association with inbreeding. The cause of hatching failure was not determined in this study therefore, it is not known whether eggs experienced infertility, embryo mortality or death during hatching. Kempanaers *et al.* (1996) suggested that unhatched eggs were not infertile but rather a consequence of inbreeding depression (i.e. a higher probability of the expression of deleterious recessive alleles led to embryo mortality in the very early stages).

A similar low rate of hatchability was found for the Chatham Island black robin, where only 67.5% of eggs hatched (Holmes 1994). Fertility in the black robin is high (approx. 90%; Merton 1990); therefore, the large proportion of eggs failing to hatch appears to be attributable primarily to females laying eggs on nest rims, rather than in the nest itself. This tendency also occurred in one of the 35 nests examined on Motuara Island. It has been suggested that this

“laying on the rim” tendency may constitute a behavioural abnormality among inbred robins (Butler & Merton 1992).

The reason for abandonment of eggs on Motuara Island is not entirely known. One possibility is inter- and intra-specific harassment. Bellbirds (*Anthornis melanura*) and blackbirds (*Turdus merula*) were often seen being aggressive towards robins, sometimes for no apparent reason. Also robins, due to their highly territorial nature, were frequently observed fighting with their neighbours or juveniles looking for a territory. Another possibility is that there is some connection between the extent of human contact and nest abandonment (e.g. how often the nests were checked). The high proportion of nests abandoned in the 1989 and 1990 breeding seasons on Motuara Island was most likely due to the disruptive nature of the poisoning operation going on at that time. Powlesland (1983) found that clutches at Kaikoura were abandoned most often in bad weather, particularly when heavy rain and strong winds continued for 2 or 3 days. This possibly also occurred on Motuara Island although it was not obvious.

A large number of eggs and chicks disappeared on Motuara Island but the exact reason for this is not known. All the chicks that suffered an unknown fate on Motuara Island seemed to have died either just before or just after they had left the nest. This was possibly due to starvation as the parents may not have been able to find enough food within their small territories to feed the chicks. The reason for the disappearance of eggs on Motuara Island seems most likely to be from inter- or intra-specific predation. A number of studies have shown that some passerine birds destroy, remove and sometimes prey on eggs and chicks of conspecifics and other species (Picman 1977a, b; Picman & Picman 1980; Belles-Isles & Picman 1986a, b; Picman & Belles-Isles 1987; Sealy 1992; Sealy 1994). At Kaikoura a South Island robin was observed removing a dunnoek (*Prunella modularis*) egg from its nest, dropping it to the ground and eating the contents (Briskie, pers. comm.). There is a general consensus that this behaviour does not appear to be a form of food provisioning but rather an interference mechanism to reduce competition for resources (Verner 1975; Picman 1977a, b; Belles-Isles & Picman 1986a, b; Scott, Weatherhead & Ankney 1992; Sealy 1992; Sealy 1994). A large number of birds are present on Motuara Island; therefore, competition for resources is strong and it would not be too surprising to find that egg predation by conspecifics is occurring in this population.

Endemic New Zealand birds are thought to have a long history of isolation and inbreeding; thus, it has been suggested that inbreeding is likely to have expressed its potential genetic disadvantages long ago (Craig & Jamieson 1988; Jamieson *et al.* 1994). Ardern and Lambert

(1997) argue that there is little clear evidence of the deleterious consequences of inbreeding associated with low genetic variation in the Chatham Island black robin. In their study, however, a hatchability rate of only 67.5% was observed. Clearly this would imply some degree of inbreeding depression. The results of my study add weight to the common view that inbreeding is detrimental in natural populations of birds. The hatchability rate observed for the inbred South Island robin population on Motuara Island was found to be 15% lower than that measured for outbred bird populations. This suggests some degree of inbreeding depression although it is not known whether this will have any long-term effect on the viability of this population. Future work on how inbreeding may affect reproductive success should also include information on survival of inbred offspring into the next generation.

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Chapter 3

Inbreeding and fluctuating asymmetry in the South Island robin

INTRODUCTION

The influence of genetic heterozygosity on phenotypic variability in plant and animal species has been recognised for over 50 years (Waddington 1942, 1957; Mather 1952; Thoday 1953, 1955; Lerner 1954). Waddington (1942) proposed that more heterozygous individuals are more developmentally buffered or “canalized” and that they will have an increased tendency to express the genetically determined phenotype of the species. Fluctuating asymmetry (FA) has been employed as an indicator of the efficiency of the canalization process or developmental stability of an organism (Mather 1953; Thoday 1953; Beardmore 1960; Reeve 1960; Soulé 1967, 1979). FA is defined as those random differences that occur between the left and right sides of a bilaterally symmetrical organism (Van Valen 1962). The underlying theory of FA proposes that the presence of environmental and/or genetic stress during ontogeny may reduce the efficiency of normal developmental processes, thus increasing the level of FA (Adams & Niswander 1967; Clarke *et al.* 1986; Clarke 1993). One important strength of asymmetry as a measure of individual variability is that it represents a deviation from a known morphological ideal, that is, perfect symmetry (Watson and Thornhill 1994).

FA is one of three types of asymmetry, each characterized by a different combination of mean and variance of the distribution of right-minus-left (R-L) differences (Palmer & Strobeck 1986). Directional asymmetry exists when a character on one side of an individual is larger than its counterpart. For example, the heart in mammals is usually larger on the left side than on the right side (Graham *et al.* 1993). Directionally asymmetric traits exhibit normally distributed R-L differences about a mean that is significantly either greater than or less than zero (Palmer & Strobeck 1986). Antisymmetry exists when asymmetry is the norm but the side containing the larger character varies. For example, the chelae in some species of lobsters is larger on one side, but which side has the larger claw is determined randomly.

Antisymmetry is distinguished by a platykurtic (broad peaked) or bimodal distribution of R-L differences about a mean of zero (Palmer & Strobeck 1986). FA differs from both directional asymmetry and antisymmetry because it has a normal distribution of R-L differences whose mean is zero. Only FA is considered to reflect a perturbation of development. Therefore, this is the only form of asymmetry that may be a useful indicator of developmental stress (Leary & Allendorf 1989).

Individuals better able to buffer themselves against developmental accidents have been argued to be at a selective advantage over less well buffered individuals (Brückner 1976), and therefore, developmental stability has been viewed as an integral component of individual fitness (Jones 1987). A number of species from populations with reduced genetic variation because of bottlenecks or founder effects have been shown to exhibit increased asymmetry relative to individuals from other conspecific populations or similar species (Vrijenhoek & Lerman 1982; Leary *et al.* 1985; Wayne *et al.* 1986; Parsons 1992). FA is also thought to aid in understanding adaptation and the evolution of populations, as well as the genetic processes associated with extinction (Leary & Allendorf 1989). Palmer (1986) has suggested that an increase in FA prior to extinction may indicate stress due to the loss of genetic variation. FA analysis may be particularly useful in New Zealand where many of our native wildlife have been reduced to low numbers or isolated populations due to the introduction of predators and habitat fragmentation. To date, however, there has been little study of FA in New Zealand wildlife populations.

In this study I examine the potential of using FA as a means of assessing the “stressfulness” of inbreeding on South Island robins. The robin populations on Motuara and Allports Islands (Marlborough Sounds) were founded by only five individuals each (Flack 1974, 1978) and are known to have low levels of genetic heterozygosity compared with outbred populations of the same species (Holmes 1994). Thus, these inbred populations might be expected to have a higher level of FA due to the genetical stress associated with inbreeding.

