Breeding season behaviour, reproductive success, and dispersal after translocation in tūturuatu *(Thinornis novaeseelandiae)*

A thesis presented in partial fulfilment of the requirements for the degree of Master of Science in Conservation Biology at Te Kunenga ki Pūrehuroa, Tāmaki Makaurau, Aotearoa (Massey University, Auckland, New Zealand).

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The cover illustration is from “The zoology of the voyage of the H.M.S. Erebus and Terror” by John Richardson and John Edward Gray, published in 1845. The artist is unknown.

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Abstract

The tūturuatu (tchūriwat’, shore plover, *Thinornis novaeseelandiae*) is an endangered shorebird endemic to Aotearoa (New Zealand). The remnant wild population of approximately 45 breeding pairs appears stable but is confined to Hokorereoro (Rangatira, South East Island), a small island in the Chatham Islands group. Since 1994 efforts to translocate captive-bred juvenile birds to other island sanctuaries free of introduced mammalian predators have met with mixed success. This study investigated the behavioural ecology of a population of eighteen tūturuatu on Motutapu, an island in the Hauraki Gulf near Tāmaki Makaurau (Auckland), which were either survivors of or descended from 92 captive-bred juveniles released between 2012 and 2017.

The behaviour of each breeding pair, and their chicks once hatched, was recorded every two minutes at their nest site or territory for two hours each day until the last chick had fledged, a total of almost 20,000 observations. Trail camera recordings of the nest site and surrounding area augmented my direct observations. Behavioural time budgets were constructed for adults and chicks allowing comparison between sexes, phases of the breeding season, and between the Motutapu population and published reports on the Hokorereoro population. Display activity was observed and circa-tidal effects on behaviour were investigated. Comparison of foraging time budgets with published reports on tūturuatu and other plover species suggested that adequate food resources were available for both adults and chicks. Display activity was primarily directed at competitive species; and increased in frequency and intensity during the chick-rearing phase compared with the earlier phases of the breeding season. I suggest that this behaviour is linked to the sudden increase in vulnerability of tūturuatu chicks after hatching rather than the gradual increase in “reproductive value” through the season. Patterns of foraging and inactive behaviour in tūturuatu appeared to be affected by circa-tidal rhythms.

Reproductive success was investigated, with an emphasis on egg survival, and chick survival to fledging. Egg survival rates were high, which I suggest is at least partly attributable to the unusual covered nest of this species. Chick mortality rates were high, with avian predation and female desertion identified as the primary causes. Female desertion is a common sequel to a male-biased adult sex ratio in other plover species but has not been observed previously in tūturuatu. Deleterious outcomes were observed both for chicks and deserted male partners, prompting wildlife management recommendations.

Thirty-six captive-bred juveniles were closely monitored after translocation to the island with the aim of distinguishing between mortality and dispersal in those that disappeared. Subsequently the records of all 128 birds translocated to the island between 2012 and 2019 were investigated to compare the effects of various predictors of detection probability. The timing of release with respect to the summer solstice was identified as a key predictor of detection probability with the most successful outcomes aligning with the timing of juvenile independence in the wild population.

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Mac McKay

CHAPTER ONE

An introduction to the biology, behaviour, and conservation of Charadrius plovers

Plate 1.1 The conjoined islands of Rangitoto and Motutapu from nearby Motukorea.

1.1 AN INTRODUCTION TO THE BIOLOGY OF CHARADRIUS PLOVERS

Plovers of the genus *Charadrius* and their close relatives number almost forty species, with many subspecies. They are shorebirds with a global distribution, inhabiting many islands, and every continent except Antarctica. Many species are long-distance migrants, some are short-distance or altitudinal migrants, and a few, like the tūturuatu (tchūriwat', shore plover, *Thinornis novaeseelandiae*), are regarded as sedentary but still may have considerable dispersal abilities (Colwell & Haig, 2019a). Charadrius plovers typically exhibit both social and genetic monogamy, and biparental care of offspring, but there is variation in breeding systems — sometimes even within a species. As inhabitants of the interface between terrestrial and aquatic environments, shorebirds represent a sensitive and visible indicator of the effects of anthropogenic change on climate, oceans, waterways, and terrestrial ecosystems (Haig, 2019).

The Charadrius plovers are thought to have originated in the northern hemisphere (dos Remedios, Lee, Burke, Székely, & Küpper, 2015) and are now widespread around the globe. They occupy niches in open, sparsely vegetated habitats of tundra and grasslands, and adjacent to water along coastlines, lakeshores, and riverbanks. Compared to other bird species, plovers exhibit high levels of population connectivity – not surprising given their high dispersal capabilities (Colwell & Haig, 2019a).

The phylogenetics of Charadrius plovers

Plovers belong to the family Charadriidae, which includes the genera *Charadrius* (plovers), *Vanellus* (lapwings), and *Pluvialis* (golden- and black-bellied plovers), as well as several other genera, each with just one or two members: *Anarhynchus*, *Elseyornis*, *Oreopholus*, *Peltohyas*, *Phegornis*, and *Thinornis* (Küpper & dos Remedios, 2019). Recent molecular DNA–based studies have indicated that four species currently placed outside the *Charadrius* genus warrant inclusion within it (dos Remedios et al., 2015). All four species are endemic to Australasia. Two of them are endemic to Aotearoa (New Zealand); the subject of this study, the tūturuatu, and the ngutuparore (wrybill, *Anarhynchus frontalis*). The hooded plover *(Thinornis rubricollis)* is endemic to southern and eastern Australia and has similarities both genetically and in appearance and behaviour to the tūturuatu. The fourth species, the black-fronted dotterel *(Elseyornis melanops)* is widespread in Australia, and since the 1950s has occurred naturally in small numbers in eastern areas of Aotearoa.

Throughout this thesis I have used the term “Charadrius plover” or simply “plover”, to refer to members of the *Charadrius* genus and the four species mentioned above that, while closely related to the genus, are currently classified outside it. This follows the taxonomic practice adopted by Colwell and Haig and their contributing authors (Colwell & Haig, 2019b). A recent review chapter on phylogenetic studies in plovers accepted the likelihood of ongoing controversy in this area and concluded by strongly advocating for field studies examining behaviour and ecology to inform the sensible biological interpretation of genetic results (Küpper & dos Remedios, 2019).

Charadrius plover species endemic to Aotearoa

Five species of Charadrius plover are endemic to Aotearoa. Four of them are closely related, forming "minor clade c" within "major clade II" of the genus *Charadrius* as proposed by dos Remedios et al. (2015). They are:

- **ngutuparore (wrybill, *Anarhynchus frontalis*)**

  This species breeds in Te Waipounamu (the South Island) and is a short-distance migrant to Te Ika-a-Māui (the North Island). The population estimate is 4500 – 5000 and the IUCN status is "Vulnerable" (Conklin, 2019; IUCN, 2021).

- **pohowera (banded dotterel, *Charadrius bicinctus*)**

  This species breeds in Aotearoa; mainly in Te Waipounamu, but also in Te Ika-a-Māui, the Chatham Islands, and Motu Maha (the Auckland Islands). They can be sedentary, or medium-distance migrants to other parts of Aotearoa, or Australia, or several Pacific islands (Conklin, 2019). The population was thought to be steady at approximately 50,000 birds (Colwell & Haig, 2019a), and is currently listed as "Near Threatened" by the IUCN (IUCN, 2021). However, a recent review found that the population on Te Waipounamu has decreased by an average of 3.7% per annum since 1962 (O'Donnell & Monks, 2020). They estimated the population at 12,730 birds and recommended reclassification of the IUCN status to "Endangered". Another conservation issue is that while some consider the Motu Maha population a sub-species (*Charadrius bicinctus exilis*) (Dowding & Moore, 2006), others consider it a full species (Holdaway, Worthy, & Tennyson, 2001), in which case the population estimate of 730 birds and constrained island habitat of this taxon would likely raise concerns over its conservation status.

- **tūturiwhatu (northern red-breasted dotterel, *Charadrius aquilonius*)**
  This species inhabits Te Ika-a-Maui, particularly northern and eastern regions, and is sedentary with some local movements. The population estimate was 2075 in 2011, and the IUCN status is “Near Threatened” (Colwell & Haig, 2019a; Conklin, 2019; IUCN, 2021)
- **tūturiwhatu (southern red-breasted dotterel, *Charadrius obscurus*)**
  This species inhabits the very southern region of Te Waipounamu and Rakiura (Stewart Island) and is a short distance altitudinal migrant. The population estimate was 120 in 2016, and the IUCN status is “Critically Endangered” (IUCN, 2021). The two species of tūturiwhatu differ in morphology and behaviour but have only moderate genetic differentiation and were previously considered a single species known as the New Zealand dotterel (*Charadrius obscurus*). They were subsequently split into two sub-species named “southern New Zealand dotterel *(Charadrius obscurus obscurus)”* and “northern New Zealand dotterel *(Charadrius obscurus aquilonius)”* (Barth, Matschiner, & Robertson, 2013). Local extirpations following the anthropogenic introduction of mammalian predators have caused the two populations to become geographically and reproductively isolated. The likelihood is that the two taxa will continue to diverge genetically, and since 2016 they have been defined as separate species by some taxonomic authorities and by the IUCN (Küpper & dos Remedios, 2019).

The fifth Charadrius plover species endemic to Aotearoa is more distantly related to the other four endemic species, being a member of “major clade I” of the genus *Charadrius* as proposed by dos Remedios et al. (dos Remedios et al., 2015). It is:

- **tūturuatu (tchūriwat’, shore plover, *Thinornis novaeseelandiae*)**
  The subject of my research efforts currently naturally inhabits one small island in the Chatham Islands group named Hokorereoro by the original Moriori settlers. The island is also known as Rangatira in te reo Māori, and South East Island in English. The tūturuatu population is sedentary with some local movements (Conklin, 2019). Anthropogenically established wild breeding populations also exist on nearby Maung’ Rē (Mangere Island), and on Waikawa (Portland) Island and Motutapu, both off-shore islands of Te Ika-a-Māui. There are also three captive breeding sites: two on Te Ika-a-Māui and one on Te Waipounamu. The entire species population estimate is 240 and the IUCN status is “Endangered” (DOC, 2019; IUCN, 2021). Tūturuatu currently share their generic name with the hooded plover *(Thinornis rubricollis)* of south-eastern Australia and appear to be closely related to this species genetically and in appearance, behaviour, and choice of habitat. They are also closely related genetically to the long-billed plover *(Charadrius placidus)* (dos Remedios et al., 2015), a species widespread throughout Asia, but the two species appear to be quite different in appearance, behaviour, and choice of habitat.

Dietary and water requirements of Charadrius plovers

Plover diets vary, with many species regarded as generalist or opportunist feeders. An example is the mountain plover *(Charadrius montanus)*, which in one study was shown to consume 2,092 different prey items, including at least sixteen families of invertebrates (Knopf, 1998). At the other end of the spectrum, the oriental plover *(Charadrius veredus)* specialises on grasshoppers in winter on grasslands in Australia (Piersma & Hassell, 2010), and the diet of Wilson's plover *(Charadrius wilsonia)* is reported to be 98.6% fiddler crabs (Morrier & McNeil, 1991). The diet of the tūturuatu has not been studied in detail but is known to include sandhoppers *(Bellorchestia quoyana)*, a common endemic talitridid amphipod. On Hokorereoro they have been observed feeding on a wide range of marine and terrestrial invertebrates including copepods, insect larvae, and amphipods (A. Davis, 1987).

Charadrius plover chicks may well have different prey species preferences from adults. This has been demonstrated in the European golden plover *(Pluvalis apricaria)* (Machin et al., 2017) which is not a Charadrius plover species. If true for Charadrius plover species, it would have implications for phenological mismatches caused by climate change as prey abundance synchrony would need to be maintained for both adults and chicks (Haig, 2019). Tūturuatu chicks on Hokorereoro were thought to be restricted in prey type by their small gape and poor feeding skills (A. Davis, 1987).

Plover chicks may also have different freshwater requirements from adults. Several authors have stated that young plovers require freshwater, as their salt gland is not developed at hatching (Haig, Murphy, Matthews, Arismendi, & Safeeq, 2019; Rubega & Oring, 2004). Tūturuatu chicks on Hokorereoro appeared to prefer freshwater seeps as feeding areas and to grow more quickly when they had access to this type of microhabitat (A. Davis, 1987). Whether this was because of prey type availability or access to freshwater is unknown. American avocet *(Recurvirostra americana)* chicks raised experimentally in environments of different salinity exhibited deleterious changes in behaviour, growth, and health related to salinity levels (Hannam, Oring, & Herzog, 2003). Foraging time and weight were highest in the group with access to freshwater and successively reduced in brackish, saline, and hyper-saline environments. However, Ehmke et al. (Ehmke, Maguire, Bird, Ierodiaconou, & Weston, 2016) recorded the selection of nesting sites by hooded plovers in the absence of freshwater.

The mass of the salt gland in adult shorebirds varies between species (Staaland, 1967). The common ringed plover *(Charadrius hiaticula)* has a comparatively large gland, which may allow it greater flexibility in habitats with increasing wetland salinisation (Rubega & Robinson, 1997). Killdeer *(Charadrius vociferus)* were not included in Staaland's study, but appear to be tied to freshwater (Plissner, Oring, & Haig, 2000). It may be that freshwater is not an absolute requirement for adult plovers but confers an advantage in that salt gland use imposes high metabolic energy demands.

While it remains unproven that access to freshwater is essential for the survival of Charadrius plover chicks, the availability and quality of freshwater are important factors to consider in a conservation setting. In Chapter Three, I explore the possibility that the artificial provisioning of fresh water on Motutapu might increase tūturuatu chick survival rates.

1.2 AN INTRODUCTION TO THE BEHAVIOUR OF CHARADRIUS PLOVERS

The breeding systems and breeding behaviour of Charadrius plovers

Breeding systems

Most Charadrius plover species (77%) are monogamous, both socially and genetically, and they exhibit biparental care during incubation and brooding; 18% are polygamous or exhibit uniparental care; and the remaining 5% are of unknown status due to insufficient study (Eberhart-Phillips, 2019). Phylogenetic analysis suggests that monogamy and biparental care are the ancestral states of Charadrius plovers (Reynolds & Székely, 1997), and this applies to all five species endemic to Aotearoa. However, plover breeding systems and parental care behaviour are diverse with both inter- and intra-specific variation documented (Eberhart-Phillips, 2019), a flexibility facilitated by the precocial state of their young (Thomas & Székely, 2005). Where polygamy and uniparental care do occur, it is usually the female that deserts the chicks to pursue further mating opportunities, leaving the male to raise the brood (Stenzel & Page, 2019).

The adult sex ratio

An unbalanced adult sex ratio (ASR) can result from differential mortality at various life-cycle stages. Differential chick mortality leading to a male-biased ASR was observed in two years out of a three year study in Great Lakes piping plovers *(Charadrius melodus)* (S. Saunders & Cuthbert, 2015). Differential adult mortality leading to a male-biased ASR has been observed in polyandrous populations of snowy plover *(Charadrius alexandrinus)* (Stenzel et al., 2011). However, Eberhart-Phillips et al. consider that ASR variation within plover populations is primarily the result of sex-biased apparent survival of juvenile birds with more female juveniles lost either through dispersal or mortality (Eberhart-Phillips, et al., 2017). The tūturuatu population on Motutapu had a strongly male-biased ASR, which contrasts with the larger remnant population on Hokorereoro where the sex ratio was consistently close to parity in all age groups (A. Davis, 1994a).

Sexual dimorphism

Sexual dimorphism in plovers is more exaggerated in polygamous taxa than in monogamous taxa (Argüelles-Ticó et al., 2016). Sexual dimorphism is also thought to be correlated with sex differences in parental care in which brightly plumaged males incubate at night when visual predators are less likely to detect them on the nest (Ekanayake et al., 2015). In tūturuatu, sexual dimorphism is present but subtle, reflecting the tendency to a monogamous breeding system. Nevertheless, Davis observed that males do most of the nocturnal incubation (A. Davis, 1994b).

Breeding season behaviour

Charadrius plovers are relatively long-lived birds with low recruitment rates. Most species studied have a maximum longevity of 12–17 years. Many plover species exhibit high inter-year site and mate fidelity, with site fidelity reportedly higher in males than females for some species (Stenzel & Page, 2019). The breeding season for tūturuatu occurs over the Austral summer from October to March. The (presumably interrelated) phenomena of breeding site fidelity and mate fidelity appear to influence site selection and pair formation in this species.

Courtship behaviour differs between monogamous and polygamous plovers. A study comparing two closely related plover species; a polygamous population of snowy plovers, and a monogamous population of Kentish plovers (*Charadrius alexandrinus*), showed that both males and females spent more time courting in the polygamous plover population than the monogamous population. In addition, courtship behaviour of males relative to females increased over the breeding season in the polygamous plover population, whereas it did not change in the monogamous population (Carmona-Isunza, Küpper, Serrano-Meneses, & Székely, 2015). In most plover species individuals breed first as yearlings, but this is not the case in wild tūturuatu on Hokorereoro, who breed for the first time at two years old (A. Davis, 1994a). Isolated cases of tūturuatu breeding as yearlings have been documented in translocated populations suggesting that resources on Hokorereoro may be the constraint, rather than physiology (Dowding, Collen, Davis, O'Connor, & Smith, 2005).

The reproductive rates of plovers are low, with small clutches. Tūturuatu usually lay a clutch of three eggs, but occasionally only two. Incubation only begins in earnest after the final egg is laid, even though there can be a considerable interval between eggs; a phenomenon known as "partial incubation" (Wang & Beissinger, 2011). Partial incubation appears to provide excellent hatching synchrony in this species; within each of the clutches observed all chicks hatched within 24 hours of each other. Renesting (the replacement of a clutch after the loss of a clutch or brood) is a common phenomenon in plovers, especially in populations breeding in temperate or tropical regions where nest loss is common and breeding seasons are long (Stenzel & Page, 2019).

Most plover species have minimal nests on the ground in open areas, which appear vulnerable. They rely on crypsis, early visual detection of potential predators, and distraction behaviours to reduce depredation (Stenzel & Page, 2019). Male and female plovers generally share incubation duties, with one parent on the nest most of the time (Eberhart-Phillips, 2019). Sexually dimorphic plover species exhibit a diurnal/nocturnal division of parental incubation, with the more brightly ornamented males incubating at night and females incubating during the day (Ekanayake et al., 2015). Although tūturuatu are only mildly sexually dimorphic, the diurnal/nocturnal division of incubation has been observed (A. Davis, 1994b).

Adult plovers are generally at heightened risk of predation through the breeding season as they are obliged to spend time on the nest, and later, time on the ground attending their brood (Ekanayake et al., 2015). Tūturuatu may be different in this respect because unlike all other plover species, their nests are almost always covered (A. Davis, 1994b; Fleming, 1939) , whether by driftwood, a rock ledge, dense vegetation, or a bank. Under natural conditions this may provide protection from avian predators, but also makes them extremely vulnerable to introduced mammalian predators.

Charadrius plovers are well-known for their distraction behaviours by which they divert the attention of a potential predator away from their clutch or brood, at some risk to themselves (Brunton, 1990; Weston & Elgar, 2005). These distraction behaviours range in intensity from a “rat-run” where the bird extends the wings, lowers the head and tail, and runs erratically in a rapid “zig-zagging” away from the perceived threat, through a “broken-wing display”, to a “dead bird” or “exhausted bird” display, a rarely observed behaviour apparently reserved for the most extreme encounters with predators.

Plover chicks are precocial. They are not fed by their parents but forage for themselves with guidance and protection from their parents until they fledge, and in many species, including tūturuatu, beyond fledging (Stenzel & Page, 2019). The degree of parental cooperation in chick-rearing is generally high but is variable both between and within species. In tūturuatu, both parents are usually highly attentive and guard their brood. Plover chicks are generally described as nidifugous; literally "nest fleeing" (Gochfeld, 1984). My studies revealed that the tūturuatu again is an exception, with the chicks using the covered nest for several days after hatching, presumably for shelter from the weather and refuge from avian predators.

The foraging behaviour of Charadrius plovers and its implications for incubation length, precocial development, and flocking behaviour

Plovers forage visually using a technique variously described as "pause-travel" or "run-stop-run", whereby they scan the area in front of them and peck at the substrate surface when they detect a prey item (Barbosa & Moreno, 1999). Most plovers have short straight bills. The exception is the ngutuparore, a species endemic to Aotearoa which is the only bird with a laterally asymmetric bill; curved to the right at an angle of 15–22° (Johnsgard, 1981).

The characteristic foraging techniques of plovers and sandpipers may explain why plovers have longer incubation periods despite similar egg volumes between the two taxa. Longer incubation in plovers is thought to be necessary for the development of complex neural tissue (the optic tectum) associated with visual foraging behaviour, compared with that necessary for tactile feeding in sandpipers (Nol, 1986).

The characteristic foraging techniques of plovers and sandpipers may also predispose the two taxa to differences in social organisation and dispersal patterns (Barbosa, 1995). Many bird species are advantaged by feeding in groups through increased vigilance for predators, but only when high density is compatible with efficient feeding. This depends on the way in which the birds detect their prey (Goss-

Custard, 1976). Plovers are able to scan almost continuously for predators while foraging, unlike other waders that search for food most of the time, whether by visual or tactile means. Charadrius plovers may also be more susceptible to intraspecific interference in feeding than tactile feeders. As a result, plovers tend to form smaller, less dense flocks than sandpipers and can avoid the inherent disadvantages of larger flocks including interference and resource suppression (Colwell, 2010).

1.3 AN INTRODUCTION TO THE CONSERVATION OF CHARADRIUS PLOVERS

Perhaps the most pervasive anthropogenic threat to shorebird populations worldwide is climate change, as it impacts so many different aspects of their ecology. Charadrius plover species occupy shoreline regions, a habitat at the interface of aquatic and terrestrial environments. This puts them in the position of being both severely threatened by climate change, but also a useful indicator of the health of the shorelines of the world (Haig, 2019). As a group, they are sensitive to water quality in both saltwater and freshwater settings. Ocean acidification and freshwater salinity are two major threats to their survival, but climate change also directly threatens their physical environment as sea levels rise and storm events increase in frequency and severity. Shorebirds in general appear to be faring poorly. A large-scale aerial shorebird survey that sampled about a third of the Australian continent from 1983–2006 found population decreases of 73% for migratory birds and 81% for resident birds. Worldwide trend data of 237 populations showed 52% in decline, and only 8% increasing (Nebel, Porter, & Kingsford, 2008).

Global climate change

Human population growth and industrial development have rapidly increased greenhouse gas emissions, with the result that the temperature of combined land and ocean surfaces increased by 0.85°C between 1880 and 2012 (IPPC, 2014). The higher temperatures and more extreme variation associated with global climate change directly threaten the thermoregulation of birds and clutches of eggs. They also contribute to the spread of algal species which can restrict shorebird foraging habitat by reducing their benthic prey. More dramatically, algal proliferation can cause toxic algal blooms which threaten waders both directly and through bioaccumulation in filter-feeding prey (Landsberg, 2002). In Aotearoa, this effect is more likely to be seen in those Charadrius plover species utilising inland habitats: the pohowera and ngutuparore. The southern species of tūturiwhatu also nests inland but migrates to coastal areas outside the breeding season (Dowding, 1994). The northern species of tūturiwhatu and the tūturuatu are primarily coastal dwellers, but still rely on clean freshwater for grooming and probably for hydration of young chicks.

Because warming trends are stronger over continental interiors than over oceans, the atmospheric pressure gradients and thus wind fields along ocean margins are intensifying (Harley et al., 2006). More frequent and intense winds, floods, and storm events threaten shorebirds in general, but particularly the vital nesting stage of coastal-nesting birds (Galbraith, DesRochers, Brown, & Reed, 2014). This is mitigated only partially by their ability to re-nest if a nest is lost early in the breeding season (Colwell & Haig, 2019b). Nesting tūturuatu and (northern) tūturiwhatu are certainly threatened by flood and storm events as they routinely nest just above the normal high tide mark and sometimes adjacent to streams. In my study I observed the effects of tidal surges and a flooded stream first-hand (see Chapter Three).

An added component to the threat of warming seas is that ocean chemistry is changing rapidly. Ocean acidification threatens the calcifying ability of many aquatic invertebrates that provide an important food source for shorebirds. This is an example of the changes in ocean chemistry that some researchers consider may be more important than changes in temperature for the performance and survival of many organisms (Harley et al., 2006). Beaches will be affected by changing ocean chemistry as they are “subsidised ecosystems”. There is very low primary production on sandy and rocky shores; these areas rely on imports of organic material from the sea to sustain terrestrial invertebrate populations that are another major food source for Charadrius plovers (Cuttriss, Weston, Maguire, & Ehmke, 2015). This has led to a novel suggestion to add “wrack” to the upper beach area for threatened populations, in addition to more conventional conservation actions (Schlacher et al., 2017). This suggestion is the exact opposite of the normal management practice for popular beaches in Aotearoa of “cleaning” the beach by removing clumps of seaweed.

Wildfires increasingly threaten birds and nests as the frequency and size of fires are worsened by climate change. This is perhaps one area where birds that feed and nest on the shore have a natural advantage over inland species. It has however been identified by the Department of Conservation (hereafter DOC) in Aotearoa as a specific risk to the remnant population of tūturuatu on Hokorereoro. (DOC, 2001).

Changes in the phenology and distribution of prey species, vegetation, and disease are expected as the climate continues to change (Machin et al., 2017). Migratory species such as Arctic nesting Charadrius plovers have already been observed nesting further north than they did historically (Both & Visser, 2001; Durant, Hjermann, Ottersen, & Stenseth, 2007; Hughes, 2000; Visser & Both, 2005). Non-migratory species like the tūturuatu may be more susceptible to phenological mismatch as they are less able to shift their range. Conversely, it has been argued that the consequences of climate change are most severe for long-distance migrants in seasonal habitats (Both et al., 2010). As mentioned earlier, plover species may present a special case in the phenological mismatch between demand and availability of food because the precocial chicks are likely to require different invertebrate prey species than adult birds (Machin et al., 2017).

Climate change also tends to decrease flow rates of freshwater systems leading to poorer water quality in general and increased salinity in particular (Haig, 2019). The drying up of some waterways, and the reduction in water quality of others has the effect of compounding the habitat loss and degradation caused by anthropogenic climate change and land-use changes. The main impact on Charadrius plovers is expected to occur during the breeding season. As previously discussed, shorebird chicks are thought to suffer severe adverse effects without access to freshwater. Adult birds may also suffer adverse effects, as the use of salt glands imposes high metabolic demands and is limited in its ability to regulate osmolality; the concentration of solutes in the plasma (Hannam et al., 2003). In areas where natural freshwater access cannot be maintained or restored it may become necessary to provide artificial sources to the breeding areas of endangered plover species.

Habitat loss and degradation

Habitat loss and degradation can be caused by global climate change but also by changes in anthropogenic land use. Sea level rise from melting polar ice caps and from thermal expansion of the oceans directly threatens the coastal habitat of shorebirds, altering or even eliminating shorebird nesting and feeding habitats (Galbraith et al., 2014; Galbraith et al., 2002; Sutherland et al., 2012). Warmer sea surface temperatures in the arctic are thought to have interacted with sea-level rise and windier conditions to have dramatically increased erosion, exacerbating the problem of coastal habitat loss (B. Jones et al., 2009).

Habitat loss and climate change also interact in the sense that a population constrained by limited habitat is more acutely threatened by adverse events triggered by climate change. As an example, the entire world population of tūturuatu in the late 1990s was restricted to the 218ha island of Hokorereoro in the Chatham Islands group. This extreme habitat limitation increased the risk imposed by other climate change mediated effects, such as fires, flooding, disease, freshwater scarcity, failing food supply, and algal blooms. Any one of these events, or indeed a combination, would have risked their extinction (Dowding & O'Connor, 2013).

Apart from climate change, the main cause of habitat loss globally is the change in anthropogenic land use: roading, urbanisation, drainage, and reclamation. For example, MacKinnon et al. (MacKinnon, Verkuil, & Murray, 2012) estimated that over the last fifty years, more than a million hectares of China’s tidal flats, and over half of coastal wetlands have been lost to agriculture, aquaculture, salt production, construction of ports and cities, and tidal energy projects. This has led to observed declines of shorebird populations of 5–9% per year. This may seem far removed from the challenges facing charadrid plovers and other shorebirds in Australia and

Aotearoa, but several species that breed in Australasia, such as the kuaka (bar-tailed godwit, *Limosa lapponica*) migrate through China and have been directly affected by these changes. More broadly, these observations are a reminder that the growth of human populations and industrialisation – the main drivers of climate change – are also the main drivers of habitat loss and degradation.

Habitat degradation can also occur through coastal pollution, specifically eutrophication, chemical contamination, and microplastic accumulation. Research on shorebird eggs in Alaska found relatively low levels of contaminants but raised concerns that several organic and inorganic contaminants including strontium were present at higher levels than in previous studies (Saalfeld et al., 2016). Aotearoa and the southern hemisphere in general are less industrialised than the northern hemisphere, but chemical pollution does occur locally, including in the relatively shallow waters of the Hauraki Gulf. Shorebirds including tūturuatu are vulnerable to contaminant exposure as they forage on invertebrates in wetlands and harbours where contaminants accumulate in sediments. A recent study on American oystercatchers *(Haematopus palliatus)* in Brazil found that all animals examined had evidence of synthetic materials in their stomach contents, most commonly plastic fragments, and pellets. The health complications of microplastic ingestion include blockage of the digestive tract, physical damage from sharp-edged fragments, and reduction in digestive tract volume. There is also a risk that synthetic material may contain chemical contaminants that are absorbed by the bird after ingestion (Rossi, Scherer, & Petry, 2019). I am unaware of similar studies in Aotearoa, but it is probable that our endemic oystercatcher, the tōrea-pango *(Haematopus unicolor)* is also exposed to microplastic contamination. The tūturuatu, and another threatened endemic plover species the tūturiwhatu, share habitat and associate closely with tōrea-pango, raising the possibility that they too could be exposed. Microplastic pollution is a global problem, and its harmful effects are unlikely to be confined to one region or a single taxon of shorebirds.

Disturbance events

In the western world, beach living, holidaying, and recreation have become an important part of the leisure lifestyle and the global tourist economy. The physical loss of plover habitat is exacerbated by human-related disturbance in shore-dwelling and particularly in shore-nesting species (Weston, 2019). Much of the research published on this topic is from Australia where beach culture is prominent and the human population is concentrated near the coast, but it is relevant to coastal areas around the world including the habitat of tūturuatu and tūturiwhatu in Aotearoa.

It is unfortunate that the breeding season for charadrid plovers in temperate regions coincides with peak visitor numbers over summer. Climate change may exacerbate this effect as warmer temperatures will likely bring more people to beaches that were otherwise occupied by plovers and other waders (Coombes, Jones, & Sutherland, 2008). In the nesting phase of the breeding season, some forms of disturbance are more likely to cause nest absence or cause a longer duration of nest absence than others. People walking or jogging down a beach cause shorter nest absences than “static disturbance” described as people sunbathing, angling, or picnicking (Weston, Ehmke, & Maguire, 2011). Joggers with or without a dog, and walkers with a dog off-leash caused more nest absences in hooded plover than people walking down a beach (Weston & Elgar, 2007). Disturbance during the chick-rearing phase of the breeding season may separate parents from chicks, reducing brooding and thermoregulation, and risking opportunistic predation of chicks. Disturbance also forces chicks into hiding, which if prolonged, interferes with their foraging time.

Large numbers of people on a beach can also decrease plover’s access to their food supply by trampling the sand (Schlacher et al., 2016). Beach management practices common in Australia and Aotearoa such as beach grooming (removing sea-weed) and construction of sea walls are also likely to decrease the suitability of beaches for plover breeding (Cuttriss et al., 2015).

Human-related disturbance to tūturuatu is minimal on two of the islands they currently inhabit. Hokorereoro is very remote, uninhabited, and a designated Nature Reserve with access limited to permit holders. Waikawa Island is privately owned but relatively remote and rarely visited by the public. Motutapu, by contrast, is a public reserve accessed by a ferry service or from private boats and is frequently visited especially during the summer breeding season. This is also true of other islands in the Hauraki Gulf that it is hoped may be colonised by tūturuatu as they breed and disperse from Motutapu.

Human-related disturbance events are likely to be more severe at high tide when the available beach area is much smaller, effectively concentrating the number of humans, dogs, or vehicles. Tūturuatu and tūturiwhatu nest near the high tide mark, and this is also the area where their chicks shelter for much of the time. They are vulnerable to human-related disturbance during the breeding season but particularly at high tide. Conservation management strategies could conceivably incorporate fencing and signage to direct the public away from high tide areas during the shorebird breeding season. Visual delineation of nest areas with the temporary installation of electric fence standards and tape (also known as “symbolic fencing”) is currently practiced on some beaches in Aotearoa including on Motutapu, and seasonal dog exclusions are practiced on many beaches. Dogs are banned all year round on Motutapu and adjoining Rangitoto Island, and while breaches certainly occur, they are unusual in the main tūturuatu and tūturiwhatu nesting areas.

Disturbance events are not just human-related: they can be caused by conspecifics, competitive species, and potential predators. While disturbance events are often brief, the display behaviours they elicit are highly energetic activities, often involving running or flying (see Chapter Two). My studies showed that most of the disturbance events affecting tūturuatu during the breeding season are caused by other tūturuatu and by tūturiwhatu; a competitive endemic Charadrius plover species. While these could be considered natural events, it is the reduced availability of suitable habitat through loss or degradation that leads to more disturbance overall.

Introduced mammalian predators

In Aotearoa and other relatively recently settled island habitats, even the pervasive threats of climate change and habitat loss are eclipsed by a more immediately devastating anthropogenic change: the introduction of new organisms that compete with or predate endemic species. This is a problem shared by just a handful of the Charadrius plovers. The birds of Aotearoa evolved in the absence of mammalian predators in the 82 million years since separation from the rest of Gondwana. Aotearoa was the last sizable landmass on the planet to be settled by humans and their attendant mammals. Pacific settlers introduced the kiore (Pacific rat, *Rattus exulans*) and kurī (Pacific dog, *Canis familiaris*) probably in the early 14th century (Walter, Buckley, Jacomb, & Matisoo-Smith, 2017), and many more species of mammalian predator accompanied European settlement in the 18th and 19th centuries. These included the domestic cat (*Felis catus*), the Norway rat *(Rattus* *norvegicus*), the ship rat *(Rattus rattus)*, the brushtail possum *(Trichosurus vulpecula)*, the hedgehog *(Erinaceus europaeus occidentalis)*, and three species of mustelid: the ferret *(Mustela furo),* stoat *(Mustela erminea)* and weasel *(Mustela nivalis).* These mammalian predators thrived in Aotearoa and decimated the endemic fauna as they spread. Of the 93 endemic species of land, freshwater and coastal birds present when humans arrived in Aotearoa, 43 are now extinct, and an estimated 29% of the remaining native or endemic bird species are currently classified as threatened (Dowding & Murphy, 2001).

