Black-fronted terns and banded dotterels: causes of mortality and comparisons of survival

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Abstract

1. The braided rivers of the South Island, New Zealand, provide feeding and breeding habitat for a range of endemic bird species. Many of these species are entirely reliant on braided river habitat for breeding, but because of a reduction in habitat quantity and quality due to weed infestation, hydroelectric power development and water abstraction, and high predation rates by introduced mammals, the survival of many of these bird species is under threat.

2. Predation is the primary cause of mortality for most braided river bird species, but most studies have only measured the effects of predation at the egg stage. In this study, I monitored breeding success of banded dotterels (*Charadrius bicinctus*) and black-fronted terns (*Sterna albostriata*) on the Ohau River, South Island, from 1998-2000, and examined the effects of predation on both species. The black-fronted tern is an endangered species about which very little is known, so I also investigated aspects of its breeding biology.

3. I used time-lapse video cameras at 39 nests of banded dotterels and determined that nest monitoring did not affect nest survival rates, nor do predators use human scent trails to locate nests. I attached radio transmitters to 49 banded dotterel chicks to assess rates and causes of mortality, but although a minimum of 18% of chicks were killed by predators, the transmitters did not provide information on the relative importance of the different predator species. Hatching success at 338 banded dotterel nests was 68%, and 48% of hatched nests fledged at least one chick.

4. Hatching success for 1022 black-fronted tern nests was 50.2%, and a minimum of 27.6% of 897 chicks survived through to fledging. Cause of mortality was assessed for 148 chick, juvenile and adult terns, and I found that predators were responsible for 47% of deaths. Feral cats (*Felis catus*) and Norway rats (*Rattus norvegicus*) were probably responsible for 19% and 51% of predator related deaths, respectively. Mortality rates remained high immediately after fledging because of predation. Annual adult mortality was estimated at 88-92% but the associated confidence intervals were wide (57-99%). I document aspects of black-fronted tern ecology such as incubation period, fledging period, egg and chick weights, and develop a preliminary method for sexing adult black-fronted terns based on body measurements. I measured black-fronted tern chick growth and survival and found that hatching asynchrony results in lower growth and survival in second hatched chicks. I collated all existing data on black-fronted tern populations and from these data estimate that the population size is less than 10 000 but conclude that better data on population size and trends are required.

5. Using population viability analysis models, I compare the survival of banded dotterels and black-fronted terns on the braided rivers. Higher productivity and shorter generation times, rather than any behavioural differences, are probably the key factors that result in stronger population growth for banded dotterels, despite both species being subject to similar levels of predation. Simulations indicate that predator control could be the most effective way to increase black-fronted tern survival.

6. This study provides the first comprehensive record of black-fronted tern breeding biology. I provide evidence that the black-fronted tern population is almost certainly in decline and the species urgently needs further research. In addition, the interrelationships between rabbit (*Oryctolagus cunniculus*) abundance, predator abundance and nest predation rates are poorly understood and urgently need attention in order to better manage braided river communities and ensure the survival of black-fronted terns and other vulnerable bird species.

Acknowledgements

Many people and organisations helped make this project possible. Each chapter has its own acknowledgements section, but here I'd like to thank people whose assistance was not specific to any one part.

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My acknowledgements would not be complete without mentioning my favourite canine friend. Without Cass, I doubt I would have discovered the effects of Norway rats and other predators on black-fronted terns, nor would my data on chick survival have been as complete without the use of his nose. He also provided a lot of entertainment and kept me sane: some days I realized the only living beings I had talked to included a dog and some birds, instead of just birds alone. Made me feel a little less mad anyway!

Finally, thanks to the terns and dotties themselves, without which this study would not exist.

Preface

Each chapter in this thesis was written as a separate paper for publication in a journal. Consequently, there is a degree of repetition and overlap between some chapters. The purpose of this preface is to detail the full references for those chapters that have been published and list the journals to which chapters have been or will be submitted. Although I have co-authors for some chapters, in all chapters my input was the greatest. I planned the research, organized the funding, carried out the fieldwork, analysed the data and wrote the manuscripts. Below I describe the roles of each of my co-authors.

Chapter 1 has been accepted for publication in *The Condor*:

> Keedwell, R. J., and M. D. Sanders. 2002. Nest monitoring and predator visitation at nests of banded dotterels. Condor.

Mark Sanders was one of my supervisors. His co-operation allowed me to carry out the research in Chapter 1 in collaboration with his on-going video monitoring of braided river bird nests.

Chapter 2 is published in *Waterbirds*:

> Keedwell, R. 2001. Evaluation of radio transmitters for measuring chick mortality in the banded dotterel. Waterbirds 24:217-223.

Chapters 3, 6 and 9 will be submitted to *Notornis*. **Chapter 4** will be submitted to *Emu.*

Chapter 5 was submitted to *Pacific Conservation Biology* in April 2002. The paper was submitted as:

> Keedwell, R. J., M. D. Sanders, M. Alley, and C. Twentyman. (submitted). Causes of mortality of black-fronted terns (*Sterna albostriata*) in the Ohau River, South Island, New Zealand.

Collaboration with Mark Sanders provided valuable video footage; and Maurice Alley and Caroline Twentyman carried out the post-mortem analyses.

Chapter 7 will be submitted to *Ibis*. **Chapter 8** was submitted to the *Journal of Field Ornithology* in May 2002. The paper was submitted as:

> Keedwell, R. J. (submitted). Does fledging equal success? Post-fledging mortality in black-fronted terns.

Chapter 10: my co-authors on this paper, Ed Minot and Murray Potter, were both my supervisors. Ed provided extensive help with the computer modelling, and both Ed and Murray provided input into the construction and write-up of this paper.

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General Introduction

Godley River. Photo: Department of Conservation

Introduction

The braided rivers of the South Island, New Zealand, provide breeding and feeding grounds for many species of river birds. Although uncommon worldwide (Peat and Patrick 2001), braided rivers are a common feature of the eastern side of the South Island's Southern Alps and many endemic bird species are specifically adapted to this habitat type (Maloney et al. 1997). Braided rivers have wide gravel riverbeds, often over four kilometres in width, and have many shallow braids that frequently change course. The wide gravel expanses, river channels, and adjacent wetlands provide both feeding and nesting habitat. Endemic species such as the black-fronted tern (*Sterna albostriata*), black-billed gull (*Larus bulleri*), wrybill plover (*Anarhynchus frontalis*) and black stilt (*Himantopus novaezelandiae*) are almost entirely dependent on braided riverbeds for breeding and feeding habitat (O'Donnell and Moore 1983, Robertson et al. 1983).

Since European colonisation of New Zealand 200 years ago, the quantity and quality of braided river habitat has been severely reduced. Introduced weed species such as willows (*Salix* sp.), Russell lupins (*Lupinus polyphyllus*) and European broom (*Cytisus scoparius*) now cover large areas of gravel that were previously nesting habitat. Weed infestations have also reduced feeding habitat by constraining the river braids into deep, swift channels. Hydroelectric power development has reduced available habitat by creation of lakes, and by redirecting river water to canals and hydro-stations. Decreased flood frequency and severity have also provided increased opportunity for invasive weed species to establish on riverbeds.

In addition to the reduction of available feeding and breeding habitat, braided river birds are also affected by a wide range of introduced mammalian predators, such as feral cats (*Felis catus*), hedgehogs (*Erinaceus europaeus occidentalis*), Norway rats (*Rattus norvegicus*), ferrets (*Mustela furo*) and stoats (*M. erminea*). Some of these predators feed primarily on the introduced European rabbit (*Oryctolagus cunniculus*), which inhabits the surrounding farmland and vegetated sections of riverbed, but predation pressure on braided river birds is high (Sanders and Maloney 2002).

The inter-relationships between all these factors and their respective impacts on braided river bird species are complex and not fully understood (Hughey 1985, Maloney et al. 1997). However, it is clear that these factors combined are detrimental to the survival of many river bird species. The conservation status of the black stilt is listed as critically endangered, the black-fronted tern has recently been upgraded to endangered, and the wrybill and black-billed gull are both listed as vulnerable (BirdLife International 2000).

Predation by introduced mammals is probably a major factor contributing to the decline of many species (Pierce 1996, Sanders and Maloney 2002). A knowledge of the importance of predation and other causes of mortality, and the relative importance of the different predator species is required to help determine the best management actions for ensuring the survival of vulnerable river bird populations. Most studies on predation of braided river birds have concentrated on measuring predation rates at the egg stage (Rebergen et al. 1998). Few studies have made any reliable measures of the effect of predation or rates of mortality at the chick and juvenile life stages, or how predation impacts at the population level. The identity of predators involved in predation of chicks and juveniles has remained largely unknown.

I aim to bridge this knowledge gap by examining rates and causes of mortality through the different life stages of two species of endemic braided river birds: one common species, the banded dotterel (*Charadrius bicinctus*) and one endangered species, the black-fronted tern.

Banded dotterels are common and widespread throughout New Zealand (Pierce 1999). Predation rates of banded dotterel eggs have been widely studied (Rebergen et al. 1998), although chick survival has received less attention. Aspects of their general ecology and population dynamics have also been examined (Pierce 1983, 1989, Rebergen et al. 1998, Pierce 1999).

In comparison, we know very little about black-fronted tern breeding success, ecology or survival, and there is an urgent need for further research on the species (Taylor 2000). Existing information on population trends for black-fronted terns suggests that the population may be in decline and the entire population size is estimated at between 5000-10000 individuals (O'Donnell and Moore 1983, Robertson et al. 1983, Maloney et al. 1997). The New Zealand conservation status of black-fronted terns was recently upgraded to ‘serious decline’ (Hitchmough in press, Molloy et al. in press). Better information about the survival of black-fronted terns is necessary to determine what, if any, management of the species is required.