METHODS

Study organism and study sites

The South Island robin is a medium-sized (32-40 g) insectivorous passerine that is patchily distributed throughout the South Island and on a number of offshore islands. Robins spend the

majority of their foraging time on or near the ground (Powlesland 1981). Of the three subspecies of New Zealand robins (*Petroica australis*), the South Island robin (*P. australis australis*) is the largest in average dimensions (Fleming 1950). Fleming (1950) also found a relationship between the wing, tail and tarsus measurements of South Island robins and geographical location. Size of these characters decreases from the top of the South Island (Marlborough Sounds) to the bottom (Otago/Southland) (See Figure 3.1).

Fluctuating asymmetry was measured in four populations of robins: Motuara, Allports and Nukuwaiata Islands (Marlborough Sounds) and St Arnaud (Nelson Lakes National Park). The robin populations on Motuara and Allports Islands are inbred while those on Nukuwaiata Island and at St Arnaud presumably are not inbred (See Chapter 2).

Measurements

Robins were caught using a hand net designed by Maloney (1991). A hand net is portable, easy to set up and causes minimal stress to the bird; therefore, its use is recommended for the capture of robins. To capture a bird a flattish area was first cleared of sticks, stones, etc; then a few *Tenebrio* larvae were thrown onto the ground. The net was held approximately 0.4 m from the ground until the robin was completely underneath it. Then it was quickly dropped, trapping the robin between the net and the ground. The robin was removed and placed into a calico bag while I set up my equipment. This usually only took a couple of minutes.

All robins were banded with a serially numbered aluminium B-sized band and those robins on Motuara Island and at St Arnaud also received a unique combination of three B-sized coloured bands. The following measurements were taken for each bird: mass; left and right bill length (from nostril to tip), bill depth (in alignment with tip end of nostril), left and right tarsus length (from joint of tibia and metatarsus to joint at the base of the middle toe), and left and right unflattened wing length. The precise starting and ending locations of these measurements are not as important as the consistency in the choice of starting and ending locations (Alford *et al.*, in press). As I measured all the birds in this study, I am confident that all measures were consistent. Mass was measured to the nearest 0.5 g using Pesola 100 g scales. All other measurements were taken to the nearest 0.1 mm using Mitutoyo calipers. Measurements were also taken from 24 South Island robin skins kept at the Canterbury Museum. I found measuring dead robins extremely difficult and the repeatability of measurements was inaccurate; therefore I did not include these birds in my analysis.

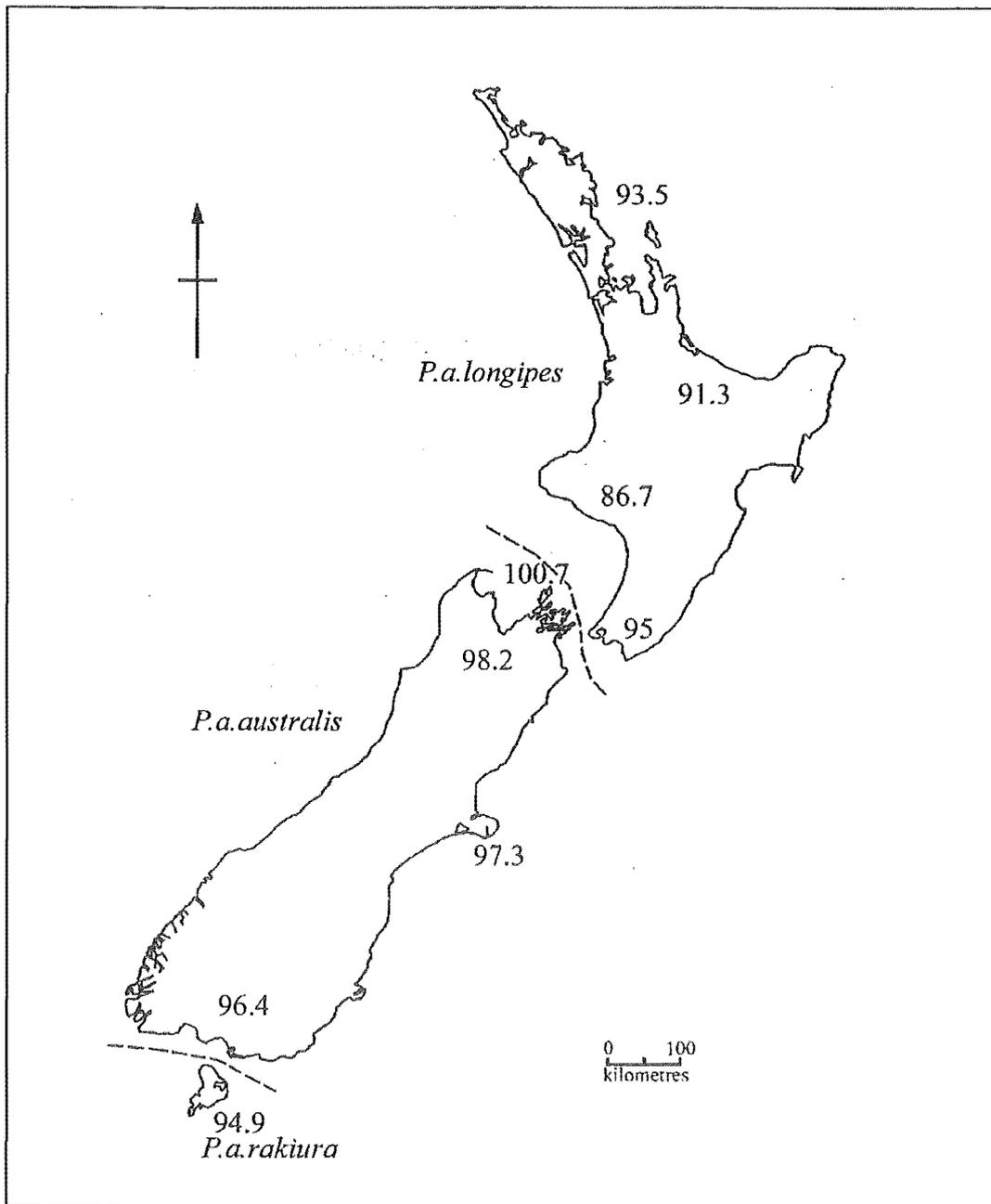


Figure 3.1 Graphical representation of the variation in wing length (mm) over New Zealand in subspecies of *Petroica australis* (from Fleming 1950).

As signed fluctuating asymmetry is characterised by a normal distribution around a mean of zero it is likely to be indistinguishable from measurement error, which shows similar properties (Palmer & Strobeck 1986; Palmer 1994; Swaddle *et al.* 1994; Merilä & Björklund 1995). This is exacerbated by the fact that fluctuating asymmetries are normally very small in relation to the trait being measured (typically less than 1% of trait size; Møller & Pomiankowski 1994). Therefore, repeated measurements should be taken from the same individual to ascertain the relative influence of measurement error on the asymmetry estimates (Møller & Swaddle 1997). However, it is also important to minimise the amount of handling time and to release the animals as soon as possible (Colwell *et al.* 1988; Hoysak & Weatherhead 1991; Arden *et al.* 1994). I took repeated measurements on the first few birds and found that these were very similar. Therefore, for the rest of the individuals sampled, I only took one measurement of each character size.

Statistical analyses

The character traits measured on each individual robin were compared among the four populations studied using a one-way analysis of variance (Statistix, Ver.2.0).

FA is defined as having a normal distribution of right-minus-left (R-L) differences around a mean of zero. A Ryan-Joiner test (similar to a Shapiro-Wilk test) for normality was used to assess if signed asymmetry (R-L) values for each character measured were normally distributed (Minitab 11.11). A one-sample two-tailed *t*-test was used to determine whether the mean signed asymmetry values for each character differed significantly from zero (Minitab 11.11). Skewness and kurtosis values were calculated to observe the nature of asymmetry in character traits (Excel 97).