Aotearoa is an archipelago of around 600 islands, which fortunately has provided some conservation opportunities. Some islands remained free of certain mammalian predators as an accident of history. The remote island of Hokorereoro in the Chatham Islands group, the last refuge of the tūturuatu, is a prime example of this as it appears never to have been invaded by any mammalian predators. On other islands more recent introductions have displaced earlier ones, for example the two rat species introduced by Europeans, the Norway rat and the ship rat, have largely displaced the kiore throughout Aotearoa. Since the 1950s the development of aerial toxin application strategies has allowed the eradication of more than 180 populations of fourteen introduced mammalian species from over 100 islands. The conjoined islands of Rangitoto and Motutapu are an example, being declared “pest-free” in 2011 (Griffiths et al., 2015). More recently the same techniques have been used to eradicate introduced mammals from “mainland islands” protected by predator-proof fences. Once “pest-free” status is achieved, major efforts in biosecurity and detection of incursions are required to maintain it. Traps to detect and kill mammalian predators are routinely deployed near the coastlines of “pest-free” islands and the periphery of “mainland islands”, with baited camera traps and specially trained dogs deployed in the case of a suspected incursion. Rats and mice are common stowaways on boats, and even more concerning are stoats, which are strong swimmers, able to colonise islands unaided. A recent survey recorded at least 84 cases of unassisted visits of stoats to islands up to about 3.0 km offshore (Veale, Hannaford, Russell, & Clout, 2012), and a stoat has been shown to swim 1.8 km in an experimental situation (King, Veale, Patty, & Hayward, 2014).

Control and elimination strategies are backed by a large research effort aimed at improving the safety and efficacy of existing methods and developing new ones, such as gene drive technology. New technologies will be required to reach the "Predator Free 2050" target supported by the major political parties in Aotearoa, which aims to rid the entire country of the worst of the introduced predators; rats, possums, and stoats by 2050 (Murphy, Russell, Broome, Ryan, & Dowding, 2019). Despite efforts by DOC and community groups, the endemic Charadrius plovers in Aotearoa are not faring well; the five currently recognised species are all listed as "Near Threatened", "Vulnerable", "Endangered", or "Critically Endangered" by the IUCN (IUCN, 2021).

Introduced and subsidised native avian competitors and predators

The presence of introduced mammalian predators on remote islands is a widely canvassed subject and the focus of much conservation effort. In Aotearoa, the issue is compounded by the introduction of avian species that may interact with endemic species as predators or competitors. Widespread landscape alteration (primarily forest clearing by fire) began with Polynesian settlement, accelerated after European settlement, and is still occurring today. The new landscapes allowed the self-introduction and successful establishment of species such as the kāhu (swamp harrier, *Circus approximans*) (Worthy & Holdaway, 1996), which was confirmed as a predator of tūturuatu during my research. Many other avian species were introduced deliberately such as the Australian magpie *(Gymnorhina tibicen)*, which was also confirmed as a predator of tūturuatu during my research.

The anthropogenically modified landscapes also altered the habitat and resources available to endemic species. In most cases the impact was negative, but some species were subsidised by the new conditions. The subsidisation of predators occurs when humans alter resource availability enabling the density of a predator population to increase above levels that would occur without the additional resources (Gompper & Vanak, 2008). Subsidised predators can drastically impact a prey population because subsidies insulate the predator population from the effect of decline in the prey population (Sinclair et al., 1998). One example of a subsidised native avian predator in Aotearoa is the karoro (southern black-backed gull, *Larus dominicanus*). My observations suggest that karoro are usually a peaceful neighbour of tūturuatu, however, they remain a potential threat as they have been known to predate tūturiwhatu chicks (Sibson, 1967).

Where introduced mammalian predators are absent, as is the case on the four islands currently supporting tūturuatu populations: Hokorereoro, Maung’ Rē, Waikawa, and Motutapu, avian competition and predation become more important influences on the factors that determine population viability: productivity, adult mortality, and juvenile dispersal (Colwell, 2019).

Tūturuatu evolved in a very different world from the one they inhabit today. They were already considered “very rare” in the 1840s (J. Richardson & Gray, 1845) during the early phase of European settlement (see Chapter Four), presumably from the combined effects of hunting, predation by kurī and especially kiore, and predation by avian species self-introduced into altered landscapes. Their survival as a species occurred through the chance absence of all these threats on the remote island of Hokorereoro in the Chatham Islands archipelago, botanically and zoologically one of the most important biological provinces of the New Zealand region (Fleming, 1939).

1.4 RESEARCH AIMS

Tūturuatu have an entire species population estimate of 240 (DOC, 2019). The population, along with many other plover species, is susceptible to the general threats outlined earlier in this chapter. The IUCN status of the species is “Endangered” (IUCN, 2021). The national Threat Classification System lists the species as: Threatened (Nationally Critical) with the qualifiers: Conservation Dependent, Climate Impact, Conservation Research Needed, Increasing, Range Restricted, and Biologically Sparse (Robertson et al., 2021). The remnant population of 45 breeding pairs of tūturuatu on Hokorereoro in the Chatham Islands of Aotearoa is stable but constrained by the very small habitat of 218 hectares. It has also been identified as being specifically at risk from adverse events such as mammalian predator introduction, flooding, fire, and disease (DOC, 2001).

Captive breeding and “reintroduction” of tūturuatu to islands free of introduced mammalian predators were identified as key strategies in the conservation of the species (DOC, 2001). Translocation has been attempted on six islands with successful establishment and persistence on two at present. Maung’ Rē, a small island approximately ten kilometres from Hokorereoro now has a small stable population of ten breeding pairs, and Waikawa off the east coast of Te Ika-a-Māui has a population of twenty breeding pairs. The habitat on Waikawa appears to be suitable for the population to establish and grow, but unfortunately it is very close to the mainland and susceptible to mammalian predator incursion. The population has had gains and losses over the years, depending on the absence or presence of rats on the island.

This study investigated a small population of tūturuatu on Motutapu, a "pest-free" island in the Hauraki Gulf close to the city of Tāmaki Makaurau. The eighteen resident tūturuatu were either survivors of or descended from 92 captive-bred juveniles successively released on the island between 2012 and 2018. The tūturuatu population on Motutapu has established but failed to grow as well as the population on Waikawa. The reasons for this were largely unknown. My study focused on behavioural ecology during the breeding season. Charadrius plovers are relatively long-lived birds with low recruitment rates (Colwell & Haig, 2019a), and chick mortality had previously been suspected as a constraint to population growth (J. E. Dowding, personal communication, 2018). In addition, adult plovers are generally thought to be at heightened risk of predation throughout the breeding season as they are obliged to spend time on the nest, and later, time on the ground attending their brood (Ekanayake et al., 2015). A better understanding of tūturuatu breeding season behavioural ecology therefore offers the potential to inform conservation and management efforts to improve both recruitment rates, and adult survival rates. The aim of my research was to contribute to this understanding by investigating **breeding season behaviour** (presented in Chapter Two) and factors affecting **reproductive success** (presented in Chapter Three). I also investigated **dispersal after translocation** (presented in Chapter Four).

In a more general sense, the aim of my project was to contribute to the global research effort into the behaviour and ecology of Charadrius plovers, which has historically been heavily biased towards northern hemisphere species. In a recent review, Haig and Colwell found that over a third of scientific publications on the 40 plover species focused on just three species: piping, snowy and Kentish plovers, and that over two-thirds of publications focused on just twelve species. Most plover species are virtually unstudied, especially in areas where conservation needs are most pressing (Haig & Colwell, 2019). This historical bias suggests an urgent need for further study of the behavioural ecology of Charadrid plovers in the southern hemisphere, especially those species or populations under threat.

CHAPTER TWO

Tūturuatu breeding season behaviour

Plate 2.1 Display behaviour between adult male tūturuatu, Motutapu, Aotearoa. Image credit to Chelsea Ralls.

2.1 INTRODUCTION

Shorebirds allocate varying amounts of time and energy to essential behaviours. These patterns of daily behaviour can be summarized in a time budget (Colwell, 2010). Time budget construction enables the quantitative description of the behaviour of an animal, or more typically a group of animals. This allows the comparison of behaviour between different groups, such as different taxa, sexes, ages, or geographically distinct populations. It also allows the temporal comparison of the behaviour of a single population, such as between seasonal phases, circadian phases or circa tidal phases. Time budget construction may be useful to inform conservation and wildlife management decisions. As a simple example, the proportion of available time spent foraging would be expected to increase if food is limited. Conversely, if suitable food is readily available, foraging time should be reduced (Nol, 2019). This information could be used to compare the adequacy of food resources between different areas of habitat, or for different age groups, sexes, or phases of the breeding season. It could also be used to track the adequacy of food resources over time in response to climate change, ocean acidification or pollution.

Charadrius plovers are relatively long-lived birds with low recruitment rates. Most species that have been studied show a maximum longevity of 12–17 years. In a population of ngutuparore (wrybill*, Anarhynchus frontalis)* in Aotearoa (New Zealand) 165 individuals, approximately 3.5% of the total population, reached at least 12 years of age (Dinsmore, 2019). The oldest recorded tūturuatu (tchūriwat’, shore plover, *Thinornis novaeseelandiae*) was 17 years of age (A. Davis, 1994a). Most plover species have minimal nests on the ground in open areas that appear vulnerable to predation or disturbance. They rely on crypsis, early visual detection of potential predators, and distraction behaviours to reduce nest depredation (Stenzel & Page, 2019). Male and female plovers generally share incubation duties, with one parent on the nest most of the time (Eberhart-Phillips, 2019). Sexually dimorphic plover species exhibit a diurnal/nocturnal division of parental incubation, with the more brightly ornamented males incubating at night and females incubating during the day (Ekanayake et al., 2015). Although tūturuatu are only mildly sexually dimorphic, the diurnal/nocturnal division of parental incubation has been observed (A. Davis, 1994b).

Adult plovers are generally at heightened risk of predation through the breeding season as they are obliged to spend time on the nest, and later, time on the ground attending their brood (Ekanayake et al., 2015). Tūturuatu may be different in this respect, because unlike all other plover species, their nests are covered (A. Davis, 1994b; Fleming, 1939). This is thought to provide protection from the avian predators found in their natural habitat and may offer advantages for thermoregulation, but also may make them extremely vulnerable to introduced mammalian predators.

Charadrius plovers are well-known for their distraction behaviours, by which they divert the attention of a potential predator away from their clutch or brood at some risk to themselves (Brunton, 1990; Weston & Elgar, 2005). The displays are primarily visual, so unsurprisingly are given only during daylight hours (Weston, 2019). Displaying plovers appear to monitor the response to their display, adjusting their behaviour when they are not followed (Ristau, 1992). I considered distraction behaviours as part of a continuum of tūturuatu responses to disturbance that I described as “display behaviour”.

Many plover species exhibit high inter-year fidelity of adults to breeding sites and mates, with site fidelity reportedly higher in males than females for some species (Stenzel & Page, 2019). For example, experienced male pohowera (double-banded plover*, Charadrius bicinctus*) nested an average of 42 m from the previous year's nest site, while females averaged 126 m (Pierce, 1989). The breeding season for tūturuatu occurs over the Austral summer from October to March. The (presumably interrelated) phenomena of breeding site fidelity and mate fidelity appear to influence site selection and pair formation in this species (H. Speed, personal communication, 2020).

Most plovers nest in open habitats with little vegetation (Stenzel & Page, 2019), which is thought to facilitate early predator detection (Muir & Colwell, 2010). The one true exception is the tūturuatu, whose nest is almost always covered, whether by driftwood, a rock ledge, dense vegetation, or a bank. To form the nest a plover rests its breast on the ground and rotates with body slanting up and tail raised, as it kicks to form a shallow cup on the ground. "This "scraping" behaviour is thought to be important in most plover species and may be linked to courtship and nest-site selection, although the details vary between species (Phillips, 1980; Stenzel & Page, 2019). Scraping behaviour has been described in tūturuatu on Hokorereoro (Rangatira, South East Island) (A. Davis, 1994b).

The reproductive rates of plovers are low, with small clutches. Tūturuatu sometimes lay a clutch of two eggs, but more normally lay three. Incubation only begins in earnest after the final egg is laid, even though there can be a considerable interval between eggs. This phenomenon, known as "partial incubation", is thought to contribute to hatching synchrony (Wang & Beissinger, 2011). Davis calculated a mean laying time of 4.1 (SD = 0.6) days (n = 20) per egg for tūturuatu (A. Davis, 1994b). Renesting (the replacement of a clutch after the loss of a clutch or brood) is a common phenomenon in plovers, especially in populations breeding in temperate or tropical regions where nest loss is common and breeding seasons are long (Stenzel & Page, 2019)

Plover chicks are precocial and nidifugous (Colwell & Haig, 2019a). They are not fed by their parents but are nurtured and protected by them as they learn to forage efficiently. Parental care continues until they fledge, and in many species, including tūturuatu, even beyond fledging (Stenzel & Page, 2019). The division of brood rearing duties between male and female plovers varies, with bi-parental care most common followed by male-biased care and very occasionally by female-biased care (Stenzel & Page, 2019). In tūturuatu, both parents are usually highly attentive and guarding of their brood. Davis reported female tūturuatu tending their brood in 83% of observations, compared with 62% in males (A. Davis, 1994b). Some species exhibit flexibility in their division of parental care (Eberhart-Phillips, 2019; Kosztolányi, Székely, Cuthill, Yilmaz, & Berberoğlu, 2006). Plover chicks rely on crypsis and immobility to avoid predation but remain extremely vulnerable until they are able to fly.

In most plover species individuals breed first as yearlings, but this is not the case in wild tūturuatu, which breed first at two years old (A. Davis, 1994a). Tūturuatu were observed to be single-brooded in the wild, possibly due to habitat constraints on Hokorereoro (A. Davis, 1994b), although they can produce several broods per season in captivity (DOC, 2019).

Aspects of tūturuatu behaviour have previously been described by Charles Fleming who visited Hokorereoro in 1937, Richard Phillips who visited in 1972 and Alison Davis who studied the same population in 1984/85 and 1986/7. Fleming visited for two weeks in December at the height of the nesting season and described courtship behaviour, nesting sites, and display behaviour including the “broken wing” display. He described parental care of newly hatched chicks and witnessed chick predation by tarāpunga (red-billed gull, *Larus novaehollandiae*) (Fleming, 1939). Phillips visited the island outside the breeding season and described the habitat, pairing, aggressive behaviour, feeding, reaction to predators and vocalisations. He recorded a number of audio-spectrograms of calls (Phillips, 1972, 1977, 1980). Davis observed all birds in each of three areas for 12 hours twice monthly during two breeding seasons. She described territory formation, mate and site fidelity, courtship, nest-building, laying and incubation, hatching and rearing of chicks, and chick survival (A. Davis, 1987, 1994a, 1994b).

2.2 RESEARCH AIMS

My study investigated a small, translocated population of tūturuatu on Motutapu, a “pest-free” island in the Hauraki Gulf close to the city of Tāmaki Makaurau (Auckland). The tūturuatu population on Motutapu has established but failed to grow over the last 10 years. The reasons for this were largely unknown.

My study focused on behavioural ecology during the breeding season, using direct observation and trail camera recordings of tūturuatu nest sites, territories, and surrounding areas including construction of time budgets to allow comparison with other populations. Chick mortality has previously been suspected as a constraint to population growth of tūturuatu on Motutapu (J. E. Dowding, personal communication, 2018). In addition, adult plovers are generally thought to be at heightened risk of predation throughout the breeding season as they are obliged to spend time on the nest, and later, time on the ground attending their brood (Ekanayake et al., 2015).

For these reasons it was hoped that a better understanding of tūturuatu behavioural ecology during the breeding season would offer the potential to improve both recruitment rates and adult survival rates, and generally better inform the conservation and management of one of Aotearoa's most threatened species.

2.3 METHODS

Study area and population

Field studies were conducted on Motutapu, a 1509-hectare island in the inner Hauraki Gulf. The study population was a group of 18 tūturuatu; 11 males, six females and one juvenile bird. The resident tūturuatu were either survivors of or descended from 92 captive-bred juveniles successively released on the island since 2012.

Motutapu, which can be translated as "Sacred Island", and the adjoining Rangitoto Island are public reserves managed by the Department of Conservation (hereafter DOC) with guidance from Ngā Mana Whenua – the local people of the area with customary rights over the land, and the DOC appointed Tāmaki Makaurau Conservation Board. There is also considerable input from a community group; the Motutapu Restoration Trust.

Motutapu and Rangitoto Island were declared "pest-free" by DOC in August 2011 following extensive eradication programs including three aerial drops of brodifacoum in winter 2009. All introduced mammalian predator species, including rats, mice, and cats were successfully removed in this process. Robust surveillance and counter-incursion procedures, including the use of specially trained dogs, provide assurance that the islands remain "pest-free". Motutapu, Rangitoto and other “pest-free” islands offer a sanctuary to endemic species that have become endangered or extinct on the other larger islands of the country.

Pre- and post-breeding season surveys

Pre- and post-breeding season surveys of the tūturuatu population were undertaken on Motutapu and three neighbouring islands: Motuihe, Motukorea and Rangitoto (see Plate 2.2).

Plate 2.2 Islands surveyed during pre- and post-breeding surveys. Yellow lines show the beaches searched during each survey.

Each survey was undertaken within two hours of high tide with observers put ashore at each island before the synchronised survey. Observers walked the beaches and noted the presence of tūturuatu and tūturiwhatu (northern red-breasted dotterel, *Charadrius aquilonius*). The location and colour-band combination of the birds were recorded. All the tūturuatu except one adult and one juvenile had individual colour-band combinations on the tarsus, so all were individually recognisable.

Twelve observers took part in each survey. Each observer surveyed several beaches, and each beach was surveyed by at least two observers. The pre-breeding-season survey was undertaken on 12th September 2018 with the high tide at 8:54 am. The post-breeding-season survey was undertaken on 23rd May 2019 with the high tide at 10:18 am. The beaches on Motutapu most favoured by tūturuatu (Gardiner Gap, Islington Bay, West Point, Pig Bay, and Sandy Bay – see Plate 2.3) were checked for several days after each survey to identify any individuals that might have been missed on the day.

Location of breeding pairs and their nests

From mid-September 2018, tūturuatu exhibiting behaviour suggestive of courtship, nest-building or territorial defence were monitored at least twice a week to identify pairs and potential nest locations. Breeding sites in the previous breeding season (2017/18) had been on the four beaches mentioned above on the west coast of Motutapu from Gardiner Gap to Sandy Bay – a distance of five kilometres (see Plate 2.3). Another site at Waikarapupu in the north had been occupied in the 2016/17 breeding season. High site and partner fidelity were expected, although several sites had been extensively modified by flood events, and I anticipated that new pairs could have formed since the previous breeding season.

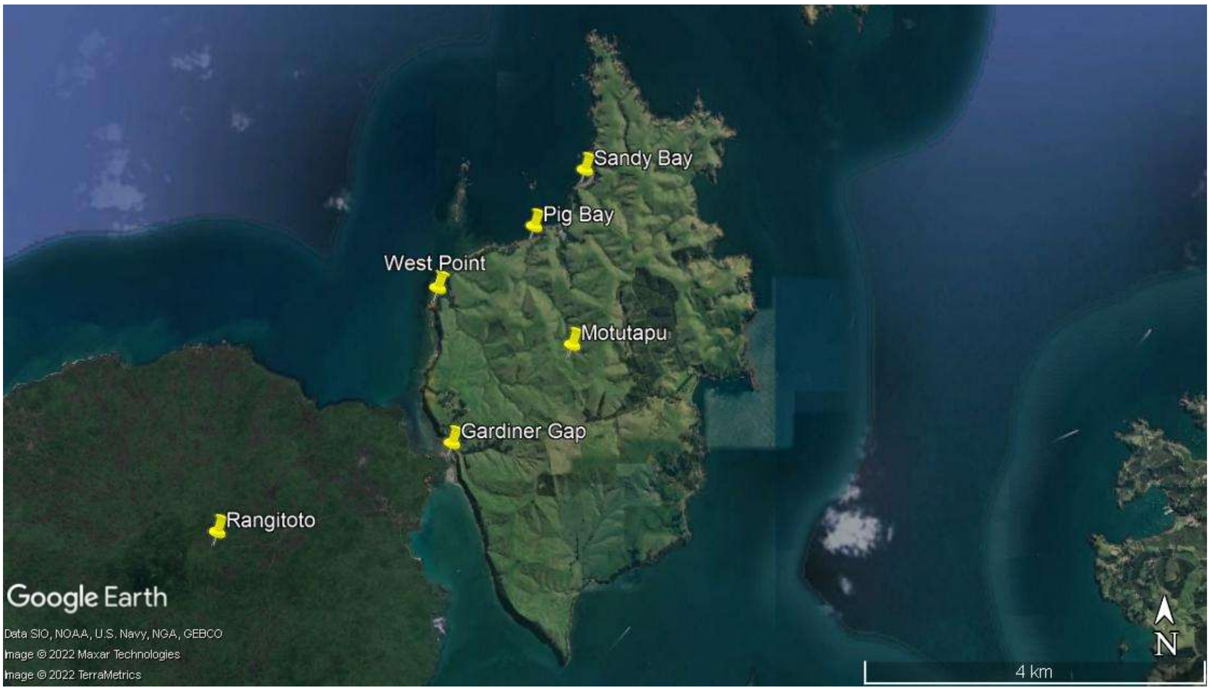

Plate 2.3 Tūturuatu breeding areas on Motutapu.

Nests were located by observing birds return to them from a distant concealed position. Egg laying dates were estimated from behavioural changes or the discovery of nests with incomplete clutches. All potential breeding habitat on Motutapu and Rangitoto was checked in September and October to try to locate all breeding pairs and sites. After losing nests, clutches, or broods, pairs were similarly monitored for replacement clutches.

Focal instantaneous sampling of behavioural states of tūturuatu nesting pairs and family groups

All nesting pairs, and their chicks once hatched, were directly observed from a concealed position with a tripod-mounted Konus 80mm spotting scope (20–60X zoom magnification). Observations were also conducted with binoculars (observers own, various brands, 10X magnification), and with the naked eye. Observers comprised myself, a succession of volunteers (including some DOC staff), and a

DOC summer intern. Observer training was conducted by me. It comprised a theory session (see Appendix B: “Advice and priorities for Tūturuatu (Shore Plover) Volunteers” and Appendix C: “Map and Species Information”), and practical sessions when I accompanied them on their first two two-hour observation periods. Health and safety briefings were conducted by Hazel Speed, a DOC ranger on the island.

A focal sampling technique was used to observe the behavioural states of a pair or family of tūturuatu. Observations were made on a daily basis and covered the entire period from the discovery of a clutch of eggs to chick fledging or disappearance. Observations were for two-hour periods at set times of the day, with the aim of varying observation times with respect to the tide. Observations were occasionally curtailed in bad weather out of concern for the safety of clutches or broods. I decided that any suggestion of observer disturbance resulting in decreased nest or brood attendance and potentially in hypothermia would be unacceptable. While this decision may have reduced the representativeness of my observations, it is an example of one of the many constraints encountered when conducting research on a highly endangered species.

Plate 2.4 Spotting telescope at the southern end of Pig Bay. A fenced-off nest area can be seen in the mid-ground.

Instantaneous sampling every 2 minutes was used to quantify the behavioural states that cover most aspects of tūturuatu behaviour. A standardised data sheet (see Appendix A) was used to directly record behavioural observations with categories based on previous studies of tūturuatu (A. Davis, 1987, 1994b), (J. E. Dowding, personal communication, 2018). The following categories were recorded:

Inactive

"Inactive" denoted a lack of movement regardless of the assumed intention. It included rest after activity, but also immobility to afford crypsis, sheltering from wind and rain, and assumed "guarding" or "sentry" behaviour characterised by immobility with alertness.

Incubating

Incubating behaviour was never observed directly as all nests were completely covered. It was inferred whenever an adult was in the nest in the presence of one or more eggs. On very rare occasions both parents were briefly in the nest together; much more common was a “tag-team” situation where one parent left the nest as the other arrived.

Brooding

I used the term “brooding” to refer to the behaviour of a parent bird when stationary beside their chick or chicks providing warmth and shelter, usually covering them with their wings. I used the same term to apply to the behaviour of the chick being brooded.

Grooming

The “grooming” category referred to two distinct behaviours: the vigorous freshwater bathing seen on occasion, particularly in the pre-nesting phase of the breeding season, and also to preening.

Foraging

“Foraging” was defined as feeding behaviour either while standing still or combined with the various forms of locomotion: hopping, walking, or running. Feeding behaviour includes pecking at the substrate for invertebrates interspersed with short bursts of movement.

Nest-building

This behaviour included carrying building materials (sticks, grass, pebbles, shells, feathers) to the nest, and re-arrangement of building materials in the nest.

Nest-building was observed only in males in the pre-nesting phase of the breeding season. It was always associated with courtship, of which it appeared to be a component. In later analyses, nest-building observations were added in with the "courtship" category.

Courtship

In a typical courtship display observed on Motutapu, the female walked quickly away from the male, stopping after a few steps to head-bob vigorously. The male followed closely behind with his head lowered and his tail raised. As the male arrived behind the female his posture changed as he raised his head higher than normal. On several occasions males were observed to incorporate a brief period of nest-building into this sequence. Courtship displays occurred close to the eventual nesting site. Davis described an initial period of aggression in courtship displays on Hokorereoro where the male lunged repeatedly at the female, which attempted to avoid contact. This was followed by a "flutter" display and a "crouch" display. During a "flutter" display, males and occasionally females faced their potential mate, lowered their heads, lifted their wings in a rapid fluttering movement, and jumped a short distance. The displaying bird called a soft "*wheet-wheet*". The "crouch" display was done mostly by males, which quietly moved up to their potential mate, hunched their body and lowered their head (A. Davis, 1994b).

Mating

During mating, the female stood still while the male stood astride her back moving his legs rapidly up and down in a "running on the spot" action. Davis described a post-copulation display similar to a "flutter" display. The male gave a soft crooning "*kwee-kwee"* call during this display, while the female shook her feathers, preened for a few seconds, and occasionally head-bobbed as she walked away. This display has not, apparently, been reported for other plover species (A. Davis, 1994b).

Locomotion

Adult tūturuatu hopped, walked, or ran to move about the beach or inter-tidal area. These behaviours were initially recorded separately but were pooled for later analysis. The rapid darting nature of their foraging behaviour made running the “default option”. Running was also the form of locomotion most often associated with agonistic interactions and display behaviour.

Flying

Tūturuatu were observed to be strong and swift in the air and flew to foraging or bathing areas but also frequently as an aspect of display activity.

Changes made during the study

Some changes to behavioural categories were made during the study. “Resting” was relabelled “inactive”. Hopping, walking, and running were initially treated as separate behaviours but were later grouped together as “locomotion”, primarily as they were functionally similar. Feeding and walking behaviours were initially recorded separately but “foraging” was quickly adopted as a category that combined the two actions. Foraging behaviour in tūturuatu typically involves rapidly alternating bursts of walking and pecking at prey. Less commonly observed behaviours were not specified in the check list on the data sheet but were simply recorded in writing when they occurred. These behaviours were brooding, grooming, courtship, nest-building, and mating. Nest-building was a rarely observed behaviour displayed only by males during courtship, so later this behaviour was incorporated into the courtship category.

After chick hatching, direct observation with a spotting telescope and binoculars continued at the same set times. The behaviour of the chicks was recorded with that of their parents on the same data sheet. Individual chicks were not identifiable, however broods were identifiable from their territories and their attendant parents. Where multiple chicks from a brood were observed they were simply recorded as C1, C2, or C3. Direct observation during daylight hours was expected to be the main source of data at this stage, as the nidifugous chicks were expected to be difficult to locate or positively identify using trail cameras. Observation sites had to be moved in some cases as the young families decamped some distance along the beach away from the nesting site, possibly to be closer to freshwater.

Focal continuous recording of display behaviour and the presence of other animals

A focal sampling technique was used to observe the display behaviour that occurred when an individual of a pair, a pair, or family of tūturuatu interacted with other animals. These observations occurred over the two-hour period used simultaneously for the observation of behavioural states. Continuous recording was used to log tūturuatu display behaviour and the presence of other animals, as instantaneous sampling is not suitable for measuring discrete events of short duration (P. Martin & Bateson, 2007). These observations were recorded on the same standardised data sheet as the behavioural state observations (see Appendix A). The number and proximity of all avian and mammalian species within 30 metres of the individual tūturuatu being studied were recorded. Avian species were categorised as non-threatening, competitor, or potential predator, as detailed in

Appendix D. There are no wild mammals on Motutapu, so all mammalian interactions (people, cattle, dogs) were considered to be human-related. Distance estimation was facilitated by the placement of coloured wands at 10-metre intervals along the beach before the breeding season. I aimed to record not just the display behaviour of tūturuatu, but also the number and proximity of the species present when the behavioural event occurred.

The display behaviours observed in tūturuatu represent a continuum of responses from interest and agitation through to distraction displays, which include injury-feigning and are potentially risky. I defined them as follows:

Display level 1 ("D1")

D1 was defined as a display of interest. It was characterised by the cessation of other behaviours such as preening or foraging, sometimes by vocalising a "peep-peep" sound, head-bobbing, and the adoption of an alert body posture. D1 included activities that could reasonably be interpreted as "guarding" behaviour of a nest, mate, clutch, or brood, and sometimes involved standing with the head higher than normal, standing on a log or pile of driftwood, and head-bobbing. As previously mentioned, adult tūturuatu maintain visual contact of their surroundings even when foraging. Weston (2019) has suggested that the "head-up" posture of Charadrius plovers appears to assist with visual monitoring of potential threats. The function of "head-bobbing" remains unknown but it could serve as a visual signal of perceived risk to conspecifics and predators (Weston, 2019), similar to tail flicking in rail species (Alvarez, 1993), or to aid distance perception in eyes that lack binocular convergence (Wilson, 1950), or to avoid retinal habituation and maintain neural responsiveness (Waldvogel, 1990).

Display level 2 (“D2”)

D2 was defined as a display of agitation. It was characterised by a markedly heightened focus on the disturbance source. It encompassed most agonistic interactions and was frequently associated with running or flying, either away from or towards the intended recipient. If the displaying bird was still, D2 was typically accompanied by vocalization and pronounced “head-bobbing”. D2 displays were also used in the context of chick-rearing where the chicks rather than the intruder appeared to be the intended recipients of the display. Once alerted to danger the chicks would hide under driftwood or in the nest. My intention was for D1 to record an increase in alertness or vigilance above normal levels that would be expected to precede higher level displays (except in the situation where a bird was surprised). In practice, D2 observations were recorded almost ten times as often as D1 observations, suggesting that the subtlety of D1 displays may have been missed by human observers. By definition, a “display behaviour” is intended to elicit a response in the recipient of the display (Beer, 1977). The competitor species may be far more adept at noticing and interpreting the nuances of display behaviour than unrelated species. Displays to mammalian species were most commonly to human members of the public.

Display level 3 (“D3”)

D3 denoted a form of distraction display called a “rat-run” or “rodent-run” common to several species of Charadrius plover. In a “rat-run” the tūturuatu extends the wings, lowers the head and tail, and runs erratically in a rapid “zig-zagging” away from the perceived threat. The intention is assumed to be to distract a potential predator away from the clutch or brood.

Display level 4 (“D4”)

D4 denoted injury feigning behaviour often known as a “broken-wing” display. This appears to be a riskier and more extreme distraction behaviour than D3 and is described in many bird species. The intention appears to be to draw the attention of a larger animal away from the clutch or brood by pretending to be a weak or vulnerable target. There is some evidence that plovers use more obvious and more risky distraction displays when their offspring are most vulnerable (Brunton, 1990).

Display level 5 (“D5”)

D5 denotes distraction behaviour feigning near-death convulsions, sometimes referred to as a “dead bird” or “exhausted bird” display. This behaviour was never observed in my study, suggesting that it is reserved for the most extreme encounters with predators.

High tide headcount

A daily survey of tūturuatu was undertaken within two hours of high tide each day (weather permitting), to allow the monitoring of movement, mortality, or re-partnering. The number of individuals of other bird species on the nesting beaches was also recorded to give an overall indication of the populations in the vicinity of tūturuatu nesting areas. High tide was chosen as the survey time to make the searching easier due to the much smaller area available to this shore dwelling species, and for consistency. High tide was also the time that tūturuatu were expected to be within their home territory, rather than away on the feeding grounds of the intertidal rock shelves at West Point.

Indirect observation of nest-sites and surrounding areas using trail cameras

Nest sites and the adjacent beaches were monitored with covert trail cameras from the time the nest was detected until fledging or disappearance of the last chick. Bushnell trail cameras (Trophy Cam HD Model 119876) were used. A camera set to "motion-triggered" mode was hidden in a hollow artificial rock positioned two to three metres from each nest to allow 24-hour monitoring of the nest site. The "nest camera" recorded 10-second video clips of activity, including infra-red imaging after dark.

Plate 2.5 Bushnell Trophy Cam HD (Model 119876) mounted on base beside Cempro artificial rock.

The artificial rocks were adapted from garden ornaments cast in fibre cement by local company Cempro. The moulds are formed from real rocks to give realistic surface detail. The "fake rocks" are spray-painted to appear like sandstone or basalt. I chose the basalt-coloured rocks to fit with the Motutapu coastal rock, and those with a steep or overhanging side so that the camera hole would be shaded and less visible. The camera was mounted on a stand with a plywood base that closely fitted the base of the rock. The system proved remarkably successful with both initial set-up, and resupply of SD cards and batteries achieved quickly with minimal disturbance to the nearby tūturuatu. With the camera settings I used, I found the 32 GB SD cards easily lasted a week. Unfortunately, I found that rechargeable batteries did not last long enough, so resorted to using new alkaline AA batteries each week.

Plate 2.6 Camera enclosed in artificial rock deployed near the entrance of a tūturuatu nest.

A second camera set to “time-lapse” mode was positioned more distantly from each site, attached to a tree or post, to monitor the surrounding area. The “beach camera” recorded one still image and one five-second video clip every five minutes during daylight hours. Both cameras also recorded weather and tidal information including storm and flood events. Camera footage review was time-consuming and as a result, was limited to three main scenarios:

1. Investigating the cause of the disappearance of a chick or nest once the approximate time had been logged from direct observation. Camera footage was a key component of my ability to diagnose the cause of each nest loss or chick death.
2. Checking nocturnal behaviour. The motion-triggered infra-red nest cameras were my only source of nocturnal information as there were no direct observations after dark.
3. Checking or confirming direct observations. Camera footage was helpful to identify individual tūturuatu in aggressive interactions or a re-partnering situation, or the occasional case of mistaken identity. It was also useful to check incubation roster changes which can be unclear to an observer. Tūturuatu cannot be directly observed incubating as the nests are completely covered. They are also quick and covert as they approach or leave the nest, making it easy for an observer to miss a change from male to female incubation.