Study area

I monitored breeding success and survival of banded dotterels and black-fronted terns in the Ohau River, which is part of the upper Waitaki Basin catchment (Figure 1). The upper Waitaki Basin probably represents up to 50% of the remaining suitable braided river habitat in New Zealand (Maloney et al. 1997). Surveys of upper Waitaki Basin rivers indicate that the area provides breeding habitat for up to 30% of the estimated black-fronted tern population, and over 20% of the national banded dotterel population (Maloney et al. 1997). The Ohau River is one of three rivers in the catchment that has high numbers of black-fronted terns. Although banded dotterels are less numerous in the Ohau River than black-fronted terns, both species are found nesting in the same habitat along the length of the river.

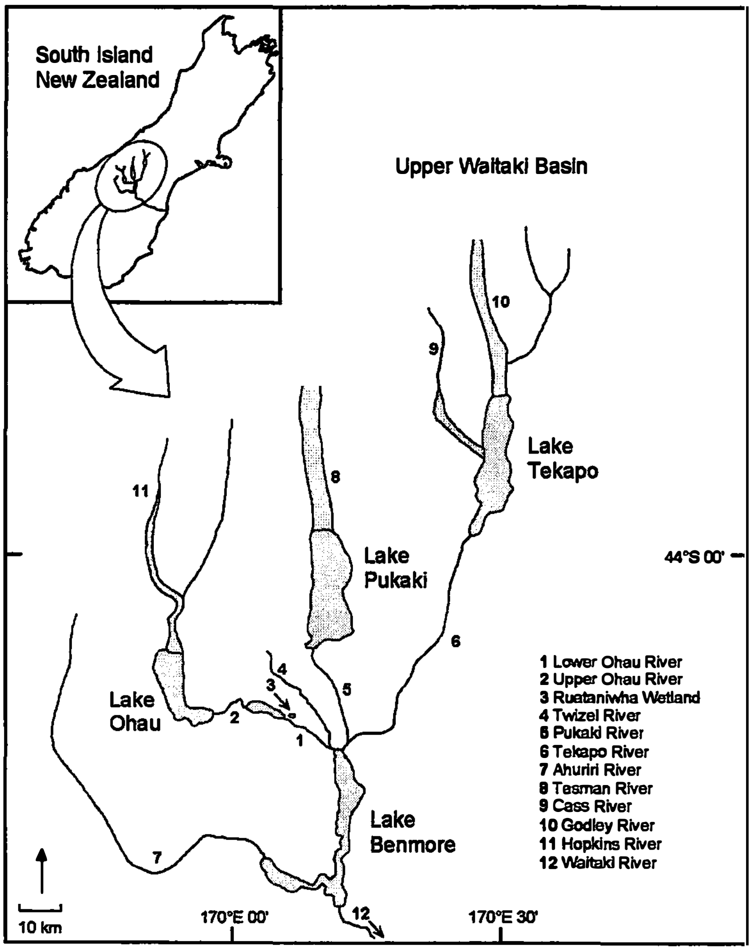

Figure 1: Location of rivers in the upper Waitaki Basin, South Island, New Zealand.

Study outline

I begin my study by using video cameras to examine whether monitoring banded dotterel nests affects nest survival (Chapter 1). Although nests of many braided river species have been monitored (Hay 1984, Pierce 1986, Rebergen et al. 1998), no studies have formally tested the impact of monitoring on nest survival. Predation is the major cause of nest failure in this environment and there are concerns that nest monitoring can affect predation rates (Götmark 1992).

Causes of chick mortality in braided river bird species are largely unknown, and this lack of knowledge hinders development of adequate management for critically endangered species such as the black stilt (Keedwell et al. 2002). Banded dotterels are common and provide an opportunity to trial methods for measuring rates and causes of mortality in chicks, before using them on more vulnerable species. In Chapter 2, I trial the use of radio-transmitters on banded dotterel chicks.

In Chapter 3, I monitor the hatching and fledging success of banded dotterels on the Ohau River. This provides increased data on fledging success in banded dotterels and allows a comparison of banded dotterel breeding success with that of black-fronted terns.

Despite the probable decline in black-fronted tern populations, the ecology and biology of the species is poorly understood (Taylor 2000). Knowledge of black-fronted tern natural history is valuable in assessing the likelihood of decline and in determining whether the increased conservation status ranking accurately represents the level of threat facing the species. The only study examining any aspect of black-fronted tern biology in depth was by Lalas (1977). I present the results of the first comprehensive study examining breeding success, natural history characteristics and survival in black-fronted terns in Chapter 4. I also document the causes of mortality of chicks, juveniles and adults and assess the impacts of different predator species (Chapter 5). I provide additional information on black-fronted tern biology by documenting characteristics of black-fronted tern eggs throughout incubation (Chapter 6), investigating effects of hatching asynchrony on chick survival (Chapter 7) and assessing whether mortality remains high after fledging (Chapter 8).

One key aspect of black-fronted tern populations that urgently needs attention is determining the population size and whether there is any reliable evidence of a decline. In Chapter 9, I gather all existing data on black-fronted terns and assess whether these data can be used to determine either population size or trends.

In my final chapter, I make a comparison between the survival of banded dotterels and black-fronted terns in the braided rivers. I use population viability analysis models to explore the influence of different parameters on projected population survival. Understanding why banded dotterels appear to do better than black-fronted terns while sharing the same habitat provides further insights into the management of black-fronted terns. I also examine the role of predator control in enhancing black-fronted tern populations (Chapter 10).

Finally, I discuss the implications of this study for the survival and management of black-fronted terns and banded dotterels on the braided rivers.

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Chapter 1:

Nest monitoring and predator visitation at nests of banded dotterels

Banded dotterel nest

Abstract

We used video-cameras to monitor 39 nests of the banded dotterel (*Charadrius bicinctus*), a ground-nesting plover endemic to New Zealand that suffers from predation by introduced mammals. To test whether monitoring nests increased the chances of nests being visited by predators, 22 of the video-monitored nests were approached on foot daily to simulate conventional monitoring and 17 unapproached nests were monitored using video cameras only. The proportions of approached nests (46%) and unapproached nests (41%) that were visited by predators did not differ significantly, nor was there any evidence that predators used human scent trails to locate nests. This study provides some evidence that monitoring banded dotterel nests by regularly checking them does not influence their risk of predation.

Introduction

Monitoring nesting success of birds involves a degree of disturbance by the researcher, and this may influence nest survival (reviewed in Götmark 1992). One effect of disturbance may be to alter predation rates, and it is widely believed that mammalian predators in particular pose a threat to nests visited by researchers (Bart 1977, Lenington 1979, Lloyd et al. 2000). However, research to date has provided contradictory results, with some studies concluding that researchers increased predation rates (Götmark et al. 1990, Esler and Grand 1993, Sandvik and Barret 2001) and others indicating that researchers either had no effect or reduced predation rates (O'Grady et al. 1996, Skagen et al. 1999, Lloyd et al. 2000). These results suggest that interactions between habitat, predator species, and prey species influence the effect of researchers on nest survival. Relatively few studies have examined this effect outside North America and Europe (Götmark 1992) and it is important to assess the effect of researchers in all nest success studies.

In the large, braided riverbed systems of the Mackenzie Basin, South Island, New Zealand, many researchers have monitored breeding success of both common and endangered ground-nesting bird species, many of which rely entirely on braided riverbeds for breeding (Maloney 1999), yet none have formally measured researcher impact on nest outcome. The main cause of nest failure in this environment is predation by introduced mammals such as feral cats (*Felis catus*), ferrets (*Mustela furo*), stoats (*M. erminea*) and hedgehogs (*Erinaceus europaeus*; Pierce 1996, Sanders and Maloney 2002).

Traditionally, assessing nest survival rates has involved regular visits to active nests. Now, remotely operated video systems are widely available and can be used to monitor nests with minimal disturbance (Innes et al. 1994, Pietz and Granfors 1996, Brown et al. 1998). We used video-cameras at nests to (1) test whether regularly approaching nests resulted in increased visitation rates by predators; and (2) assess whether mammalian predators used human scent trails to locate nests. We also compared predation rates at video-monitored nests and nests that were inspected regularly but not video-monitored, to test whether the video cameras affected nest survival.

Methods

We placed video-cameras at nests of a small, common plover, the banded dotterel (*Charadrius bicinctus*) in the Ohau River, South Island, New Zealand (44°20'S, 170°11'E) from mid-September to the end of December, 1998 to 2000. We found nests by following breeding adults to their nests. Banded dotterels usually lay three eggs in a shallow hollow in the gravel. Both parents share the incubation of the eggs (usually 28 days), average nest hatching success is 56% (Rebergen et al. 1998), and 83% of chicks leave the nest within two days of the last chick hatching (Sanders and Maloney 2002).

Cameras and infrared lights were placed 1-2 m from nests and connected to a video recorder and 12 V battery that were hidden 30-60 m away. Nests were filmed continuously until hatching or failing, and tapes and batteries were changed daily. Full details of the camera configuration are available in Sanders and Maloney (2002).

Nests monitored with cameras were alternately assigned one of two treatments: 'approached,' where nests were approached on foot daily from the same direction each time (simulating traditional nest monitoring); and 'unapproached,' where nests were not approached after the initial camera setup, until incubation had finished. Approached and unapproached nests were distributed evenly over the length of the river (11 km) in each year. For approached nests, we used the same direction of approach as we had when the nest was first located.