One possible problem in measuring and interpreting levels of asymmetry is that the measured values of right-minus-left differences may be correlated with character size (Palmer & Strobeck 1986). I calculated Pearson correlation coefficients for the absolute R-L differences against character size, for each character, to determine whether scaling of the R-L differences was necessary (Statistix, Ver.2.0).

Various methods to measure FA have been described (for reviews see Palmer & Strobeck 1986). I measured FA by the same method as Eldridge *et al.* (1999); the absolute R-L differences were divided by mean character size ($FA = |R-L|/\{(R-L)/2\}$). Following this, two different one-way analyses of variance (ANOVA) were used to determine whether there were significant differences in FA among and within populations (SAS, Ver.6.04).

Another method that is thought to be sensitive to small variations in FA, provided that three conditions are met, is the F-max test (Palmer & Strobeck 1986; Sarre & Dearn 1991). These three conditions are: (1) FA values are independent of character size; (2) directional asymmetry is absent; and (3) antisymmetry is absent. As this method is based on the variance of R-L differences I did not use it because of the great differences in my sample sizes.

All statistical analyses are considered significant at the $\alpha=0.05$ level.

RESULTS

The mean values for bill length, bill depth and wing length differed significantly among the four populations (Table 3.1).

If FA is present, as opposed to other forms of asymmetry, then signed values of (R-L) asymmetry should be normally distributed with a mean of zero (Palmer & Strobeck 1986). In the populations studied, I found that skewness and kurtosis values often departed from normality (Table 3.2). Visual inspection of the histograms of frequency against signed asymmetry values for each character trait showed that these departures from normality were not obvious, except for bill length in the Nukuwaiata Island population which showed a skewed distribution to the right. Except for bill length in the Motuara Island population, all mean signed asymmetry values did not differ significantly from zero (Motuara bill: $t=-5.28$, $df=27$; Motuara tarsus: $t=-1.19$, $df=48$; Motuara wing: $t=-0.47$, $df=48$; Allports bill: $t=-1.57$, $df=10$; Allports tarsus: $t=0.58$, $df=10$; Allports wing: $t=-1.29$, $df=10$; Nukuwaiata bill: $t=-1.95$, $df=30$; Nukuwaiata tarsus: $t=0.69$, $df=30$; Nukuwaiata wing: $t=-0.57$, $df=30$; St Arnaud tarsus: $t=-1.46$, $df=48$; St Arnaud wing: $t=-1.78$, $df=48$; Table 3.2).

Unsigned R-L asymmetry did not vary significantly with mean trait size for bill and tarsus length but did show a positive correlation for wing length in the Motuara and Nukuwaiata Island populations (Figure 3.2). Therefore, to measure FA I divided the unsigned asymmetry values of each character by the mean character size for each individual robin. A one-way ANOVA showed no significant differences in the FA of each character trait among the four populations examined (Table 3.3). Using a one-way ANOVA no significant differences in FA were found within populations either (Table 3.4).

Table 3.1 Morphological characteristics of the South Island robin from two inbred populations (Motuara and Allports Islands) and two outbred populations (Nukuwaiata Island and St Arnaud).

	Motuara Island			Allports Island			Nukuwaiata Island			St Arnaud			P*
	Mean	SE	<i>n</i>	Mean	SE	<i>n</i>	Mean	SE	<i>n</i>	Mean	SE	<i>n</i>	
Bill length (mm)	10.55	0.10	77	11.54	0.09	22	10.84	0.06	62	10.36	0.09	49	<0.001
Bill depth (mm)	5.31	0.04	49	5.41	0.06	11	5.22	0.03	31	5.15	0.03	49	0.001
Tarsus length (mm)	37.53	0.14	98	37.45	0.19	22	37.34	0.17	62	37.48	0.17	98	0.88
Wing length (mm)	95.88	0.40	98	95.55	0.74	22	95.07	0.37	62	94.16	0.43	49	0.02
Weight (g)	38.08	0.50	49	39.05	0.64	11	39.26	0.58	31	37.51	0.37	49	0.07

* Based on a one-way analysis of variance (Statistix Ver 2.0)

Table 3.2 Statistical descriptors of asymmetry in South Island robins from two inbred populations (Motuara and Allports Islands) and two outbred populations (Nukuwaiata Island and St Arnaud).

	Motuara Island						Allports Island					
	Mean unsigned asymmetry (± SE)	Signed R – L asymmetry					Mean unsigned asymmetry (± SE)	Signed R – L asymmetry				
		Mean (± SE)	P(t)†	Skewness	Kurtosis	P‡		Mean (± SE)	P(t)†	Skewness	Kurtosis	P‡
Bill	0.22 (0.03)	-0.19 (0.04)	<0.001	0.45	1.43	>0.10	0.16 (0.06)	-0.09 (0.06)	0.15	-0.57	0.99	>0.10
Tarsus	0.40 (0.05)	-0.09 (0.08)	0.24	-0.77*	0.09	0.03	0.35 (0.07)	0.07 (0.13)	0.58	0.48	-0.11	>0.10
Wing	1.24 (0.15)	-0.11 (0.23)	0.64	1.13**	1.90**	<0.01	1.80 (0.52)	-0.93 (0.72)	0.22	0.79	1.69	>0.10

	Nukuwaiata Island						St Arnaud					
	Mean unsigned asymmetry (± SE)	Signed R – L asymmetry					Mean unsigned asymmetry (± SE)	Signed R – L asymmetry				
		Mean (± SE)	P(t)†	Skewness	Kurtosis	P‡		Mean (± SE)	P(t)†	Skewness	Kurtosis	P‡
Bill	0.23 (0.03)	-0.09 (0.05)	0.06	1.46**	2.84**	<0.01	—	—	—	—	—	—
Tarsus	0.32 (0.04)	0.05 (0.07)	0.49	-0.16	-0.58	>0.10	0.35 (0.20)	-0.10 (0.07)	0.15	-0.79*	1.83**	<0.01
Wing	1.23 (0.26)	-0.20 (0.34)	0.57	-1.52**	4.23**	<0.01	1.56 (0.05)	-0.52 (0.29)	0.08	-0.48	2.25**	0.07

† Probability that mean signed asymmetry does not differ from zero (one-sample *t*-test).

‡ Probability that signed asymmetry is normally distributed (Ryan-Joiner test; Minitab 11.11).