The phases of the breeding season

I defined the phases of the breeding season as follows:

- **“pre-nesting”**; a pair having no eggs or chicks at the time. This phase included periods between nesting attempts.
- **“nesting”**; a pair having one to three eggs in the nest and no chicks.
- **“chick-rearing”**; a pair having one to three live unfledged offspring and no eggs.

Some observations were recorded during hatching when a pair had both eggs and chicks. The synchrony of hatching was such that the number of these observations was very small, so it was decided not to include them in the analyses in order to use the simple definitions above. Behavioural observations for each nest were made during all three phases.

Time budget construction

Proportional time budgets were calculated for each individual adult bird by adding the number of observations of the behavioural states defined above and dividing by the total number of observations made during an observation period. The mean proportional time budget was simply the mean of these individual values for the data set being considered, whether the whole adult population throughout the breeding season, or smaller groupings by sex or phase of the breeding season. This methodology was not feasible for chicks as they were not individually identifiable. The data for the chicks of each brood were aggregated, and the time budgets calculated as the mean proportion of time each brood spent in each of the behavioural categories.

Each nest site or territory was observed for two hours at the same time every day, effectively varying the data set with respect to tidal state. The tidal state for each observation was recorded using data from Te Ratonga Tirorangi (the Meteorological Service of New Zealand) based on the tidal reference point at Matiatia Bay on nearby Waiheke Island, which appeared to best match the tidal state on the western beaches of Motutapu. This enabled investigation of the effect of circa tidal rhythm on tūturuatu behaviour. No attempt was made to investigate semilunar or lunar temporal influences.

Bias avoidance

Tūturuatu nest sites and surrounding areas were managed as normal. The standard practice on Motutapu is to encircle the nest areas with electric fencing tape 3 – 5m from the nest and erect signs asking people to stay outside the area, a practice termed “symbolic fencing”. Observers and cameras were quiet and covert as far as possible, and no patrolling activity was undertaken. A great deal of effort was made to minimise disturbance to tūturuatu and other wildlife, and to train volunteers to be consistent in this approach. Observation posts were approached from the inland aspect of the nest area, rather than by walking down the beach. Observers had to remember to wear “Hi-Viz” vests while walking around the island, but to remove them before coming close to the observation area. The “beach camera” SD cards and batteries were almost always changed by me. This involved quickly removing the camera from its hiding place in the fake rock, then retiring to a distant position to make the changes and check the timer and settings, before replacing it again. In the event of cold wet weather, observations for the day were cancelled as the risk of disturbance to clutches or broods was deemed to be unwarranted.

The high tide headcount was the one monitoring event that was deliberately disturbing to the tūturuatu, but again this was kept to a minimum. The observer walked the beach close to the water; several metres below the high tide mark where the nests are located noting the identity of all tūturuatu present, and the number of all other avian and mammalian species present. I judged this to be no more disturbing than a member of the public walking quietly along the beach.

Statistical analysis

All analyses were conducted in R v4.1.3 (R Core Team, 2022). The proportion of each behaviour within each observation period for each individual was calculated as the count of observations for a behaviour divided by the total number of observations in that period. The mean proportion of each behaviour was then calculated and compared between sexes using generalised linear mixed models; lme4 package (Bates, Mächler, Bolker, & Walker, 2015) with a binomial family specified. Sex and behavioural category were included as fixed effects, with individual ID nested within pair included as a random factor. Interaction terms between behaviour and sex were also included. Chi-squared tests were applied to compare the counts of display behaviours towards different avian species and between phases of the breeding season.

2.4 RESULTS AND DISCUSSION

Pre- and post-breeding season surveys

Nineteen tūturuatu were identified during the pre-breeding survey in September 2018; eighteen on Motutapu and one on nearby Motukorea. One adult female disappeared before my daily behavioural observations started in November, leaving a total of eighteen (six females, eleven males, one immature). Six more tūturuatu (five adults, one immature) disappeared from Motutapu by the time of the post-breeding survey in May 2019 (Table 2.1). The single bird identified on Motukorea in the first survey moved to Motutapu during this time. Eighteen tūturuatu were identified during the post-breeding survey in May 2019. The twelve survivors from the pre-breeding survey were joined by six juvenile birds, five from the translocated captive-bred birds, and a single island-bred bird.

Territory occupation and nest-building

Territory occupation by six pairs began in September, leaving an additional five single adult males, and the immature bird. Courtship behaviour and mating were observed from October through to January. I did not observe tūturuatu performing the scraping behaviour commonly associated with courtship in other plover species (Phillips, 1980), however this has been described in tūturuatu on Hokorereoro (A. Davis, 1994b). I suggest that tūturuatu nests on Motutapu are so well-hidden that this behaviour would be difficult to observe. The location of a nest on Motutapu was only evident once the first egg had been laid. Two of the six nesting pairs on Motutapu at the start of the 2018/19 breeding season occupied the same sites as the previous season. An additional five individual birds exhibited site fidelity but had re-partnered following the disappearance of their mates.

Table 2.1 The results of pre- and post-breeding season surveys.

Tūturuatu band	Sex	Age	Island bred	Pre-breeding	Post breeding
GO-WB	M	2 years		✓	✓
Unbanded male	M	1 year	2018	✓	✓
WB-OB	M	4 years		✓	✗
GO-WO	M	2 years		✓	✓
WB-RY	F	3 years		✓	✓
GO-GW	M	2 years		✓	✓
BO-	F	2 years	Jan 2017	✓	✓
GB-GY	M	4 years		✓	✗
GO-OY	F	2 years		✓	✓
GO-GY	F	3 years		✓	✓
BO-YO	M	2 years	Jan 2017	✓	✓
WB-YR	M	4 years		✓	✓
GB-BY	F	4 years		✓	✗
RY-RB	M	3 years		✓	✓
GB-GB	M	4 years		✓	✗
WB-GO	F	4 years		✓	✗
WB-RW	M	2 years		✓	✓
GB-BO	M	4 years		✓	✗
Unbanded immature		1 year	2018	✓	✗
Unbanded juvenile		5 months	Jan 2019		✓
RG-OR	2nd release	5 months			✓
WO-YG	2nd release	4 months			✓
WO-	1st release	6 months			✓
RG-WO	2nd release	4 months			✓
WO-RO	1st release	5 months			✓

✓ = Detected, ✗ = Not detected

Three of the nests were hidden in piles of driftwood on a sandy shore, two were in hollows in banks above the high tide mark of a sandy shore, and one was beneath grasses on a rocky platform adjacent to a sandy shore. Virtually all the behaviour observed and recorded over the breeding season occurred on sandy beaches close to the nest sites. Nest-building behaviour was observed on six occasions, all exhibited by male birds, and all associated with courtship behaviour. This behaviour may be an example of the phenomenon whereby male birds signal their condition, health, or parental disposition by pre-mating displays of nest-building (Moreno, 2012). Three pairs re-nested after losing their clutch or brood so a total of nine nests were observed.

Egg production

During the 2018/19 breeding season on Motutapu, one-third of nests (3/9) had two eggs and two-thirds of nests (6/9) had three eggs: a mean of 2.66 (SD = 0.51) eggs per nest. These results are similar to those on Hokorereoro in the 1984/5 and 1985/6 breeding seasons where of 119 clutches, 23 contained two eggs, and 96 contained three eggs (a mean of 2.8 eggs per nest) (A. Davis, 1994b). Davis calculated a mean laying time of 4.1 (SD = 0.6) days (n = 20) per egg (A. Davis, 1994b), however, on one occasion I observed a much longer period of eight days between two eggs being laid, with eventual successful hatching of the whole clutch. Partial incubation appeared to provide excellent hatching synchrony in this species with all the clutches observed hatching within 24 hours. My observations revealed that tūturuatu chicks frequently returned to the nest, a behaviour thought to be unique among Charadrius plover chicks which are generally described as nidifugous.

The covered nest of this species continues to provide refuge from competitors and predators, and shelter from the elements for at least a few days after hatching.

In most plover species, individuals breed first as yearlings (Colwell & Haig, 2019a) but this is not the case in wild tūturuatu, which breed first at two years old (A. Davis, 1994a). Tūturuatu were previously thought to be single-brooded in the wild, possibly due to habitat constraints on Hokorereoro (A. Davis, 1994b), although they can produce several broods per season in captivity. My observations revealed that tūturuatu can produce replacement clutches in the wild on Motutapu and recently even double brooding (renesting after successfully rearing a brood) has been observed in the wild on Motutapu (H. Speed, personal communication, 2020). Double brooding was not observed on Hokorereoro (A. Davis, 1994b) but has been reported on the off-shore island sanctuaries of Waikawa and Mana (Dowding & O'Connor, 2013).

Adult tūturuatu breeding season time budgets

The nine nest sites were observed for up to 2 hours on 341 occasions in total, yielding a total of 19,357 focal instantaneous samples of behavioural states of tūturuatu nesting pairs and family groups. Adult tūturuatu of both sexes spent more than half their time budget during the breeding season engaged in just three behaviours: inactivity, incubation, and foraging (see Figure 2.1). A key difference between these behaviours is that inactive behaviour and foraging occurred throughout the different phases of the breeding season, but incubation occurred only in the nesting phase. The rarely observed behaviours: brooding, grooming, courtship, and mating are combined into a single “other” category in Figure 2.1; these are explored further in Figure 2.2.

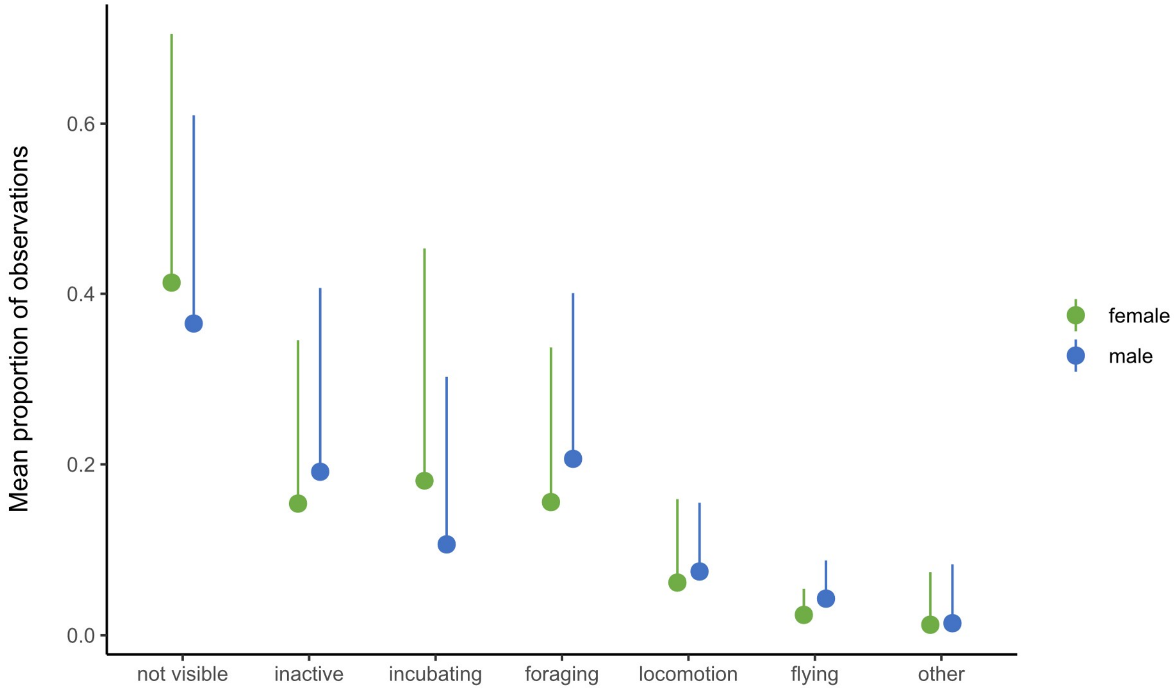

Figure 2.1 Mean proportion (+SD) of observations for each sex and most frequently observed behaviours. The category ‘other’ is a grouping of rarely observed behaviours (<5% observations) that is explored further in Figure 2.2. Data represent 6 females with a mean of 53.2 observation sessions of up to 2 hours each (range 36 – 82), and 8 males with a mean of 42.6 observation sessions of up to 2 hours each (range 20 – 62).

Foraging

The mean proportional time (±SD) adult tūturuatu spent foraging over the breeding season was approximately 0.17 (± 0.17) for females, and 0.23 (± 0.19) for males. My observations captured foraging only when it occurred at or near the nest site. Foraging at distant sites such as the inter-tidal rock platforms at West Point was not recorded. When food supplies are limited plovers can be expected to forage for a large proportion of their time both day and night (Nol, 2019), although this behaviour is likely to be influenced by metabolic demands (such as egg production) and time constraints (such as incubation). Analysis of time budgets of other plover species shows that the proportion of time spent foraging often exceeds 0.5 (Nol, 2019). The proportional foraging budgets for piping plover *(Charadrius melodus)* in coastal Alabama were between 0.5 and 0.9 of daylight hours depending on the time of year (Johnson & Baldassarre, 1988). In coastal Cuba, both semipalmated plover *(Charadrius semipalmatus)* and killdeer *(Charadrius vociferus)* diurnal foraging budgets exceeded 0.6 (Nol, MacCulloch, Pollock, & McKinnon, 2014). At the other end of the spectrum, pohowera (Auckland Island banded dotterel, *Charadrius bicinctus exilis*) were observed to spend only 15–20% of daylight time foraging (Pierce, 1980). Unfortunately, the methodology used in these studies is variable and sometimes unclear, making direct comparison of figures unreliable. Despite these caveats, the comparatively low foraging time budgets I observed in adult tūturuatu on Motutapu are suggestive that adequate food resources are available, an important conservation implication.

Adult tūturuatu on Hokorereoro during the breeding season had foraging budgets, when visible, of 0.35, but birds often left the nest area, apparently to forage elsewhere unobserved (A. Davis, 1987). On Motutapu the comparable figure was 0.30, with birds similarly often seen to leave their nest sites or territories to forage unrecorded on the inter-tidal rock platforms at West Point.

Inactive behaviour

Although proportional time budgets for foraging may be confounded by periods when the birds are not visible, the time budgets for resting ("inactive behaviour") give some additional insight into the adequacy of food supplies. The mean proportional time (±SD) adult tūturuatu were inactive was 0.18 (± 0.19) for females, and 0.21(± 0.22) for males, and possibly more when unobserved. These are higher proportions of their time budgets than the plover species in the studies mentioned above (Johnson & Baldassarre, 1988; Nol et al., 2014). Time budgets for tūturuatu on Hokorereoro had different categories of behavioural states, making direct comparison difficult. Their time budget when visible for “roosting” was 0.17, but two other behavioural categories: “scanning” 0.03, and “chick care” 0.27, would also have had a component of inactivity (A. Davis, 1987). These figures are comparable with a time budget for “inactivity” when visible of 0.28 for tūturuatu on Motutapu.

The comparatively high time budgets for inactive behaviour I observed in adult tūturuatu on Motutapu add some weight to the suggestion that adequate food resources are available.

Differences in breeding season behaviour between female and male tūturuatu

Female tūturuatu breeding season behaviour

Female breeding season behaviour could be characterised as more passive and physically supportive for clutches and broods than male behaviour. Females spent almost twice as much time incubating as males (see Figure 2.1) with the caveat that all direct observations were made during daylight hours. A generalised linear mixed model (GLMM) analysis showed significant interaction between sex and incubating behaviour ($z = 3.07$, $p = 0.002$). Although the data set was very small, females also appeared to brood more than males (see Figure 2.2). Female breeding season behaviour was less active overall than male behaviour. Females spent a lower proportion of their time inactive, but this was more than offset by a higher proportion spent incubating, and less time spent foraging, locomoting, and flying. Females may conserve energy because of the high metabolic demands of egg production, particularly given the possibility that a replacement clutch might be required. The overall female time budget for diurnal foraging was 0.17, lower than that of males at 0.23. Assuming female energetic demands equate to or even exceed those of males, it seems likely that females make up this shortfall by foraging nocturnally.

A difference in diurnal/nocturnal incubating and foraging times between the sexes could be responsible for differential survival rates, depending on the prevalence of diurnal or nocturnal predators. There may be occasional cases of predation from the same diurnal avian species that threaten tūturuatu chicks (see Chapter Three) but adult tūturuatu are vigilant and feisty on the ground, and strong and swift on the wing. They also take advantage of the strong presence and non-threatening manner of tōrea-pango (variable oystercatcher, *Haematopus unicolor*), for example by choosing to alight beside them when returning to a beach. A small native owl, the nocturnal ruru (morepork, *Ninox novaeseelandiae*) is the only confirmed predator of adult tūturuatu on the island and appears to be their major predatory threat. If female tūturuatu are more nocturnally active than males during the breeding season, they may well be at increased risk of predation than males. This is one possible mechanism by which the male-biased ASR (adult sex ratio) observed on Motutapu might have occurred. Further studies using transmitters would be helpful to establish the fate of adult tūturuatu that disappear.

Male tūturuatu breeding season behaviour

Male breeding season behaviour could be characterised as more active and “guarding” than female behaviour. Males spent a slightly higher proportion of their time being inactive than females (0.21 vs. 0.18), but were still more active overall, spending less time incubating and more foraging, in locomotion, and flying (see Figure 2.1). GLMM analysis showed significant interaction between sex and foraging behaviour ($z = 2.27$, $p = 0.0.02$). Males also engaged in display activity more than females, particularly in the chick rearing phase (see Figures 2.5 and 2.6). The "inactive" behavioural category may suggest a "resting" state, but in both sexes was often accompanied by D1 display behaviour (interest, alertness) suggestive of a "guarding" role.

Although females spent almost twice as much time incubating as males diurnally, males may do more of the nocturnal incubating as suggested by Davis (A. Davis, 1994b). If correct this appears to support the theory that "the bright incubate at night", where the more brightly coloured sex of a dimorphic species is thought to reduce diurnal incubation and increase nocturnal incubation to reduce the risk of visual detection by a predator (Ekanayake et al., 2015). However, such a strategy has no relevance in a species with a completely covered nest, as both sexes are virtually invisible while incubating. An alternative explanation is that there are advantages to females in being nocturnally active. These might include feeding on abundant prey such as "sandhoppers"; talitrid amphipods which are more active at night, and having the opportunity to incubate during the warmer daylight hours (Colwell, 2010). Indirect nocturnal observations using motion-triggered infra-red trail cameras recorded some nocturnal activity, including foraging on sandhoppers, but were not sensitive enough to regularly capture incubation shift changes. Further research using either GPS transmitters or microchips would be required to describe the nocturnal incubation behaviour of tūturuatu, and would also facilitate the study of diurnal incubation, given their covered nests and covert behaviour.

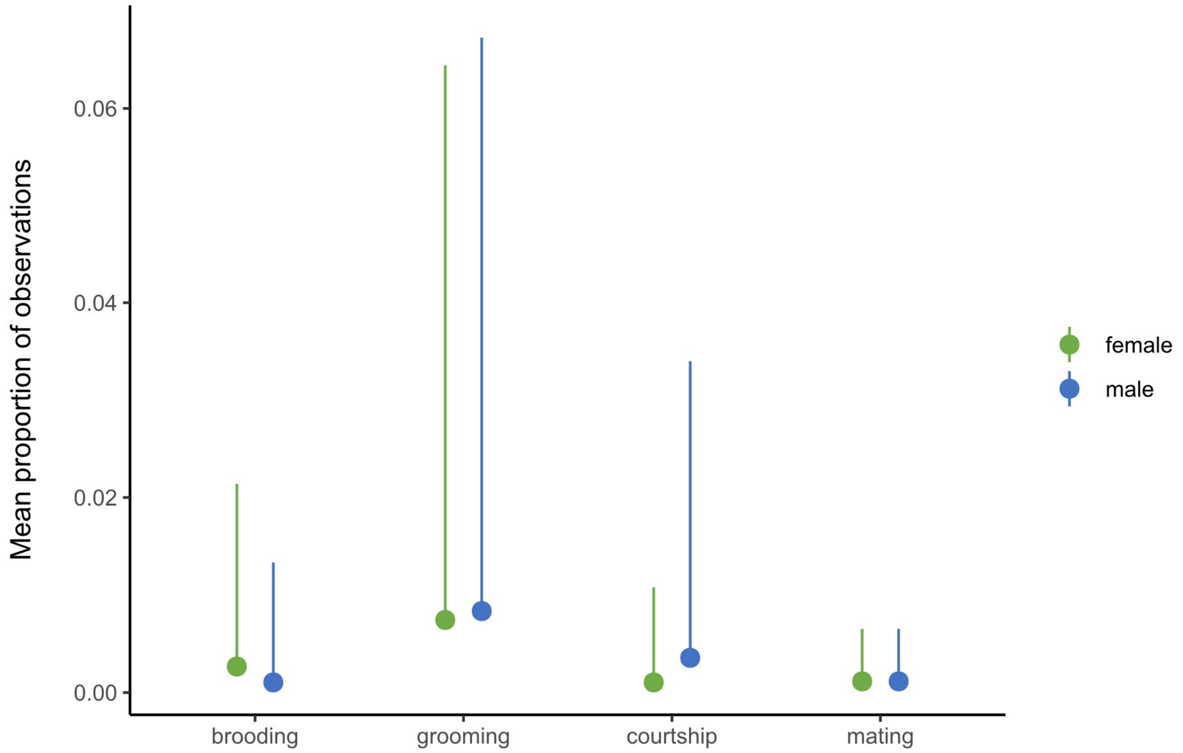

Figure 2.2 Mean proportion (+SD) of observations for each sex and rarely observed behaviours (<5% observations). No analysis was conducted due to the small sample size. Data represent 6 females with a mean of 53.2 observation sessions of up to 2 hours each (range 36 – 82), and 8 males with a mean of 42.6 observation sessions of up to 2 hours each (range 20 – 62).

Rarely observed behaviours

Males and females spent similar proportions of their time budgets grooming: both bathing in freshwater and preening. The amount of time spent on courtship behaviour by both sexes was very small, as expected in this preferentially monogamous species. Monogamous Charadrius plover species are known to spend significantly less time courting than polygamous species (Carmona-Isunza et al., 2015). There was a difference between sexes in the amount of time spent courting; male birds spent approximately twice as much time courting as female birds. Male birds also occasionally incorporated nest building behaviour into their courtship display. This behaviour is thought to signal their condition, health, or parental disposition to their mate. In some bird species this behaviour is extended to the construction of elaborate nests that are not always used for breeding (Moreno, 2012). Mating behaviour was observed on just 26 occasions through the study.

Differences in behaviour between phases of the breeding season

There were differences between phases of the breeding season both in time budgets and display behaviour (see Figures 2.3, 2.4, and 2.6). Some of these variations were self-explanatory, for example, the fact that incubation occurred only during the nesting phase, and that courtship and mating occurred predominantly during the pre-nesting phase.

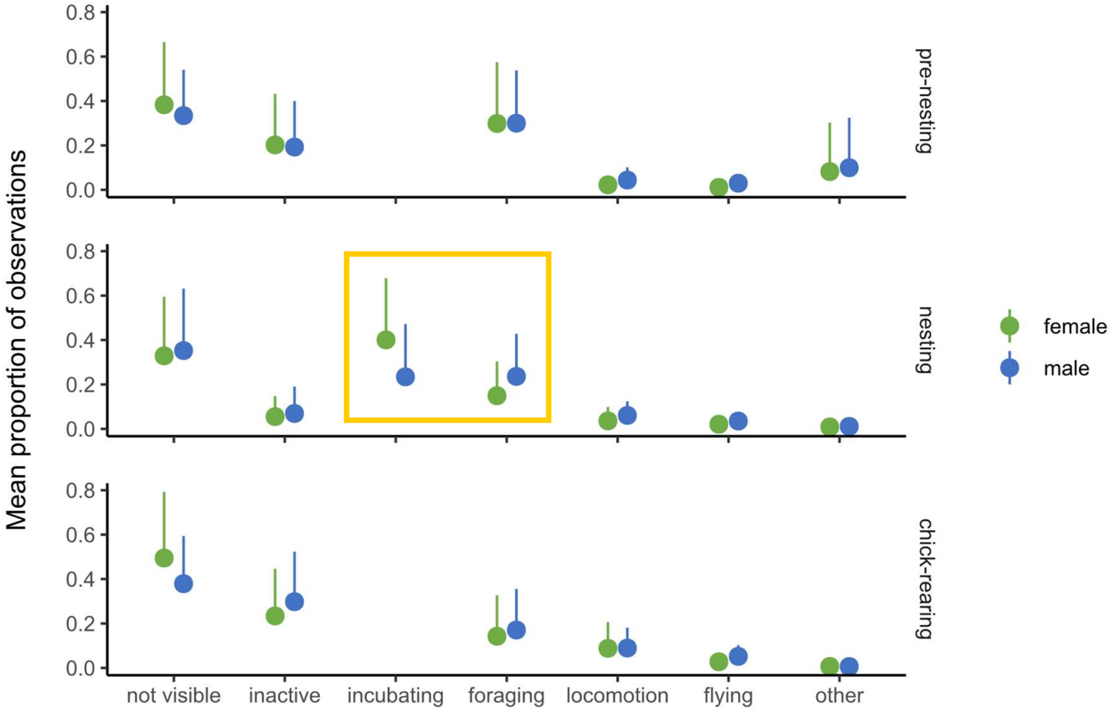

Figure 2.3 Mean proportion (+SD) of observations for each sex and most frequently observed behaviours separated by phase of the breeding season. The category ‘other’ is a grouping of rarely observed behaviours (<5% observations) that is explored further in Figure 2.4. The yellow box in the nesting phase observations indicates the driver of the significant interaction between sex and the behaviours foraging and incubating observed in the GLMM analysis. Data represent 6 females with a mean of 53.2 observation sessions of up to 2 hours each (range 36 – 82), and 8 males with a mean of 42.6 observation sessions of up to 2 hours each (range 20 – 62).

The pre-nesting phase

The pre-nesting phase was characterised by low levels of locomotion and flying, high levels of inactivity, and much higher time budgets for grooming than subsequent phases for males and females (see Figures 2.3 and 2.4). Tūturuatu are known to moult directly after breeding (Dowding & Kennedy, 1993) in a “pre-basic” moult, which represents the transition from breeding (“alternate”) plumage to non-breeding (“basic”) plumage. Although it has not been described to my knowledge in the tūturuatu, most plover species also undergo a ‘pre-alternate’ moult (Conklin, 2019) which would result in increased grooming behaviour in the early phase of the breeding season.

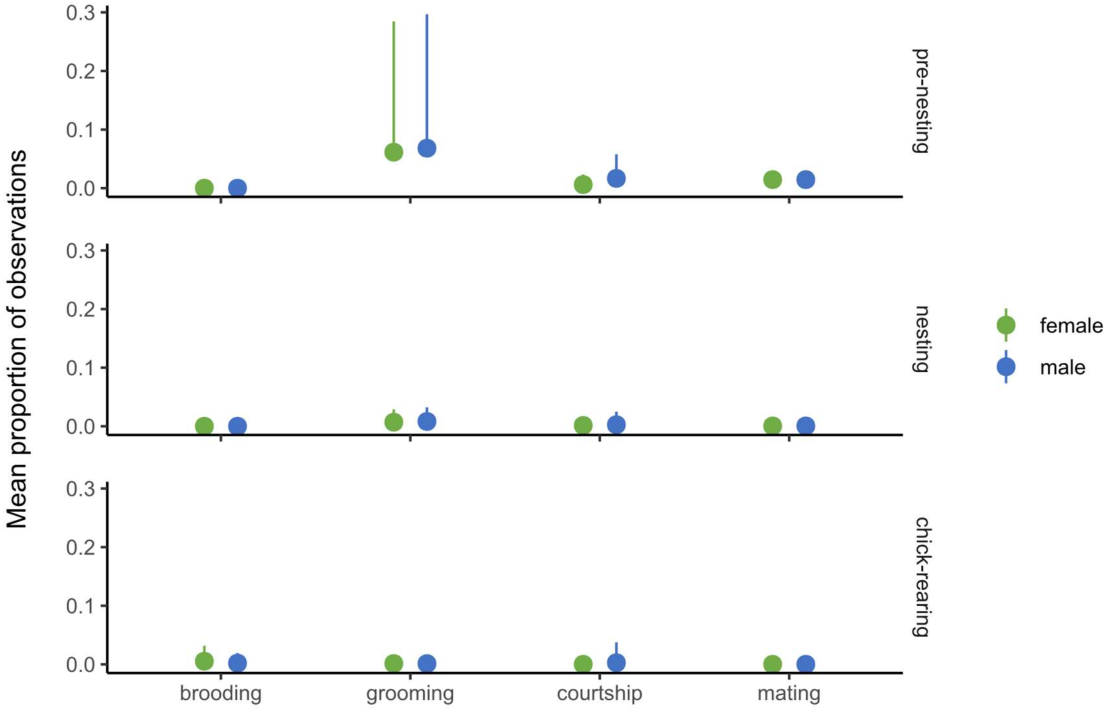

Figure 2.4 Mean proportion (+SD) of observations for each sex and rarely observed behaviours (<5% observations) separated by phase of the breeding season. No analysis was conducted due to the small sample size. Data represent 6 females with a mean of 53.2 observation sessions of up to 2 hours each (range 36 – 82), and 8 males with a mean of 42.6 observation sessions of up to 2 hours each (range 20 – 62).

The nesting phase

The time budget for inactive behaviour decreased dramatically from the pre-nesting phase to the nesting phase for both sexes but was more than offset by the time spent incubating. This was most notable in females who spent approximately half their nesting phase time budget on these two behavioural categories (see Figure 2.3). Time budgets for foraging varied only slightly between breeding season phases. Male time budgets for foraging were similar in the pre-nesting and nesting phases, while female time budgets for foraging decreased from the pre-nesting phase to the nesting phase. The time demands on females of incubation may reduce the time available for them to forage. Females may also supplement diurnal foraging with nocturnal foraging during the nesting phase, as mentioned above. However, other factors may impact a female's ability to forage nocturnally, including the weather, tidal state, lunar cycle, and the presence of ruru. Incubating killdeer (*Charadrius vociferus*) have been observed to preferentially forage at night and incubate during the day if nocturnal light levels suffice. It has been suggested that the choice would depend on both prey availability and perceived predation risk, which would vary from site to site (Eberhart-Phillips, 2016).

The chick-rearing phase

Inactive behaviour increased from the nesting phase to the chick-rearing phase for both sexes, although the high levels of display activity seen during this phase suggest a "guarding" aspect to this behaviour (see Figure 2.6). Increased time budgets for the high energy output behaviours of locomotion and flying during the chick-rearing phase were not matched by an increase in foraging time budget in either sex. Male foraging time budget decreased slightly from the nesting phase to the chick-rearing phase, and female foraging time budget increased, but only slightly. One or both parents stayed with the brood throughout the chick rearing phase, potentially reducing their opportunity to fly to high-quality foraging sites. It is likely that the cooperation of both parents was needed to produce the successful outcome of chick fledging and adult survival. Just one single parent was observed to raise a chick to fledging. He appeared devoted to this task but died shortly after his chick fledged. The cause of death was unknown.

The chick-rearing phase of the breeding season is the time of the annual cycle when tūturuatu appear to be most susceptible to negative impacts from human-related disturbance. A person jogging down the beach may cause parents to separate from chicks, potentially leaving the chicks vulnerable to opportunistic predation. Another effect of human-related disturbance can be to force the chicks into hiding, significantly restricting their time budget for foraging (Weston & Elgar, 2005). It is unfortunate that the chick-rearing phase on Motutapu tends to coincide with peak visitor numbers over the Christmas holidays.

Time budgets for locomotion and flying behaviours increased steadily through the breeding season to peak during the chick-rearing phase. These behaviours can be associated with defence, but not exclusively. Increased locomotion was also associated with chick-rearing. Chicks cannot fly until fledged so an adult accompanying them tends to walk, run, or hop more than they would without chicks to care for.

Display behaviour

Display behaviour was elicited most commonly (61%) in response to the presence of two competitive avian species: conspecific tūturuatu, and tūturiwhatu, a larger competitive congener (females: $\chi^2 = 113.3$, $p < 0.001$, males: $\chi^2 = 104.2$, $p < 0.001$; see Figure 2.5). Displays to potential predator species (18%) and non-threatening species (21%) were less common (see Figure 2.5). Displays to the two competitive species were approximately equal in number, with males displaying slightly more to other tūturuatu, and females slightly more to tūturiwhatu. An important finding with relevance to conservation management is that the presence of tūturiwhatu accounted for approximately 30% of the display behaviour observed in tūturuatu overall. I suggest that having to share breeding habitat with tūturiwhatu is likely to cause considerable energy expenditure and stress to tūturuatu and may impact both adult survival and chick survival to fledging.

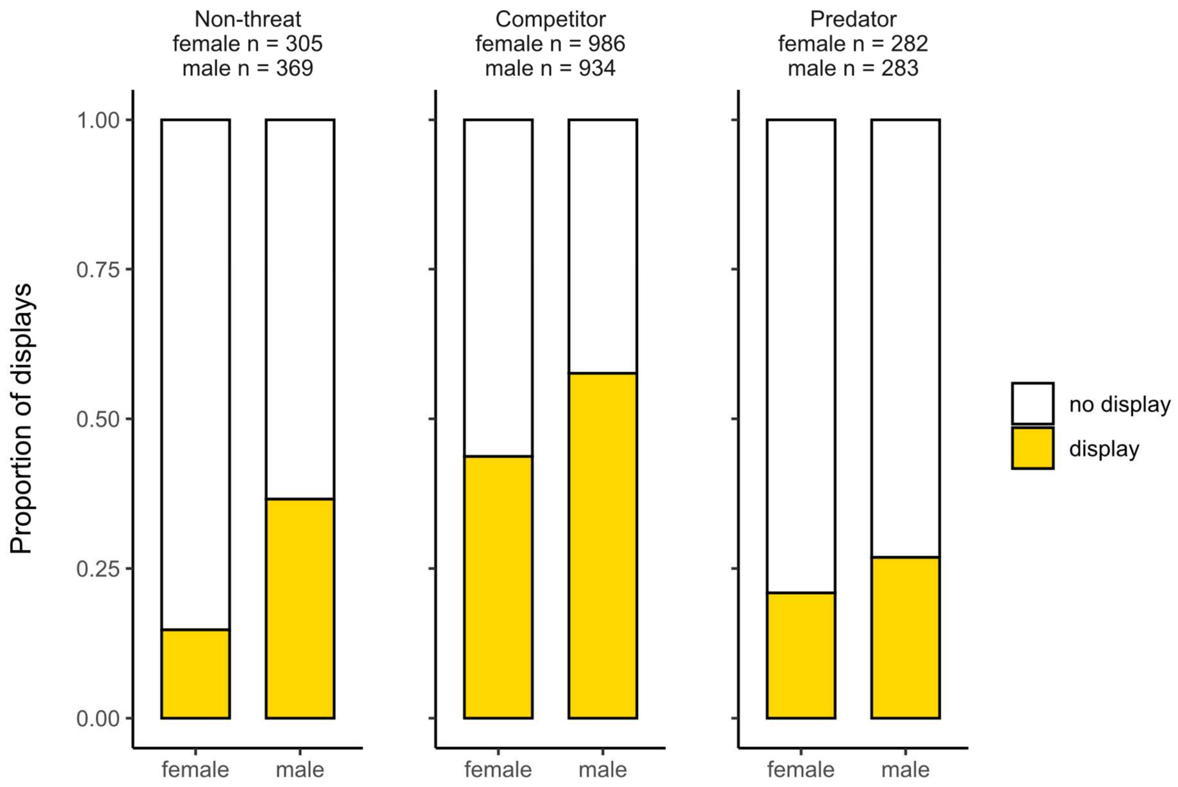

Figure 2.5 Proportion of encounters with other bird species where tūturuatu displayed, for each sex towards birds considered non-threatening, competitors, and predators. For a list of the three categories of avian species, see Appendix D. Sample sizes indicate the number of encounters observed with species in the vicinity of the focal animal (within an estimated 30m) where display behaviour was observed.