Videotapes were watched daily and nests were categorized as visited or not visited by predators. The proportions of approached and unapproached nests that were visited were compared using contingency table analyses. Data from all three years were pooled because sample sizes were too small to test for differences among years. Ten nests that hatched or failed within three days of the camera setup were excluded from the data set to rule out any potential effects of the initial camera setup, and because we considered that human scent trails would still be fresh at unapproached nests for at least this length of time.

To assess whether predators followed human scent trails to the nest, the direction of predator and human approaches to the same nest were compared using the Rayleigh test for circular uniformity (Zar 1999). The direction of human approach was set at 0° and each predator visit was categorized into one of 12 30° segments relative to the human approach path (0°, 30°, 60°, etc., up to 360°).

To assess whether the video-cameras affected predation rates, we used contingency table analysis to compare predation rates at the 39 video-taped nests with those at 227 banded dotterel nests that were monitored by field observers in a concurrent study on the Ohau River (Chapter 3). Nests were classified as preyed upon if one or more eggs were lost to predators. Human-monitored nests were visited every 2-4 days until the nesting attempt ended. As with the video-monitored nests, nests that hatched or failed within three days of discovery were excluded from analysis. There were no significant differences in predation rates at video-monitored and human-monitored nests among years; thus, data from all three years were pooled. Percentages are reported with 95% binomial confidence intervals.

Results

We video-taped outcomes for 22 approached nests and 17 unapproached nests over the three years. Filming effort (mean days filming per nest ± SE) was similar at approached (15.3 ± 1.3 days) and unapproached (13.8 ± 1.8 days) nests.

We recorded predator visits to 10 approached nests and seven unapproached nests. Two visits resulted in the predation of newly hatched chicks and at one of those nests an adult was also taken. Seven visits were nonlethal and during the remaining visits one or more of the eggs were preyed upon (Table 1). The same species of predators were recorded at both approached and unapproached nests. Listed in decreasing order of visits, they included feral cats, hedgehogs, mice (*Mus musculus*), Australian magpie (*Gymnorhina tibicen*) and Australasian harrier (*Circus approximans*).

The proportion of approached (46%, 24-68% CI) and unapproached (41%, 18-67% CI) nests visited by predators did not differ significantly ($\chi^2_1 = 0.1$, $P > 0.7$). There was no evidence to suggest that the directions of approach by visiting predators and by humans were correlated ($n = 9$; $z = 0.8$, $P > 0.20$; magpie visit excluded). The proportions of video-monitored (31%, 17-48% CI) and human-monitored (24%, 18-30% CI) nests that were depredated did not differ significantly ($\chi^2_1 = 0.5$, $P = 0.46$).

Table 1: Details of predator visits to video-monitored banded dotterel nests that were either approached daily (approached nests) or not approached after the initial camera set-up (unapproached nests). Unless otherwise stated, each item represents a single nest. Numbers in parentheses indicate the difference in degrees between the approach paths of humans and predators. No angle is given for the magpie visit because it approached from above.

	Predator visits to nests	
Year	**Approached nests (n = 22)**	**Non-approached nests (n = 17)**
1998	Cat eats 1 of 2 eggs (30°) Mouse visits nest (300°)	Mouse visits nest, 5 days later cat eats 1 of 3 eggs Australian Magpie eats 3 chicks Cat visits same nest 3 different nights
1999	Cat eats eggs at 3 nests (30°, 180°, 180°) Cat eats 3 chicks and 1 adult (120°) Hedgehog eats 3 eggs (210°) Cat visits nest (120°)	Cat eats 3 eggs Hedgehog visits nest
2000	Hedgehog eats 3 eggs (210°) Australian Magpie visits nest	Hedgehog eats 3 eggs Australasian Harrier eats 3 eggs
Total nests visited	10	7

Discussion

In this study, sample sizes in each year were small, a direct limitation of the number of cameras available. Although the proportions of approached and unapproached nests visited by predators were similar, a power analysis of the data indicated that with the given sample size, 0.44 was the minimum difference between the two proportions that could have been detected (with $\alpha = 0.1$, $\beta = 0.9$). Therefore, there may have been a difference in visitation rates between the two treatments that we could not detect. However, we approached nests daily, which is more frequent than usual for nest monitoring, and the lack of a strong effect of frequent monitoring on predator visitation rates suggests that traditional nest monitoring every 2-4 days is even less likely to influence nest survival.

Our results also suggest that approaching nests had little influence on how predators located nests. Again, sample sizes were small, but predators approached nests from seemingly random directions that did not correlate with human scent trails to nests. Observations of predator behaviour have shown that cats tend to use visual cues to locate nests (Fitzgerald 1990, Sanders and Maloney 2002), whereas ferrets and hedgehogs use olfactory cues (Lavers and Clapperton 1990, Sanders and Maloney 2002). No ferret predations were recorded in this study, but ferrets were responsible for 21% of 69 video-taped predations at braided river bird nests (Sanders and Maloney 2002). If ferrets do hunt by smell, there is a possibility that monitoring nests may increase ferret predation rates. However, given that cats and hedgehogs together account for over two thirds of depredations at nests (Sanders and Maloney 2002), and that there was no evidence that either of these species used human scent trails to locate nests (this study); it is unlikely that nest monitoring has any appreciable effect on nest survival in this braided river environment.

Our comparison of predator visits to nests assumes that videos yield an unbiased picture of what happens at nests. This is difficult to test because any method of observation potentially has an effect. Conspicuous nest markers, such as video cameras, may increase nest predation rates (Götmark 1992). The video-cameras used in our study were up to 40 cm high, and some of the infrared lights emitted small amounts of visible light at night; thus the cameras or lights may have provided visual cues to attract either mammals or birds to the nests. However, our comparison showing no difference in predation rates at video-monitored and human-monitored banded dotterel nests suggests this is not the case. Also, behavioural observations have shown that mammalian predators approached the nests and not the camera (Sanders and Maloney 2002); and although avian predators such as Australasian harriers and Australian magpies are abundant in the braided river environment (Keedwell and Brown 2001) they were responsible for fewer than 3% of 69 video-taped predations (Sanders and Maloney 2002) and are therefore unlikely to be using video-cameras to locate nests. Video-monitored and human-monitored nests of the black-fronted tern (*Sterna albostriata*), a species that shares the habitat of the banded dotterel, also showed no significant difference in survival between the two treatments (RJK unpubl. data, Sanders and Maloney 2002), which further suggests that video-cameras do not have a detrimental effect on nest survival.

The use of video-cameras helped us investigate the effects of nest monitoring because the cameras recorded nest fates without physical nest checks. Without cameras, the only other method for testing researcher effect is to alter the frequency of monitoring, because nests must be approached at some stage to determine outcome (e.g., Nichols et al. 1984, Major 1990, Sandvik and Barret 2001). Video-cameras also increase the amount of information available by providing data on whether predators use human scent trails to locate nests and whether nest monitoring attracts different species of predators.

Video-monitoring provides valuable opportunities to compare different methods of nest monitoring on other species. Although the financial costs associated with running video-cameras may be high, we believe video monitoring provides a comprehensive method for investigating the relationships among nest survival, nest monitoring, and the effects of predators.

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Chapter 2:

Evaluation of radio transmitters for measuring mortality of banded dotterel chicks

Banded dotterel chick with transmitter

Abstract

Radio transmitters have potential for measuring rates and causes of mortality in precocial chicks. To assess their utility, elastic harnesses were used to attach radio transmitters to 49 newly hatched banded dotterels (*Charadrius bicinctus*), a bird breeding along braided rivers of the South Island, New Zealand. Twelve chicks either lost their transmitters or the transmitters were removed, six chicks survived to fledging, 26 chicks died and the outcome was unclear for the remaining five chicks. A minimum of 18% of chicks that died were taken by predators, but predator identity was clear in only one case. The transmitters did not appear to affect growth rates of radiomarked chicks but three chicks died from harness entanglement. This technique provided only limited information about causes of mortality in banded dotterel chicks, and radio transmitters attached with elastic harnesses are not suitable for young chicks of endangered braided river birds.

Introduction

Radio transmitters attached to birds can provide valuable information about a species' ecology. Radio transmitters have been used to provide information on habitat use and foraging behavior (Massey et al. 1988, Knopf and Rupert 1996, Whittingham 1996); rates of mortality (Pietz et al. 1995, Korschgen et al. 1996a, Riley et al. 1998), and causes of mortality (Knopf and Rupert 1996, Korschgen et al. 1996a, Flint and Grand 1997, Stephenson et al. 1998). Radio transmitters may affect the survival and behavior of animals (Hooge 1991, Dzus and Clark 1996, Bro et al. 1999). Hence, negative effects of transmitters could bias survival rates; therefore evaluating the utility of transmitters on birds is critical (Perry et al. 1981, Caccamise and Hedin 1985, Mauser and Jarvis 1991, Bakken et al. 1996, Dzus and Clark 1996).

Estimating seasonal survival rates of young birds, particularly from the time of nest exodus to fledging, is important for understanding processes of recruitment. Much research has been devoted to studying ecology of radio-equipped adult birds, but fewer studies have investigated demographics of pre-fledged chicks (Mauser and Jarvis 1991, Bakken et al. 1996, Korschgen et al. 1996a, Korschgen et al. 1996b, Riley et al. 1998). Most studies involve young of common waterfowl, such as Mallard (*Anas platyrhynchos*). Transmitters cannot be attached to chicks using a standard harness because they will quickly outgrow it. Transmitters can be successfully glued to young chicks that are feathered (e.g., megapode chicks as detailed in Goeth and Jones 2001) but this technique does not work on young, downy chicks (R. Keedwell, unpubl. data). Subcutaneous or abdominal implants have worked on ducklings (Korschgen et al. 1996b, Davis et al. 1999) but the attachment process is time consuming, intrusive, and may pose too high a risk for use on threatened or endangered species (Olsen et al. 1992, Dzus and Clark 1996).