* P<0.05

** P<0.01

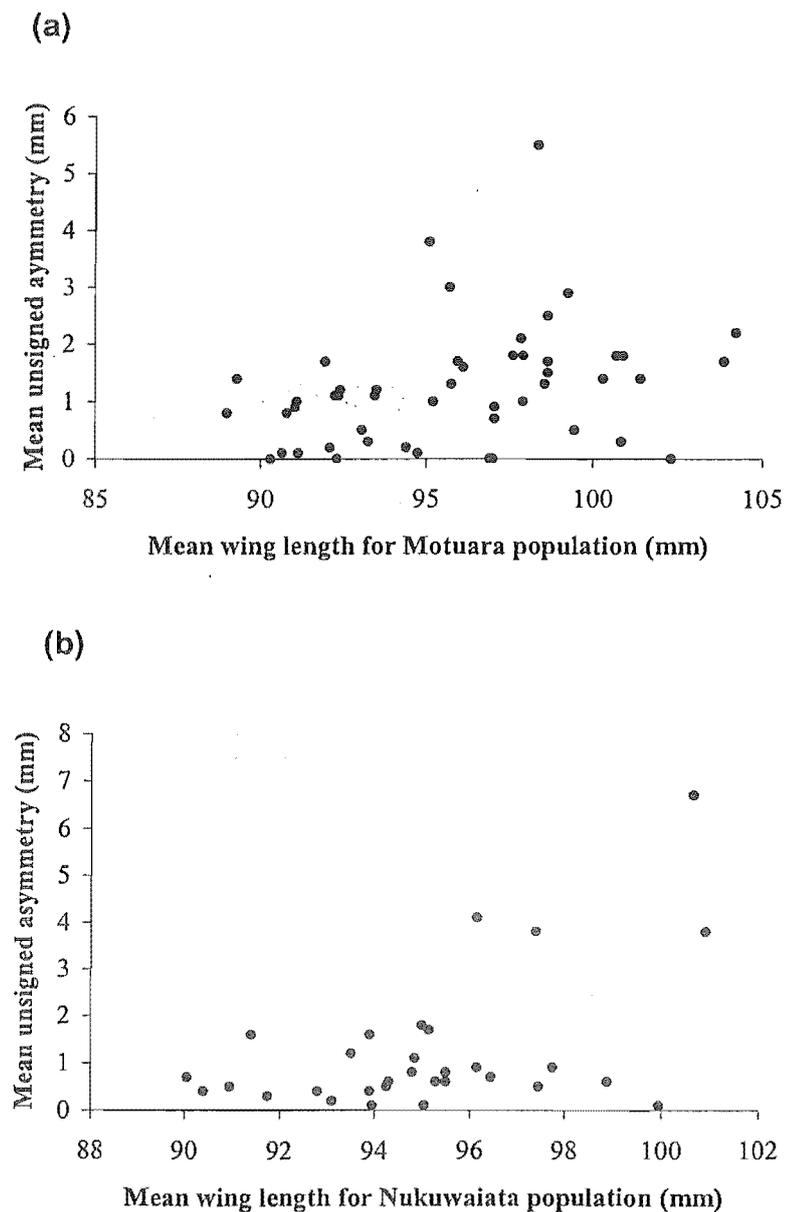


Figure 3.2 Unsigned R-L differences correlated with wing length for the Motuara Island (a) and Nukuwaiata Island (b) robin populations. Using the Pearson correlation coefficient, unsigned asymmetry varied significantly with wing size for Motuara Island ($r=0.3201$, $P=0.025$, $n=49$) and for Nukuwaiata Island ($r=0.4964$, $P=0.005$, $n=31$) but did not vary significantly for any other character traits examined (Allports bill: $r=0.2749$, $P=0.41$, $n=11$; Allports tarsus: $r=0.1457$, $P=0.67$, $n=11$; Allports wing: $r=-0.2184$, $P=0.52$, $n=11$; Motuara bill: $r=0.1680$, $P=0.39$, $n=28$; Motuara tarsus: $r=0.1055$, $P=0.47$, $n=49$; Nukuwaiata bill: $r=-0.0733$, $P=0.70$, $n=31$; Nukuwaiata tarsus: $r=0.1485$, $P=0.43$, $n=31$; St Arnaud tarsus: $r=0.0932$, $P=0.52$, $n=49$; St Arnaud wing: $r=0.0223$, $P=0.88$, $n=49$).

Table 3.3 Statistical descriptors of fluctuating asymmetry (FA) among populations as measured by dividing the absolute R-L differences for each character by character size ($FA = |R-L|/\{(R+L)/2\}$).

	Allports Island			Motuara Island			Nukuwaiata Island			St Arnaud			P*
	Mean	SD	n	Mean	SD	N	Mean	SD	n	Mean	SD	n	
Bill length	0.0141	0.0109	11	0.0217	0.0136	28	0.0212	0.0150	31	—	—	—	0.2818
Tarsus length	0.0092	0.0058	11	0.0106	0.0098	49	0.0085	0.0058	31	0.0095	0.0095	49	0.7682
Wing length	0.0190	0.0186	11	0.0129	0.0108	49	0.0127	0.0147	31	0.0166	0.0148	49	0.3332

* Based on a one-way analysis of variance (SAS, Version 6.04)

Table 3.4 Statistical descriptors of fluctuating asymmetry (FA) *within* populations as measured by dividing the absolute R-L differences for each character by character size (FA = |R-L|/((R+L)/2)).

	n	Mean		Standard deviation		F-value	P*
		Right side	Left side	Right side	Left side		
Allports Island							
Bill length	11	11.49	11.58	0.38	0.45	0.26	0.6171
Tarsus length	11	37.49	37.42	0.88	0.99	0.03	0.8569
Wing length	11	95.09	96.02	3.55	3.52	0.38	0.5452
Motuara Island							
Bill length	28	10.11	10.30	0.70	0.72	0.95	0.3338
Tarsus length	49	37.49	37.58	1.38	1.38	0.11	0.7424
Wing length	49	95.83	95.94	3.98	4.00	0.02	0.8916
Nukurwaiata Island							
Bill length	31	10.80	10.89	0.47	0.49	0.59	0.4468
Tarsus length	31	37.37	37.32	1.28	1.45	0.02	0.8895
Wing length	31	94.97	95.17	2.65	3.20	0.07	0.7931
St Arnaud							
Tarsus length	49	37.43	37.53	1.64	1.70	0.09	0.7586
Wing length	49	93.90	94.42	4.19	4.28	0.37	0.5428

* Based on a one-way analysis of variance (SAS, Version 6.04)

DISCUSSION

Researchers have argued that higher quality individuals should have greater developmental stability and lower fluctuating asymmetry on average (e.g. Møller 1992, 1993; Thornhill 1992). Evidence from studies on fluctuating asymmetry in inbred populations suggests that populations with low levels of genetic variation tend to have high fluctuating asymmetry values (Vrijenhoek & Lerman 1982; Leary *et al.* 1985; Clarke *et al.* 1986; Wayne *et al.* 1986; Sarre & Dearn 1991; Eldridge *et al.* 1999). In contrast, my results provide no evidence to support the hypothesis that greater levels of fluctuating asymmetry are found in inbred populations. Measures of fluctuating asymmetry in each character trait were not found to vary significantly among or within the four populations of robins studied. Hence, I did not find that any one population had a higher level of asymmetry compared to other populations. These findings agree with those of Handford (1980) and McAndrew *et al.* (1982). Handford (1980) examined fluctuating asymmetry in the Rufous-collared sparrow, *Zonotrichia capensis*, and suggested that the reason he failed to find any associations between genetic variation and fluctuating asymmetry may be because he was examining an endotherm, and that any such associations may be more striking in invertebrates and ectotherms. However, Eldridge *et al.* (1999) found a higher level of fluctuating asymmetry associated with inbred populations of the black-footed rock wallaby, *Petrogale lateralis*, compared to outbred populations. Thus, the endotherm-ectotherm hypothesis does not seem to explain the absence of any associations between fluctuating asymmetry and heterozygosity.

When examining the relationship between heterozygosity and developmental stability it is important to ascertain that the data show fluctuating asymmetry and not directional asymmetry or antisymmetry. This is because fluctuating asymmetry in bilateral characters represents a departure from the *a priori* optimal state, perfect symmetry (Van Valen 1962), and therefore relative deviations can be easily measured (Watson & Thornhill 1994; Palmer 1996). The significant departure from normality for wing length in the Nukuwaiata Island population and the departure from zero for bill length in the Motuara Island population were both due to the asymmetry distribution being skewed to the right. This would usually imply directional asymmetry within the population; however, these values probably indicate only a measurement bias stemming from the “handedness” of the measurer. In both cases the left-sided trait was measured as being larger than the right-sided one. This was most probably due to the fact that I had to use my left hand to measure left-sided traits whereas I am right-handed. Brown & Brown (1998) also assumed that departures from zero in mean signed asymmetry were due to

the “handedness” of the measurer. Thus, even though these departures imply directional asymmetry, I have assumed that my data follow the assumptions of fluctuating asymmetry i.e. a normal distribution around a mean of zero.