Male and female tūturuatu encountered other birds in approximately equal numbers, but males were more likely to respond with display behaviour (see Figure 2.5). This effect occurred in all three avian categories but was most notable for non-threatening birds.

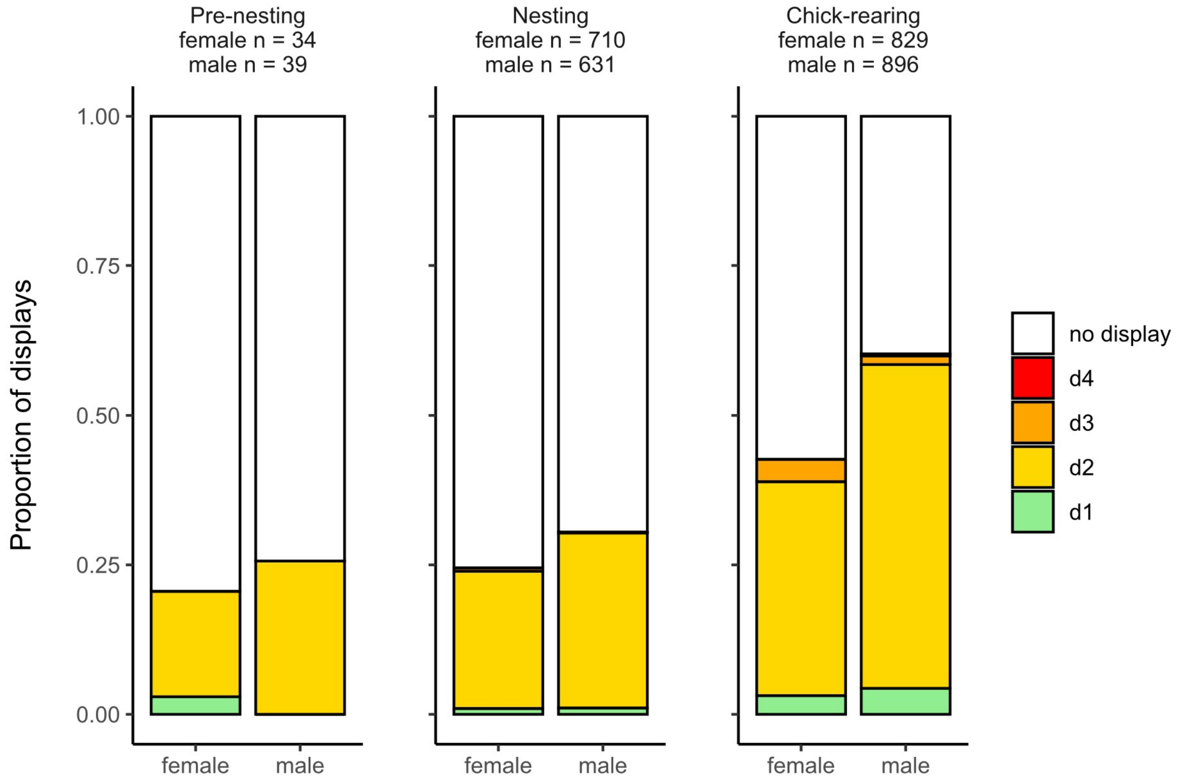

Figure 2.6 Proportion of each type of display in each phase of the breeding season in response to the presence of other animals. Sample sizes indicate the number of encounters observed with species in the vicinity of the focal animal (within an estimated 30m) where display behaviour was observed.

Display behaviour frequency increased significantly for each sex in the chick-rearing phase compared to the earlier phases of the breeding season: pre-nesting, and nesting (females: $\chi^2 = 69.6$, $p < 0.001$, males: $\chi^2 = 148.0$, $p < 0.001$; see Figure 2.6). The greatest increase was seen in display level 2 (D2). Most of the more intense displays (D3, D4) were observed during the chick-rearing phase. Two hypotheses have been advanced to explain the change in frequency and intensity of display activity over the breeding season in other avian species. The first is based on the expected future survival and “reproductive value” of the offspring increasing with age (Andersson, Wiklund, & Rundgren, 1980). The second hypothesis is that greater vulnerability of the offspring demands more frequent and intense defence efforts (Brunton, 1990). My results appear to support the latter explanation for tūturuatu. In the pre-nesting phase, tūturuatu defend their territory and mate, but neither can be considered vulnerable. In the nesting phase, the cryptic and covered clutch and incubating parent also have very low vulnerability, at least in the natural situation the species evolved in. No depredation occurred, and a high egg survival rate was recorded in tūturuatu on Motutapu, in marked contrast to their congener the tūturiwhatu which has an open nest. In the early part of the season the six tūturuatu nests produced a hatching success rate of 81%, while the six tūturiwhatu nests on the same beaches were all lost. On hatching the chicks are suddenly extremely vulnerable, a situation that persists until fledging allows them to fly from danger. The change in frequency and intensity of display behaviour observed matches the sudden increase in vulnerability of the chicks after hatching, rather than the gradual increase in the age and reproductive value of the offspring through the breeding season.

In addition to these factors, the behaviour of the chicks themselves was sometimes observed to trigger agonistic inter-specific encounters. Chicks sometimes wander into a neighbouring territory while seeking food or freshwater leading to “border skirmishes” between their parents and other tūturuatu and tūturiwhatu.

Circa-tidal rhythms of behaviour

Foraging behaviour

Patterns of foraging behaviour in tūturuatu appeared to be affected by tidal cycles. The response varied between phases of the breeding season, and between sexes (see Figure 2.7). In the pre-nesting phase of the breeding season, foraging by both sexes of tūturuatu steadily decreased as the tide came in. After high tide, foraging increased as the falling tide exposed favoured inter-tidal feeding areas. Female foraging increased rapidly to peak approximately four hours after high tide. Male foraging increased more slowly but was more sustained, peaking six hours after high tide.

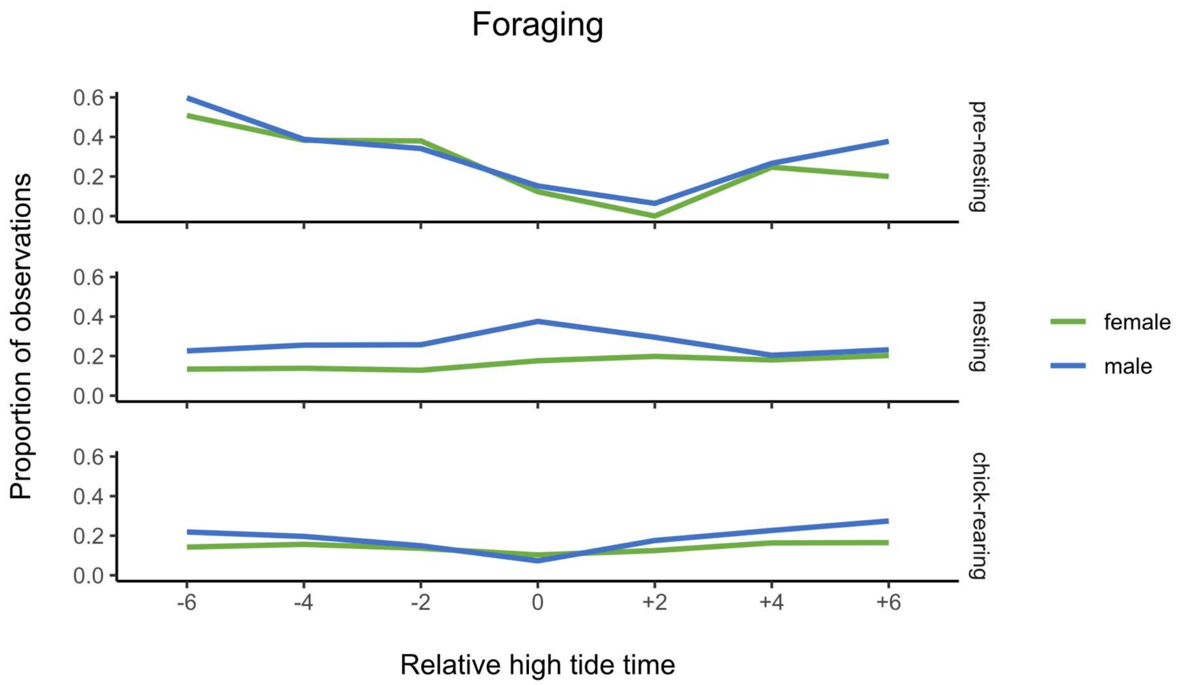

Figure 2.7 Proportion of observations recorded as foraging relative to high tide time and phase of the breeding season. Negative values on the x-axis indicate the incoming tide, zero indicates high tide, and positive values indicate the outgoing tide, in hours. Data represent 6 females with a mean of 53.2 observation sessions of up to 2 hours each (range 36 – 82), and 8 males with a mean of 42.6 observation sessions of up to 2 hours each (range 20 – 62).

During the nesting phase, one parent was incubating virtually all the time, so if a female was foraging her male partner would be incubating, and vice versa. Females spent almost twice as much diurnal time incubating as males so their opportunities to forage (diurnally) were markedly reduced from the pre-nesting phase. The only discernible circa tidal rhythm observed in females during the nesting phase was a gradual increase in foraging behaviour through the six hours of ebbing tide. In contrast, male foraging behaviour increased as the tide came in to peak around high tide. This unusual pattern contrasts not only with the female foraging pattern for the nesting phase, but also with the behaviour of both sexes in other phases of the breeding season. The inter-tidal zone is the main feeding ground of the tūturuatu on both sandy beaches and rock platforms. The first few hours after high tide are the highly favourable foraging time as the receding waters expose feeding grounds that have been inaccessible for several hours. The unusual pattern of male foraging behaviour I observed during the nesting phase suggests that females may have priority over males in their choice of foraging time. The nutritional requirements of females may still be greater than males during the nesting season though they are no longer producing eggs. Females may still be recovering from the metabolic demands of egg production in the pre-nesting phase but also must maintain a state of physiological preparedness for re-nesting if required by the loss of their clutch.

During the chick-rearing phase, foraging opportunities were more equally shared between male and female birds, as incubation duties were no longer required. Both sexes now had a role in nurturing and protecting their precocial chicks as they learned to forage efficiently. To some extent, adults were able to forage and care for their brood at the same time. Females appeared to forage at low levels all day long unrelated to the tide. Male foraging followed the same pattern as during the pre-nesting period with minimal foraging at high tide, however the curve was flatter with peak foraging levels only half what they were in the pre-nesting phase.

Inactive behaviour

Patterns of inactivity also appeared to be affected by tidal cycles. The response varied between phases of the breeding season, but with little difference between the sexes (Figure 2.8). In the pre-nesting and chick-rearing phases, females and males rested more around high tide when foraging opportunities are reduced. In the nesting phase, both sexes displayed much less inactive behaviour overall. There also appeared to be negligible tidal influence on the timing of a period of inactivity. It appeared that incubating behaviour largely took the place of inactive behaviour during this phase (see Figure 2.3 and earlier discussion).

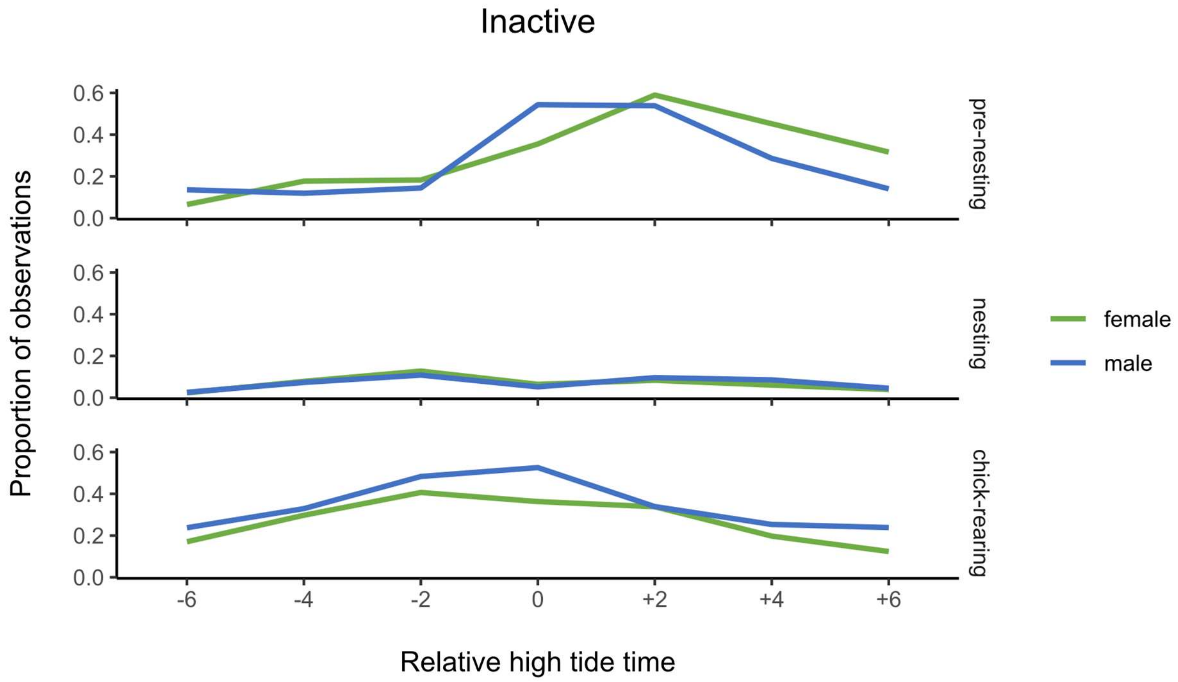

Figure 2.8 Proportion of observations recorded as inactive relative to high tide time and phase of the breeding season. Negative values on the x-axis indicate the incoming tide, zero indicates high tide, and positive values indicate the outgoing tide in hours. Data represent 6 females with a mean of 53.2 observation sessions of up to 2 hours each (range 36 – 82), and 8 males with a mean of 42.6 observation sessions of up to 2 hours each (range 20 – 62).

While the above figures suggest that the tide may have some influence on tūturuatu behavioural rhythms, the behavioural rhythms of shorebirds are likely to be subject to complex temporal influences including circadian, circa-tidal, semi-lunar, lunar, and seasonal. They may also be affected by the behaviour of conspecifics (especially their partner), and other species; prey, competitor, and predator (Bulla, Oudman, Bijleveld, Piersma, & Kyriacou, 2017). It is perhaps unsurprising that clear circa tidal patterns are difficult to identify as individual shorebirds manage the interplay between these factors.

<u>Tūturuatu chick time budgets</u>

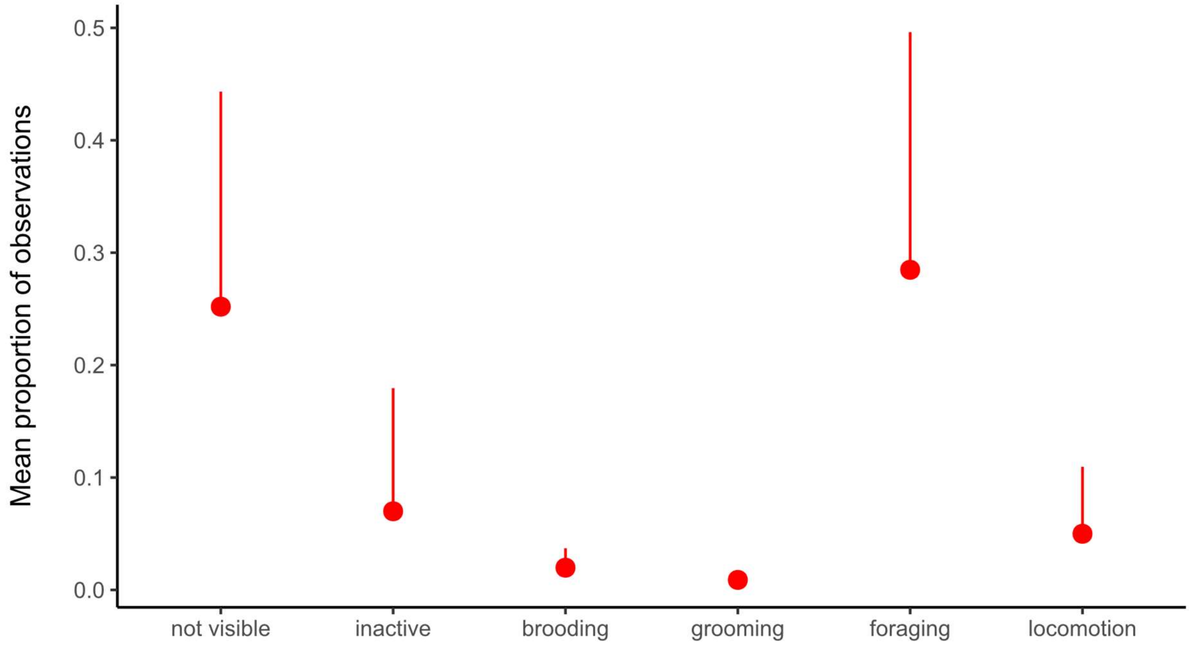

Figure 2.9 Mean proportion (+SD) of observations for the most frequently observed chick behaviours. As individual chicks could not be identified, the observations of chicks in each brood were combined.

The time budget for chicks on Motutapu is shown in Figure 2.9. Chicks spent the highest proportion (0.3) of their time foraging, with time budgets for inactive behaviour and locomotion less than 0.1. Grooming and "brooding" (in this case actually being brooded by a parent) were also observed in chicks. The proportion of observations for which chicks were not visible was less than adults simply because they lacked the ability to fly away from the nest site area. However, they are extremely cryptic and almost impossible to see when not moving. My observations may therefore be biased towards more active behaviours, and against more sedentary behaviours.

The foraging time budget for chicks (0.3) on Motutapu was far higher than adults (0.21). In contrast to adult plovers, chick foraging rates and time budgets tend to be higher in more favourable habitats (Loegering & Fraser, 1995). As an example, American avocet (*Recurvirostra americana*) chicks raised with access to freshwater spent a significantly higher proportion of time feeding (0.23 vs. 0.09) than those raised in a hypersaline environment (Hannam et al., 2003). Foraging time and weight were highest in the group with access to freshwater and successively reduced in brackish, saline, and hyper-saline environments.

Comparison of foraging time budgets between Motutapu and Hokorereoro when chicks were actually visible showed a strong similarity between Motutapu (0.77) and the favoured "Northern Shore" area (0.8) of Hokorereoro, rather than the "Southern Coast" (0.55) and "Clears" (0.14) areas (A. Davis, 1987). The implication for wildlife management is that the resources available to chicks on Motutapu, including food and freshwater, were comparable to the area on Hokorereoro where chicks had high growth and fledging rates. While a small gape size and inefficient foraging technique have been suggested as reasons for chicks having a higher foraging time budget than adults (A. Davis, 1987), a more compelling explanation is their requirement to grow as rapidly as resources allow. Tūturuatu chicks remain extremely vulnerable to predation until they fledge, and weight rather than age appears to be the key determinant of the time of fledging (A. Davis, 1994b). I suggest that the main driver of the high foraging rates observed in chicks in favourable habitats is selective pressure to maximise their growth rate.

Summary and wildlife management recommendations

Adult tuturuatu had mean proportional time budgets for foraging of 0.17 (± 0.17) in females and 0.23 (± 0.19) in males, and for inactive behaviour of 0.18 (± 0.19) in females and 0.21(± 0.22) in males. These figures are relatively low for foraging and high for inactive behaviour when compared to published reports from other plover species (Johnson & Baldassarre, 1988; Nol et al., 2014) and the tūturuatu population on Hokorereoro (Rangatira, South East Island) (A. Davis, 1987). When food supplies are limited plovers can be expected to forage for a large proportion of their time both day and night (Nol, 2019), although this behaviour is likely to be influenced by metabolic demands (such as egg production) and time constraints (such as incubation). My observations suggest that adequate food resources are available for adult tūturuatu on Motutapu.

Female tūturuatu incubate significantly more than males diurnally and may be more active nocturnally during the nesting phase of the breeding season. This behaviour is seen in other plover species where it is thought to reduce diurnal predation of males (Ekanayake et al., 2015b). No such benefit is likely in tūturuatu as the incubating partner is hidden in the covered nest unique to this species. An alternative explanation is that nocturnal activity benefits the female, for example by allowing access to nocturnal prey species (Kuwae, 2007). On Motutapu, nocturnal foraging may also predispose females to predation by ruru and is one possible mechanism for the development of a male-biased ASR.

Display behaviour in tūturuatu was elicited significantly more commonly in response to two competitive species: other tūturuatu, and tūturiwhatu, than to potential predators or non-threatening species. While interaction with other tūturuatu is unavoidable, I suggest that having to share breeding habitat with tūturiwhatu is likely to cause considerable energy expenditure and stress to tūturuatu and may impact both adult survival and chick survival to fledging.

The covered nest of this species provides shelter and crypsis to the clutch and newly hatched chicks. The increase in display behaviour observed in adult tūturuatu through the breeding season was not gradual as would be expected if it was related to increasing “reproductive value” of the off-spring (Andersson et al., 1980). Display behaviour by both sexes increased suddenly and significantly during the chick-rearing phase as would be expected if it was related to the vulnerability of the off-spring (Brunton, 1990). The vulnerable phase unfortunately coincides with a heightened risk of human disturbance as visitor numbers peak over summer, but wildlife management practices can take advantage of the fact that chick-rearing occurs over a relatively limited time.

Patterns of foraging and inactive behaviour in tūturuatu appeared to be affected by circa-tidal rhythms. In general, foraging occurred preferentially during the hours after high tide as the receding waters exposed feeding grounds to the hungry birds, and inactive behaviour occurred preferentially around the high tide when foraging options were limited. The response varied between phases of the breeding season, and between sexes. In the nesting phase the time budget for inactive behaviour in both sexes decreased markedly and appeared to be decoupled from circa-tidal rhythm. The decrease in inactive behaviour was more than offset by the time spent incubating. Opportunities for females to forage diurnally during the nesting phase were markedly reduced from the pre-nesting phase as they spent almost twice as much diurnal time incubating as males. Interestingly my results suggest that during the nesting phase females appeared to have priority over males in their choice of foraging times with respect to the tidal state. They were observed to gradually increase foraging behaviour during the highly favourable six hours of ebbing tide as normal. In contrast, male foraging behaviour in the nesting phase increased as the tide came in to peak around high tide. This pattern contrasts not only with the female foraging pattern for the nesting phase, but also with the behaviour of both sexes in other phases of the breeding season, and is suggestive of an unusual form of cooperation between the sexes. Behavioural rhythms of shorebirds are likely to be subject to complex temporal influences including circadian, circa-tidal, semi-lunar, lunar, and seasonal. They may also be affected by the behaviour of other species; prey, competitor, and predator (Bulla et al., 2017), and conspecifics — especially their partner.

My observations revealed that tūturuatu chicks frequently return to the nest, a behaviour thought to be unique among Charadrius plover chicks which are generally described as nidifugous (Gochfeld, 1984). Chick rearing was centred on the nest area for most broods with only 25% (2/8) decamping, apparently to gain access to freshwater. The mean proportional time budget for foraging in chicks was 0.3 (± 0.21), comparable to the most favoured area on Hokorereoro for chick growth and survival (A. Davis, 1987), suggesting that adequate food resources are also available for tūturuatu chicks on Motutapu. In contrast to adult plovers, chick foraging time budgets tend to be higher in more favourable habitats (Loegering & Fraser, 1995).

Tūturuatu chicks remain extremely vulnerable to predation until they fledge, and weight rather than age appears to be the key determinant of the time of fledging (A. Davis, 1994b). I suggest that the main driver of the high foraging rates observed in chicks in favourable habitats is selective pressure to maximise their growth rate.

Food resources are a key component of habitat suitability. They are threatened by climate change and habitat degradation and are an important consideration in translocation biology. While I did not directly measure food availability, my study demonstrated in principle the feasibility of assessing the adequacy of food resources of a site by comparing the foraging time budget of the population with that of another known site.

CHAPTER THREE

Reproductive success of tūturuatu on Motutapu

Plate 3.1 Newly hatched tūturuatu chick and two eggs at Sandy Bay, Motutapu, Aotearoa.

3.1 INTRODUCTION

Breeding biology figures prominently in the management and conservation of Charadrius plovers. The reproductive potential of an avian population varies under the influence of a number of elements, including age of first reproduction, clutch size, hatching success/egg survival, and fledging success/chick survival (Evans & Pienkowski, 1984). Shorebirds are conservative breeders in that they have small fixed clutch sizes (Colwell, 2010). Nest predation is the primary source of nest losses across a wide diversity of species, habitats, and geographic locations, accounting for 80% of nest losses on average (T. Martin, 1993), and this is especially true for ground nesting birds (Colwell, 2010). Tūturuatu (tchūriwat', shore plover*, Thinornis novaeseelandiae*) may be different in this respect because unlike all other plover species, their nests are covered (A. Davis, 1994b; Fleming, 1939). This is thought to provide protection from the avian predators found in their natural habitat but may also make them vulnerable to introduced mammalian predators. Other natural challenges and constraints on recruitment include climatic and nutritional factors, disease, and predation of chicks and adults (Stenzel & Page, 2019). Adult plovers are generally at heightened risk of predation through the breeding season as they are obliged to spend time on the nest, and later, time on the ground attending their brood (Ekanayake et al., 2015), although tūturuatu may again be an exception. Conservation challenges for many plover species include high levels of egg and chick loss from habitat loss and degradation, disturbance events, and introduced and subsidised native predators (Stenzel & Page, 2019). The subsidisation of predators occurs when humans alter resource availability, enabling the density of a predator population to increase above levels that would occur without the additional resources (Gompper & Vanak, 2008). Subsidised predators can drastically impact a prey population because subsidies insulate the predator population from the effect of decline in the prey population (Sinclair et al., 1998). In addition to these factors, inbreeding suppression of hatching rate appears to be a common phenomenon observed in bird populations that have experienced a severe population bottleneck (Brekke, Bennett, Wang, Pettorelli, & Ewen, 2010; Briskie & Mackintosh, 2004).

Detailed studies of chick survival have been conducted on just six of the forty Charadrius plover species (Dinsmore, 2019). This type of research is challenging because of the small size, mobility and crypticity of the chicks. Technological advances leading to smaller transmitting devices may help, but the presence of the transmitter and the handling required may affect their survival (Dinsmore, 2019), and were outside the remit of my research in this endangered species. A review of the relevant literature suggests that my study may have been the first to attempt to ascertain the cause of death of each individual in a population of wild plover chicks.

A study on piping plover (*Charadrius melodus*) chick survival tested the hypotheses of differential food resources, predation, and (human) disturbance explaining differences in chick survival in three different habitats (Loegering & Fraser, 1995). The study noted that most chick mortality occurred in the first ten days of life, and that foraging rates and time spent foraging were higher in the more favourable habitats. It concluded that differential food resources were the primary reason for the observed differences in chick survival rates. Another study investigated the effect of great-horned owl (*Bubo virginianus*) trapping on chick survival (Catlin, Felio, & Fraser, 2011). It showed that owl removal significantly increased the daily survival of piping plover chicks in one year, and increased survival in the second year, but not significantly. The authors commented that other studies have shown predator control failure for reasons including incomplete control and increasing pressure from non-target predators.

A study on mountain plover (*Charadrius montanus*) demonstrated that chicks tended by females had a higher survival rate than chicks tended by males, and that chick survival generally increased through the nesting season (Dinsmore & Knopf, 2005). These findings are unlikely to be applicable to other plover species because of the unusual rapid multi-clutch mating system of this species. The female is thought to lay a complete clutch for the male first, and then a second clutch at a different site for herself.

A six-year study on snowy plover (*Charadrius nivosus nivosus*) in California established that most chick mortality occurred before chicks were six days old (Warriner, Warriner, Page, & Stenzel, 1986). Loggerhead shrike (*Lanius ludovicianus*), a relatively small passerine predator, were observed to predate 14 chicks in one year. On one occasion a chick died after its parents had a prolonged confrontation with a pair of American avocet (*Recurvirostra americana*). Another study on snowy plover compared reproductive success between beach and river habitats (Colwell et al., 2005). River-nesting males consistently tended fewer eggs, hatched similar numbers of chicks, and fledged significantly more young than beach-nesting males. The authors suggested that the beach habitat may provide poorer crypsis for nests and chicks, that prey availability may be lower, and that human disturbance may be greater. Another study by the same group investigated the age-related survival and behaviour of chicks (Colwell, Hurley, Hall, & Dinsmore, 2007). Chicks were most likely to die in the first three days of their 28-day pre-fledging period. Lower survival of younger chicks was associated with a tendency to lie motionless when approached by humans; nearly all older chicks responded to human approach by running to evade danger. Another study on snowy plover investigated the effect of predator management on chick survival (Dinsmore, Gaines, Pearson, Lauten, & Castelein, 2017). The predator species removed were primarily corvids (88%), non-native foxes (*Vulpes vulpes*) (5%) and striped skunks (*Mephitis mephitis*). The authors were able to demonstrate a significant improvement in productivity from 1.06 chicks fledged per breeding male prior to predator control to 1.32 chicks with predator control.

A study on Kentish plover (*Charadrius alexandrinus*) in Spain showed that larger eggs produced heavier chicks, and within broods, heavier chicks were more likely to be recruited into the breeding population (Amat, Fraga, & Arroyo, 2001). However, chick characteristics at hatching did not appear to be related to recruitment in the entire population.

A study on ringed plover (*Charadrius hiaticula*) in England and Greenland investigated the behaviour, growth, and survival of chicks over three years (Pienkowski, 1984). In contrast to some of the studies mentioned above, it found that growth rates were remarkably similar in a wide range of situations, and that feeding conditions did not normally affect growth or survival of chicks. Cause of death was established for only two broods when drowning resulted from exceptionally high tides. Most chick losses appeared to take place at night, with foxes (*Vulpes vulpes*), rats (*Rattus norvegicus*), and short-eared owls (*Asio flammeus*) among the possible predators.

Perhaps surprisingly, the plover species where chick survival appears to have been most extensively studied is the tūturuatu, specifically the remnant population on Hokorereoro (Rangatira, South East Island) in the Chatham Islands group of Aotearoa (New Zealand). Chick mortality in tūturuatu on Hokorereoro was low on the first day after hatching, but increased rapidly to peak at four days old (A. Davis, 1994b). Davis compared chick foraging behaviour, time to fledging, and survival rate between different habitats on the island. On the favoured northern shore, chicks foraged 80% of time when visible compared with 55% on the southern shore (A. Davis, 1987), comparable to the findings of Loegering and Fraser in piping plover (Loegering & Fraser, 1995). Northern shore chicks on Hokorereoro fledged significantly earlier as fledging time appeared to be determined by weight rather than by age (A. Davis, 1987, 1994b). Chick survival from hatching to fledging varied considerably from 43% on the northern shore in 1984/5 to just 7% on the southern shore in 1985/6 with an overall rate for the population of 25% over the two seasons. Causes of chick mortality on the island included starvation, drowning by large waves, and predation by tarāpunga (red-billed gull, *Chroicocephalus novaehollandiae scopulinus*). Starvation was thought to be the major cause of death on the southern shore, where underweight and malnourished chicks were observed (A. Davis, 1994b). Subsequent research on the freshwater requirements of shorebird chicks (Haig et al., 2019; Hannam et al., 2003; Rubega & Oring, 2004) lead me to suggest that some of these effects may have been caused by lack of access to freshwater on the southern shore, rather than lack of food.

Monitoring of tūturuatu at Hokorereoro and other sites has shown that egg survival rates are normally very high compared with other species (perhaps as high as 80%), but that chick survival to fledging is low. Mortality during the period from hatching to fledging (typically 35–45 days) was thought by earlier investigators to be a key constraint on population growth (J. E. Dowding, personal communication, 2018). The aim of the research detailed in this chapter was to investigate the specific causes of chick mortality of tūturuatu on Motutapu to better inform ongoing conservation efforts.

3.2 METHODS

Field studies

Field studies were conducted on a small population of tūturuatu on the island of Motutapu in the Hauraki Gulf. Refer to Chapter Two for details of the population and Motutapu. Direct observation of chicks was conducted via spotting scope and binoculars at all nine nest sites over 660 observation periods. These were usually of two hours each but were occasionally curtailed by bad weather. Indirect observations were recorded throughout this time by trail camera, as outlined in more detail in Chapter Two. All nest-sites were monitored day and night by a motion-activated trail camera from the time the first egg was laid until the time the last chick fledged or disappeared. The adjacent area was monitored during daylight hours by a time-lapse trail camera recording a still image and a five second video clip every five minutes through the same time period. The thousands of stills and thousands of hours of video were a key component of my ability to diagnose the cause of each nest loss or chick death once the approximate time had been logged by observers. Camera recordings were also helpful to identify individual tūturuatu in aggressive interactions or a re-partnering situation, or in the occasional case of mistaken identity in the direct observation records.

Statistical analysis

Egg production and hatching success rates were calculated for first nests, second nests, and overall. Egg production and hatching success rates were also calculated per adult female, all of which were breeding. Chick survival rates from hatching to fledging were calculated for first nests, second nests, and overall, with the overall probability of survival to fledging plotted. The rate of chick survival to fledging per breeding female, was calculated.