In braided river habitats of the South Island, New Zealand, attempts to reverse the decline of threatened and endangered river birds, such as black stilts (*Himantopus novaezelandiae*) and black-fronted terns (*Sterna albostriata*), are hindered by a lack of knowledge of rates and causes of chick mortality. Chicks of New Zealand braided river birds are generally precocial and the few existing data on chick survival suggest mortality rates are high (Rebergen et al. 1998), probably because of predation by introduced mammals. Further information about causes of river bird chick mortality is needed to enable accurate management of declining populations.

In this study, the use of elastic harness radio transmitters on chicks of a small (60 g), common plover, the banded dotterel (*Charadrius bicinctus*) was evaluated. The objectives were to: 1) assess the effects of an elastic harness as a method of transmitter attachment on chicks; 2) determine whether radio transmitters affect chick growth and survival; and 3) assess whether radio transmitters can provide accurate information on both rates and causes of mortality for this species.

Study site

Banded dotterels were studied on a 11 km stretch of the Ohau River, South Island, New Zealand (44°20'S, 170°11'E) from September 1998 to January 1999. The Ohau River is a braided riverbed with large expanses of sparsely vegetated gravels interspersed with numerous 'braids' or channels of the river. It varies in width from 50-300 m. Most of the river water has been diverted to hydroelectric canals for power supply, leaving an average flow of <5 m^3sec^{-1} in only one channel for much of the river. Introduced predators, such as cats (*Felis catus*), ferrets (*Mustela furo*), stoats (*M. erminea*) and Australian magpies (*Gymnorhina tibicen*), and two native avian predators southern black-backed gulls (*Larus dominicanus*) and Australasian harriers (*Circus approximans*) are found throughout the braided rivers (King 1990).

Methods

Banded Dotterel nests were located by observing breeding adults return to their nests. Adults were trapped on nests using a drop-trap, and each bird was color-banded with an individual combination. When possible, both male and female were banded, to monitor the family group after hatching.

Nests were checked daily; and nests usually contained three eggs. At hatching, chicks were caught and weighed, and individually colored with non-toxic ink on the down of their abdomens. One chick per brood was randomly selected for radiomarking, then the chicks were returned to where they were found. Total handling time was usually less than five minutes for the entire brood. Often, only one or two chicks were colored and weighed, because I could not always locate all three chicks.

The single-stage radio transmitters weighed 0.75 g (HOLOHIL Systems Ltd., Canada), had transverse lugholes through the epoxy resin for harness attachment, and a 12.5 cm whip antenna. I shortened the antenna to 10 cm during the study after observing the long antenna getting snagged between rocks. The lifespan of the transmitters was five weeks.

Transmitters were attached only to chicks with masses greater than 6.5 g. Chick mass (mean ± SE) at hatching was 7.5 ± 0.1 g; and only two chicks weighed ≤ 6.5 g at hatching. Thus, transmitters plus harness (0.8 g total) initially represented approximately 8-11% of chick body mass, but this declined to <2% by fledging.

The transmitters were attached using 2-3 strands of fine elastic yarn threaded through the lugholes, creating two leg loops. Transmitters were positioned on chicks' backs with the elastic loops around the top of the legs securing the transmitters in place (as detailed in Rappole and Tipton 1991). Contact adhesive (Ados F2) was put on the elastic knot and at the transmitter holes to prevent any lateral movement of the transmitter along the harness. When attaching transmitters to chicks, the elastic was stretched over each leg and the transmitter pulled into position. A harness that fitted well held the transmitter in place on the chick's back without the elastic pressing into the chick's flesh.

Radiomarked chicks were located daily using a Merlin 12 receiver and a hand-held three-element Yagi antenna. Radiomarked chicks were handled each day to ensure that their harness still fitted correctly. They were weighed every 3-7 d. The harnesses were changed every 4-14 d as needed. When a radiomarked chick was found dead, the area up to 5 m around the chick was checked for any signs of predation (scat, footprints, blood or feathers). Cause of mortality was assessed from the recovery location of the carcass or transmitter and evidence on the carcass or transmitter. If the transmitter was found detached from the chick, the family group was observed closely to confirm whether the radiomarked chick was missing or still alive. If the carcass was found fresh, it was packed in ice and sent overnight to the Institute of Veterinary, Animal and Biomedical Sciences, Massey University, New Zealand for post-mortem examination. These carcasses were given a complete pathological examination and selected histopathological tests.

Radiomarked chicks were color-banded at 21-30 d and the transmitters removed at 30-34 d to enable recovery of the units before battery failure. Chicks were considered to have fledged if they reached 35 d of age. It was not always possible to monitor chicks past this age because the family group would often leave the territory immediately after fledging.

The unmarked siblings of radiomarked chicks were weighed when encountered by chance or by watching the parents from a distance and then capturing the chicks. It was difficult, however, to locate the unmarked chicks because the parents apparently learned to recognise me and would give alarm calls, causing their chicks to hide when I was still several hundred metres away. To increase the available data on the growth of unmarked chicks, I also weighed chicks from clutches of known ages that were being monitored in a concurrent study on the Ohau River (Chapter 3).

Differences in survival of radiomarked and unmarked chicks were examined by fitting survivor curves to both groups of chicks using the Kaplan-Meier estimator (Allison 1995). The log rank tests (Mantel-Haenszel) were used to test for differences between survival of radiomarked and unmarked chicks (Allison 1995). Survival estimates for radiomarked chicks were based on the last day that they were alive and still radiomarked. Survival estimates for unmarked chicks were probably over-estimates because when a chick disappeared, I conservatively assigned its age at death on the last day the chick could have lived, as opposed to the midway point between when it was last seen alive and when it was determined missing. Unmarked chicks older than four weeks were right-censored (i.e., removed from the model without reference to their fate) on the last day they were seen alive if their fate was unclear (i.e. they could have fledged or died). Radiomarked chicks that lost their transmitter after 3 d were right-censored on the last day they were seen alive with their transmitter; radiomarked chicks that lost their transmitter within 2 d of attachment were excluded from analyses.

Results

Cause of mortality

Transmitters were attached to 49 banded dotterel chicks; six chicks survived to fledging age, 26 died, and the fates of 17 were undetermined (Table 1). Fates were not determined for 12 chicks because the transmitter was removed (n = 4) or the transmitter detached (n = 8) prematurely. Two of the transmitters were removed because the elastic harness lacerated the skin on the chicks' legs, a third transmitter failed and I removed the fourth transmitter because flooding had limited my access to the area. The elastic was still intact on six of the eight transmitters that became detached. On six other occasions, chicks slipped their transmitters with intact harnesses but they were recaptured and their transmitters reattached. No chicks older than 11 d of age slipped their transmitter.

Table 1: Outcomes for 49 radiomarked banded dotterel chicks

	Age (weeks)					
Outcome	**<1**	**1-2**	**2-3**	**3-4**	**>4**	**Total**
Transmitter removed by investigator	0	3	1	0	0	**4**
Transmitter on ground, chick still alive	5	2	1*	0	0	**8**
Transmitter on ground, chick survival unknown	2	0	0	0	0	**2**
Unknown outcome – transmitter failure	2	1	0	0	0	**3**
Fledged	-	-	-	-	6	**6**
Dead	11	9	3	0	3	**26**
Total						**49**

*Transmitter fell off when harness broke after 14 days of continuous attachment.

Seventy-seven percent (n = 26) of chick mortality occurred during the first two weeks of life (Table 2). Predators were linked to four deaths but predator identity was clear in only one case, and that was because the transmitter was found in a cat scat. I inferred that the cat preyed upon, rather than scavenged, the chick because the entire family group disappeared overnight, suggesting all three chicks in the clutch were eaten.

On seven occasions, transmitters were found on the ground and the chick was not seen again despite extensive observations. In five instances, the brooding parents ceased chick-guarding behavior (e.g., alarm calling) following the disappearance of the radiomarked chick, indicating total brood loss.

Table 2: Causes of mortality of 26 radiomarked banded dotterel chicks

	Age (weeks)					
Cause of mortality	**<1**	**1-2**	**2-3**	**3-4**	**>4**	**Total**
Predation		3	1			**4**
Trauma[a]		1				**1**
Degenerative myopathy			1			**1**
Pulmonary oedema	1					**1**
Cardiomyopathy					1	**1**
Fence[b]	1					**1**
Rosehip bush[c]		1				**1**
Starvation			1		1	**2**
Harness entanglement	3					**3**
Possible handling shock		1				**1**
No diagnosis:						
Carcass too old	2					**2**
Transmitter on ground, chick confirmed missing	5	2			1	**8**
Total	**11**	**9**	**3**	**0**	**3**	**26**

[a] Chick died of respiratory failure caused by a small wound to the windpipe – it is unlikely the wound was predator inflicted

[b] Chick was unable to pass through a fence to where its parents were feeding on the opposite side.

[c] Chick found impaled on a thorn of a briar bush (*Rosa rubignosa*) alongside its dead but unmarked sibling (also impaled).