In a recent model, Leung & Forbes (1997a) have identified that a leptokurtic population distribution of asymmetry values can arise due to developmental stability, and hence can be thought of as indicating fluctuating asymmetry. This model therefore implies that researchers could assume that asymmetry data that follow a normal or leptokurtic distribution represent fluctuating asymmetry (Møller & Swaddle 1997). All significant kurtosis values in this study showed a leptokurtic distribution of signed R-L differences for each character. Hence, they are still thought of as representing fluctuating asymmetry.

The presence of antisymmetry can be perceived by a platykurtic (broad-peaked or bimodal) departure from normality in the distribution of R-L values (Palmer & Strobeck 1986). No platykurtic distributions were found in my data; thus, antisymmetry was not present. If antisymmetry were present, reliable conclusions about variation in fluctuating asymmetry among samples should not be made because they may be confounded by differences in antisymmetry (Palmer & Strobeck 1986).

A significant positive correlation was found between unsigned R-L differences and wing length in the Motuara and Nukuwaiata Island populations. This is not surprising considering the amount of territorial aggression that occurs in robins. It was not uncommon to see robins ‘locked in battle’, usually over territorial disputes but also occasionally due to male robins asserting dominance over females or juveniles. It is likely that larger robins have more damaged wing feathers because they presumably would be involved in more disputes owing to their hierarchical status. In some ways this may reflect a part of the handicap principle proposed by Zahavi (1975). The larger robins with damaged wing feathers (and therefore higher asymmetry) have persisted in the population whereas there were no small robins with high wing asymmetry. Hence, the larger robins have persevered even though they may have been handicapped by their higher wing asymmetry.

Two other factors that can cause negative results are insufficient sample size and measurement error. Both of these could possibly influence my results. Only eleven robins were sampled from the Allports Island population and sample sizes from the other three populations were not huge either ($n = 31-49$). Also measurement error could not be accounted for in my results because I did not take repeated measurements for each character on individual birds. Although I took repeated measurements to check for measurement accuracy, for future

research projects I would recommend taking repeated measurements of each character trait so that measurement error can be controlled for in subsequent analyses.

Other researchers (e.g. Sarre & Dearn 1991) have suggested that meristic characters be used for fluctuating asymmetry analysis because they are independent of body size and because the error involved in counting such characters is considered to be less than the error in measurement of bilateral characters. However, rather than choosing a particular trait because of its ease of measurement, traits used in fluctuating asymmetry analyses should have some biological significance (Houle 1998).

While it is not possible to exclude all possible confounding factors, the simplest and most likely explanation for my results is that fluctuating asymmetry is not consistently related to genetic variation in the populations of organisms studied. Leung & Forbes (1997b) also drew this conclusion when examining fluctuating asymmetry in relation to indices of quality and fitness in the damselfly. One possible reason for this is that phenotypic quality is a function of both genetical and environmental factors.

Møller's (1997) review of the literature concluded with the message that most studies show a clear negative relationship between developmental instability and fitness components. However, recent reviews on this topic (e.g. Clarke 1995a, b; Houle 1998) have found a weak, heterogeneous and somewhat ambiguous relationship between stability and fitness (Clarke 1998). Also, I found only a small number of papers that showed no association between stability and fitness (Handford 1980; McAndrew 1982; Leung & Forbes 1997b). Perhaps negative results may occur more often but authors and/or editors hesitate to accept such results for publication. Therefore, more studies are needed before it can be concluded that fluctuating asymmetry is a good predictor of the environmental and/or genetic stresses occurring in a population. Further research should try to determine which species and characteristics may be useful in detecting such stress.

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Chapter 4

The effects of colonization and population bottlenecks on the song diversity of the South Island robin

INTRODUCTION

The founding of new populations in geographically isolated areas, such as islands, is of great interest to biologists. Although the genetic effects of population bottlenecks have been well documented (e.g. Nei *et al.* 1975; Chakraborty & Nei 1977), the cultural effects of bottlenecks have only recently received increased attention (Mundinger 1980; Cavalli-Sforza & Feldman 1981; Boyd & Richerson 1985; Baker & Jenkins 1987; Lynch 1996; Payne 1996; Burnell 1998). In many species of birds, young males learn their songs from other individuals and therefore, bird song has been cited as a classic example of a cultural trait in non-human animals (Mundinger 1980, 1982; Kroodsma & Baylis 1982).

Populations of birds introduced by humans to geographically isolated areas provide excellent opportunities to investigate the effects of colonization and population bottlenecks on the evolution of cultural traits such as bird song (Baker & Jenkins 1987). Two main hypotheses have been put forward to predict how bird song might evolve in island populations (Naugler & Smith 1993). First, founder effects may constrain song structure and lead to a reduction in song variation and/or complexity (Mirsky 1976; Lynch & Baker 1986; Naugler & Smith 1991). This may be due either to the fact that islands are often colonised by young birds that have not yet learnt their songs (e.g. Thielcke 1973) or because young birds are exposed to fewer kinds of songs and song elements owing to a population bottleneck (e.g. Baker & Jenkins 1987). Alternatively, birds in an island population may have more complex songs because they are subject to weaker selective pressures for species-specific signals than are mainland populations (Marler & Boatman 1951; Marler 1957, 1960; Miller 1982). As a general rule, small islands have a lower diversity of breeding species than the mainland, and there are fewer closely related species on islands (Lack & Southern 1949; Marler & Boatman 1951; Thielcke 1973). Lack & Southern (1949) suggested this would reduce the necessity for

species-specific differences in song. Marler (1960) noted that what tends to happen in such cases is that the songs become simpler but more variable.

In New Zealand, birds and other endangered animals are routinely transferred to offshore islands for conservation purposes. In 1973, five South Island robins, *Petroica australis australis*, were transferred to Motuara Island (Marlborough Sounds). This transfer was part of a bigger project aimed at designing a recovery plan for the closely related Chatham Island black robin, *P. traversi*, which is highly endangered. The five birds involved in the transfer were from Nukuwaiata Island (Marlborough Sounds), which supports a natural, presumably outbred, population of South Island robin. Although it is possible that a single pair founded the robin population on Motuara Island (Flack 1974), the current population size is approximately 250-300 pairs (pers. obs.). The genetic effects of the population bottleneck that occurred in the Motuara Island robin population have been studied by Holmes (1994). It was found that a lower level of genetic diversity was present in this population compared to its source population on Nukuwaiata Island. In this chapter I investigate the cultural effects of colonization and population bottlenecks that may have occurred in the South Island robin population on Motuara Island. In particular, I examine the song diversity of the Motuara Island robin population and compare it to two other robin populations: one on Nukuwaiata Island and the other on the mainland at St Arnaud.

METHODS

Study sites and sampling dates

Songs of male South Island robins were recorded from populations on Motuara and Nukuwaiata Islands (Marlborough Sounds) and from a mainland population at St Arnaud (Nelson Lakes National Park)(refer to Figure 2.1). For a detailed description of forest composition and structure on Motuara Island and at St Arnaud refer to Chapter 2. Nukuwaiata Island is very similar in forest composition to Motuara Island in that they are both classified as coastal broadleaf forests.

The robin populations on Motuara Island and at St Arnaud were colour banded; therefore individual identification was possible. On Nukuwaiata Island, birds were banded with a metal band only. To ensure that the same bird was not recorded twice, I only made recordings from within known territories. Robin territories were determined by close observation over the first

few days of my visit. Songs were recorded on Motuara Island from November 1998 – January 1999, on Nukuwaiata Island from 12-18 January 1999 and at St Arnaud from 16-20 March 1998 and 17-21 August 1998. Most songs were recorded before dawn, when robins would usually sing continuously for long periods of up to approximately 20 minutes. However, on Nukuwaiata Island, cicada noise was so great also in the morning that robin song was recorded at other times throughout the day. Robins have been found to sing less frequently during their moult (Jan-Feb) and most frequently during prelaying (Powlesland 1980). I recorded songs from as many male robins in each population as possible, however, due to moulting and sampling time constraints, sample sizes are quite small. Twelve males were recorded from Motuara Island, seven from Nukuwaiata Island and eight from St Arnaud.