3.3 RESULTS

Egg production and hatching success rate

Six pairs of tūturuatu nested on four beaches from late October 2018. There were three pairs at Pig Bay, and one each at Gardiner Gap, West Point and Sandy Bay. Two to three eggs were laid at each nest over several days. The maximum interval between individual eggs being laid was eight days. A total of 16 eggs was laid in these first six nests. One nest of three eggs at Sandy Bay was destroyed by a high tide storm event on 3rd December; the other 13 eggs hatched successfully.

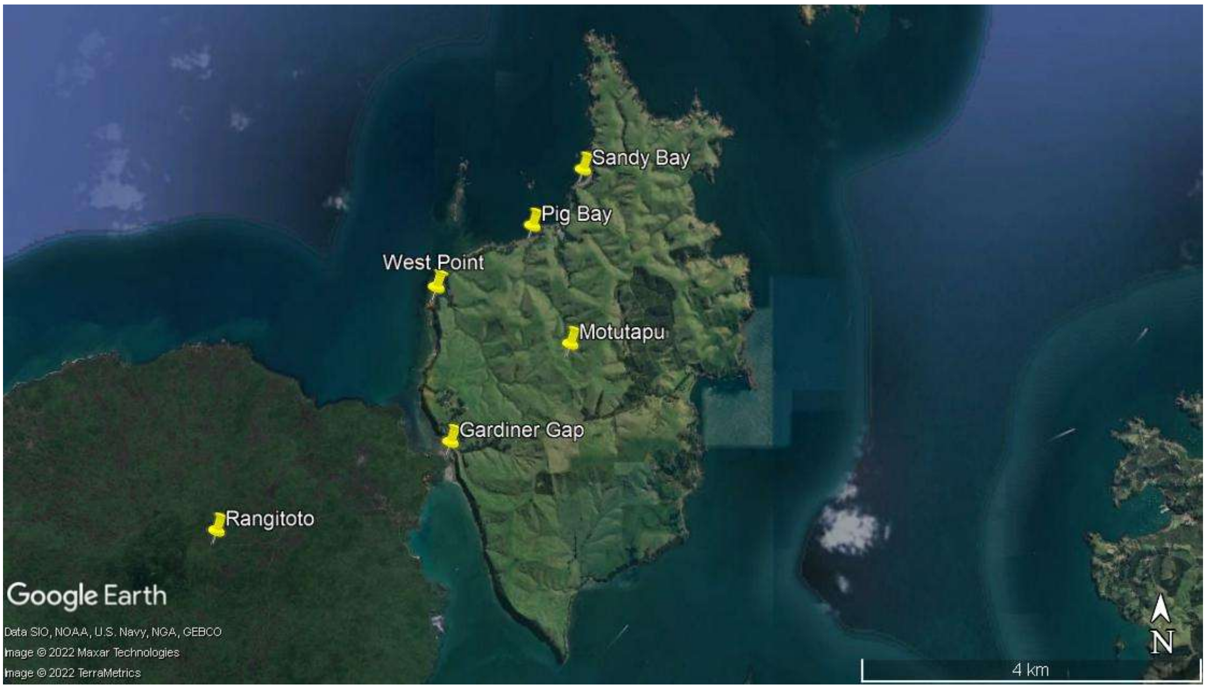

Plate 3.2 Tūturuatu nesting areas on Motutapu in the 2018/19 season.

Re-nesting occurred at three sites in late December following loss of the first nest at Sandy Bay, and the early mortality of all the chicks from the first nest at Gardiner Gap and the first nest at West Point. At Sandy Bay, the original pair re-nested. At Gardiner Gap and West Point, the original males were usurped by new males, then attacked and driven off by the new pair. At Gardiner Gap the new male was in turn usurped by a third male. All three of the deserted males died or disappeared within a week. A total of eight eggs was laid in the three re-nesting sites, from which six chicks hatched successfully.

Table 3.1 Summary of egg production and hatching success rate on Motutapu.

	First nests	Second nests	Overall
Nests	6	3	9
Eggs	16	8	24
Mean eggs/nest	2.66 (SD = 0.51)	2.66 (SD = 0.58)	2.66 (SD = 0.5)
Mean eggs/female			4 (SD = 1.67)
Chicks hatched	13	6	19
Hatching success rate	0.81	0.75	0.79
Mean chicks hatched /nest	2.17 (SD = 1.17)	2 (SD = 1)	2.1 (SD = 1.05)
Mean chicks hatched /female			3.17 (SD = 1.72)

Apart from the single clutch that was lost to a high-tide storm event, all the eggs laid during the first part of the season hatched successfully. In the re-nesting part of the season no clutches were lost, and six out of eight eggs hatched successfully. Two eggs appeared to be infertile. I observed no evidence of nest depredation, despite the presence of karoro (black-backed gull, *Larus dominicanus*), pūkeko (*Porphyrio melanotus*) and kāhu (swamp harrier, *Circus approximans*): all known egg predators of other birds. The nest survival of tūturuatu was in sharp contrast to that of tūturiwhatu (northern red-breasted dotterel, *Charadrius aquilonius*) nesting concurrently on the same beaches. In the early part of the breeding season before Christmas, five out of the six tūturuatu clutches survived to hatching, while all six tūturiwhatu clutches were lost. The causes of clutch loss in tūturiwhatu on Motutapu are unknown. A study on the mainland, Te Ika-a-Māui, over two years in the 1980s found that nest survival was low, with 86% of all nesting attempts failing to hatch. Predation by introduced mammals, which are absent on Motutapu, was the greatest cause of nest failure (Dowding & Murphy, 2001). Other possible causes include avian predation of adults or eggs, high tide flood events, and human disturbance or damage.

Chick survival from hatching to fledging

The percentage of hatchlings to successfully fledge on Motutapu was 15.4% (2/13) for the first batch of chicks, and 33% (2/6) for the second batch, giving an overall figure of 21% (4/19). As a comparison, chick survival to fledging on Hokorereoro varied over two years from 7% to 43% for more favourable and less favourable seasons and habitats, with an overall figure of 25% (A. Davis, 1994b).

Cause of death was established to a high degree of confidence in 66.6% (10/15) of chicks that died on Motutapu, by a combination of direct observation, and indirect observation from nest cameras and beach cameras (see Table 3.2). Perhaps surprisingly only 27% (4/15) of chick mortality was due to predation, with 27% (4/15) also dying as a result of female desertion. A further 13% (2/15) died from accidental drowning and illness/starvation/dehydration, leaving 33% (5/15) where the cause of death could not be established.

Table 3.2 Outcome for each chick on Motutapu: fledged or cause of mortality.

Chick ID	Date hatched	Date last seen	Days alive	Fledged/Cause of death
1	27-Nov	5-Dec	9	Female desertion
2	27-Nov	18-Feb	84+	Fledged (after hand-rearing)
3	5-Dec	8-Dec	4	Female desertion
4	5-Dec	8-Dec	5	Female desertion
5	5-Dec	8-Dec	5	Female desertion
6	21-Dec	22-Dec	2	Predation by kāhu (swamp harrier, *Circus approximans*)
7	21-Dec	1-Jan	12	Unknown cause of death
8	21-Dec	15-Jan	26	Predation by Australian magpie (*Gymnorhyna tibicen*)
9	27-Nov	8-Jan	43	Illness/dehydration
10	27-Nov	16-Jan	51+	Fledged
11	30-Nov	9-Dec	10	Predation by kāhu
12	30-Nov	9-Dec	10	Predation by kāhu
13	30-Nov	1-Jan	33	Unknown cause of death
14	31-Jan	26-Feb	27	Unknown cause of death
15	31-Jan	12-Mar	41+	Fledged
16	27-Jan	27-Jan	1	Drowning/hypothermia
17	27-Jan	29-Jan	3	Unknown cause of death
18	27-Jan	7-Feb	12	Unknown cause of death
19	14-Jan	24-Feb	42+	Fledged

Note: More detail of the outcome for each individual chick is available in Appendix E.

The survival curve for tūturuatu chicks on Motutapu this season (Figure 3.1) is similar to published data from Hokorereoro in 1984/5 and 1985/6 (A. Davis, 1994b). As on Hokorereoro, chick mortality was high in the first 12 days of life with only 42% of chicks surviving past this point.

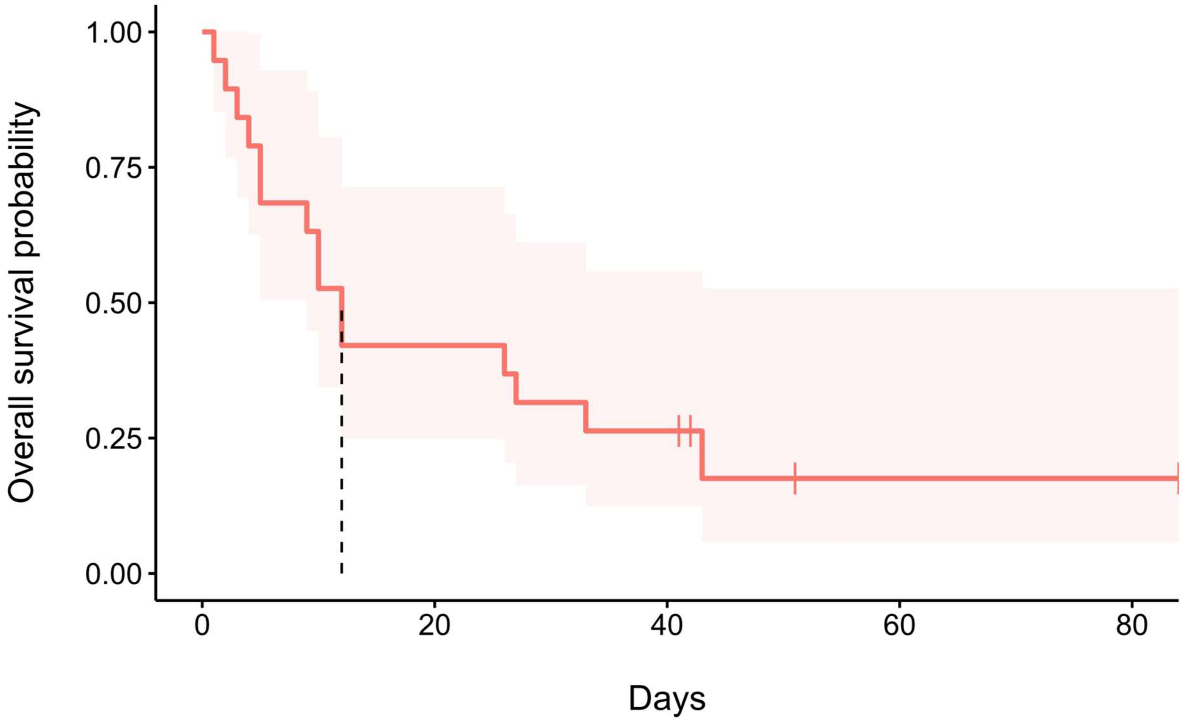

Figure 3.1 Tūturuatu chick survival in days after hatching on Motutapu 2018–19. Note: The dotted black line indicates the median value of 12 days. The shaded area represents 95% CI.

The survival data were affected by the fact that one of the chicks was rescued after female desertion, hand-reared at Te Whare Kararehe o Tāmaki Makaurau (Auckland Zoo), and subsequently released with a cohort of captive-bred birds. In a study of endangered animals with such low numbers, a small stochastic effect can have a large impact on the data.

The overall productivity on Motutapu of 0.66 (four fledged juveniles from six females) was almost identical to the mean on Hokorereoro over six years of 0.638 (SD = 0.13) (A. Davis, 1994a).

Adult survival

Four adult males died or disappeared during the breeding season, three of them (WB-OB, GB-BO, GB-GY) within a week of intra-specific fights over their breeding territory and partner, following female desertion of the brood. One of these, WB-OB was subsequently found to have been predated by a ruru (morepork, *Ninox novaeseelandiae*). The only adult female to die or disappear during the season was WB-GO, the partner of GB-GB. She was last seen on 24th January when their chick was ten days old. Her partner (GB-GB) was the fourth male to die after successfully raising his single offspring to fledging as a solo parent.

Table 3.3 Tūturuatu adult mortality and intra-specific aggression on Motutapu 2018–19.

Band	Sex	Intra-specific aggression date	Date last seen	Comments
WB-OB	Male	7-Dec – 8-Dec	8-Dec	Ruru predation
GB-BO	Male	8-Dec – 9-Dec	9-Dec	Disappeared
GB-GY	Male	8-Dec – 9-Dec	15-Dec	Disappeared
WB-GO	Female		24-Dec	Disappeared
GB-GB	Male		2-Apr	Found dead

3.4 DISCUSSION

Egg production and hatching rate

The mean egg production rate of four (SD = 1.67) per female on Motutapu compares favourably with the remnant population of tūturuatu on Hokorereoro in 1984/5 and 1985/6. There, the mean number of eggs per female was 3.35 (SD = 0.4) overall, varying from 3.0 to 3.9 for different areas and seasons (A. Davis, 1994b). The hatching success rate on Motutapu of 0.79 was comparable with an overall hatching rate on Hokorereoro of 0.83, varying from 0.79 to 0.88 for different areas and seasons (A. Davis, 1994b). The effects of inbreeding depression on hatching rate commonly observed in populations that have undergone a severe bottleneck (Brekke et al., 2010; Briskie & Mackintosh, 2004) do not appear to be a factor in this species. Of the 24 tūturuatu eggs laid on Motutapu in the season I observed, one nest of three eggs was swept away by a tidal surge during a storm. Nineteen of the 21 remaining eggs hatched – a hatching success rate of 0.9, suggesting that there is no suppression of fertility from the population bottleneck. The hatching success rate figures in tūturuatu are considerably higher than those published for most other plover species (Dinsmore, 2019). One study of reproductive success in piping plover appeared to report similar success rate figures of 0.75–0.88 (Harris, Duncan, Franken, McKinnon, & Dundas, 2005). However, this study used the "Mayfield method" to estimate nest success where nests were considered successful if at least one egg hatched and are not directly comparable to my results.

Many plover species lay their eggs sequentially over several days and only start incubation proper once the whole clutch is laid; a phenomenon known as "partial incubation" (Wang & Beissinger, 2011). The longest interval I observed between individual eggs being laid was eight days, with all the eggs from the nest eventually hatching synchronously. There was no nest depredation during my season on Motutapu despite the almost ubiquitous presence of three known egg predator species: the karoro, pūkeko and kāhu. The covered nest appears to confer a substantial advantage to the egg survival rate of this species during the latter part of the pre-nesting phase (when the eggs are being laid), and during the incubation phase.

Chick survival from hatching to fledging

Before the study began, I hypothesised that human related disturbance (including cattle and dogs) and high tide storm events might have major impacts on chick survival, but this was not confirmed by my observations. I also suspected that pūkeko, ruru, and karoro might predate tūturuatu chicks, but saw no evidence of this. On several occasions I witnessed a tūturuatu chick closely approach a group of karoro without confrontation. I confirmed predation of tūturuatu chicks by kāhu, and recorded evidence of predation of tūturuatu by Australian magpie (*Gymnorhina tibicen*) for the first time.

The observation of female desertion as a major cause of chick loss between hatching and fledging was an unexpected finding. It should be noted that the term “female desertion” is not meant in a pejorative sense but simply to best describe what I observed. “Parental desertion” seems inaccurate because in the situations I observed the original male did not appear to willingly desert his brood, but rather was driven from the territory, primarily by the new male. “Male intrusion” has been suggested as an alternative term, but it describes the initiating event rather than the cause of chick death. The new male behaved with some hostility towards the brood, but more importantly the female completely ignored them. The propensity for “female desertion” to occur as a response to a male-biased ASR is well recognised in other Charadrius plover species (Eberhart-Phillips, 2019), but has not been previously reported in tūturuatu.

While the sample sizes are very small, the fledging rates from the first and second clutches of chicks were quite different, with chicks hatching from a first nest having a survival rate of 15.4%, compared with 33% from a re-nest. The compelling explanation for the observed difference is that female desertion caused significant chick mortality from the first clutches but did not occur during rearing of the re-nesting broods. The risk of female desertion may have reduced because the ASR (adult sex ratio) was closer to parity later in the breeding season following the death/ disappearance of the three deserted males (see later discussion).

An inherent problem in the study of extremely endangered animals is the small population size and the potential for stochastic events (and the assumptions made around them) to dramatically affect results. An example of this was the decision whether to include or exclude the hand-reared chick in the tally of successful fledglings. The decision to uplift the chick and hand-rear it was based on the judgement that it would almost inevitably die if left in its natural environment. It could have been excluded from the tally on the basis that it did not survive under natural conditions or included on the basis that it did actually fledge despite the unusual circumstances. This decision affected the productivity figure for the small population for the season. The rescue and hand-rearing of the chick was a valuable exercise demonstrating that intervention in these cases can have a positive outcome. Not only was the chick reared successfully, but the mother re-nested with her new partner and raised a second chick successfully to fledging.

The period from hatching to fledging appears to be by far the most dangerous phase of the tūturuatu lifecycle. Only 21% of tūturuatu hatchlings on Motutapu fledged successfully this season, and while this is similar to the 25% overall success on Hokorereoro over the 1984/5 and 1985/6 seasons, it is still disappointing. Published chick survival rates in plover species are highly variable. The methodology used can also be variable and confusing (Dinsmore, 2019). The probability of surviving the fledging stage (4–6 weeks in most plover species) ranged from 8% to 65% in the Kentish plover, 6% to 80% in the snowy plover, 8% to 75% in the piping plover, 6% to 26% in the mountain plover (Dinsmore, 2019) and as previously mentioned, 7% to 43% in tūturuatu on Hokorereoro (A. Davis, 1994b).

The identification and prevention of the causes of mortality through this crucial period could be an important contribution to the conservation of this endangered species.

Avian predation

Avian predation accounted for 40% of chick mortality where the cause of death was established. Motutapu is free from introduced mammalian predators, which are widely considered to be the major cause of the extirpation of tūturuatu from their former habitat. However, Motutapu remains a highly modified environment. It is a working farm with some areas of remnant or re-planted native forest and wetland. The avian species present reflect this – the predominant predators of tūturuatu chicks are kāhu and Australian magpie, neither of which inhabited Aotearoa in pre-human times. Kāhu are considered a subsidised native species that established naturally in Aotearoa only after extensive anthropogenic habitat change (Gompper & Vanak, 2008; Worthy & Holdaway, 1996). Australian magpies were deliberately introduced to New Zealand in the 1860s and 1870s as a control measure for agricultural pests (McIlroy, 1968). Control of avian predators might have a positive impact on tūturuatu chick survival on Motutapu but could be harmful without a better understanding of their ecological role in this habitat. As mentioned above, other studies have shown predator control failure for reasons including incomplete control, and increasing pressure from non-target predators (Catlin et al., 2011). As an example, on Motutapu, if kāhu alone were controlled it might allow the proliferation of pūkeko or Australian magpies with an overall negative impact on tūturuatu.

Female desertion

Female desertion was also identified as an important factor reducing chick survival to fledging, accounting for 40% of chick mortality where the cause of death was established. The pattern observed on three occasions was for the female to desert her brood and her partner to form a new partnership with a single male. The new pair remained in the original territory with the new male harassing the brood and attacking the original male, and the female ignoring the brood. Not only did this cause the mortality of four chicks, an equivalent impact on chick survival as all predators combined, it also appeared to have a devastating effect on the deserted adult males. All three deserted males died or disappeared within a week of desertion, accounting for 60% of adult tūturuatu deaths for the breeding season. A fifth deserted chick was uplifted and successfully hand-reared at Te Whare Kararehe o Tāmaki Makaurau, and later released on the island as a fledgling.

The adult sex ratio (ASR) on Motutapu at the start of the breeding season was heavily male-biased, with eleven adult males, six adult females, and one juvenile male. This contrasts with the remnant tūturuatu population on Hokorereoro where the sex ratio was consistently close to parity in all age groups (A. Davis, 1994a). The mechanism(s) by which the bias in the ASR occurred in this population is unknown. Most of the adults (12/17), were originally bred in captivity and released on the island as juveniles. Unfortunately, only 51% (39/76) of the birds translocated over the period 2012–2016 had their sex determined before release, but known male translocations outnumbered females by 22 to 17. It is possible that non-parous release rather than differential dispersal or mortality may have contributed to the male-biased ASR of this anthropogenically established population. The propensity for female desertion to occur as a response to a male-biased ASR is well recognised in other Charadrius plover species (Eberhart-Phillips, 2019), but has not been previously reported in tūturuatu. The deleterious nature of the outcomes observed on the abandoned brood and partner suggest that female desertion may be an aberrant phenomenon in this species.

Most Charadrius plover species (77%) are monogamous, both socially and genetically, and exhibit biparental care during incubation and brooding (Eberhart-Phillips, 2019). Phylogenetic analysis suggests that this is the ancestral state (Reynolds & Székely, 1997), and is the case for all five species endemic to Aotearoa. Plovers exhibit several breeding systems with both inter- and intra-specific variation documented (Eberhart-Phillips, 2019), a flexibility facilitated by the precocial state of their young (Thomas & Székely, 2005). Where polygamy and uniparental care do occur, it is usually the female that deserts the chicks to pursue further mating opportunities, leaving the male to raise the brood.

Uniparental care, usually by males and occasionally by females, can be successful in some plover species; it is normal in six of the forty species, and common in another two (Eberhart-Phillips, 2019). My observations suggest that this is not the case for tūturuatu, as deserted males are likely to be injured or killed by the new partners, leaving the brood unattended. I witnessed a single case of male uniparental care after a female died or disappeared, leaving her partner to raise their 10-day old chick. He raised his chick successfully but may have neglected his own nutritional needs, as he was found dead in poor body condition five weeks after the chick fledged.

Food and water

Although not measured in this study, the abundance of prey species suitable for young chicks (which might vary through the season) could be a factor affecting chick survival, as suggested in tūturuatu on Hokorereoro (A. Davis, 1994b), and in piping plover (Loegering & Fraser, 1995) and snowy plover (Colwell et al., 2005). Young plovers are also thought to require freshwater, as their salt gland is not developed at hatching (Haig et al., 2019; Rubega & Oring, 2004). Chicks on Motutapu had easy access to freshwater from only two of the six nest sites: West Point, and Pig Bay North. Chicks from Pig Bay Mid and Pig Bay South were obliged to cross the territory of the Pig Bay North pair, and also the territory of a tūturiwhatu pair to gain access to freshwater. Chicks at Gardiner Gap and Sandy Bay were obliged to travel from their nest sites at the southern end of each beach to access freshwater at the northern end. On Hokorereoro tūturuatu chicks appeared to prefer freshwater seeps as feeding areas, and grew more quickly with access to freshwater seeps than those reared on saltmeadow turf (A. Davis, 1987). The chicks raised on freshwater seeps averaged 36 days to fledging, whereas those raised on saltmeadow turf averaged 56 days. Davis suggested the differences observed might be caused by different prey type availability, but freshwater access is a compelling explanation. Lack of access to freshwater may be a direct cause of mortality in plover chicks (Rubega & Robinson, 1997). It may also delay fledging by negatively impacting growth rate, as has been shown experimentally in American avocet chicks (Hannam et al., 2003). Any delay in fledging prolongs the most vulnerable phase in the life cycle, potentially leading to higher mortality from other factors such as predation.

The crucial period

The survival curve for tūturuatu chicks on Motutapu this season (Figure 3.1) was similar to that published for piping plover (Loegering & Fraser, 1995), snowy plover (Colwell et al., 2007), and tūturuatu on Hokorereoro (A. Davis, 1994b). The crucial twelve-day period from hatching appears to be the most dangerous part of the tūturuatu life cycle, and the time in which conservation efforts can potentially have the most impact. The rescue and hand-rearing of a chick during this phase was a successful intervention but also a demonstration of the fact that stochastic events and the assumptions made around them can significantly affect the outcomes for such a small population.

Overall productivity

The measure of productivity I used was the number of fledged young per breeding female. In any bird population this is a combination of the three parameters discussed above: egg production rate, hatching rate, and chick survival rate from hatching to fledging. The productivity for the season of my study was 0.66, consisting of four fledged juveniles from six females. This is almost identical to the mean productivity reported from the larger population on Hokorereoro of 0.64 (SD = 0.13) over six years (A. Davis, 1994a). However the mean productivity on Motutapu since the population was first established is 0.5, which compares unfavourably with

Hokorereoro and two other translocation sites: Waikawa Island and Mana Island (Dowding, 2019).

Juvenile and adult survival and dispersal

The mean annual survival rate of juvenile tūturuatu on Motutapu between 2012 and 2018 has been reported as 0.337 (Dowding, 2019). There was a marked difference between captive-bred birds released on the island at 0.283 (n = 92) and those bred on the island at 0.889 (n = 9). As a comparison, the mean annual survival rate of juveniles on Hokorereoro over two years was 0.26. Tūturuatu are not known to disperse from Hokorereoro so any losses can be attributed to mortality (A. Davis, 1994a), but they are known to disperse from Motutapu. Dowding's figures do not distinguish between dispersal and mortality, and although the net result to the population size may be the same, understanding the mechanism of loss is critical to inform management decisions (Drummond, Parker, Lovegrove, & Armstrong, 2019). I suggest that a difference in dispersal rate between the captive and wild bred juvenile birds is a more compelling explanation for the reported figures than a difference in resident survival rate. This theme is explored in Chapter Four "Dispersal of captive-bred tūturuatu after translocation".

The mean adult annual survival rate of tūturuatu on Motutapu between 2012 and 2018 has been reported as 0.710 (Dowding, 2019). This compares to an adult annual survival rate of 0.7 in the Hokorereoro population in 1985 and 1986 (A. Davis, 1994a), but values in the range of 0.86–0.88 in other (translocated) populations from 2005–2010 (Dowding, 2019). During my research project the adult tūturuatu population on Motutapu suffered losses of 28% (5/18) between September and April. This figure seems high, but adult tūturuatu do appear to be more vulnerable during the breeding season; on Hokorereoro 92% of adult mortality occurred between September and April (A. Davis, 1994a).

Summary and wildlife management recommendations

The viability of the tūturuatu population on Motutapu will ultimately be determined by the interaction of the parameters discussed above. As an example, a low fledging rate may not necessarily lead to a decreasing population if adult survival rates are high. It is important to target wildlife management inputs on those parameters where the population is performing poorly, which are often, but not always, associated with the breeding season.

Egg production and hatching rate are two parameters where the tūturuatu population on Motutapu appeared to perform well. The egg production rate was higher, and the hatching rate was similar to that recorded on Hokorereoro. The hatching rate was also considerably higher than those published for other plover species and for (congeneric) tūturiwhatu nesting on the same Motutapu beaches suggesting that the unusual, covered nest of the tūturuatu is beneficial in this respect.

Chick survival from hatching to fledging is the parameter where the population performed most poorly, with a survival rate of 21%, compared with Hokorereoro at 25%. Without human intervention to rescue and hand-raise one chick this figure would have been lower still. Published chick survival figures in other plover species are widely variable but include some that are considerably higher than those recorded on Motutapu. Wildlife management input has the potential to improve performance in this area. Female desertion resulted in the death of four chicks and threatened a fifth chick that was eventually hand-reared. Female desertion has not been reported in tūturuatu previously but is a common phenomenon in some other plover species and is thought to occur as a response to a male-biased ASR (Eberhart-Phillips, 2019). The sex-determination of all translocated birds would help to prevent such losses in the future. A prudent policy would be to release sex-balanced cohorts, or in the event of an established population with a biased ASR, to release a counter-biased cohort to achieve parity.

While unproven, lack of access to freshwater may be a factor that reduced chick growth and survival rates, as has been shown in other shorebird species. A prudent wildlife management strategy would be to provide access to freshwater near each nest for the first week or two after hatching. This would not only ensure access to freshwater but also allow chicks to stay near the shelter and refuge of the nest, rather than being forced to cross hostile territory or decamp to a distant and unprotected part of the beach.

I saw no evidence of human-related disturbance impacting chick survival rates. On this basis it seems prudent to advocate for the continuation of the current practice of placing symbolic fencing and signage around nesting sites.

Avian predator control is a controversial subject in wildlife management, particularly when the predator involved is a native species, like the kāhu. There are also inherent practical difficulties and a risk of increasing pressure from non-target predators (Catlin et al., 2011). I recorded no evidence of chick predation from three suspected avian species: karoro, pūkeko, and ruru and on this basis would not advocate for their control. My figures suggest that chick losses to avian predators may be sustainable if losses due to female desertion were avoided.

Juvenile tūturuatu bred on Motutapu demonstrated an exceptionally high survival rate at 0.889 (n = 9) (Dowding, 2019) compared with a rate of just 0.26 over two years on Hokorereoro (A. Davis, 1994a). Perhaps even more exceptional is the fact that these birds did not disperse permanently from Motutapu, in marked contrast to the high disappearance rates of captive-bred birds translocated to the island (see Chapter Four). This very high survival and retention rate raises some intriguing possibilities, for example: could similar results be expected if a captive-breeding facility were established on the island?

The mean adult annual survival rate on Motutapu was 0.71 (Dowding, 2019), similar to that reported from Hokorereoro of 0.7 (A. Davis, 1994a). The known causes of adult mortality during my research were ruru predation and intra-specific aggression following female desertion of brood and mate, affecting three birds in total. One adult male, injured in intra-specific aggression following female desertion was predated by a ruru, while the other two deserted males disappeared. Two other adults died or disappeared from unknown causes. Ruru are not present in the Chatham Islands, and were implicated in the failure to establish a translocated tūturuatu population on Motuora, another island in the Hauraki Gulf (Aikman, 1999). While it may be possible for a tūturuatu population to establish and grow in the presence of ruru, the ideal translocation site would not have this additional threat.

Female desertion was an unexpected finding of my research. Also unexpected was the prolonged intra-specific aggression between the new partners and the deserted male. This has not, to my knowledge, been reported in other plover species. Female desertion appeared to significantly alter the population dynamics on the island by causing the death of four chicks and also the death or disappearance of three deserted male partners. Simple wildlife management strategies to ensure a parous population as discussed above, would be a sensible precautionary approach to try to prevent such losses.

CHAPTER FOUR

Dispersal of captive-bred juvenile tūturuatu after translocation

Plate 4.1 Juvenile tūturuatu, Waikawa (Portland Island), Aotearoa (New Zealand).

4.1 INTRODUCTION

Captive breeding and translocation

Animal translocations by humans have been numerous and widespread since prehistoric times (Grayson, 2001). Translocations where conservation of the target species was the primary objective are a much more recent phenomenon. An early example was the translocation of hundreds of kākāpō (*Strigops habroptilus*) and kiwi pukupuku (little spotted kiwi, *Apteryx owenii*) by Richard Henry in the 1890s (A. Saunders & Norton, 2001). These ground-dwelling endemic birds were threatened by the spread of introduced mammalian predators, primarily stoats (*Mustela erminea*). Henry moved the birds from mainland Te Waipounamu (the South Island) of Aotearoa (New Zealand) to a large offshore island named Tau Moana (Resolution Island). Ultimately these efforts were unsuccessful as stoats invaded the island in 1900, but they created a template for the widespread use of translocation as a conservation tool in Aotearoa. Early successes included Don Merton's work with the two species of tīeke (saddleback, *Philesturnus rufusater* and *P. carunculatus*) in the 1960s, and the karure (kakaruia, Chatham Island robin, *Petroica traversi*) in the 1970s (C. Jones & Merton, 2012). Early successes outside Aotearoa included the translocation of peregrine falcon (*Falco peregrinus*) in North America in 1975 (Watts et al., 2015), and captive breeding and translocation of Arabian oryx (*Oryx leukoryx*) to Oman in 1982 (Spalton, Lawrence, & Brend, 1999). There were also many projects with low success rates; reviews of the literature from the 1970s and 1980s concluded that the majority of wildlife translocations failed to establish (Griffith, Scott, Carpenter, & Reed, 1989; Wolf, Griffith, Reed, & Temple, 1996).

The first translocation of plovers was recorded in 1982. Fifty independent mountain plover *(Charadris montanus)* chicks on the verge of fledging were captured in Colorado and transported to Kansas to an area within their historical range. Some chicks were kept enclosed with supplementary food for 1–2.5 days in what is now termed a “soft” release while others were released immediately in what is now termed a “hard” release. The “soft” release birds stayed within 350 m of their pen for 2–13 days before dispersing. The “hard” release birds foraged within 460 m of the release site for just a single day before dispersing. The authors concluded: “The success of this project may remain a mystery for several years. Though waterfowl prove to return to the area from which they fledge, it is unknown if other birds will respond in the same manner.” (Ptacek & Schwilling, 1983)

Captive rearing of Charadrius plovers first occurred in North America in 1989 with killdeer *(Charadrius vociferus)* eggs collected from the wild and artificially incubated (Powell & Cuthbert, 1993). The chicks were raised in captivity until fledging and released into the wild in sibling groups where their survival rates and behaviour were compared to wild-reared birds. The knowledge gained from this research was successfully applied to the captive rearing of endangered piping plover *(Charadrius melodus)* in 1991, using eggs recovered from abandoned nests (Powell, Cuthbert, Wemmer, Doolittle, & Feirer, 1997).

Tūturuatu (tchūriwat’, shore plover, *Thinornis novaeseelandiae*) were first bred in captivity at Pūkaha (Mount Bruce) near Whakaoriori (Masterton) in the early 1990s (Dowding & O'Connor, 2013). There are now two other captive-breeding facilities: Isaac Conservation and Wildlife Trust in Ōtautahi (Christchurch) and the recently established Cape Sanctuary in Te Matau-a-Māui (Hawkes Bay), with a total of thirteen breeding pairs in captivity at the time of writing.

Husbandry practices in Aotearoa have gradually been refined to the point that captive breeding is a regular aspect of conservation management for tūturuatu.

Multiple brooding of captive pairs is encouraged by the removal of clutches for artificial incubation. Some pairs have produced as many as five clutches through the long breeding season that runs through the Austral summer from September to February. Diseases such as Staphylococcal plantar pododermatitis ("bumblefoot") and Avian Pox Virus Disease continue to present challenges, resulting in variable productivity.

In a "typical" breeding season like 2018–19, the number of eggs laid per captive breeding pair is between six and eight, and the productivity, defined as chicks fledged per breeding pair, is between three and four. This level of productivity is considerably higher than that achieved in the wild (A. Davis, 1994a) and has allowed the translocation of 322 juvenile birds to six offshore islands around the coast of Aotearoa between 2009 and 2019 (DOC, 2019).

The captive breeding of tūturuatu is now an established and successful practice but their translocation is still fraught with difficulty. Tūturuatu populations have established on only three of the six islands they have been released on: Maung' Rē (Māngere) near Hokorereoro (Rangatira, South East Island) in the Chatham Islands, Waikawa (Portland Island) near the Māhia peninsula of Te Ika-a-Māui (the North Island), and Motutapu in the Hauraki Gulf near Tāmaki Makaurau (Auckland). The population on Motutapu has failed to grow despite the successful on-island breeding of some individuals, and the release of a total of 128 tūturuatu between 2102 and 2019.