Four of the 26 chick deaths were attributed to radiomarking. In two cases, the harness partially slipped off the chick and the loose end became entangled in vegetation, trapping the chick. In the third case, the harness snagged on vegetation while still on the chick. All three of these chicks were less than 7 d old when they died. A fourth chick died after its transmitter was changed on a cold day. It became stressed during handling, which may have contributed to its death soon afterwards.

When the 17 undetermined outcomes and four transmitter-related mortalities are excluded, fledging success for the 28 chicks that were successfully radiomarked was 21.4% (95% CI: 7-36%). Predation was possibly the cause of death for at least 18% (95% CI: 5-40%) of the 22 chicks that died.

Growth

Body mass data were gathered from 34 unmarked chicks, with an average of two masses obtained per chick over time. Data were also collected from 28 radiomarked chicks for which there were two or more masses through time, with an average of four weighings per chick. Chick mass from hatching to fledging was slightly higher for radiomarked than for unmarked chicks (Figure 1).

Comparisons of individual growth curves or of body masses at fledging for radiomarked and unmarked chicks would have provided the best tests for transmitter effect on growth. However, there were not enough data to construct individual growth curves, and too few chicks survived to fledging to give data for the latter. Therefore, based on the approximate growth curve in Figure 1, chicks that had been weighed during the most active period of growth (between the ages of 12-29 days) were selected. For chicks that had been weighed more than once during this period, the mass taken closest to 22 days of age was selected. This gave a sample of masses for 14 radiomarked and 10 unmarked chicks. A multiple regression on these, taking into account age and transmitter (i.e. radiomarked or unmarked) indicated that, at the midpoint of growth, the radio transmitter did not have a significant effect on chick growth.

Effect of transmitters on survival

Survival was analysed for 128 chicks from 52 clutches, and 39 of these chicks were wearing transmitters. Of the 89 unmarked chicks, at least 16 (18%; 95% CI: 11-27%) survived to fledging, but if nine chicks with unknown outcomes are included as fledged, fledging success could have been as high as 28% (95% CI: 19-38%). The survivorship

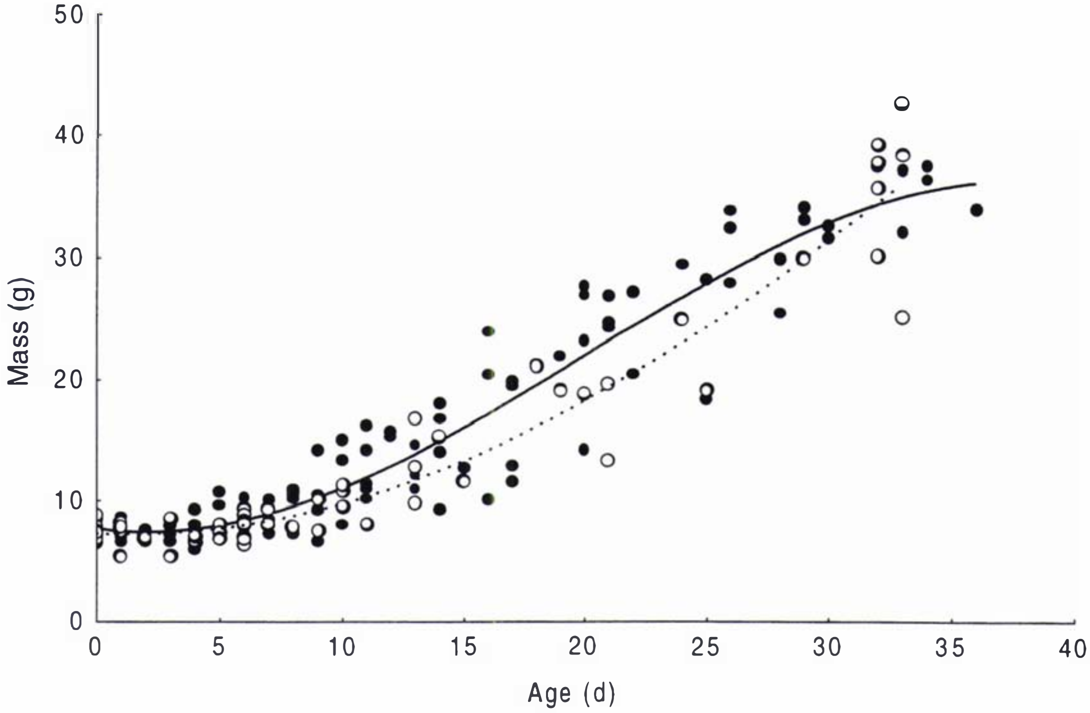

Figure 1: Weights of 28 radiomarked (closed circles, solid line) and 34 unmarked (open circles, dotted line) banded dotterel chicks, from hatching through to fledging. Line is a computer-fitted polynomial curve.

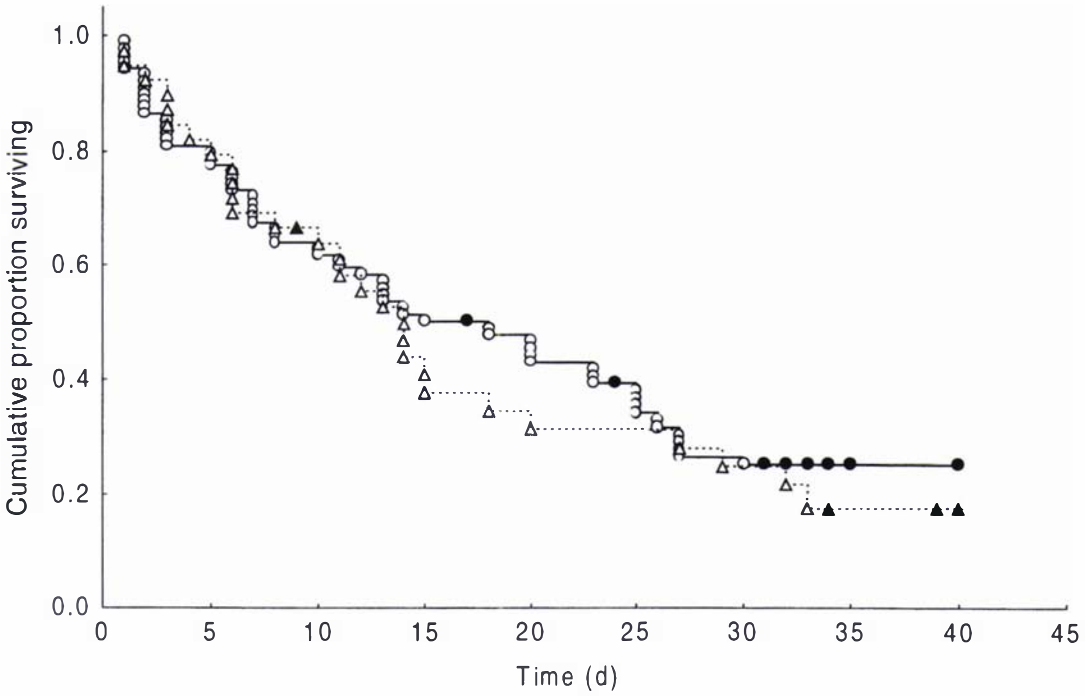

Figure 2: Survival curves for radiomarked (triangles, dotted line; n = 39) and unmarked (circles, solid line; n = 89) banded dotterel chicks. An open triangle or circle represents a known outcome (died), a closed triangle or circle represents a right censored individual (fate unknown or fledged).

curve for unmarked chicks was slightly higher than, but not significantly different from, the curve for radiomarked chicks ($\chi^2_1 = 0.60$, n.s.; Figure 2).

Discussion

Elastic harnesses

Elastic harnesses are not an effective way to attach transmitters to young chicks. Although they present a lightweight attachment method that is quick and simple to use, harnesses carry a risk of entanglement, even in the sparsely vegetated riverbed environment. A "weak link" in the harness may have overcome this problem. However, it would be difficult to incorporate a link weak enough for a chick to break, but strong enough to keep the harness intact throughout the study, without substantially increasing the weight of the transmitter package.

Although elastic harnesses require low handling time for initial attachment, this study involved daily handling to assess the harness fit. Two proximate causes of mortality recorded in this study were myopathies, which could possibly be linked to handling stress. Handling stress has been linked to death in wild species of mammals (Bartsch et al. 1977, Joubert and Stander 1990, Beringer et al. 1996). This has been termed "capture myopathy" and has more recently been found in birds (Spraker et al. 1987, Bollinger et al. 1989, Bailey et al. 1996, Finlay and Jeske 1998). If elastic harnesses were used again, daily handling would be unnecessary because properly attached transmitter harnesses fitted well for at least 5 days. Alternatively, other attachment methods may reduce this risk; for example suturing transmitters onto chicks would involve only one handling session (Raim 1978, Mauser and Jarvis 1991, Korschgen et al. 1996a, Korschgen et al. 1996b). However, deaths can result directly from intrusive attachment processes such as those requiring surgery (Dzus and Clark 1996, Korschgen et al. 1996a).

Effect of transmitter on growth and survival

The transmitters in this study had no apparent effect on the growth of chicks, despite the transmitter initially weighing as much as 11% of the chicks' body mass. Other studies using transmitters attached to chicks' backs by glue-on or surgical methods also found the transmitters had no effect on growth (Mauser and Jarvis 1991, Ewing et al. 1994, Goth and Jones 2001).

The transmitters did have a direct effect on chick survival through harness entanglement and possible also through handling stress. Although the survival analysis indicates there was no significant difference in survival, the survival curve of radiomarked chicks from 14 days onwards drops below that of unmarked chicks, resulting in an 8% difference in survival. Most other studies using transmitters on chicks did not find that transmitters increased mortality (Krementz and Pendleton 1991, Mauser and Jarvis 1991, Kenward et al. 1993, Goth and Jones 2001), although transmitters attached to wings of chicks had a detrimental effect on survival (Kenward et al. 1993). The lower survival of radiomarked chicks in my study may have been due to the high degree of handling involved as well as the method of attachment.