Recording equipment and song analysis

All songs were recorded on a Sony TC-D5M Stereo Cassette-Corder. At St Arnaud a Sennheiser ME-80 microphone was used, while on Motuara and Nukuwaiata Islands a Beyerdynamic TGX480 microphone was used. Songs were displayed on a Gateway2000 computer using the Signal program (Version 3.0). Spectrograms were produced using a FFT size of 1024 and an anti-alias filtering device set at 10000 Hz with a gain of 10 dB.

Mundinger (1975) defined a syllable as the basic structural unit of a song, separated from adjacent syllables by a silent period of 0.02-0.20 seconds. Syllables can be either singular or as part of group of identical syllables known as a phrase (Catchpole & Slater 1995; Figure 4.1). The number of repetitions of a syllable in a phrase is quite variable both within and between individuals (Slater & Ince 1979, 1982; Lynch & Baker 1993). Therefore, song was identified as an array of syllables disregarding the number of repetitions. Syllables were classified into different types by visual inspection, based on differences in their morphologies. Previous studies have found that this method is more satisfactory than laborious techniques such as digitization in recognising homologous forms of a syllable (Lynch & Baker 1986; Baker & Jenkins 1987; Lynch *et al.* 1989). Within syllable types, related variants have presumably arisen by small copying errors during the learning process (Jenkins & Baker 1984; Lynch *et al.* 1989; Lynch & Baker 1994). I did not differentiate between syllable variants and syllable types; thus all my analyses were restricted to the use of syllable types only.

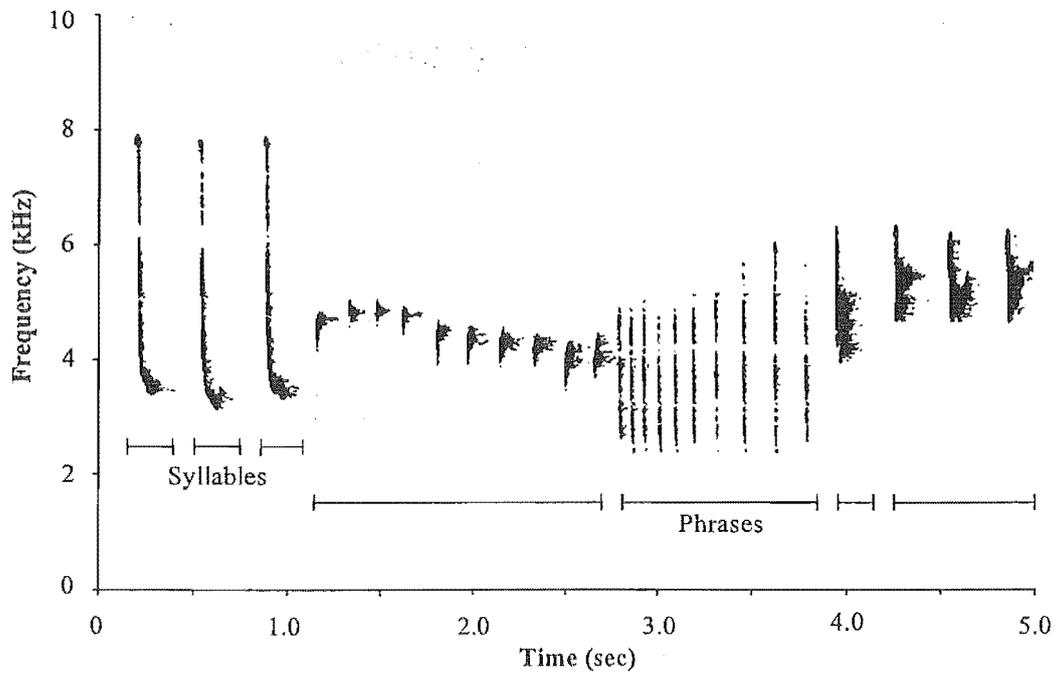


Figure 4.1 A sonagram showing an example of five seconds of a robin's song. Also illustrated is the division of song into syllables and phrases.

Robin song is different to that of most other passerine species songs in that it is composed of a continuous series of phrases taken from a total repertoire of approximately 200 different syllable types (pers. obs.). An individual would often sing continuously for periods of up to 20 minutes or more and it was not possible to determine where one song ended and another began. Therefore, analyses were not made on robin song as a whole but only on the syllables.

Syllable diversity

Syllable diversity was measured by examining the distinctiveness and repetition of individual syllable types. Two different methods of analysis were employed. First, I calculated the bird's approximate repertoire size by plotting the number of new syllable types introduced as the song progressed against time (see Figure 4.2). The time taken for a bird to sing the majority of its syllables varied between individuals from 3-9 minutes. At first the number of new and distinct syllable types increased linearly as the song progressed. Then, as the bird approached the probable limit of its repertoire, the rate of introduction of new syllable types decreased asymptotically. I ascertained that the asymptote had been reached when the number of new syllable types entering a song was approaching zero i.e. only one or two new syllables types were sung over a time period of approximately 1-2 minutes. The first method of analysis included only those recordings that were long enough to calculate the probable limit of the bird's repertoire. Hence, graphs in which the asymptote had not been reached were not included. Performing the analysis in this way meant that only two recordings from the Nukuwaiata Island population could be utilized. As I have already mentioned, I had to sample during the daytime for this population instead of at dawn. Robins do not sing for long periods during the day (Powlesland 1983), therefore, recordings were relatively short.

The second method of analysis involved equalizing the time frame examined for all three populations. Only seven individuals were recorded from the Nukuwaiata Island population. Thus, to compare with the other two populations, I randomly chose (using a random numbers table) seven individuals from each. One-minute samples from each individual were randomly selected for analysis. A one-minute time period was decided upon because some of the individuals in the Nukuwaiata population were only recorded singing for a period of one minute.

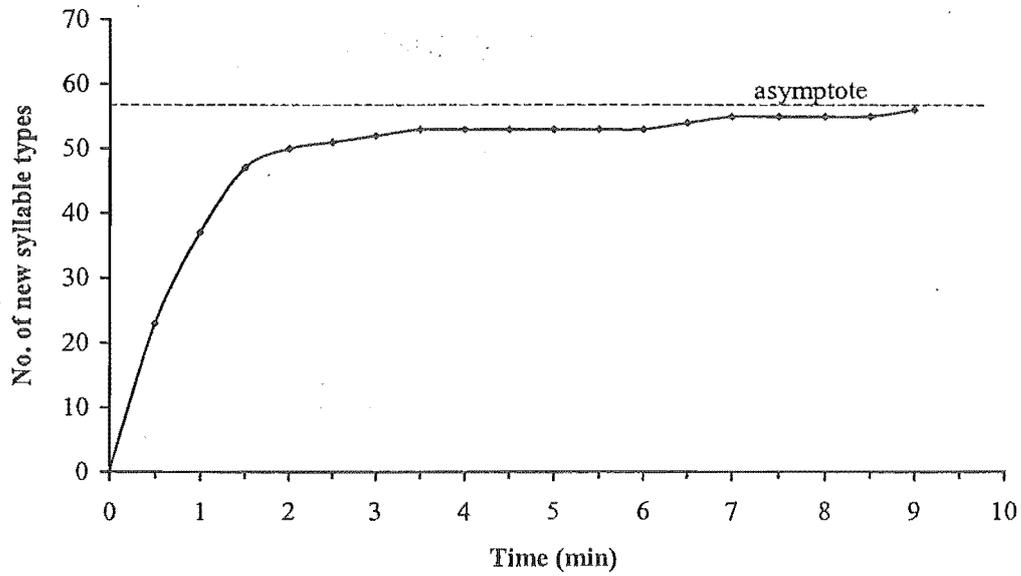


Figure 4.2 Syllable diversity of an individual male robin in the Motuara Island population. The probable limit of the bird's repertoire is reached when the number of new syllable types entering the song approaches zero.