<u>Disappearance after translocation: dispersal or mortality?</u>

The disappearance of captive-bred juvenile tūturuatu after translocation is a significant constraint on conservation efforts for this species (Dowding & O'Connor, 2013). The net result of dispersal and mortality to the population is essentially the same: the loss of the demographic and genetic potential of the individuals (C. Jones & Merton, 2012). However, determining the mechanism of this loss, by distinguishing between dispersal and mortality, may well be informative for strategies to maximize future establishment success (Drummond et al., 2019; Tweed et al., 2003).

The dispersal ability of tūturuatu

Dispersal ability varies greatly between species and in many cases is constrained by the lack of connectivity between habitat areas. The remnant population of tūturuatu on Hokorereoro has been described as sedentary, but it is perhaps more helpful to think of it being constrained by lack of habitat. Many Charadrius plover taxa flock away from their breeding territories during the non-breeding season, and about half are migratory (Haig, 2019). Tūturuatu movements recorded in the Chatham Islands have been between Hokorereoro, Rangihaute (Rangiauria, Pitt Island), and Maung' Rē islands; all movements less than 15 km, with water barriers of 2–3 km.

Translocations of tūturuatu around mainland Aotearoa have revealed their true dispersal ability. Birds have returned from release sites to the facilities where they were bred; from Waikawa Island to Pūkaha, a distance of 250 km, and from Mana Island to the Isaac Wildlife and Conservation Trust, a distance of 325 km. Between November 2012 and January 2013, a female released on Mana Island in 2009 was seen at Plimmerton, Lake Ellesmere, the Manawatu Estuary, and back at Plimmerton; a round-trip of over 850 km. Three individual tūturuatu are known to have crossed Te Moana-o-Raukawa (Cook Strait) (one of them twice); a minimum water crossing of 22 km (Dowding & O'Connor, 2013). The considerable dispersal ability of tūturuatu presents a challenge to translocation projects, but the greater challenge is to elucidate the factors affecting the individual’s decision to settle or disperse.

The drivers of dispersal

The phenomenon of dispersal is increasingly studied in conservation biology but remains poorly understood (C. Jones & Merton, 2012). Some instances of translocation dispersal are thought to be driven by “homing” towards the natal site, others by “exploration” from it (Linnell, Aanes, Swenson, Odden, & Smith, 1997). Exploratory behaviour can have profound effects on the selection of future breeding habitat, particularly in birds with high site fidelity whose initial choice could represent a lifetime investment in fitness (K. Davis et al., 2017). As with the distinction between dispersal and mortality, the net result of homing and exploration may be the same but investigating the drivers of translocation dispersal may provide valuable information for future management. For example, radio-tracking of re-introduced brown treecreepers *(Climacteris picumnus)* in Australian woodlands found birds preferentially established in forested areas with extensive leaf litter, a previously unknown habitat preference (Bennett et al., 2012; K. Richardson, Doerr, Ebrahimi, Lovegrove, & Parker, 2015).

The propensity of translocated animals to disperse may be subject to many factors other than a simple “homing” or “exploration” drive. They may be stressed from iatrogenic factors such as capture, transportation, or change in diet (Dickens, Delehanty, & Romero, 2010). They may be socially stressed if held in captivity with unfamiliar conspecifics pre-release, or through encounters with wild conspecifics post-release. These factors can result in translocation dispersal behaviour being quite different in type and scale from “natural” dispersal behaviour such as natal dispersal patterns and seasonal movements (Dickens et al., 2010; Parker et al., 2012).

The tendency of reintroduced animals to disperse depends not just on intrinsic behavioural factors, but on the availability of habitat (K. Richardson, 2015). This may include not only the physical landscape and the availability of food suitable for various life-cycle stages, but also the presence or absence of conspecifics, competitor species, predators, and parasites. The habitat requirements of a species may not always be well understood, especially where an endangered species has a current or relict habitat distribution reflecting a predation refuge rather than true habitat preference (Beauchamp & Worthy, 1988). For example, the remnant tūturuatu population on Hokorereoro persists on a rocky coastline, but the clear preference of translocated birds is to nest adjacent to sandy beaches, and areas with a mix of rock platform and sandy beach (A. Davis & Aikman, 1997). Similarly, takahē *(Porphyrio hochstetteri)* were assumed to be adapted only to the alpine grassland habitat where they were rediscovered in 1948. Subsequent examination of subfossil evidence has shown that they were widespread in lowland forests before their range was restricted by anthropogenic change (Beauchamp & Worthy, 1988).

The positive and negative aspects of dispersal

Dispersal behaviour has positive aspects in driving individuals to colonise new areas, and promoting gene flow between isolated established populations (K. Richardson et al., 2015). There can also be negative consequences to dispersal. Moving from the natal site risks decreased availability of essential resources, increased competition and/or predation, and incurs energy costs. In the context of the translocation of a highly endangered species, individuals that move from the managed release area could suffer from threats that led to the extinction of the wild population in the first place (van Heezik, Ludwig, Whitwell, & McLean, 2008). Integrated landscape management, which considers the availability of habitat in the surrounding landscape and its connectivity to the reintroduction site for the species concerned, is increasingly recognised in translocation programs (Jamieson and Lacy, 2012). These issues are of acute concern in tūturuatu, a species with strong dispersal abilities that is particularly vulnerable to the mammalian predators widespread on mainland Aotearoa.

The selection of Motutapu as a release site for tūturuatu offers examples of the potential for both positive and negative effects of dispersal. Successful establishment followed by dispersal of some individuals holds the prospect of a self-sustaining meta-population scattered over the many “pest-free” sanctuaries of the Hauraki Gulf, consisting of islands within the Gulf and mainland coastal sanctuaries adjacent to it. Conversely, dispersal to most mainland areas is currently likely to result in separation from conspecifics, very low potential for breeding, and rapid mortality from predation by introduced mammals.

Translocation: reintroduction or assisted colonisation?

The term “reintroduction” is used for translocation to an area within the indigenous range of the species, but this is not well documented in the case of the tūturuatu (Dowding & Kennedy, 1993). It is possible that the translocation of tūturuatu to islands around Te Ika-a-Māui (the North Island) is an example of “assisted colonisation” whereby organisms are translocated to an area outside their indigenous range. This is not just a semantic consideration as assisted colonisation is more controversial and inherently riskier than reintroduction (Seddon, Moro, Mitchell, Chauvenet, & Mawson, 2015). The IUCN guidelines for reintroductions state that introducing a species outside its indigenous range should only be considered if there is no suitable habitat within that range, so it follows that assessing the indigenous range of a species proposed for translocation is a fundamental part of the decision making process (IUCN/SCC, 2013) (Armstrong & Seddon, 2008).

4.2 RESEARCH AIMS

The small remnant population of tūturuatu on Hokorereoro is stable in numbers but constrained by a small habitat of 218 hectares and at risk from adverse events such as mammalian predator introduction, flooding, fire, and disease (A. Davis, 1994a). Captive breeding and translocation to islands free of introduced mammalian predators are key strategies in the conservation of tūturuatu (DOC, 2001), but their disappearance after release has been identified as a significant constraint on these efforts (Dowding & O'Connor, 2013).

In this study I closely monitored three cohorts of captive-bred juvenile tūturuatu released on Motutapu in 2019, with the principal aim of distinguishing between dispersal and mortality in those that disappeared. I also investigated some of the factors affecting the tendency to disperse or settle in the 128 captive-bred tūturuatu released on the island over the years 2012–2019.

4.3 METHODS

Study area and population

Field studies were conducted on Motutapu, a 1509-hectare island in the inner Hauraki Gulf near the city of Tāmaki Makaurau in Aotearoa (see Chapter Two for more detail). The study population was a group of 36 juvenile tūturuatu released on the island in three cohorts in late summer 2019. The birds were bred in captivity at one of two facilities: the National Wildlife Centre (NWC), and the Isaac Conservation and Wildlife Trust (ICW).

Pre-translocation preparation

Preparation at both captive breeding facilities included weighing, assessment of body condition, examination for external parasites, and examination for lesions suggestive of Staphylococcal plantar pododermatitis ("bumblefoot") and Avian Pox Virus. Disease screening for *Salmonella* and *Yersinia* was undertaken 7–10 days before translocation. A clean bill of health for each bird was a prerequisite for translocation. All fledglings were fitted with coloured plastic tarsal bands for field identification, along with a metal identification band on the tibia.

Motutapu pre-release aviary set-up and husbandry

Two pre-release aviaries were erected on a flat grassy area a few metres above the beach in Islington Bay. They were furnished with sand, shingle, and rocks from nearby beaches. Driftwood, wooden A-frame shelters, and trays of fresh and saltwater were also installed.

On arrival on the island, the juvenile tūturuatu were offered their familiar captive diet of ground cat biscuits and oxheart mince/wombaroo insectivore mixture in ramekins twice daily with mealworms scattered about the aviaries. In addition, several buckets full of fresh sand and seaweed containing sandhoppers *(Bellorchestia quoyana)*, an endemic Talitrad amphipod, were placed next to the salt-water trays and scattered around the aviaries twice daily. Some sandhoppers made their way into the saltwater trays, which encouraged the tūturuatu to forage in the saltwater as well as the sand. The aims were to provide some natural food, allow the development of foraging skills, and provide behavioural enrichment.

The juvenile tūturuatu were observed at least every second day with binoculars to check for leg lesions or any other abnormality. They were captured with a hand-net the day before release and examined more thoroughly, to confirm their fitness for release.

Release

The first cohort of twenty juveniles was released on the 18th February 2019, by which time the birds had spent between six and thirteen days on the island. The variation in time was not deliberate but dependant on transport and logistics. One bird (the second cohort) was held back for treatment at Te Whare Kararehe o Tāmaki Makaurau (Auckland Zoo) and released on the 27th of February 2019. The third cohort of fifteen juveniles was released on the 4th April 2019. All birds from this cohort had spent nine days on the island. The releases were timed to coincide with an outgoing low tide, to maximise foraging opportunities. The birds were fed as usual early on the morning of the release. At release time, the doors of the aviaries were opened and tied back. The birds were allowed to find their own way out in their own time to avoid panic. Any birds that had not left the aviary within a couple of hours were gently encouraged out so they could join the rest of the flock and take advantage of the low tide foraging opportunities. Once the last bird had left the aviaries the doors were closed.

Post-release monitoring

All areas of tūturuatu habitat on Motutapu and Rangitoto Island were monitored by me, Department of Conservation (hereafter DOC) staff, and volunteers, for the presence of translocated birds and evidence of injury or fatality. Established tūturuatu habitat (the most favoured beaches where tūturuatu have settled previously) was searched within an hour of high tide each day for three weeks. Observers walked the beaches and searched with binoculars (observer's own, 10X magnification) recording the identity of all tūturuatu seen. The observations were conducted at high tide for consistency and to make searching easier due to the much smaller beach area available.

Other areas of possible habitat were searched close to high tide every second or third day through this time. After three weeks the intensive searching was scaled back to routine monitoring once or twice a month by DOC staff. The presence and location of the released juveniles were also noted during the post-breeding season survey on 23rd May 2019. The data from the three cohorts were aggregated and plotted as the number of birds still present over days after release.

Evaluating time to dispersal – statistical methods

I expanded the scope of this study to include a review of the records of all 128 captive-bred juvenile tūturuatu translocated to Motutapu between 2012 and 2019. I plotted the probability of detection over time for this entire period. I then plotted the probability of detection over time for each of the twelve cohorts released, focussing on the 60-day post-release period. Survival analysis was conducted in R v4.1.3 (R Core Team, 2022) using a Cox proportional hazard regression model survival package (Therneau, 2021) to compare the effects of sex, place of origin, rearing method, age at release, and release date, on the risk of dispersal during the 60-day post-release period. This statistical method is typically used to assess the effect of several simultaneous risk factors on survival time, although in this case “survival time” was actually time to dispersal.

The sex of the birds was not always known; it was determined in 58% (75/128) of individuals prior to release. I also fitted binomial logistic regression models (R Core Team, 2022) comparing the probability of detection at the 60-day post-release period with age at release, and release date (measured in days after the summer solstice). This statistical method is useful when there are two mutually exclusive possible outcomes of a trial, in this case the dispersal or non-dispersal of each individual translocated bird.

4.4 RESULTS AND DISCUSSION

Disappearance after translocation 2019

Five birds from the first cohort disappeared immediately, leaving fifteen able to be detected one day after release. The single bird from the second cohort also disappeared immediately after release. Numbers then decreased more gradually until Day 11 when there were four birds still present.

Five birds from the third cohort disappeared immediately, leaving ten able to be detected one day after release. Numbers then decreased more gradually until Day 6, when there were three birds still detectable on the island. The data from the three cohorts released have been pooled to create Figure 4.1.

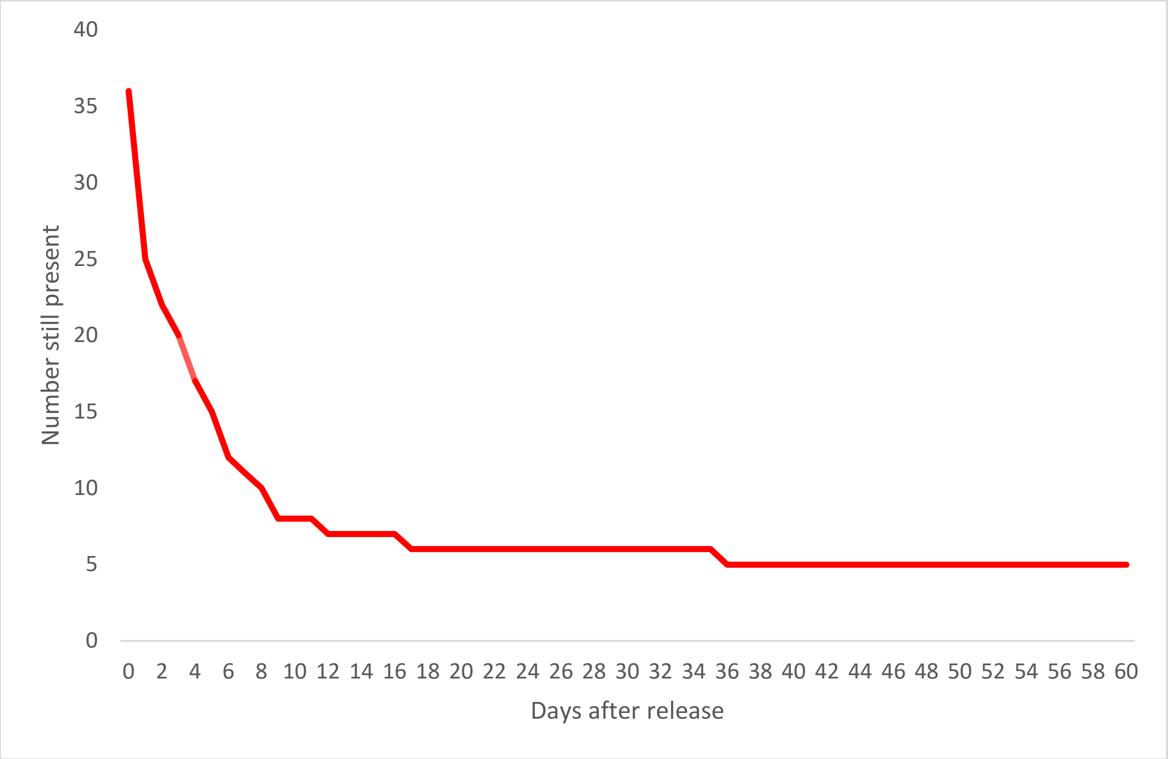

Figure 4.1 Number of captive-bred juvenile tūturuatu detected on Motutapu (from three cohorts) plotted against days after release on the island in 2019.

Disappearance after translocation: dispersal or mortality?

Most of the juvenile tūturuatu released on Motutapu in 2019 disappeared within a few days of release, almost one-third (11/36) within 24 hours. This rapid fall in numbers occurred during the three-week period after each release when established tūturuatu habitat and all beaches identified as suitable habitat were being closely monitored. No evidence of predation, injury, or fatality from any cause was seen through this period. While this does not exclude the possibility that on-island fatalities occurred, it is likely that the cause of disappearance in most (if not all) cases was dispersal. In particular it seems very unlikely that the five birds that disappeared within a day after the release of the first and third cohorts died on the island. Another piece of evidence supportive of the idea that dispersal rather than mortality was responsible for the disappearances is the high survival rate reported in juvenile tūturuatu bred on Motutapu between 2012 and 2018 of 0.889 (n = 9) (Dowding, 2019). As a comparison, the overall annual survival rate of juveniles on Hokorereoro over two years was 0.26 (A. Davis, 1994a).

One male bird was not detected on the island from Day 16 but subsequently returned to settle. This individual (WO-BG) was reported by members of the public at Whitford Beach on the mainland south of Motutapu on the 7th March and the 19th July, but returned to become resident on the island from December 2019. The other birds from the 2019 cohorts that were no longer detectable on Motutapu have not been reported since and are assumed to have been predated on the mainland.

Dispersal after translocation 2012–2019

When the data from all 128 birds translocated to Motutapu between 2012 and 2019 were considered, translocation to the island was characterised initially by the rapid disappearance of individual birds, shown in Figure 4.2 as a reduction in the probability of detection over time to a median value at 26 days.

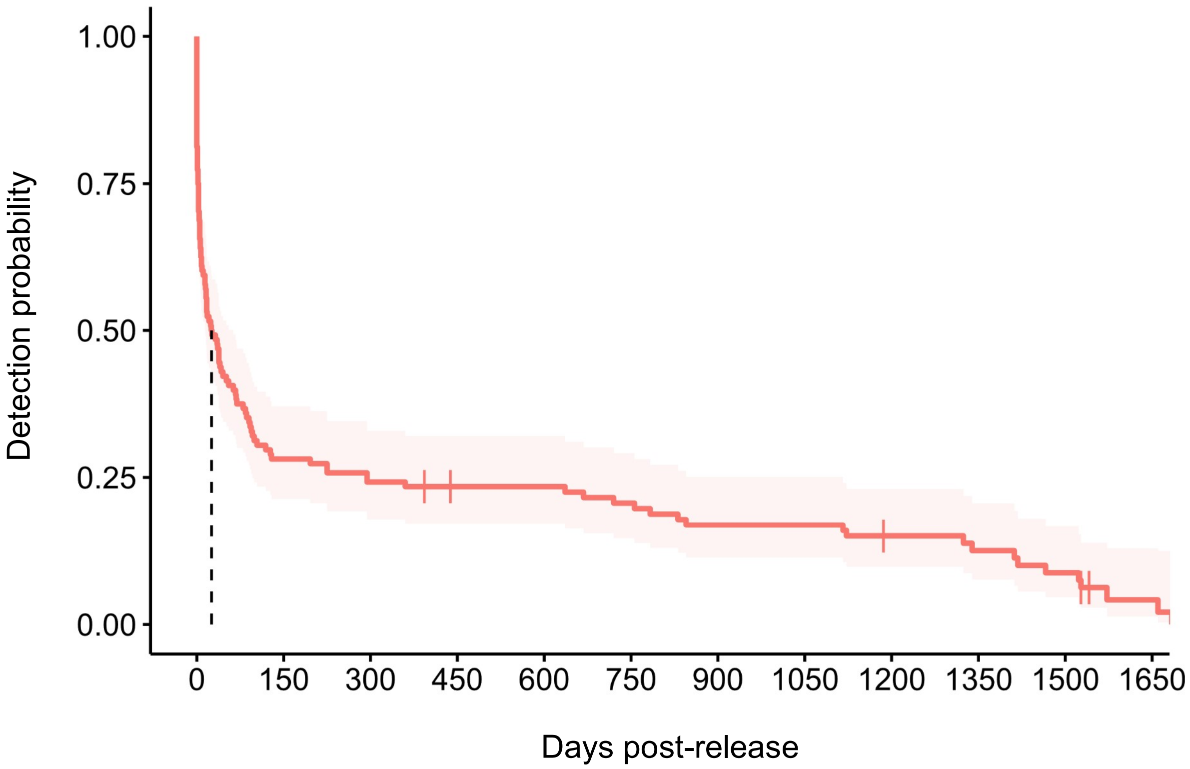

Figure 4.2 Overall probability of detection by days after translocation. The dotted black line indicates the median value of 26 days. Vertical bars represent individuals still present. The shaded area represents 95% CI.

There was considerable variation between cohorts particularly in the immediate 60-day post-release phase (see Figure 4.3).

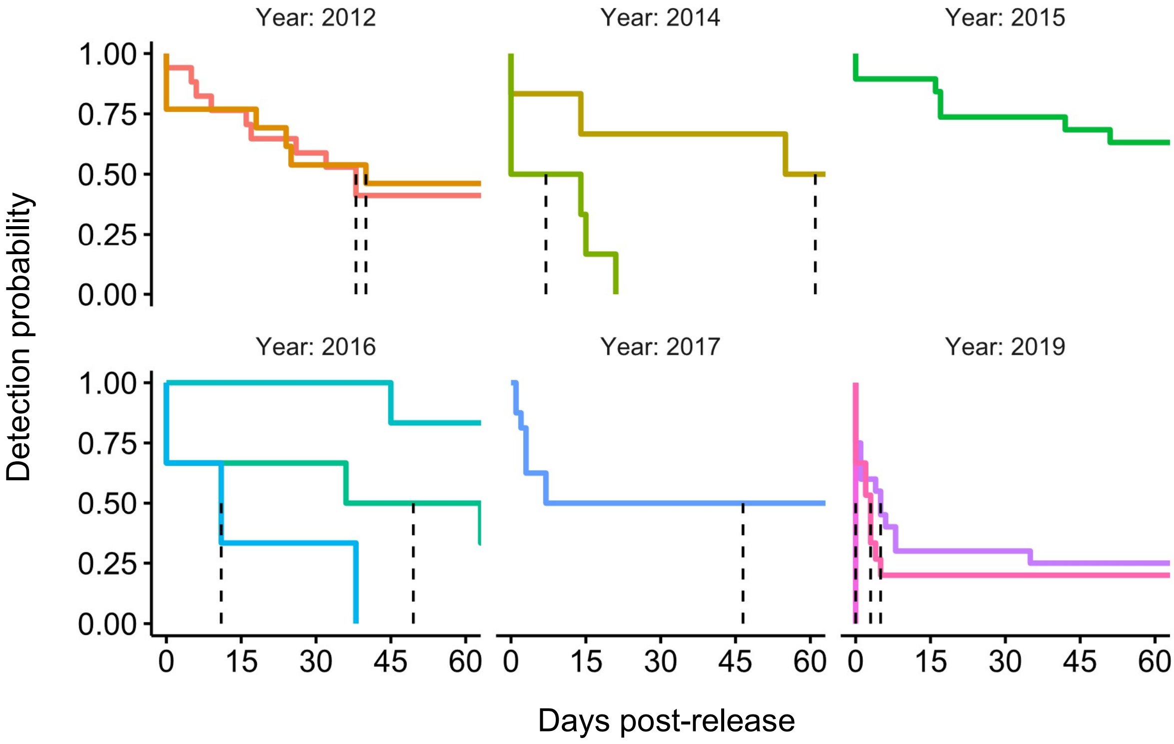

Figure 4.3 Probability of detection over time over the 60-day post-release period for each cohort of birds released on Motutapu from 2012–2019. The dotted black lines indicate the median values. Vertical bars represent individuals still present. The 95% CIs are not shown for clarity.

The rapid disappearance and considerable variation between cohorts seen on Motutapu are commonly observed phenomena in reintroduction biology but represent a major constraint on conservation efforts for tūturuatu (Dowding & O'Connor, 2013).

The predictors of probability of detection

I investigated five possible predictors of the possibility of observation using a Cox proportional hazards regression model as shown below in Figure 4.4.

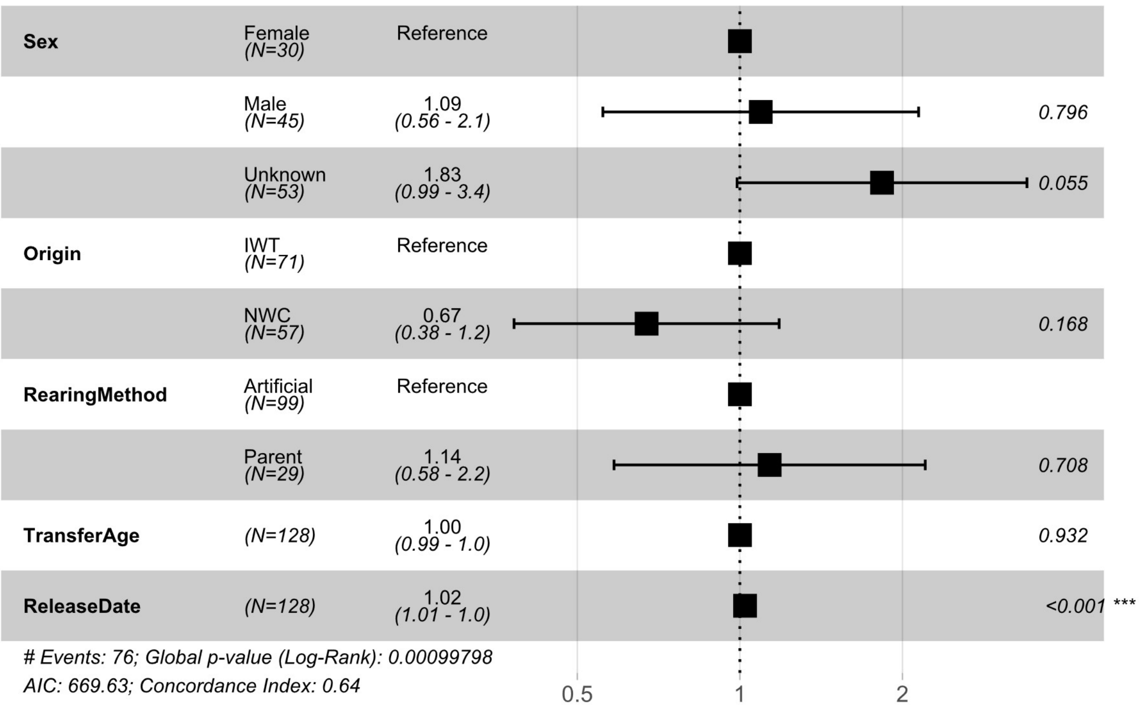

Figure 4.4 Comparison of hazard ratios for each predictor of probability of detection using a Cox proportional hazards regression model. Black squares represent the hazard ratio for each factor level compared to the reference level for that predictor. Black horizontal bars represent the 95% CI. Values greater than 1 indicate an increase in hazard (a decreased probability of detection) suggestive of increased dispersal. Values less than 1 indicate reduced hazard (an increased probability of detection) suggestive of decreased dispersal.

Sex

There was no significant difference in probability of detection over time between the female reference group and males (p = 0.796), and unknown (p = 0.055) (see Figure 4.4). The unknown group refers to the 53/128 captive-bred juveniles that had not had their sex determined prior to their release on Motutapu.

An unexpected finding was that twelve birds from seven of the twelve cohorts disappeared within 60 days of release but reappeared to become long-term residents on the island. More than half of these birds (7/12) disappeared on the day of release, with a mean time to disappearance of six days. The time to reappearance was not always recorded exactly but varied from seven months to three years with a mean of 11.6 months. The proportion of birds that disappeared within 60 days of release was approximately equal in known males: 64% (29/45) and known females: 60% (18/30), but there was a noticeable sex difference in the proportion that reappeared: 24% of known males (7/29), compared with 11% of known females (2/18). I suggest that successful return to the translocation site after dispersal might be more likely on Motutapu than in other parts of the country, as it is one of approximately forty wildlife sanctuaries around the Hauraki Gulf that are free of introduced mammalian predators.

I also suggest that differential return to settle long-term after early dispersal is a possible mechanism contributing to the male-biased ASR observed in the Motutapu population prior to the 2018/19 breeding season. At that stage (considering just the cohorts released from 2012–2016) the proportion that disappeared within 60 days of release was again approximately equal in males: 50% (11/22) and females: 47% (8/17), and the proportion that reappeared to settle was again male-biased: 36% of males (4/11), compared with 12% of females (1/8).

Place of origin

There was no significant difference (p = 0.168) in probability of detection over time between the two places of origin (see Figure 4.4) despite a marked difference in the distances involved. Motutapu is approximately 500 km north of NWC, and 900 km north of IWT (see Plate 4.2). Tūturuatu have been known to travel considerable distances to return from release sites to the facilities where they were bred; from Waikawa Island to NWC (250 km), and from Mana Island to IWT (325 km) (Dowding & O'Connor, 2013). These examples may represent “homing” towards the natal site, rather than "exploration" from the release site (Linnell et al., 1997). However, translocation dispersal may be driven by different factors from natal dispersal (K. Richardson & Ewen, 2016) and may result in behaviour that is quite different in type and scale from "natural" dispersal (Dickens et al., 2010; Parker et al., 2012). The high survival (and non-dispersal) rate reported in juvenile tūturuatu bred on Motutapu between 2012 and 2018 of 0.889 (n = 9) (Dowding, 2019) raises the intriguing possibility of captive rearing on the island in an attempt to reduce juvenile dispersal.

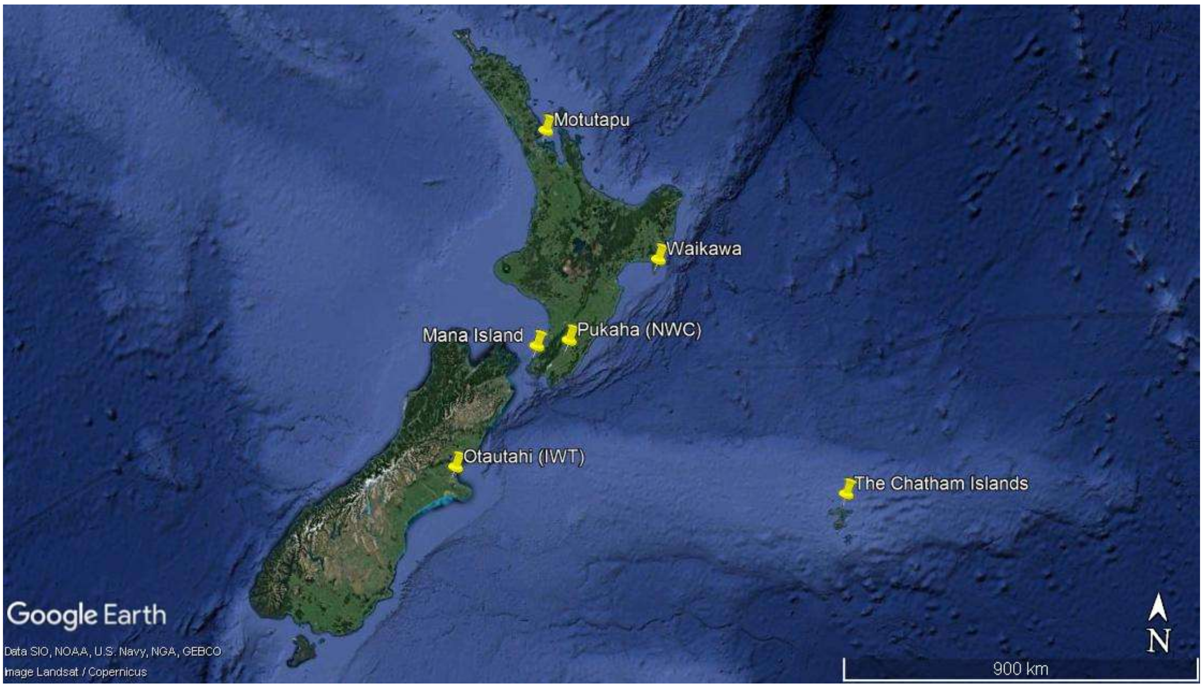

Plate 4.2 Aotearoa showing breeding centres: Pukaha (NWC) = (Mt. Bruce) National Wildlife Centre; Ōtuatahi (IWT) = Isaac Wildlife and Conservation Trust. Also shown are the sites of wild populations of tūturuatu: Motutapu, Waikawa, Mana, and the Chatham Islands.

Rearing method

There was no significant difference ($p = 0.708$) in the probability of detection over time between the two rearing methods; artificial ("hand") rearing, and parental rearing (see Figure 4.4).

Age at release

The relationship between the probability of detection and age at the time of release was not statistically significant ($p = 0.932$) (see Figure 4.4). However, the binomial distribution curve was suggestive of a trend, with over 50% of the youngest birds remaining observable, decreasing to 25% of the oldest birds (see Figure 4.5).

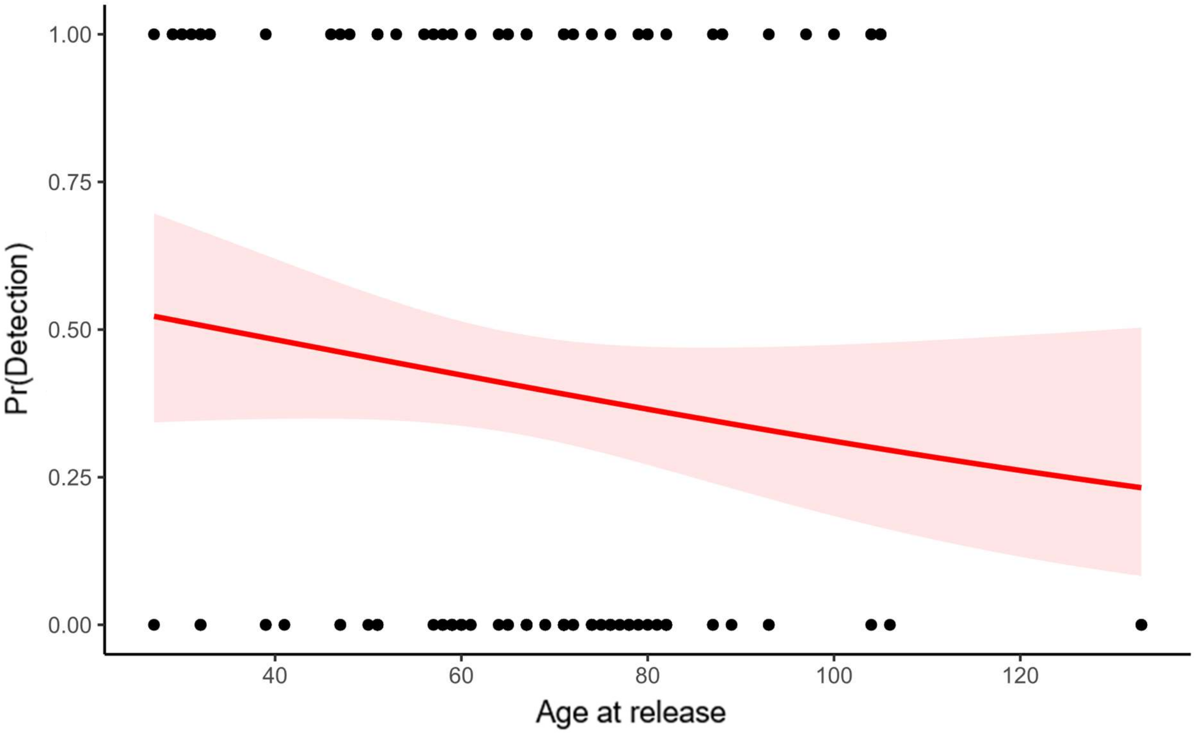

Figure 4.5 The probability of detection (during the 60-day post-release period) by age at release in days. Binomial distribution curve with 95% CI shaded.