Measuring rates and causes of mortality

Transmitters attached with elastic harnesses provided only limited data on the causes of chick mortality, and could not clearly quantify the impact of predation or the relative importance of the different predator species. Predators were responsible for at least 18% of deaths, but a further seven deaths are unexplained where the transmitter was found on the ground with the chick missing. Predator identity was particularly difficult to ascertain from remains left after a predation event. The best information on predator identity was gained when the predator consumed the entire chick and its transmitter, as observed with the cat predation. In New Zealand, cats are an important predator of eggs of river birds (Sanders 1997) therefore accurately assessing their impact on chicks is important. Other methods of transmitter attachment such as implantation are more likely to provide evidence of predator identity when the prey is consumed whole because there is more chance the transmitter will be consumed and found in scat or predator den sites (Krementz and Pendleton 1991). Further research is needed to develop and test methods for studying rates and causes of chick mortality in the braided river habitat.

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Chapter 3:

Breeding success of banded dotterels on the Ohau River, South Island, New Zealand

Day-old banded dotterel chicks in the nest

Abstract

I monitored hatching and fledging success of banded dotterels on the lower Ohau River, from 1998 to 2000. Hatching success was 68% (n = 338 nests) and fledging success was 48% (n = 153). Hatching success did not vary among years, but fledging success was slightly, although not significantly, elevated in 2000 compared with the previous two years. This pattern was similar in hatching and fledging success rates for black-fronted terns monitored on the lower Ohau River over the same period. Hatching and fledging success rates of banded dotterel nests are not strongly correlated, and future studies need to measure both egg and chick survival to measure reproductive output and the effects of predation.

Introduction

The banded dotterel (*Charadrius bicinctus*) is a common, endemic plover that is widespread throughout both the main islands of New Zealand. Commonly found in the braided river habitat of the South Island, the species also breeds on pasture and in coastal areas (Marchant and Higgins 1993). The breeding success of banded dotterels in the braided river environment has been widely studied, and predation is the main cause of nest failure (Rebergen et al. 1998). However, although nesting success through to hatching has been monitored, few studies have assessed survival rates through to fledging (Rebergen et al. 1998). Survival to hatching and fledging may be affected differently by predation, and both need to be known if an assessment of population trends is to be made.

In this study, I monitored the breeding success of banded dotterels on the Ohau River for three years. My aims were to:

1) increase available information on banded dotterel breeding success, including nest hatching and fledging success rates;
2) compare the success rates of banded dotterels with that of black-fronted terns monitored in the same habitat;
3) and compare hatch and fledge success rates to determine whether the two are correlated.

Methods

I searched for breeding adult banded dotterels along the lower Ohau River from September until January, 1998-2000. I located nests by following adults and marked nests with a small rock cairn 2-3 m on the true left side. Both adults were trapped and colour-banded where possible, to facilitate nest monitoring after hatching.

Nests were monitored every 1-3 days until hatching or failing. Outcomes were classified into five categories: 'hatched' – chicks seen in the nest or the adults were displaying chick behaviour (agitated or performing distraction displays); 'failed' – no eggs in the nest and the adults absent or unconcerned with my presence, and/or presence of eggshell, ants or flies in the nest bowl; 'deserted'; 'flooded'; or 'unknown' – newly located nests that ended before adult band combinations were confirmed, therefore fate of nest could not be confirmed.

After hatching, I continued to monitor the family group every 2-4 days through to fledging or failure. Where possible, I banded chicks once they reached 3 weeks but because locating and catching chicks was extremely difficult, only a small proportion of chicks were banded. Family groups that disappeared prior to five weeks were presumed failed if they were not relocated after searching adjacent territories. Chick outcomes were classified as: 'fledged' – one or more chicks fledged; 'failed' – adults stopped displaying chick behaviour or disappeared before five weeks; or 'unknown' – usually because one adult was not banded and the family group could not be monitored through to fledging if the banded adult abandoned the brood.

Survival parameters are presented as: 'hatching success' – percent of nests that hatched one or more eggs; 'egg success' – percent of individual eggs that hatched; 'fledging success' – percent of hatched nests that fledged one or more chicks; and 'egg fledging success' – percent of all monitored nests of known outcomes that fledged one or more chicks. Unknown outcomes are excluded from percentage calculations.

Results

I monitored 347 nests over three years, with outcomes determined for all but nine nests. Hatching success for 338 nests was 68% (Table 1). Of the remaining nests, 5% were deserted, 0.6% were flooded and 26% failed due to predation. Hatching success did not vary among years ($\chi^2 = 0.312$, df = 2, $P = 0.99$).

Hatching success using the Mayfield method (Mayfield 1975) was 53% and ranged from 50.4-55.4% each year. Mayfield egg success ranged from 51.8-60.4%, with 57% egg success overall.

I monitored 184 nests after hatching, for which 31 had unknown outcomes. Fledging success of known nests for all years pooled was 48% (Table 1), and fledging success in 2000 was higher than, but not significantly different to fledging success in the previous two years (Table 1; $\chi^2 = 7.379$, df = 2, $P = 0.117$).

I banded 246 adults (150 females, 96 males) and 53 chicks. The mean number of eggs per nest for 347 nests was 2.9.

Table 1: Hatching and fledging success of banded dotterel nests in the lower Ohau River, 1998-2000. See text for descriptions of categories. Data presented are: %, *n* [95% binomial confidence interval].

Year	Hatching success	Egg success	Fledging success	Egg fledging success
1998	69.3, *127* [60-77]	65.0, *314* [59-70]	41.5, *53* [28-56]	23.2, *95* [15-33]
1999	66.4, *110* [57-75]	63.2, *315* [58-69]	40.4, *52* [27-55]	22.5, *89* [14-33]
2000	67.3, *101* [57-76]	64.5, *287* [59-70]	64.6, *48* [49-78]	36.9, *84* [27-48]
Overall	67.8, *338* [62-73]	64.2, *916* [61-67]	48.4, *153* [40-57]	27.2, *268* [22-33]

Discussion

The 66-69% hatching success that I recorded on the Ohau River was similar to those published for rivers in the upper Waitaki Basin and elsewhere. The mean (± 1 SD) nest success rate for 13 sites presented in Rebergen et al. (1998) was 60 ± 18%. The only other study of banded dotterel breeding success on the Ohau River reported a hatching success of 32% in 1992. Predation in that study was correspondingly high (66%), compared to only 26% in my study. The high predation rates in 1992 were probably due to recent rabbit poisoning operations causing predator-prey switching (Rebergen et al. 1998), and probably are not representative of predation rates on the Ohau River in most years.

Banded dotterel fledging success was slightly elevated in 2000 compared to 1999 and 1998, and I found a similar result with chick survival in black-fronted terns (Chapter 4). For both species, egg predation rates on the lower Ohau River remained similar in all three years, but chick survival increased in 2000. Cats were not videoed at nests of banded dotterels (Chapter 1) or black-fronted terns (Chapter 4) during 2000, yet were regular predators in all previous years (Sanders and Maloney 2002). If cats are one of the main predators of braided river bird chicks (Chapters 2 and 5), lower cat density in 2000 may have increased chick survival. However, until further study is undertaken on the relative importance of different predator species in a range of braided rivers, it is not clear exactly what impact cats have on the annual variation in chick survival.

Although hatching success of banded dotterels has been frequently studied, fledging success was measured in only five of the 15 years of data presented in Rebergen et al. (1998). Even fewer studies provided measures of productivity. In this study, I did not measure productivity because of the time required to monitor the fate of individual chicks, and because the large area of river covered meant I could not ensure all breeding attempts of each known female were monitored. Productivity estimates from other studies range from 0.55-1.72 chicks/female/year, with an average of 1.0 (A. Rebergen, unpubl. data, Sanders and Brown 2000, 2001, Keedwell and Sanders 2002). To measure the reproductive output of banded dotterels, and to assess the impacts of predation at different life stages, measures of egg and chick success are needed. If the hatching and fledging success data from all existing studies are compared (this study, Rebergen et al. 1998, Sanders and Brown 2000, 2001, Keedwell and Sanders 2002), the survival rates at each life stage are positively, but not significantly, correlated ($r_{10} = 0.52$, $P = 0.08$; Fig 1). Therefore, although monitoring hatching success may be the easiest way to measure breeding success for banded dotterels, it may not provide an entirely accurate assessment of productivity or the effects of predation at the different life stages.