Syllable sharing between populations

The amount of syllable sharing between populations was examined to see if any two populations were more closely related with respect to the syllable types found in each. Examination of each population for an equal amount time was employed here in the same way as it was for syllable diversity. One-minute samples from seven individuals in each population were analysed. Pairwise comparisons were made between all three populations. The number of syllables shared between two of the populations was divided by the total number of syllables found in both populations to give the percentage of shared syllables. A chi-squared test of independence was performed on proportions to assess if any pair of populations was significantly different from the other pairs.

RESULTS

Syllable diversity

Overall, I classified 200 distinct syllable types for the three South Island robin populations studied. Each individual male robin had a total repertoire range of 38-60 different syllables. Using the first method of analysis, i.e. an individual's entire repertoire, a one-way analysis of variance showed that the mean syllable diversity differed significantly among populations ($F=8.61$, $d.f.=2,14$, $P=0.004$; Table 4.1). A Tukey test (Zar 1996) for a post hoc comparison of means revealed that birds in the Motuara Island population used a significantly larger number of distinct syllable types in their song compared to both the Nukuwaiata Island and St Arnaud populations (Table 4.1).

Using the second method of analysis, i.e. a one-minute sample from each individual, a one-way analysis of variance showed that the mean syllable diversity did not differ significantly among the populations ($F=2.13$, $d.f.=2,18$ $P=0.148$; Table 4.2).

Syllable sharing

Using one-minute samples from each individual, a total of 136 syllable types were identified in the syllable pool of all three populations. Of these 81 (59.6%) were unique to individual populations, whereas 24 (17.6%) are shared among all three populations. A

Table 4.1 Syllable diversity in three South Island robin populations; calculated using the mean number of different syllable types found in an individual's repertoire.

Robin population	Sample size	Mean	S.D.	Range	Post hoc test*
Motuara Island	8	54.0	5.15	44-60	A
Nukuwaiata Island	2	43.5	0.70	43-44	B
St Arnaud	7	43.7	5.50	38-54	B

* The post hoc test employed was a Tukey test ($\alpha=0.05$). A different letter signifies that the means are significantly different from each other.

Table 4.2 Syllable diversity in three South Island robin populations; calculated using the mean number of different syllable types found in a one-minute random sample from each individual.

Robin population	Sample size	Mean	S.D.	Range
Motuara Island	7	24.7	7.02	16-38
Nukuwaiata Island	7	21.1	3.29	17-26
St Arnaud	7	26.7	4.31	21-33

Table 4.3 Pairwise comparisons of syllable sharing between populations. (Mot = Motuara Island; Nuku = Nukuwaiata Island; StAr = St Arnaud).

	Mot-Nuku	Mot-StAr	Nuku-StAr
No. of syllables shared between populations	33	38	31
No. of syllables unique to one population	62	82	81
Total no. of syllables found in both populations	95	120	112

pairwise comparison of the populations revealed that Nukuwaiata and Motuara Islands share 34.7%, Motuara Island and St Arnaud share 31.6% and Nukuwaiata Island and St Arnaud share 27.7% of their syllable types (Table 4.3). No significant difference is apparent in the amount of syllable sharing among populations ($\chi^2=1.213$, d.f.=2, $P=0.55$).

DISCUSSION

The isolated South Island robin population on Motuara Island, established by just five individuals carrying only a small part of the genetic and behavioural information of the parental population, might be expected to possess limited song variability. Instead, this robin population exhibits greater song variability than either its parent population on Nukuwaiata Island or a mainland population at St Arnaud.

Several hypotheses have been put forward to explain the development of song in island populations or, more generally, in populations isolated by unsuitable habitat. First, colonization by only a few individuals or a decline in the population size due to a bottleneck event may both lead to a reduction in song variation. Thielcke (1973) suggested that colonization often involves young birds that have not yet learnt their songs from adults in the ancestral population. Consequently, they develop a homogeneous song which is transmitted from generation to generation and thus becomes a new cultural tradition. A reduction in song variation can also arise because a small number of founders who had already learnt their song from adults before colonizing would introduce only a subset of the syllables present in the ancestral population (Baker & Jenkins 1987). However, neither colonization nor the bottleneck event that occurred in the robin population on Motuara Island can account for the variation in song found there. The 'founder effects' hypothesis states that there would be a loss in song variation, and this is the opposite of what I have found in this study.

Increased song variation in island populations may result from the lack of need for species-specific distinctness where there are few other species with which confusion might result. Songs are signals that not only serve as intraspecific communication to attract females and repel rival males, but also as sexual isolating mechanisms. If two closely related species were sympatric then, presumably, there would be a need for song distinctness so that interbreeding did not occur. Gill & Murray (1972) found the songs of blue-winged and golden-winged warblers to be less variable where the two species occurred together than in areas where only one was found. Marler & Isaac (1961) used this concept to explain the considerable song

variability in a Mexican population of *Junco phaenotus* in an environment with a small number of bird species. Likewise, variance in pulse rate of *Litoria ewingi* (a frog species introduced into New Zealand from Australia) was found to be greater in samples from the South Island of New Zealand compared to samples from Tasmania (Littlejohn *et al.* 1993). The authors attributed this increase in variation to the absence of sympatric closely related species. I suggest that the greater song variability I found on Motuara Island has resulted from the lack of need for species-specific signals. The tomtit, *P. macrocephala macrocephala*, a closely related species of the robin, is found both on Nukuwaiata Island and in St Arnaud. During the Chatham Island black robin recovery program, workers observed a hybrid chick produced from the mating of a Chatham Island tit and a black robin (Butler & Merton 1992). Thus, interbreeding is possible between tit and robin species. There are no tomtits present on Motuara Island and hence, presumably due to the absence of closely related species, robins have increased their song repertoire.

A further explanation for the differences in song variation that may occur between populations, relates to the sound transmission properties of the habitat in which the bird lives (Morton 1975; Marten & Marler 1977; Marten *et al.* 1977; Wiley & Richards 1978; Hunter & Krebs 1979; Richards & Wiley 1980; Jenkins & Baker 1984). The general consensus is that species living in forested areas tend to avoid high frequency sounds and rapid repetition of syllables due to degradation from reverberation. However, this last hypothesis can be discounted as a possible explanation for the observed differences in song variation among the three South Island robin populations because Motuara Island, Nukuwaiata Islands and St Arnaud are all forested areas with a similar vegetation structure. Hence, the sound transmission properties of each habitat are relatively similar and robin song would have evolved accordingly.

Hay (1979) found that the developing song of juvenile robins is influenced by the songs of adults in surrounding territories. As only five robins were originally transferred to Motuara Island, the offspring of these birds would have had ample space in which to disperse after reaching independence. Therefore, some juveniles may not have been situated within earshot of an adult male's territory and may have learnt parts of their song by trial and error or by copying notes from other species. In contrast, young birds in areas where the habitat is more saturated with robins, may have more opportunities to accurately copy the song of neighbouring adults. Robins are sedentary birds and because no immigration occurs to Motuara and Nukuwaiata Islands, new syllable types can only be added to these isolated populations by copying errors in the learning process.

The robin population on Motuara Island was founded by individuals from Nukuwaiata Island and consequently these two populations might be expected to have more syllables in common than either of these populations would have with the mainland robin population at St Arnaud. However, a pairwise comparison revealed no significant difference in the amount of syllable sharing between populations. At present, I have no explanation for this pattern.