The younger chicks released best match the natural age of independence in this species. Tūturuatu on Hokorereoro reached independence at 41–67 days (A. Davis, 1994b). The time to fledging varied between 29 and 63 days, and fledglings stay with their parents for 4–36 days, with those taking longer to fledge usually remaining with their parents for a shorter time. The release of young birds 1–4 weeks after fledging best approximates the natural situation and may offer the highest chance of success.

Interestingly, adult tūturuatu have also been translocated on occasion, notably on Motuora (another island in the Hauraki Gulf) in the late 1990s where a higher proportion of adults than juveniles remained detectable on the island for more than a month; 57% of adults (8/14) compared with 26% of juveniles (10/39) (Aikman, 1999).

Release date

There was a significant relationship (*p* < 0.001) between probability of detection over time and the release date (see Figure 4.4). The reference number of 1.02 indicates a 2% decrease in the likelihood of detection for each additional day after the summer solstice. The binomial distribution curve (see Figure 4.6) illustrates the trend with close to 60% of birds in the in the earliest releases remaining detectable, decreasing to 20% in the latest releases.

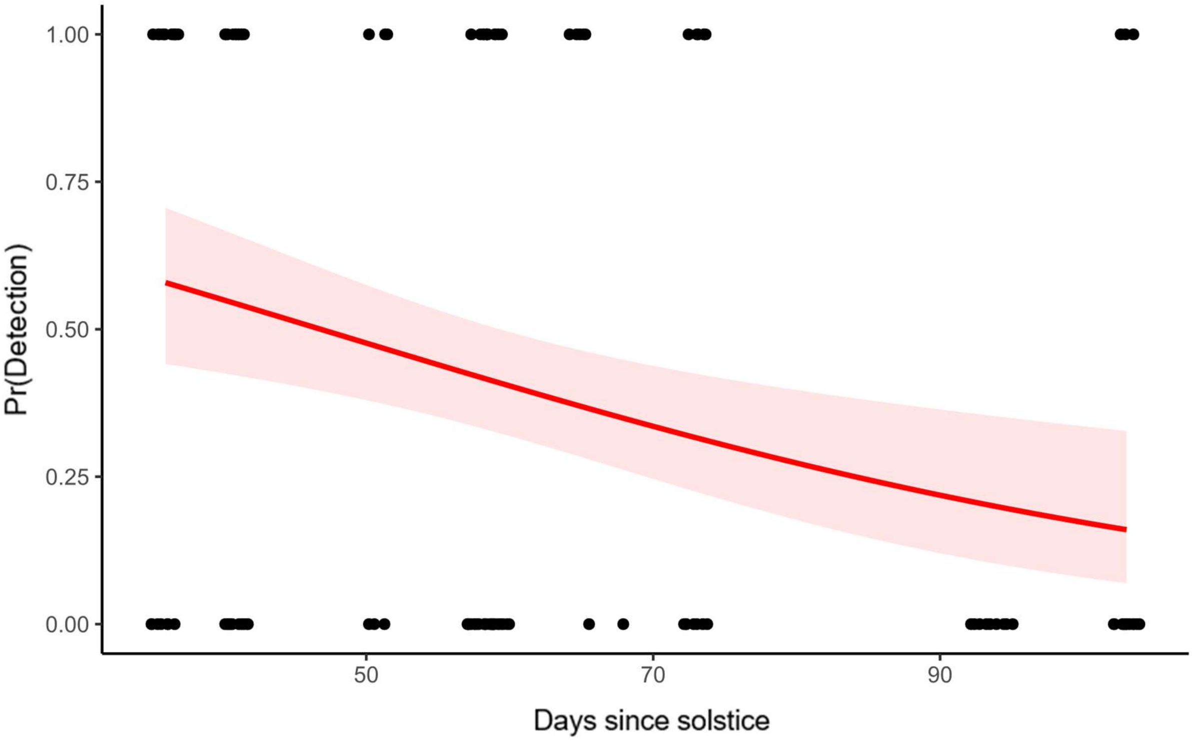

Figure 4.6 Probability of detection (during the 60-day post-release period) by release date (days after summer solstice). Binomial distribution curve with 95% CI shaded.

Juvenile tūturuatu translocated to Motutapu were most likely to remain detectable on the island when released in January, and significantly less likely when released in March or April. January is the peak of the Austral summer, and the time that best matches the fledging of wild-hatched tūturuatu from first clutches on the island. In the breeding season I observed, eggs from the first clutches all hatched between 27th November and 21st December, with surviving chicks expected to fledge in January.

These findings suggest that the timing of release may be an important factor in translocation success in juvenile tūturuatu. Current management policy for captive breeding encourages pairs to re-nest by removing clutches for artificial incubation and rearing, with the result that captive pairs have been known to produce up to five clutches in a season. These findings suggest that more modest production, with more emphasis on the timing of release, might lead to more successful translocation outcomes.

Other possible drivers of dispersal of tūturuatu from Motutapu

Indigenous range

Motutapu is approximately 800 km north of the documented indigenous range of tūturuatu (see later in this chapter for more detail). Translocations in the core of the indigenous range tend to achieve the highest success rates (Griffith et al., 1989). Allowing for climate change, the recommendation should perhaps be to translocate to sites in the cooler end of the indigenous range. It is possible that the latitudinal distance of Motutapu from the indigenous range is a driver for dispersal.

Presence of predators

The presence of easily detected avian predators including kāhu (swamp harrier, *Circus approximans*) and ruru (morepork, *Ninox novaeseelandiae*) may act as a driver for dispersal. It was suggested that translocated tūturuatu dispersed from nearby Motuora as a response to nocturnal harassment by ruru (Aikman, 1999).

Presence of competitive congeners

The presence of tūturiwhatu (northern red-breasted dotterel, *Charadrius aquilonius*), a larger competitive congener may be a driver for dispersal. The two species interact frequently; my behavioural observations on Motutapu showed that approximately half of adult tūturuatu display behaviour during the breeding season is to tūturiwhatu (see Chapter Two).

Presence of conspecifics

The presence of conspecifics is unlikely to act as a driver of dispersal. In the Chatham Islands, tūturuatu rarely disperse from Hokorereoro to other islands, even though there is a much greater population density there than on Motutapu. In early translocations to nearby Maung' Rē, tūturuatu usually returned to Hokorereoro (Dowding & O'Connor, 2013). Conversely, the presence of other tūturuatu might act as a driver to settle, as juvenile tūturuatu have been observed to stay around their parents for a variable time (4–36 days) after fledging (A. Davis, 1994b).

Resource availability

There appear to be adequate resources of food for adult tūturuatu on Motutapu as evidenced by the establishment and persistence of a small population, and my observations of a low adult foraging time budget comparable to the stable population on Hokorereoro (A. Davis, 1987). My observations of a high chick foraging time budget were comparable to the favoured “Northern Shore” area on Hokorereoro (A. Davis, 1987) suggesting that food resources and freshwater necessary for chicks are not limiting factors. The high survival and non-dispersal rate of island-born juvenile tūturuatu (Dowding, 2019) is further evidence that resources on Motutapu are adequate.

Historical and subfossil records of tūturuatu

Mainland Aotearoa: Te Waipounamu and Te Ika-a-Māui

Our knowledge of the distribution of tūturuatu around Aotearoa before the arrival of humans is limited. Until recently, many authors, e.g. (A. Davis, 1994a) assumed that the species was widely distributed around the coast of both main islands; Te Waipounamu, and Te Ika-a-Māui. However, the historical and subfossil evidence for this is sparse. A single specimen referred to initially as a “sandpiper” *(Charadrius torquatula)*, was collected by Johann Reinhold Forster on 16th April, 1773 at Dusky Sound in the southwest of Te Waipounamu during Captain James Cook’s second voyage to Aotearoa (Forster & Hoare, 1982). What was almost certainly the same specimen was painted by Forster’s son George, the assistant naturalist and natural history draughtsman on the voyage. The specimen was later incorrectly assumed to have been collected from Queen Charlotte Sound by Dr J. Latham, who described the new species as the New Zealand Plover *(Charadrius novaeseelandiae)* (Medway, 2007). No mention is made of tūturuatu being seen or collected at Queen Charlotte Sound despite the voyage visiting the area three times. Queen Charlotte Sound is approximately 800 km distant from Dusky Sound, on the north-east aspect of Te Waipounamu. It appears that this single historical error led to the assumption that the species was widespread around the coast of Te Waipounamu, and perhaps by extension the whole of Aotearoa.

A second single specimen was collected during the voyage of The Erebus and Terror from the Auckland Islands in 1840 (J. Richardson & Gray, 1845). This bird (possibly a juvenile) is assumed to have been either a straggler or mislabelled as to its place of collection (Turbott, 1990). The same expedition reported the sighting of a pair on the Otago coast by Earl, who described the species as "very rare" (J. Richardson & Gray, 1845). Potts also describes sighting three pairs in the same area, probably in 1872 (Potts, 1873). The species also appears on a list of the wildlife in the Okarito district of Westland in 1878 (Hamilton, 1878), but no specific sightings or specimens are mentioned. In addition to the historical records, subfossils from whēkau (laughing owl, *Ninox albifacies*) sites in the Waikari Valley in North Canterbury are evidence of tūturuatu distribution inland along riverbeds in the late Holocene (< 5000 years B.P.) (Worthy & Holdaway, 1996). I have used the recently recommended reclassification of whēkau from the monotypic genus *Sceloglaux* to the genus *Ninox* (Wood et al., 2017).

It remains unclear whether tūturuatu ever existed in Te Ika-a-Māui. Buller in his "Manual of the Birds of New Zealand" briefly described the species range as "Both Islands" (Buller, 1882). In his later work "A History of the Birds of New Zealand" Buller wrote: "Till of late years this handsome Wader appears to have been of very rare occurrence…" and mentioned three specimens in collections, two of them from the Chatham Islands. He went on to write: "Owing, however to the increased activity of ornithological research in the colony, it has been discovered to be comparatively plentiful on various parts of our coast, both north and south. The mouth of the Piako river, in the Hauraki Gulf, the broad flats of the Manukau harbour, and the sand-spits off Tauranga are some of the localities where flocks have been met with in the spring and autumn." (Buller, 1888).

This report is now considered doubtful by some authors (Sibson & Howard, 1982; Turbott, 1990; Woodley, 2012). One point is that tūturuatu do not flock in the spring. They could also be confused with a returning migrant: the ruddy turnstone *(Arenaria interpres)* as Fleming's description indicates: "On the wing the Shore Plover is reminiscent of the Turnstone, the wing pattern, glistening white breast, dark collar, orange legs and general manner of flight being remarkably similar" (Fleming, 1939). In addition, I have been unable to find any recorded specimens, eye-witness accounts, midden, or subfossil remains of the species from Te Ika-a-Māui.

The Chatham Islands

The Chatham Islands lie approximately 950 km east of mainland Aotearoa. The date of human arrival is unknown but is estimated at 450 years ago (Millener, 1999). At that time tūturuatu were probably widespread around the islands – they were certainly present on the south-western aspect of Rēkohu (the largest island) as indicated by subfossil remains (Marshall, Scarlett, & Sutton, 1987).

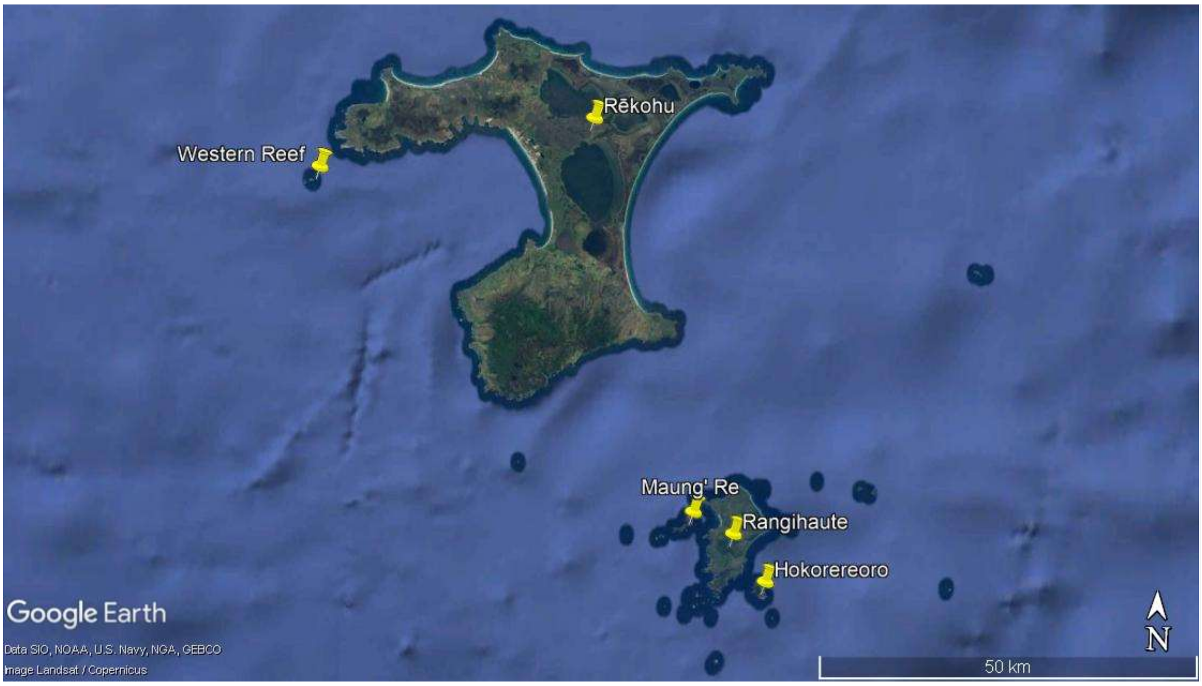

Plate 4.3 The Chatham Islands.

Discovery of a new population

For most of the 20th century, it was believed that the remnant population of 110–140 tūturuatu was confined to Hokorereoro (Dowding & O'Connor, 2013). In 1999, a small, apparently isolated population of about twenty birds was discovered on Western Reef, a tiny (6 hectare) reef approximately 80km to the north-west of Hokorereoro. Sawyer and de Lange described the physical geography of the reef : “Most of the reef is subject to tidal wash, and that portion lying above the approximate mean high tide mark is mostly of such low relief that it would be partially submerged and wave swept in only moderate swells. Indeed, according to local crayfishermen, the whole reef is frequently wave swept, and during particularly severe storms it can be completely submerged” (de Lange & Sawyer, 2008). Whether because of the inclement conditions, or an expanding fur seal colony on the reef, the tūturuatu population declined, with the last surviving bird taken into captivity in 2003 (Dowding et al., 2005).

Summary of documented distribution of tūturuatu

To summarise the documented distribution of tūturuatu from convincing historical and subfossil records, the species was present in the south-west of Te Waipounamu (Dusky Sound), present in the east of Te Waipounamu including coastal Otago and north Canterbury, and present in the Chatham Islands. There is little to no convincing evidence tūturuatu were once widespread on Te Ika-a-Māui.

The impact of introduced mammalian predators

The evolution of the avifauna of Aotearoa in the absence of terrestrial mammals, and their susceptibility to mammalian predators following anthropogenic introduction is well documented e.g. (Dowding & Murphy, 2001). Tūturuatu are relatively small shorebirds, nest on the ground adjacent to open areas of coastline, have covered nests, and have defence behaviours including injury feigning and attacking intruders; all factors that make them easy prey for a mammalian predator.

The first two mammalian predators; the kiore (Pacific rat, *Rattus exulans*) and the kurī (Polynesian dog, *Canis familiaris*) were introduced to Aotearoa centuries ago by Polynesian settlers. The effect of kiore predation on tūturuatu populations is unknown, but experience with other coastal ground-nesting birds suggests it may have been significant. In Marotere (the Hen and Chicken Islands), productivity of Pycroft's petrel *(Pterodroma pycrofti)* and little shearwater *(Puffinus assimilis haurakiensis)* was measured before and after the removal of kiore from two islands (Pierce, 2002). Productivity was significantly lower for both species in the presence of kiore, down to almost total failure in some years. Video surveillance of little shearwater burrows documented predation of eggs by kiore, which was the probable cause of up to 75% of the nest failures (Booth, Minot, Fordham, & Innes, 1996).

Further south on Hauturu-o-Toi (Little Barrier Island), widespread predation by kiore on chicks of Cook's petrel *(Pterodroma cookii)* contributed to 100% failure of studied burrows in three years of monitoring between 1996 and 1999, whereas the same species on Whenua Hou (Codfish Island) achieved over 85% breeding success after removal of kiore (Atkinson & Towns, 2001).

Kiore were introduced to the Chatham Islands by Polynesian settlers (Matisoo-Smith, Sutton, Ladefoged, Lambert, & Allen, 1999). They established on Rēkohu, but do not appear to have established on the other smaller islands of the group (Tennyson & Millener, 1994). The combined effects of human hunting, habitat modification, and kiore predation devastated the endemic avifauna. Thirteen species (36% of the original terrestrial avifauna) were extirpated from the Chatham Islands between the arrival of the first humans and about 300 years ago (Millener, 1999). Others, including the tūturuatu, were extirpated from Rēkohu to become small remnant populations on the smaller islands.

The extirpation of tūturuatu from Rēkohu and Te Waipounamu

The documented extirpation of tūturuatu from Rēkohu in pre-European times suggests that a similar process may have occurred on a much larger scale on Te Waipounamu. Kiore were introduced to Te Waipounamu by successive waves of Polynesian settlers several centuries earlier than on Rēkohu (Atkinson & Towns, 2001). The time of arrival of the first settlers is unknown but is generally estimated at 800 years ago. Archaeological evidence supports a rapid exploration and dispersal around the coastline of Aotearoa. The vast protein resources available year-round allowed rapid increases in both human and kiore populations (McGlone, Anderson, & Holdaway, 1994).

Some authors have linked the extirpation of tūturuatu from mainland Aotearoa to the introduction of cats *(Felis catus)* and Norway rats *(Rattus norveigicus)* e.g. (Dowding & Murphy, 2001). It certainly occurred before the spread of ship rats *(Rattus rattus)* in Te Waipounamu, and the introduction of the three mustelid species: stoats, ferrets (*Mustela furo*), and weasels (*Mustela nivalis*) in the 1870s. However, the historical records from the 1800s consist of the sighting of a pair on the Otago coast by Earl, who described the species as “very rare” (J. Richardson & Gray, 1845), and the sighting of three pairs by Potts in the same area, probably in 1872 (Potts, 1873). It seems likely that tūturuatu, if not quite extirpated, were in decline from predation by kiore before the arrival of cats and Norway rats.

The remaining tūturuatu on Te Waipounamu faced additional challenges from avian predators absent from the Chatham Islands. Two species of owl are known to have predated tūturuatu: the now extinct whēkau (Worthy & Holdaway, 1996) and the ruru (Aikman, 1999). Interestingly the ruru, while very widespread around forested areas of Aotearoa, is uncommon on the Otago coast where the last documented sightings of tūturuatu on the mainland occurred.

In the Chatham Islands, cats and Norway rats were present on Rēkohu by 1840 (Fitzgerald, 1990; Moors, 1990), but tūturuatu had not been recorded there by earlier European settlers. Tūturuatu survived on Maung’ Rē, on parts of the coast of Rangihaute (where they were reported by Travers in 1872 (Travers & Travers, 1872), and on Hokorereoro – the eventual stronghold of the remnant population. Cats were introduced to Maung’ Rē in the early 1890s and tūturuatu, though still present in 1892 (Forbes, 1893), were last seen there in 1898 (Fleming, 1939). Cats were also introduced to Rangihaute where they remain the single mammalian predator species today. Tūturuatu have not established on the island since, although the occasional straggler is reported (Fleming, 1939).

Predator Free 2050

A major initiative in Aotearoa that could transform integrated landscape management for translocations, and wildlife management in general, is the Predator Free 2050 program. The combination of political will and developing new technologies allow for at least the aspiration of the elimination of introduced mammalian predators from the whole of Aotearoa. The Hauraki Gulf currently has forty pest-free sites consisting of relatively small offshore islands, and peninsulas protected by predator-proof fencing. As the Predator Free 2050 project gathers momentum, it is possible to imagine the eradication of mammalian predators from the larger inhabited islands of Aotea (Great Barrier) and Waiheke, and from the Coromandel Peninsula. This would create substantial additional habitat for many endemic species, including translocated tūturuatu. Aotea and Waiheke already have the advantage that each island is free of one important predator: the stoat on Aotea, and the brushtail possum *(Trichosurus vulpecula)* on Waiheke.

Cat eradication from Rangihaute

In the Chatham Islands, the eradication of a single predator species — the cat — from Rangihaute would make available substantial additional habitat to the remnant tūturuatu population on adjacent Hokorereoro. Rangihaute at 65 square kilometres is far larger than Hokorereoro at 218 hectares, it is only three km distant, and cats are the only mammalian predator species present. A feral cat control program on St. Helena Island increased nest survival of the critically endangered St. Helena plover *(Charadrius sanctaehelenae)* by more than threefold in one study area, but only marginally in another area. The difference was thought to be the presence of rats in the second area, which increased their activity and predation once the apex predator was removed (Oppel et al., 2014). The single management action of eradicating cats on Rangihaute may well represent the best chance of tūturuatu surviving as a species in the medium term.

Translocation: reintroduction or assisted colonisation?

The historical evidence strongly suggests that the translocation of tūturuatu to islands around Te Ika-a-Māui is an example of “assisted colonisation” whereby organisms are released outside their indigenous range, rather than “reintroduction”, where the release is inside their indigenous range. This is not just a semantic consideration. Assisted colonisation is more controversial and inherently riskier than reintroduction (Armstrong & Seddon, 2008; Seddon et al., 2015). Translocations into the core of species indigenous ranges are generally more successful than those on the periphery of, or outside, indigenous ranges (Griffith et al., 1989). One justification for assisted colonisation is to counteract the effect of climate change, for example to translocate a species to a cooler latitude to offset the effects of environmental warming. It would appear to be counter-productive to deliberately translocate a species to a warmer latitude. Despite this logic, the successful establishment, growth, and persistence of a population of tūturuatu on Waikawa Island off the east coast of Te Ika-a-Māui as part of DOC’s recovery program demonstrates that the species can thrive at this latitude.

Assisted colonisation also tends to focus on the restoration of a species rather than an ecosystem (Lunt et al., 2013). It may be that the ecosystem services provided by the organism in its indigenous range are either not required outside that range or are provided by other species. A move outside the indigenous range could also bring an organism into contact with new competitors, predators, parasites, or diseases. Alternatively, such a move could expose indigenous species to competition or predation by the colonist species – a scenario we are all too familiar with in Aotearoa where introduced mammals and birds compete with and predate endemic species.

Summary and wildlife management recommendations

Most of the juvenile tūturuatu released on Motutapu in 2019 disappeared within a few days of release, almost one-third (11/36) within 24 hours. This rapid fall in detectable numbers occurred during the period after each release when established tūturuatu habitat and all beaches identified as suitable habitat were being closely monitored. No evidence of predation, injury, or fatality from any cause was seen through this period. While this does not exclude the possibility that on-island fatalities occurred, it is likely that the cause of disappearance in most (if not all) cases was dispersal. When the data from all 128 birds translocated to Motutapu between 2012 and 2019 were considered, translocation to the island was characterised initially by the rapid disappearance of individual birds to a median value at 26 days, although there was considerable variation between cohorts. These findings suggest that a focus on researching and reducing dispersal is important for future translocation projects in tūturuatu.

Release date was the only predictor investigated that showed a significant relationship (p < 0.001) with the probability of detection in the 60-day post-translocation period. There was a 2% decrease in the likelihood of detectability for each additional day after the summer solstice. This timing aligns with the fledging of wild-hatched tūturuatu from first clutches on the island, all of which were expected to fledge in January. Current management policy for captive breeding encourages pairs to produce multiple clutches with production extending late in the season. These findings suggest that a shorter captive breeding season with a focus on translocation early in the year would reduce dispersal and lead to more successful outcomes.

Translocation of tūturuatu to Motutapu is likely an example of “assisted colonisation” rather than “reintroduction”, as the release site is well outside the documented latitudinal range of the species. Assisted colonisation is more controversial and inherently riskier than reintroduction and does not align well with an ecosystem restoration approach. The eradication of cats on Rangihaute would allow reintroduction or natural colonisation of tūturuatu from Hokorereoro to a large area of habitat in the heart of their indigenous range and potentially improve the long term viability of the species.

CHAPTER FIVE

Summary and conservation implications

Plate 5.1 Male tūturuatu on Motutapu, Aotearoa. Image credit to Chelsea Ralls.

5.1 INTRODUCTION

The tūturuatu (tchūriwat’, shore plover, *Thinornis novaeseelandiae*) is an endangered shorebird endemic to Aotearoa (New Zealand). The remnant wild population of approximately 45 breeding pairs appears stable but is confined to Hokorereoro (Rangatira, South East Island), a small island in the Chatham Islands group. Since 1994 efforts to translocate captive-bred juvenile birds to other island sanctuaries free of introduced mammalian predators have met with mixed success. This study investigated the behavioural ecology of a population of eighteen tūturuatu on Motutapu, an island in the Hauraki Gulf near Tāmaki Makaurau (Auckland), which were either survivors of or descended from 92 captive-bred juveniles released between 2012 and 2017.

5.2 TŪTURUATU BREEDING SEASON BEHAVIOUR

The behaviour of each breeding pair, and their chicks once hatched, was recorded every two minutes at their nest site or territory for two hours each day until the last chick had fledged, a total of almost 20,000 observations. Trail camera recordings of the nest site and surrounding area augmented my direct observations. Behavioural time budgets were constructed for adults and chicks allowing comparison between sexes, phases of the breeding season, and between the Motutapu population and published reports on the Hokorereoro population. Display activity was observed and circa-tidal effects on behaviour were investigated.

Time budget construction

Proportional time budgets were calculated for each individual adult bird by adding the number of observations of the behavioural states defined above and dividing by the total number of observations made during an observation period. The mean proportional time budget was simply the mean of these individual values for the data set being considered, whether the whole adult population throughout the breeding season, or smaller groupings by sex or phase of the breeding season. This methodology was not feasible for chicks as they were not individually identifiable. The data for the chicks of each brood were aggregated, and the time budgets calculated as the mean proportion of time each brood spent in each of the behavioural categories.

Adult tūturuatu breeding season time budgets

Adult tuturuatu had mean time budgets for foraging of 0.17 (± 0.17) in females and 0.23 (± 0.19) in males, and for inactive behaviour of 0.18 (± 0.19) in females and 0.21(± 0.22) in males. These figures are relatively low for foraging and high for inactive behaviour when compared to published reports from other plover species (Johnson & Baldassarre, 1988; Nol et al., 2014) and the tūturuatu population on Hokorereoro (Rangatira, South East Island) (A. Davis, 1987). When food supplies are limited plovers can be expected to forage for a large proportion of their time both day and night (Nol, 2019), although this behaviour is likely to be influenced by metabolic demands (such as egg production) and time constraints (such as incubation). My observations suggest that adequate food resources are available for adult tūturuatu on Motutapu.

Differences in breeding season behaviour between male and female tūturuatu

Female tūturuatu incubate significantly more than males diurnally and may be more active nocturnally during the nesting phase of the breeding season. This behaviour is seen in other plover species where it is thought to reduce diurnal predation of males (Ekanayake et al., 2015a). No such benefit is likely in tūturuatu as the incubating partner is hidden in the covered nest unique to this species. An alternative explanation is that nocturnal activity benefits the female, for example by allowing access to nocturnal prey species (Kuwae, 2007). On Motutapu, nocturnal foraging may also predispose females to predation by ruru and is one possible mechanism for the development of the male-biased adult sex ratio (ASR) observed.

Display behaviour

Display behaviour in tūturuatu was elicited significantly more commonly in response to two competitive species: other tūturuatu, and tūturiwhatu, rather than to potential predators or non-threatening species. While interaction with other tūturuatu is unavoidable, I suggest that having to share breeding habitat with tūturiwhatu is likely to cause considerable energy expenditure and stress to tūturuatu and may impact both adult survival and chick survival to fledging.

The covered nest of this species provides shelter and crypsis to the clutch and newly hatched chicks. The increase in display behaviour observed in adult tūturuatu through the breeding season was not gradual as would be expected if it were related to increasing “reproductive value” of the off-spring (Andersson et al., 1980). Display behaviour by both sexes increased suddenly and significantly during the chick-rearing phase as would be expected if it were related to the vulnerability of the off-spring (Brunton, 1990). The vulnerable phase coincides with a heightened risk of human disturbance as visitor numbers peak over summer, but wildlife management practices can take advantage of the fact that chick-rearing occurs over a relatively limited time.

Circa-tidal rhythms of behaviour

Patterns of foraging and inactive behaviour in tūturuatu appeared to be affected by circa-tidal rhythms. In general, foraging occurred preferentially during the hours after high tide as the receding waters exposed feeding grounds to the hungry birds, and inactive behaviour occurred preferentially around the high tide when foraging options were limited. The response varied between phases of the breeding season, and between sexes. In the nesting phase the time budget for inactive behaviour in both sexes decreased markedly and appeared to be decoupled from circa-tidal rhythm. The decrease in inactive behaviour was more than offset by the time spent incubating. Opportunities for females to forage diurnally during the nesting phase were markedly reduced from the pre-nesting phase as they spent almost twice as much diurnal time incubating as males. Interestingly my results suggest that during the nesting phase females appeared to have priority over males in their choice of foraging times with respect to the tidal state. They were observed to gradually increase foraging behaviour during the highly favourable six hours of ebbing tide as normal. In contrast, male foraging behaviour in the nesting phase increased as the tide came in to peak around high tide. This pattern contrasts not only with the female foraging pattern for the nesting phase, but also with the behaviour of both sexes in other phases of the breeding season and is suggestive of an unusual form of cooperation between the sexes. Behavioural rhythms of shorebirds are likely to be subject to complex temporal influences including circadian, circa-tidal, semi-lunar, lunar, and seasonal. They may also be affected by the behaviour of other species; prey, competitor, and predator (Bulla et al., 2017), and conspecifics — especially their partner.

Tūturuatu chick behaviour

My observations revealed that tūturuatu chicks frequently return to the nest, a behaviour thought to be unique among Charadrius plover chicks which are generally described as nidifugous (Gochfeld, 1984). Chick rearing was centred on the nest area for most broods with only 25% (2/8) decamping, apparently to gain access to freshwater. The mean time budget for foraging in chicks was 0.3 (± 0.21), comparable to the area on Hokorereoro most favoured for chick growth and survival (A. Davis, 1987), suggesting that adequate food resources are also available for tūturuatu chicks on Motutapu. In contrast to adult plovers, chick foraging time budgets tend to be higher in more favourable habitats (Loegering & Fraser, 1995). Tūturuatu chicks remain extremely vulnerable to predation until they fledge, and the key determinant of the time of fledging appears to be weight rather than age (A. Davis, 1994b). I suggest that the main driver of the high foraging rates observed in chicks in favourable habitats is selective pressure to maximise their growth rate.

The use of behavioural studies to assess the adequacy of food resources

Food resources are a key component of habitat suitability. They are threatened by climate change and habitat degradation and are an important consideration in translocation biology. While I did not directly measure food availability, my study demonstrated in principle the feasibility of assessing the adequacy of food resources of a site by comparing the foraging time budget of the population with that of another known site.

5.3 REPRODUCTIVE SUCCESS OF TŪTURUATU ON MOTUTAPU

Egg production and hatching rate

The viability of the tūturuatu population on Motutapu will ultimately be determined by the interaction of reproductive parameters (egg production, hatching rate, and chick survival to fledging) with survival rates of various age groups. The age of first reproduction is another contributing factor, as is dispersal both to and from the island. As an example, a low fledging rate may not necessarily lead to a decreasing population if adult survival rates are high. It is important to target wildlife management inputs on those parameters where the population is performing poorly, which are often, but not always, associated with the breeding season.

Egg production and hatching rate do not appear to be constraints to reproduction success for tūturuatu on Motutapu, despite the commonly observed occurrence of fertility depression in populations that have undergone severe bottlenecks (Brekke et al., 2010; Briskie & Mackintosh, 2004). The egg production rate was higher, and the hatching rate was similar to that recorded on Hokorereoro (A. Davis, 1994b). The hatching rate was also considerably higher than those published for other plover species. The failure rate of tūturiwhatu nests on Motutapu was very high, whereas tūturuatu nesting on the same beaches lost only one nest to an exceptionally high tidal surge during a storm. The covered nests of tūturuatu appear to afford protection from avian depredation, and to some extent, human-related disturbance, compared to the open nests of other plovers. The importance of this to conservation efforts is simply that the pre-nesting and nesting phases of the breeding season are of less concern, allowing efforts to be concentrated on the chick-rearing phase. Public access to beaches could safely continue during the earlier phases of the breeding season if the principles established from the study of human-related disturbance to nesting plovers were applied. Some examples are allowing walking but not static beach use in nesting areas (Weston et al., 2011), having dogs strictly on a leash where they are allowed at all (Weston & Elgar, 2007), fencing off the high tide area, or banning access at high tide. Conservation efforts could be focussed on the chick-rearing phase, including the possibility of preventing public access altogether through this time.

Chick survival from hatching to fledging

Chick survival from hatching to fledging appears to be the phase of the life cycle when tūturuatu are at their most vulnerable, and to provide the greatest opportunity for enhancement of productivity. Only 21% of tūturuatu hatchlings on Motutapu fledged successfully this season, and while this is similar to the 25% overall success on Hokorereoro over the 1984/5 and 1985/6 seasons (A. Davis, 1994b), it is still disappointing. Published chick survival rates in plover species are highly variable. The methodology used can also be variable and confusing (Dinsmore, 2019). The probability of surviving the fledging stage (4–6 weeks in most plover species) ranged from 8% to 65% in the Kentish plover, 6% to 80% in the snowy plover, 8% to 75% in the piping plover, 6% to 26% in the mountain plover (Dinsmore, 2019) and 7% to 43% in tūturuatu on Hokorereoro (A. Davis, 1994b). Wildlife management input has the potential to improve performance in this area. The two major causes of chick mortality observed on Motutapu were avian predation and female desertion. In addition, one chick drowned in a flooded creek and others may have failed to thrive from a lack of access to freshwater. The artificial provision of safe freshwater would help to address both issues and would allow chicks to stay near the shelter and refuge of the nest, rather than being forced to cross hostile territory or decamp to a distant and unprotected part of the beach.