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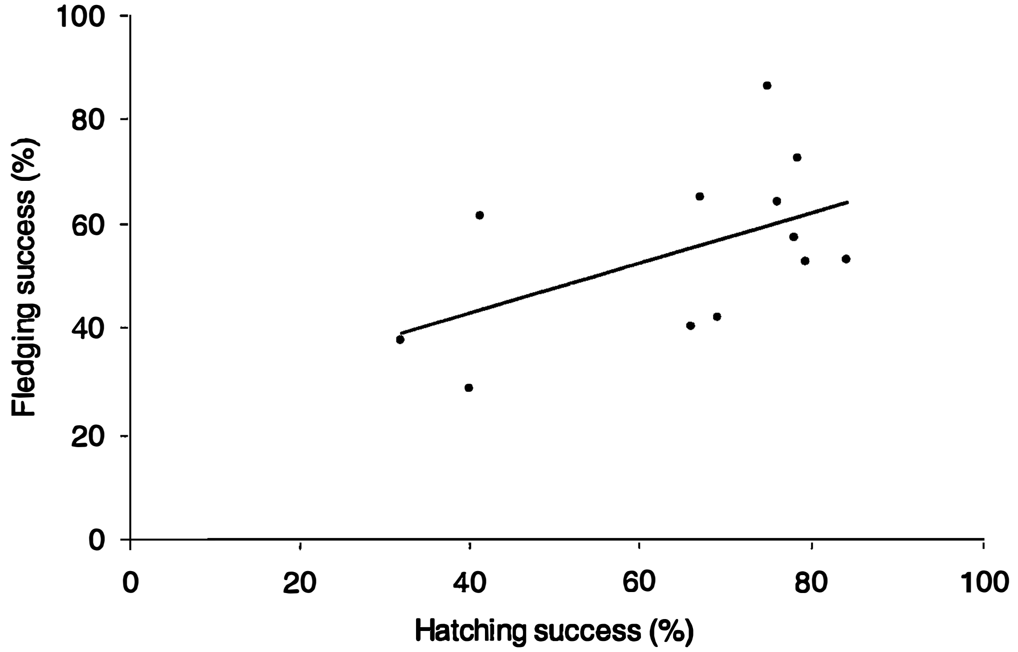

Figure 1: Hatching success and corresponding fledging success rates of banded dotterels. Equation of linear regression: $y = 0.4766x + 23.755$, $R^2 = 0.27$. See text for data sources.

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Chapter 4:

Ecology, breeding biology and survival of the black-fronted tern *Sterna albostriata* on the Ohau River, South Island, New Zealand

Black-fronted tern on nest. Photo: Dave Murray

Abstract

I monitored aspects of black-fronted tern (*Sterna albostriata*) breeding ecology for three years and survival for four years on the Ohau River, South Island, New Zealand, from 1998-2001. Over 3 years, 50.2% of 1022 nests successfully hatched. Predation (24.6%) and desertion (21.4%) were the main causes of nest failure. At least 28% of all hatched chicks (n = 897) survived to fledge. Hatching and fledging rates at individual colonies ranged from zero success to 74% hatching or 50% fledging, largely because of the impacts of predation by introduced predators. Seventy-two adult terns were banded and annual survival was estimated at 0.88-0.92, but the associated confidence intervals were wide (0.57-0.99). The majority of banded adults were resighted nesting either in the colony in which they were banded or elsewhere on the Ohau River. Adult terns could be sexed with 80% accuracy using mass, tarsus length and bill depth, but the method needs validating. Survival of fledglings through to first breeding could not be accurately determined. First-time breeders usually returned to the Ohau River to nest but there was evidence of some dispersal to adjacent rivers. This is the first comprehensive study on the breeding biology of black-fronted terns and provides baseline information about rates of survival and information essential to the future management of the species.

Introduction

The black-fronted tern (*Sterna albostriata*) is endemic to New Zealand and breeds inland on the wide, sparsely vegetated braided riverbeds of the South Island. The species is probably in decline, primarily because of predation by introduced mammalian predators (Higgins and Davies 1996, Sanders and Maloney 2002). A reduction in the quantity and quality of available braided river habitat because of the development of hydroelectric dams and canals has reduced the availability of habitat for black-fronted terns. Increased vegetation cover on braided rivers has provided favourable habitat for the introduced European rabbit (*Oryctolagus cunniculus*) and its associated predators which, in turn, prey on black-fronted terns (O'Donnell and Moore 1983, Balneaves and Hughey 1989, Maloney 1999). Their global conservation status was recently upgraded from threatened to endangered (BirdLife International 2000) and the entire population probably numbers fewer than 10 000 individuals (Chapter 9).

Despite mounting evidence that black-fronted terns are in decline (Chapter 9), no nationwide census of the population has been conducted. The only research on the species focussed on their feeding ecology (Lalas 1977). Limited data exist on their breeding ecology (Lalas 1977, Higgins and Davies 1996), much of it based on small sample sizes, casual observation and anecdotal information. Black-fronted terns urgently need further research and conservation effort (Taylor 2000).

Even the most fundamental question of whether the population is in decline cannot be answered because basic natural history and survival data are so limited. Such data are also essential for determining the most appropriate methods for managing the species. The aims of this study were to document the breeding ecology and survival of black-fronted terns, and to provide baseline measures of survival against which future studies can be compared.

Study site

I studied black-fronted tern breeding biology along the 11 km lower Ohau River and at one island colony on the upper Ohau River, South Island, New Zealand (44°20'S, 170°11'E). The lower Ohau River is a braided riverbed with large expanses of sparsely vegetated gravels. It varies in width from 50 to 300 m. The upper Ohau consists primarily of a single channel with only small areas of exposed gravel and the riverbed is up to 100 m wide. The two sections of river are separated by a hydro-lake. Both the upper and lower Ohau are bordered by introduced species of willows (*Salix* spp.) and by grass and tussock covered river terraces. Most of the river water has been diverted to hydroelectric canals for power supply, leaving an average flow of < 5 m^3sec^{-1} and 18 m^3sec^{-1} in the lower and upper Ohau River, respectively. Introduced mammalian predators, such as cats (*Felis catus*), ferrets (*Mustela furo*) and stoats (*M. erminea*), which feed mainly on the European rabbit are found throughout the braided rivers of the upper Waitaki Basin (Keedwell and Brown 2001).

In 2001, I regularly visited other areas of the Waitaki catchment to search for colour-banded black-fronted terns. These sites included the Tekapo, Pukaki, Twizel, Ahuriri, Tasman, Cass, and Waitaki Rivers, and Ruataniwha Wetland (see map page 5).

Methods

Egg survival

I monitored breeding success during the summers of 1998-2000. I searched the river for tern colonies from early September until January of each season and marked all nests with a small rock cairn 1-3 m from the nest. Colonies were visited every 1-4 days to search for new nests, to record the status of existing nests and to search for chicks. Nest sites were mapped using GPS and colony locations are provided in Appendix 1. Nest outcomes were classified into five categories: 'hatched' – chicks were evident in the nest or the nest was surrounded by faeces; 'preyed on' – broken egg shell or egg contents were in the nest, or the eggs were missing and there was no sign of chicks; 'deserted' – the eggs were cold and unattended; 'other' – flooding or other rare events; and 'unknown' where I could not be sure of the outcome. I also used laying date, where known, to confirm nest outcome. Hatching success was calculated as the number of nests that hatched one or more eggs (i.e., apparent hatching success), not Mayfield success, because the fate of each nest was probably not independent of other nests within the colony (Mayfield 1975, Johnson 1979).

Chick survival

In 1999 and 2000, all chicks at nests on the lower Ohau River were banded, within 3 days of hatching, with numbered metal bands. I searched the colonies for banded chicks every 1-4 days. Chicks were located by walking through the colony and catching any running chicks, or by sitting back 20-40 metres and waiting until chicks called out to incoming adults. I recorded the band numbers of any chicks found and released them where caught. I also recorded the bands of dead chicks, and placed rocks over any unbanded dead chicks to avoid counting them twice. A trained dog was used to sniff out chicks from their hiding places, but use of the dog was confined to areas of the colony where there were no adults incubating eggs to avoid any potential risk of nest desertion. In 1998, chicks were not banded until after two weeks of age, but so few chicks survived at each colony that the number of chicks fledged could be monitored without banding. The colony on the upper Ohau River was visited only every 3-4 days and consequently many chicks were banded after they left the nest when their exact age and nest site could not be determined.

Chick outcomes were classified as: 'fledged' – the chick was seen flying or it had a wing chord length greater than 140 mm when last seen; 'dead' – the chick's body was recovered; 'presumed dead' – the chick was no longer found during regular searches, or all chicks in the colony disappeared after a predation event; 'unknown' – the chick was last seen at up to 12 days of age but because of the large size of some colonies, I was not confident that I had caught all chicks present and therefore could not confirm survival. Fledging success was calculated as the percentage of hatched chicks that survived to fledge. Where there were chicks with unknown outcomes, the fledging success calculation ranged from a minimum (minimum number of chicks known to fledge) to a possible maximum number (minimum fledged plus unknown outcomes) of chicks that fledged.

Some 1999 and 2000 fledglings were radio-marked, which provided information on movements after fledging. Full details of methods of transmitter attachment and survival rates after fledging are presented in Chapter 8. In 2000, 26 fledglings were sexed, using DNA analysis of feather samples, to determine the sex ratio of fledglings produced.

In all three years, chicks were banded prior to fledging, with a cohort combination of plastic leg bands indicating the year and colony from which the chick fledged. From 1999-2001, I recorded the locations of nesting terns with cohort band combinations to assess natal site fidelity. The proportions of banded fledglings resighted in each year were calculated.

Renesting and adult characteristics

In 1999 and 2000, I was confident I found all nests on the lower Ohau River and I estimated the largest number of nests that were active at one time. This allowed me to estimate the minimum number of breeding pairs on the lower river and the proportion of nests that were renests. Nests were classified as 'early' (hatched or failed on or before 30 November) or 'late' (after 30 November) season. I used log-linear analysis to test whether season (i.e., early or late) affected the proportion of nests fledging chicks in each year.

As part of a joint study with the New Zealand Department of Conservation's "Project River Recovery", predator identity was recorded at black-fronted tern nests by placing time-lapse video cameras at 50 nests during 1998-2000. Cameras and infrared lights were placed 1–2 m from nests and connected to a video recorder and 12-V battery that were hidden 30–60 m away. Nests were filmed continuously until hatching or failing, and tapes and batteries were changed daily. Full details of the camera configuration are available in Sanders and Maloney (2002). The video cameras provided additional information on hatching intervals, nest attendance and effects of nocturnal disturbance.