A second method of analysis of syllable diversity showed that no variation occurred among the three populations studied. However, using one-minute samples from each individual does not really give a true representation of its syllable diversity. By chance, an individual may repeat a small number of syllables over and over again within this minute and the rest of its song might contain a diverse array of syllable types. Therefore, even though only a small sample size could be obtained for the Nukuwaiata Island population, I used the more accurate method of analysing the mean number of syllable types in an individual's entire repertoire and comparing this among populations.

Most work on song evolution in New Zealand bird populations has been done on the chaffinch, *Fringilla coelebs* (Jenkins & Baker 1984; Baker & Jenkins 1987; Lynch *et al.* 1989). Baker and Jenkins (1987) found that the syllable pool in the isolated Chatham Island chaffinch population is depauperate relative to that in the New Zealand mainland population. They concluded that the Chatham Islands were colonized by a small number of founders who had already learnt their syllables and songs from adult conspecifics and that this 'founder effect' had led to a reduction in syllable diversity. Results from my study imply that the isolated robin population on Motuara Island has increased its syllable diversity since being founded in 1973. This suggests that a drastic reduction in the genetic diversity of a population does not necessarily or inevitably lead to a concomitant reduction in its cultural diversity.

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General Conclusion

In this study I found that: (1) South Island robins (*Petroica australis australis*) from an inbred population on Motuara Island exhibited lower clutch size, number of clutches per season, and hatching success compared to outbred robin populations; (2) there was no evidence of an association between lowered heterozygosity and levels of fluctuating asymmetry; and (3) the robin population on Motuara Island has evolved greater song variation than either its source population on Nukuwaiata Island or another robin population found on the mainland.

The lower rate of hatching success reported for the inbred population on Motuara Island suggests that this population is suffering from inbreeding depression. A number of other studies on inbred populations of birds have found the same pattern (Sittman *et al.* 1966; Bensch *et al.* 1994; Kempnaers *et al.* 1996). The effect of lowered hatching success on the long-term survival of the Motuara Island population is currently unknown. The high density at the present time suggests that the lower rate of hatchability due to inbreeding has not been sufficiently deleterious to limit the population size. However, further declines in hatchability could eventually prevent sufficient recruitment and lead to a decline in this population.

Other measures of reproductive success that showed significant differences between inbred and outbred populations, such as lower clutch size and number of clutches per season, are also consistent with the hypothesis of inbreeding depression. However, both of the latter could also be explained by island population dynamics rather than inbreeding depression. For example, the robin population on Motuara Island seems to be near the carrying capacity for this environment; therefore, it might be expected that robins can only produce a certain number of offspring per year as competition for resources is so intense. In contrast, outbred mainland populations of robins, such as the one at St Arnaud, occur at much lower densities and have greater space and resources for the production of offspring.

A recent article by Sarre *et al.* (1994) detailed the potential application of fluctuating asymmetry for monitoring animal populations as part of conservation biology programs. Numerous other studies have proposed that fluctuating asymmetry may be used as a surrogate for more direct assessments of fitness that use parameters such as fecundity, survival or fertility (Leary & Allendorf 1989; Parsons 1992; Graham *et al.* 1993; Clarke 1995; Markow 1995). The results of this study, however, found no evidence for greater fluctuating asymmetry in the

inbred robin population on Motuara Island. This was somewhat surprising because, as mentioned above, there is evidence of inbreeding depression in this population as manifested by a low hatching success. It has been proposed that differences in fluctuating asymmetry among samples are generally small (Palmer 1996). Thus, confounding factors such as measurement error, directional asymmetry, and antisymmetry may make up a sizable fraction of the variance in a sample (Palmer & Strobeck 1986). Careful measurement and analysis of fluctuating asymmetry is therefore essential. Although fluctuating asymmetry looks like a seemingly simple tool to achieve a precise measure of developmental instability, I agree with Clarke (1996) in that there does not seem to be enough evidence to make generalizations or to promote the widespread application of fluctuating asymmetry as a surrogate for measuring fitness. More studies are needed to determine which species and characters may be useful in detecting stress or reduced fitness within a population.

Two main hypotheses have been proposed to explain the evolution of bird song in island populations. First, there may be a reduction in song diversity due to founder effects and second, there may be an increase in song diversity resulting from the lack of need for species-specific signals. Only five individuals founded the robin population on Motuara Island; thus it might be expected to have limited song variability due to only a small number of songs and song elements being transferred from the parent population. Instead, this island population exhibits greater song variability than either its parent population on Nukuwaiata Island or a mainland population at St Arnaud. I have suggested that this increase in song diversity has resulted from a lack of sympatric and closely related species on the island. On Nukuwaiata Island and at St Arnaud the tomtit (*P. macrocephala macrocephala*) is present and this species is known to hybridize with other robin species (Butler & Merton 1992). Thus on Motuara Island, where there are no tomtits present, robins may have been able to expand their repertoire due to the lack of need for species-specific signals which may be used as reproductive isolating mechanisms. The results of this study imply that a reduction in the genetic diversity of a population does not necessarily or inevitably lead to a concomitant loss of cultural diversity as measured by song variation.

Opportunities for future research

The inbred population of robins on Motuara Island provides valuable opportunities to study both the long-term effects of inbreeding on population viability as well as how inbreeding affects success at the individual level. In this study, I observed a reduced rate of hatching in the Motuara Island robin population. However, the exact cause of this reduced hatchability is not known. Further studies could look at a number of possibilities, such as the production of abnormal sperm by some males, increased embryo mortality, or improper incubation behaviour of the female to explain the lower hatching rate. In the Chatham Island robin, much of the hatching failure was due to females laying eggs on the rim of the nest, rather than in the nest cup (Butler & Merton 1992). Such abnormal behaviour was only observed in one out of the 35 nests examined on Motuara Island; however, it is possible that other behavioural problems occur and may account for the low hatchability.

While I have noted that inbreeding has affected reproductive success of some individuals, there are also many other factors which it may affect and which I was unable to study. A number of studies have correlated homozygosity with an increase in susceptibility to parasitic infections (e.g. Allendorf & Leary 1986; Watkins *et al.* 1991). Disease susceptibility is of particular importance in New Zealand where many of our endangered species have been, and continue to be, transferred to new environments such as offshore islands (see Armstrong & McLean 1995). In such cases, the transfer of infected individuals could have disastrous consequences. Therefore, it would be of interest to know how well the robin population on Motuara Island could resist a disease outbreak if ever one occurred. Deliberately infecting robins may be difficult to justify, but a measure of immunocompetence could be obtained by challenging birds with a standard antigen (e.g. sheep red blood cells; Deerenberg & Apanius 1997; Pastoret *et al.* 1998).

Theoretical models of mate choice suggest that inbreeding depression should lead to selection mechanisms to avoid inbreeding (Kempnaers *et al.* 1998). In this context, it would be interesting to look for the presence of sex-biased dispersal (Greenwood 1980), kin recognition (Bateson 1982), or mate choice within inbred populations of robins. For example, do robins avoid close kin? Is dispersal limited on islands and does this alter the criteria individuals use in mate choice?

The robin population on Motuara Island could also be used to study ways of restoring genetic diversity to a population. Perhaps selective removal of infertile birds would improve the genetic make-up of this population? Would the addition of new birds increase the genetic

diversity enough to curb inbreeding depression and reduce problems associated with hatchability? How much genetic diversity is required to prevent any effects of inbreeding depression?

In the future, the conservation of some species may be wholly dependent on survival in small populations, whether it be in a captive environment or in the wild. Thus, the study of population bottlenecks and how they affect various types of organisms is highly important for the generation of management strategies and continued perseverance of small populations.

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