Avian predation

Avian predation is a natural challenge to chicks of many species. On Hokorereoro for example, the predation of tūturuatu chicks by tarāpunga (red-billed gull, *Larus novaehollandiae*) has been documented (Fleming, 1939), and can be considered a natural phenomenon. On Motutapu, neither of the two avian species I observed to predate tūturuatu chicks can be considered a natural predator. The kāhu (swamp harrier, *Circus approximans*) self-introduced and established in Aotearoa (New Zealand) only after extensive anthropogenic habitat alteration (Worthy & Holdaway, 1996), and the Australian magpie *(Gymnorhina tibicen)* was deliberately introduced in the 1860s and 1870s (McIlroy, 1968). Other potential avian predators of tūturuatu chicks on Motutapu include the pūkeko *(Porphyrio melanotus)*, karoro (black-backed gull, *Larus dominicanus*), and spur-winged plover *(Vanellus miles)*, all of which are either self-introduced or natives subsidised by anthropogenic habitat alteration.

Given that tūturuatu are highly endangered, and that all the diurnal avian predators or potential predators mentioned above are common, non-endemic species, control of these birds is worth considering, at least in the early stage of establishing a new population. Control measures have been considered by the Department of Conservation (hereafter DOC) but pose moral and practical issues.

The karoro population on the island offers an example of each type of issue. Karoro have been observed predating tūturiwhatu chicks (J. E. Dowding, personal communication, 2018). However, they have never been recorded predating tūturuatu, and are commonly observed interacting peaceably with adults and chicks, making lethal control morally questionable. There is also a major breeding site for karoro on adjacent Rangitoto island, making eradication from Motutapu impractical. Given the constrained geography and time frame of the chick-rearing phase, I suggest it would be preferable to rely on human patrol measures, non-lethal removal methods, or bird scaring technology to reduce avian predation of chicks.

Female desertion and male-biased adult sex ratio

My observations revealed female brood desertion in tūturuatu for the first time. I suggest that this behaviour may be a response to a male-biased adult sex ratio (ASR). Brood desertion by both sexes has been observed in some other species of Charadrius plover where it is associated with a non-parous ASR and may represent an ancestral behaviour pattern (Eberhart-Phillips et al., 2018). It should be noted that my use of the term “female desertion” is not intended in a pejorative sense but simply to best describe what I observed. “Parental desertion” seems inaccurate because in the situations I observed the original male did not appear to willingly desert his brood, but rather was driven from the territory, primarily by the new male. “Male intrusion” has been suggested as an alternative term, but it describes the initiating event rather than the cause of chick death. The new male behaved with some hostility towards the brood, but more importantly the female completely ignored them.

In tūturuatu, female desertion appears to be deleterious not only for the deserted chicks but also for the deserted male which has not, to my knowledge, been reported in other plover species. All the deserted chicks died or had to be rescued within a few days, and all three deserted males died or disappeared within a week.

At the start of the breeding season, the population on Motutapu had a ratio of eleven males to six females, but the mechanism(s) by which this male-biased ASR arose in the population is unknown. One possibility is that differential release during the establishment of the population may have contributed to the biased ASR. Most of the adults (12/17), were originally bred in captivity and released on the island as juveniles. Unfortunately, only 51% (39/76) of the birds translocated over the period 2012–2016 had their sex determined before release, but known male translocations outnumbered females by 22 to 17.

A second possibility is that differential reappearance on the island after disappearance contributed to the biased ASR. The proportion of translocated juveniles that disappeared within 60 days of release was approximately equal in males: 50% (11/22) and females: 47% (8/17), but the proportion that reappeared to become resident was male-biased: 36% of males (4/11) compared with 12% of females (1/8).

A third possible explanation is differential nocturnal predation of adult tūturuatu during the nesting phase of the breeding season. Female tūturuatu incubate significantly more than males during the day, safe from diurnal avian predators in their covered nests. Males are thought to incubate more than females at night (A. Davis, 1994b), and similarly would be expected to be safe from nocturnal avian predators. On Motutapu, in the absence of introduced mammalian predators, the main predatory threat to adult tūturuatu appears to be a small native owl, the nocturnal ruru (morepork, *Ninox novaeseelandiae*). If female tūturuatu are more active nocturnally than males during the nesting phase of the breeding season, they may well be at increased risk of predation than males.

The numbers I observed were too small to allow firm conclusions but suggest that a biased ASR may lead to deleterious outcomes in this species. I recommend that future wildlife management ensures that populations have a parous ASR. This can be achieved by determining the sex of all released birds, the initial release of a parous population, and if necessary, by subsequent biased releases to correct for any differential survival.

Juvenile and adult survival

Juvenile tūturuatu bred on Motutapu 2012 to 2018 demonstrated an exceptionally high survival rate at 0.889 (n = 9) (Dowding, 2019) compared with a rate of just 0.26 on Hokorereoro over two years (A. Davis, 1994a). Perhaps even more exceptional is the fact that these birds did not disperse permanently from Motutapu, in marked contrast to the high disappearance rates of captive-bred birds translocated to the island. This very high survival and retention rate raises some intriguing possibilities, for example: could similar results be expected if a captive-breeding facility were established on the island?

The mean adult annual survival rate on Motutapu from 2012 to 2018 was 0.71 (Dowding, 2019), similar to that reported from Hokorereoro over two years of 0.7 (A. Davis, 1994a). The known causes of adult mortality during my research were ruru predation and intra-specific aggression following female desertion of brood and mate, affecting three birds in total. One adult male, injured in intra-specific aggression following female desertion was predated by a ruru, while the other two deserted males disappeared. Two other adults died or disappeared from unknown causes. My observation of ruru predation may be the first documented predation of tūturuatu by ruru, although there was strong circumstantial evidence that ruru predated four tūturuatu released on Motuora (another island in the Hauraki Gulf) in the 1990s and were implicated in their failure to establish there (Aikman, 1999). Ruru are widespread on mainland Aotearoa, including many offshore islands, but are not present in the Chatham islands. While it may be possible for a tūturuatu population to establish and grow in the presence of ruru, the ideal translocation site would not have this additional threat.

The final observation regarding adult mortality was a single case of an adult male whose partner disappeared when their chick was ten days old. He managed to rear the chick successfully, but this appears to have been at some cost to his own health. He was found dead, apparently of natural causes, shortly after his chick fledged. This is only one case, but the suggestion is that single-parent chick-rearing may be extremely difficult for tūturuatu.

5.4 DISPERSAL OF CAPTIVE-BRED TŪTURUATU AFTER TRANSLOCATION

Captive breeding

Captive breeding of tūturuatu is well established and successful with high productivity helped by multiple brooding in captivity (DOC, 2019). Genetic diversity is augmented by the occasional transfer of eggs from the remnant population on Hokorereoro to the captive-breeding facilities. Tūturuatu in the wild produce replacement clutches after early loss of a clutch or brood. Double brooding (renesting after successfully rearing a brood) was not seen on Hokorereoro (A. Davis, 1994b), but has been observed on one occasion on Motutapu (H. Speed, personal communication, 2020) and on the off-shore island sanctuaries of Waikawa and Mana (Dowding & O'Connor, 2013).

Factors affecting the probability of detection after translocation

My observations established that most of the juvenile tūturuatu translocated to Motutapu were no longer detectable on the island within a few days of release, and that very few, if any, died on the island. The tendency for released birds to disappear from Motutapu and other sites is a key constraint to conservation efforts for this species (Dowding & O'Connor, 2013). The problem is compounded by the fact that introduced mammalian predators are common and widespread on mainland Aotearoa. Tūturuatu that disperse to the mainland are thought to be at high risk of predation.

The factors affecting an individual’s decision to settle or disperse after release are not well understood (C. Jones & Merton, 2012). Do they assess the adequacy of resources, the presence of competitors and predators, the climate? The decision-making process may be affected by the stresses involved in the physical translocation process such as being caught, handled, transported, and mixed with unfamiliar conspecifics (Dickens et al., 2010). Some instances of translocation dispersal are thought to be driven by “homing” towards the natal site, others by “exploration” from it (Linnell et al., 1997).

Analysis of the data relating to the translocation of 128 birds to Motutapu from 2012–2018 considered five possible predictors of the probability of detection. Release date was the only predictor investigated that showed a significant relationship ($p < 0.001$) with the probability of detection. There was a 2% decrease in the probability of detection for each additional day after the summer solstice. This timing aligns with the fledging of wild-hatched tūturuatu from first clutches on the island, all of which were expected to fledge in January. Current management policy for captive breeding encourages pairs to produce multiple clutches with production extending to later in the season. These findings suggest that more modest production, with more emphasis on the timing of release, might lead to more successful translocation outcomes.

The importance of the indigenous range

The location of a release site in relation to the indigenous range was shown to be an important factor in translocation success rates in a large survey (Griffith et al., 1989). Releases into the core of the indigenous range had a mean success rate of 76%, compared with those on the periphery or outside the indigenous range of 48%. In Chapter Four, I extensively reviewed the historical records for tūturuatu and concluded that, despite the commonly held view that they were widespread around coastal Aotearoa, there is no reliable evidence that their indigenous range extended any further north than Canterbury in Te Waipounamu (the South Island). On this basis, I recommend that future translocations occur at a significantly lower latitude. The most promising area to provide additional habitat for the species appears to be the island of Rangihaute (Rangiauria, Pitt Island) in the Chatham Islands group. Just two kilometres distant from Hokorereoro and offering 65 square kilometres compared with 218 hectares on Hokorereoro, it is in “the core of the indigenous range” with respect to latitude. A single introduced mammalian predator species, the domestic cat *(Felis catus)* is present on the island. If cat eradication efforts prove successful tūturuatu will likely re-establish on Rangihaute without the need for translocation, leading to the possibility of a greatly enlarged meta-population. The species would have significantly greater resilience to three of the four adverse events currently identified as risks by DOC: mammalian predator introduction, flooding, and fire (DOC, 2001). The risk of disease might not be significantly changed but would be mitigated somewhat by increased genetic diversity.

The precautionary principle and its application to translocation projects

Translocation of endangered species involves difficult decisions, often without adequate evidence. Behavioural and biological research to inform these decisions is crucial but inherently risky; examples are the catching, banding, and transportation of birds that made my study possible. The luxury of the perfect translocation site is not always available; if it was perhaps the species in question would already be there!

The precautionary principle holds that when deviating from a natural situation, caution should prevail, though the potential adverse effects might not be fully understood. Wildlife management in general, and translocation projects in particular, should aim to recreate as natural a situation as possible, informed by minimally invasive behavioural and biological research. This approach includes translocating within the indigenous range of a species (thus reducing potential issues with climate, predation, and competition); releasing into an area that has been assessed as having adequate resources for a self-sustaining population; determining the sex of translocated individuals and establishing a parous ASR; and releasing captive-bred individuals at the age, stage, and time of year that they would naturally become independent. We may not yet have convincing scientific evidence that other approaches are harmful, especially for species of conservation importance, but we should err on the side of caution.

5.5 CONSERVATION CHALLENGES FOR TŪTURUATU

Charadrius plovers worldwide are severely threatened by climate change. They occupy shoreline regions, a habitat at the interface of aquatic and terrestrial environments, making them vulnerable to both ocean acidification (Harley et al., 2006), and freshwater salinity (Haig et al., 2019). Climate change also directly threatens their physical environment as sea levels rise, and as storm events increase in frequency and severity. The second major threat to Charadrius plovers worldwide is habitat loss, mainly attributable to changes in anthropogenic land use (MacKinnon et al., 2012).

In Aotearoa and other relatively recently settled islands, even the threats of climate change and habitat loss are eclipsed by the introduction of new organisms that compete with or predate endemic species. Introduced mammalian predators are common and widespread on mainland Aotearoa, and control or elimination of these is the focus of much conservation effort. The issue has been compounded by anthropogenic landscape alteration which has allowed the establishment of avian species which compete with or predate endemic species. In Aotearoa all five endemic Charadrius plover species are now considered to be Near Threatened, Vulnerable, or Endangered (Colwell & Haig, 2019a; O'Donnell & Monks, 2020).

“Pest-free” islands around the coast of Aotearoa offer sanctuary to endemic birds extirpated from the mainland, or other islands. A small number of these islands, such as Hokorereoro, the strong-hold of the remnant tūturuatu population, remain “pest-free” largely as an accident of history. Others, such as Waikawa and Motutapu, which support translocated tūturuatu populations, have been systematically cleared of mammalian predators. Conservation efforts on these two islands have been severely undermined at times by the incursion of mammalian predators.

5.6 TŪTURUATU RESEARCH PRIORITIES

Charadrius is one of the major genera of shorebirds, numbering about forty species, and many sub-species. They are similar in appearance, and occupy broadly similar shoreline habitats worldwide, but vary considerably in their behaviour, particularly with respect to migration and breeding systems (Colwell & Haig, 2019a). Their choice of habitat brings them into frequent contact with humans; sometimes there is conflict, but often there is admiration for these handsome and plucky birds that share our shorelines.

Charadrius plover research to date has focussed on northern hemisphere species, their biology and behaviour, and in particular their migration (Haig & Colwell, 2019). Their fascinating variety of breeding and parental care systems have been studied for their own sake, but also to inform theoretical models of the evolution of these systems. As anthropogenic change increasingly threatens their existence, plover research has tended to focus on the effects of climate change, habitat loss, and human disturbance. As inhabitants of the interface between terrestrial and aquatic environments, they represent a sensitive and visible indicator of the effects of anthropogenic change on climate, oceans, waterways, and terrestrial ecosystems (Haig, 2019).

Southern hemisphere species, particularly those of conservation interest, are much less studied. Here the research priorities are for basic biological and behavioural information to urgently inform practical wildlife management. The endemic plover species of Aotearoa all face the anthropogenic threats mentioned above including the somewhat overlooked predation and competition from introduced and subsidised native avian species. Priority should be given to any research that investigates these threats in relation to the behavioural ecology of the species involved. Some suggestions for tūturuatu research include:

- experimental provision of artificial freshwater supplies to chicks
- radio-tracking any future releases of captive-bred birds to better inform knowledge of dispersal
- investigation of the feral cat population on Rangihaute: population dynamics and trapping/control techniques
- experimental “growing on” of captive-bred tūturuatu to be translocated as yearlings rather than juveniles
- further evaluation of behavioural studies as a tool to investigate habitat suitability
- investigation of the potential to establish captive breeding facilities, or incubation and hatching facilities at the translocation site

Tūturuatu and the other plover species of Aotearoa often have small study populations and remote study areas in extensively modified landscapes but are deserving of greater research effort. They deserve it aesthetically because these birds are interesting and attractive. They deserve it practically because they supply ecosystem services to the shoreline, a vital and vulnerable habitat at the interface of aquatic and terrestrial environments. They deserve it morally as co-inhabitants of our planet, especially as their decline in numbers to their current Near Threatened, Vulnerable, or Endangered status has been caused by anthropogenic change.

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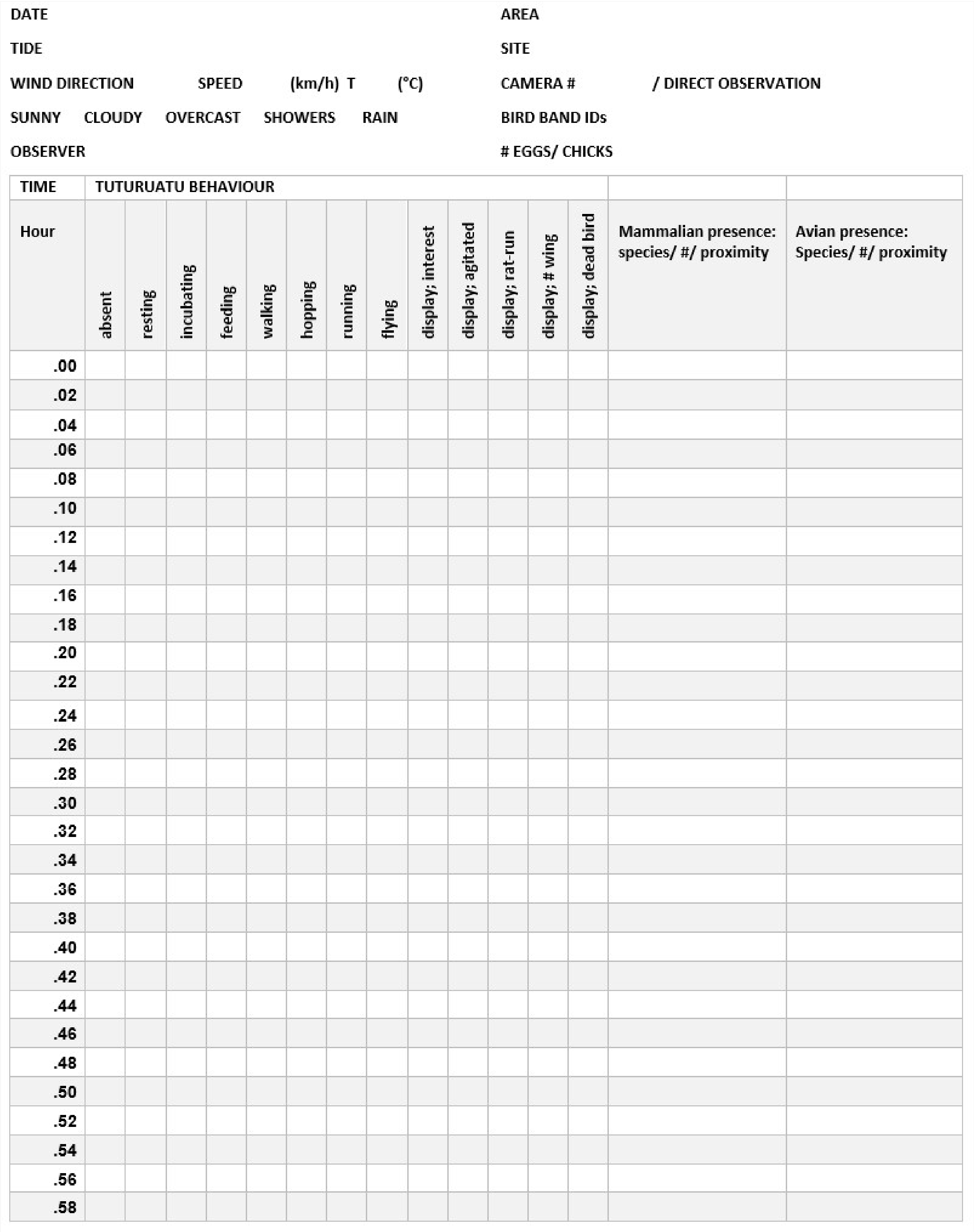
APPENDIX A



DATE

AREA

TIDE

SITE

WIND DIRECTION SPEED (km/h) T (°C)

CAMERA # / DIRECT OBSERVATION

SUNNY CLOUDY OVERCAST SHOWERS RAIN

BIRD BAND IDs

OBSERVER

EGGS/ CHICKS

TIME	TUTURUATU BEHAVIOUR														
Hour	absent	resting	incubating	feeding	walking	hopping	running	flying	display; interest	display; agitated	display; rat-run	display; # wing	display; dead bird	Mammalian presence: species/ #/ proximity	Avian presence: Species/ #/ proximity
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TIME	TUTURUATU BEHAVIOUR														
Hour	absent	resting	incubating	feeding	walking	hopping	running	flying	display; interest	display; agitated	display; rat-run	display; # wing	display; dead bird	Mammalian presence: species/ #/ proximity	Avian presence: Species/ #/ proximity
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APPENDIX B

Advice and priorities for tūturuatu (shore plover) volunteers

1. The first priority is to minimise observer disturbance and interference with tūturuatu behaviour. Some practical suggestions to help with this:
    - Walk well above the high-tide mark if possible, or well below it if necessary. These birds nest and are most active around the high tide mark.
    - Walk calmly and quietly and never wear HI-VIS on the beach.
    - Do not investigate nests unless absolutely necessary. Generally this will be done by Mac on a weekly basis when he is already close to the nest site to change camera batteries and SD cards.
    - High tide head counts involve walking along the beach near the birds and will inevitably cause some disturbance. This should be done once a day only, and never immediately before an observation period. If the observation period is close to high tide do the observations first; then the high tide head count afterwards.
    - Please abandon observations and especially high tide head counts if it is cold, windy or rainy. If agitated the birds may leave the nest or chicks allowing them to get cold very quickly.
    - It is always preferable to abandon observations than risk causing mortality or nest failure.
2. The second priority is to stick to the schedule of monitoring each nest site on a daily basis at the set time and completing a high-tide head count of all species on the beach once a day. It is tempting to drop everything to focus attention on new chicks, but they are adequately observed with this schedule, and doing so risks losing information on other sites. Only observations recorded during the set times will ultimately be used, so punctuality and organisation are important. Sandy Bay is a longer walk than the other sites but that is not a good reason for the number of observations there to be just over half that of the other sites.
3. The third priority is to fill in the observation records thoroughly and correctly. You are at the site for 2 hours so there should be no excuse for gaps or incorrect entries. Examples of incorrect entries so far include:
    - No observer name
    - The wrong date, or no date at all
    - No record of the bands of the birds being observed (birds can change partners and sites – so we always need to check which couple is at the site!)
    - Nest sites incorrectly recorded
    - The male and female being muddled up for the entire session

    - No time entered – the times are standardised but need to be recorded as a double check

4. It's a good idea to familiarise yourself with the species you are likely to encounter, and also the standard abbreviations for them to avoid having to write such things as "Australasian harrier" or "variable oyster catcher" over and over.
5. What we are really after is data – so be scientific in your recordings. The estimated distance of an adult to a chick or the nest site is always good data, as is the closest proximity and duration of any disturbance event. It is OK to record 2 or more different behaviours at one time for a single bird; for example flying and agitated display. Another example; people on the beach should be recorded as Hx4 say, with the distance from the nest site recorded at each 2 minute interval AND the total duration and closest proximity recorded.
6. One of the most important documents is the "high tide head count" sheet which is actually a daily summary sheet. Please fill it in properly while the information is still fresh in your mind, on your phone, or in your notebook and note any unusual events or changes. If a chick is suspected to be lost or a nest has been washed away or a bird has re-partnered this is where it should be recorded. Often this is done at the end of the day as different observers have done the high tide head counts on different beaches. This is a great time to compare notes of any changes or suspicions so that everyone is in the know. Remember that Mac and Hazel would appreciate a txt or call with any developments and are happy to respond to questions. The high tide head count needs to be done within an hour (or two at most) of high tide to be consistent. We use the tides for Matiatia Bay (on Waiheke Island) as they seem to be closer to the Motutapu tides than the Auckland city tides.
7. If you are recording any data from cameras (a great wet-weather job!) please prioritise periods of time when we suspect significant changes occurred – a chick was lost or a female re-partnered. There may be multiple relevant sources of data that need to be cross correlated; direct observations, stills AND video from a beach camera in hybrid mode, video from one or more nest cameras. Any clues can be noted; for example, the sudden disappearance of BBGs resting on the beach may indicate KAHU hunting the area – which might then be spotted in the sky in a still image from another camera.
8. Last but not least; have fun out there. You are making a substantial contribution to the conservation of one of our most endangered taonga on a beautiful island in the south Pacific – please enjoy the moment!

APPENDIX C


Three Sisters
Fowlhouse Bay
Rakino
Channel
South Point
South Island
Awash Rock
Pohutukawa
Billy Goat Point
Waikalabubu Bay
Pohutukawa Track
Sandy Bay
Station Bay
Wetland Track
Administration Bay
Historic gun emplacements
Camp
A9LN
107m
93
Mullet Bay
A9LP
91m
105
Rotary Centennial Wlky
Airstrip
Access Track
B2JC
111m
Motutapu Island
MOEC
63
Historic gun emplacements
Home Bay Campsite
Home Bay
116
Gardiner Gap
69
113
100
70
72
73
A5XF
121m
Walkway
Track
Motutapu Track
Islington Bay
Yankee Wharf
Emu Point Track
Otahuhu Point
Emu Bay
Channel
Coastal Track
Emu Rock
Emu Point
Motuihe
Te Tumurae Point
Gun emplacement
NZ Topo Map


Tuturuatu female


Tuturuatu male


Tuturuatu male in flight


Tuturuatu nest and eggs


Tuturuatu chicks and egg


Tuturuatu older chick


Banded dotterel **BD**


New Zealand dotterel **NZD**


Variable oystercatcher **VOC**


Black-backed gull **BBG**


Australasian harrier **KAHU**


Pukeko **PUK**


Red-billed gull **RBG**


Morepork **RURU**


Spur-winged plover **SWP**

APPENDIX D

Bird species considered non-threatening, competitors, or potential predators.

Non-threatening species

blackbird	(*Turdus merula*)
chaffinch	(*Fringilla coelebs*)
goldfinch	(*Carduelis carduelis*)
greenfinch	(*Carduelis chloris*)
house sparrow	(*Passer domesticus*)
kawau	(shag or cormorant, various species)
korimako	(bellbird, *Anthornis melanura*)
kōtare	(kingfisher, *Todiramphus sanctus*)
myna	(*Acridotheres tristis*)
pātake	(brown teal, *Anas chlorotis*)
pihoihoi	(pipit, *Anthus novaeseelandiae*)
pūtangitangi	(paradise shelduck, *Tadorna variegata*)
redpoll	(*Carduelis flammea*)
skylark	(*Alauda arvensis*)
song thrush	(*Turdus philomelos*)
starling	(*Sturnus vulgaris*)
swallow	(*Hirundo neoxena*)
tākapu	(Australasian gannet, *Morus serrator*)
tara	(tern, various species)
tōrea-pango	(variable oystercatcher, *Haematopus unicolor*)
yellowhammer	(*Emberiza citrinella*)

Competitor species

tūturiwhatu	(northern red-breasted dotterel, *Charadrius obscurus*)
tūturuatu	(tchūriwat’, shore plover, *Thinornis novaeseelandiae*)

Potential predator species

kāhu	(swamp harrier, *Circus approximans*)
karoro	(black-backed gull, *Larus dominicanus*)
magpie	(*Gymnorhyna tibicen*)
pūkeko	(*Porphyrio melanotus*)
spur-winged plover	(*Vanellus miles*)
tarāpunga	(red-billed gull, *Larus novaehollandiae*)
white-faced heron	(*Egretta novaehollandiae*)

APPENDIX E

Detail of tūturuatu chick mortality 2018–2019.

Chick 1

Hatched on 27th November 2018 at Gardeners Gap.

Parents: WB-OB (male) and GO-WO (female).

Chick last seen on 5th December 2018 at eight days old.

Cause of death: female desertion.

The mother of this chick, GO-WO, re-partnered with GO-WB, who was first observed in the natal territory on 6th December. The new male GO-WB and the mother GO-WO were observed defending the nest site from a tūturiwhatu (northern red-breasted dotterel) on the 8th , and mating on the 9th. The original male WB-OB was last seen on 8th December after repeated fights with the new male GO-WB and subsequently his remains were found below a ruru (morepork) nest.

GO-WB and GO-WO went on to successfully raise Chick 15.

Cause of death has been ascribed to female desertion as GO-WO was visibly distracted from the morning of the 6th by the appearance of GO-WB.

Chick 2

Also hatched on 27th November 2018 at Gardeners Gap.

Parents: WB-OB (male) and GO-WO (female).

Chick last definitively seen on 18th February 2019 at 83 days old.

Fledged successfully after hand-rearing.

The second chick from the nest was uplifted from the site on 13th December and successfully hand-reared at Auckland Zoo. This followed fears for its safety as it was repeatedly driven away by the new male GO-WB and ignored by its mother GO-WO. The chick was subsequently released with the first cohort of captive-bred juveniles on 18th February and appeared to have excellent natal philopatry, although in the absence of colour-banding it could not be definitively distinguished from other island-bred juveniles.

Chick 3

Hatched on 5th December 2018 at West Point.

Parents: GB-BO (male) and WB-RY (female).

Chick last seen on 8th December 2018 at three days old.

Cause of death: female desertion.

All three chicks from this nest are thought to have died primarily from female desertion. Chick 3 was last seen on 8th December. A new male GB-GY appeared in the natal territory that day and fought vigorously with the original male GB-BO on the 8th and 9th. GB-BO was last seen on the 9th. The new male GB-GY was observed attempting to mate with the female WB-RY on the 10th December, but she subsequently paired with another male GO-GW.

Chick 4

Hatched on 5th December 2018 at West Point.

Parents: GB-BO (male) and WB-RY (female).

Chick last seen on 8th December 2018 at three days old.

Cause of death: female desertion.

All three chicks from this nest are thought to have died primarily from female desertion. Chick 4 was last seen on 8th December. A new male GB-GY appeared in the natal territory that day and fought vigorously with the original male GB-BO on the 8th and 9th. GB-BO was last seen on the 9th. The new male GB-GY was observed attempting to mate with the female WB-RY on the 10th December, but she subsequently paired with another male GO-GW.

Chick 5

Hatched on 5th December 2018 at West Point.

Parents: GB-BO (male) and WB-RY (female).

Chick last seen on 9th December 2018 at four days old.

Cause of death: female desertion.

All three chicks from this nest are thought to have died primarily from female desertion. Chick 5 was last seen on 9th December. A new male GB-GY appeared in the natal territory that day and fought vigorously with the original male GB-BO on the 8th and 9th. GB-BO was last seen on the 9th. The new male GB-GY was observed attempting to mate with the female WB-RY on the 10th December, but she subsequently paired with another male GO-GW.

Chick 6

Hatched on 21st December 2018 at Pig Bay (South).

Parents WB-YR (male) and GO-OY (female).

Chick last seen on 22nd December 2018 at one day old.

Cause of death: predation by kahu (Australasian harrier, *Circus approximans*)

Video footage indicates that this chick was predated by a kahu (Australasian harrier).

Chick 7

Hatched on 21st December 2018 at Pig Bay (South).

Parents WB-YR (male) and GO-OY (female).

Chick last seen on 1st January 2019 at 11 days old.

Cause of death: unknown.

Chick 8

Hatched on 21st December 2018 at Pig Bay (South).

Parents WB-YR (male) and GO-OY (female).

Chick last seen on 15th January 2019 at 25 days old.

Cause of death: predation by Australian magpies *(Gymnorhyna tibicen).*

Video footage suggests that this chick was probably predated by 4 magpies which spent 30 minutes at the natal site in the evening where the chick had been seen most of the afternoon including twenty minutes earlier.

Chick 9

Hatched on 27th November 2018 at Pig Bay (Mid).

Parents RY-RB (male) and BO- (female).

Chick last seen on 8th January 2019 at 42 days old.

Cause of death: illness/ starvation/ dehydration.

This chick, although theoretically old enough to fledge, appeared to die of illness and/or malnourishment/ dehydration. The previous day it had rested in shade all day while its sibling fed. Its body was found in the nest and sent to Massey University for an autopsy, but no conclusive cause of death was established.

Chick 10

Hatched on 27th November 2018 at Pig Bay (Mid).

Parents RY-RB (male) and BO- (female).

Chick last seen on 16th January 2019 at 50 days old.

Assumed to have fledged successfully.

This chick was never seen flying but is assumed to have fledged. It was last seen at 50 days old. By comparison Chick 19 was seen to have fledged at 41 days old.

Chick 11

Hatched on 30th November 2018 at Pig Bay (North).

Parents BO-YO (male) and GO-GY (female).

Chick last seen on 9th December 2018 at nine days old.

Cause of death; predation by kahu (Australasian harrier, *Circus approximans*).

Chicks 11 and 12 both disappeared during a single hour when the observers at the site were away at lunch. A review of video footage and still photographs shows a pair of kahu (Australasian harriers) actively hunting the beach over a period of 12 minutes, with no evidence of any other disturbance.

Chick 12

Hatched on 30th November 2018 at Pig Bay (North).

Parents BO-YO (male) and GO-GY (female).

Chick last seen on 9th December 2018 at nine days old.

Cause of death; predation by kahu (Australasian harrier, *Circus approximans*).

Chicks 11 and 12 both disappeared during a single hour when the observers at the site were away at lunch. A review of video footage and still photographs shows a pair of kahu (Australasian harriers) actively hunting the beach over a period of 12 minutes, with no evidence of any other disturbance.

Chick 13

Hatched on 30th November 2018 at Pig Bay (North).

Parents BO-YO (male) and GO-GY (female).

Chick last seen on 1st January 2019 at 32 days old.

Cause of death unknown.

Chick 14

Hatched on 31st January 2019 at Gardiners Gap (the second clutch at this site).

Parents GO-WB (male) and GO-WO (female).

Chick last seen on 26th February 2019 at 26 days old.

Cause of death unknown.

Chick 15

Hatched on 31st January 2019 at Gardiners Gap (the second clutch at this site).

Parents GO-WB (male) and GO-WO (female).

Chick last seen on 12th March 2019 at 40 days old.

Fledged successfully.

Chick 16

Hatched on 27th January 2019 at West Point (the second clutch at this site).

Parents GO-GW (male) and WB-RY (female).

Chick last seen on 27th January 2019 at less than one day old.

Cause of death: drowning/ hypothermia.

This chick fell from a piece of driftwood into a stream in cold wet conditions on the day it hatched. An observer attempted to resuscitate it but it could not be revived.

Chick 17

Hatched on 27th January 2019 at West Point (the second clutch at this site).

Parents GO-GW (male) and WB-RY (female).

Chick last seen on 29th January 2019 at two days old.

Cause of death: unknown.

Chick 18

Hatched on 27th January 2019 at West Point (the second clutch at this site).

Parents GO-GW (male) and WB-RY (female).

Chick last seen on 7th February at 11 days old.

Cause of death: unknown.

Chick 19

Hatched on 14th January 2019 at Sandy Bay (the second clutch at this site).

Parents GB-GB (male) and WB-GO (female).

Chick last seen definitively on 24th February 2019 at 41 days old.

Fledged successfully.

The first clutch of three eggs at this site was destroyed by high waves in a storm on 3rd December 2018. The pair nested again but had two infertile eggs, with only this one chick hatching successfully. The female WB-GO was last seen on 24th January, which left the male GB-GB to raise the chick alone. He was extremely attentive and managed this successfully; the chick was observed to be fledged on 24th February at 41 days old. Unfortunately, the male GB-GB was found dead with no obvious sign of injury on 3rd April. His body was sent to Massey University for an autopsy, but no conclusive cause of death was established.