I caught 72 adult terns with a hand net and banded them on the tarsi with individual colour combinations. The white rumps of banded birds were painted yellow with picric acid so that banded birds could be easily identified within a season. I took nine body measurements from all adults (Table 1) and 39 birds were unambiguously sexed using DNA analysis from a feather sample. I used a discriminant function analysis to determine whether body size reliably predicted sex.

At one colony in 2000, I carried out nest checks at dusk at five nests where one of the adults was banded, had a dyed yellow rump and had been sexed from feather samples. I noted which bird was incubating at dusk to determine which sex incubated the eggs overnight. Data from videoed black-fronted tern nests showed that the bird on the nest at dusk remained so for the rest of the night unless disturbed by a predator.

Table 1: Summary of measurements. All measurements taken with Vernier callipers unless noted otherwise.

Measurement	Description
Mass	Taken with 300 g Pesola scale.
Wing chord	From leading edge of the wrist joint to tip of longest primary using a stopped rule. Wing chord not flattened.
Tarsus	From the rear of the intertarsal joint to the distal edge of the last complete scale before the toes begin.
Tail tip	From base of tail feathers to tip of longest rectrix, using a metal ruler.
Tail fork	From base of tail feathers to tip of shortest rectrix in the fork of the tail, using a metal ruler.
Head and bill	From back of head to bill tip.
Bill length	Distance from bill tip to top of nostril.
Bill width	Width of bill at top of nostril.
Bill depth	Depth of bill at top of nostril.

Adult survival and site fidelity

I recorded band resightings of adults from 1999-2001 to assess survival rates and site fidelity. The banded adults included 32 adults banded in 1998, 12 in 1999 and 25 in 2000. I looked for banded terns while searching for nests or in roosting flocks at the start and end of the breeding season in 1999 and 2000. In 2001, I spent two months during the breeding season searching for banded black-fronted terns (birds banded as either adults and fledglings) in other rivers of the upper Waitaki Basin, and in the lower Waitaki River. For 2001, search effort concentrated in the Ohau River and rivers that were near the Ohau, and I determined the ratio of banded to unbanded birds seen in each flock or colony site to assess which locations had the highest proportion of banded birds.

I used MARK 2.1 (White and Burnham 1999) to determine adult survival estimates. Survival was modelled using the Cormack-Jolly Seber (CJS) model for live recaptures (Lebreton et al. 1992). I used the CJS model $\{\phi_t, P_t\}$, which assumes survival and resighting probabilities are constant among individuals, as the global model for the analysis and assessed the fit of the model using RELEASE (available within MARK). I then sought the most parsimonious model describing adult survival. Because more effort was put into searching for bands in 2001, I had an *a priori* reason to suspect that resighting probabilities were higher in 2001 than in previous years. Accordingly, I included a model that reflected this difference in resightings. In addition to the global model, I considered five reduced models where survival was either constant through time $\{\phi\}$ or varied through time $\{\phi_t\}$, and where resighting was constant through time $\{P\}$, varied through time $\{P_t\}$, or was constant in 1999 and 2000 but varied in 2001 $\{P_{1\text{-}2,3}\}$. Models were compared using the quasi Akaike's Information Criterion corrected for bias (QAICc, Burnham and Anderson 1998). The overdispersion parameter *c* was estimated from the global model using the bootstrapping routine in MARK.

Statistical tests were carried out using STATISTICA (StatSoft 1998) or SAS (SAS Institute 1996). All means are reported ± 1 SD unless stated otherwise.

Results

Colony size and location

I monitored 1022 nests at 11 colony locations from 1998-2000. Colony size ranged from 5 to 223 nests with 48 nests/colony on average. The mean nest density in colonies was 0.4 nests/100 m^2 but this ranged from 0.1 to 2.9 nests/100 m^2. Six solitary nests were also found but none of these survived to hatching. Three colony sites were used in all four years (1998-2001), five were used for three years, one was used for two years and two sites were used for only one year. If a colony site had high chick survival in one year (i.e. >20 chicks fledged), it was always used the following year (Table 2), but this effect was not independent of colony size. All four colony sites that had high chick survival were sites that were used in at least three or more years of the study.

Table 2: Presence and absence of black-fronted tern colony sites on the Ohau River, 1998-2001, in relation to how many chicks were fledged. Data represent the number of chicks fledged in year$_t$ in a given colony location in relation to whether that colony was present or absent in year$_{t+1}$. Data are from 11 colony sites in total.

No. of chicks fledge in year$_t$	No. colonies present at same site in year$_{t+1}$	No. colonies absent at same site in year$_{t+1}$
0	5	2
1-5	3	4
6-10	0	2
11-15	0	0
16+	5	0

Adults and immatures were observed periodically roosting at colony sites up to three weeks prior to the first egg being laid. Each year, the first eggs were laid in the last week of September or first week of October, and the last chicks hatched by mid-January. Hatching rates peaked in November (Figure 1). Nest formation within colonies was often asynchronous and the nest-laying period varied widely among individual colonies. At most colonies, 75% of nests were laid within five weeks of the earliest nest, but the last eggs could be laid up to 11 weeks after colony initiation.

Egg laying

In 1998-2000, 15.5% of 965 nests were 1-egg nests, 83.0% were 2-egg nests and 1.5% were 3-egg nests with a mean of 1.9 ± 0.4 eggs/nest, excluding potentially incomplete clutches. Eggs were laid 1-2 days apart. Incubation usually began when the first egg was laid, but was not always continuous until the clutch was completed. In 2001, I found two 4-egg nests. All the eggs in both 4-egg nests were fertile and successfully hatched, but in both cases, two chicks died in the nest shortly after hatching. In 2000, a black-fronted tern laid two eggs in a banded dotterel nest and then continued to incubate all five eggs. Both tern eggs hatched but the dotterel eggs were addled by the end of incubation.

The mean incubation period for 72 nests was 24.9 ± 1.8 days (range = 22-31). Two additional nests had incubation periods of 36 and 41 days respectively, and although they each hatched one chick, in both cases the chicks were underweight and died within three days of hatching. One pair incubated eggs for 52 days before their nest was flooded, and another two pairs incubated eggs for more than 40 days before deserting. Females were incubating at dusk in 52% of 23 evening observations made over five nests, indicating that nighttime incubation was shared between males and females.

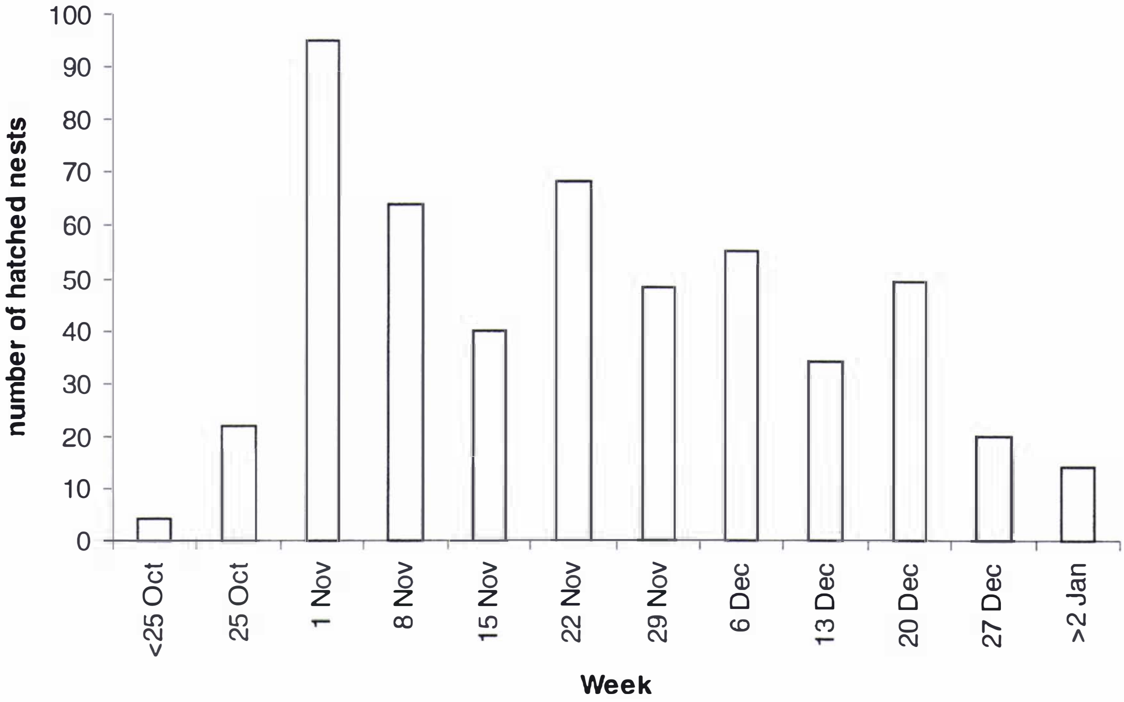

Figure 1: Number of black-fronted tern nests hatching each week of the breeding season, 1998-2000 pooled, on the Ohau River.

Egg survival

Hatching success varied among years, with 45%, 60% and 40% of all nests hatching one or more eggs in 1998, 1999 and 2000, respectively (Table 3). Overall, predation (24.6%) and desertion (21.4%) were the primary causes of nest failure but hatching, predation and desertion rates varied widely among colonies (Appendix 1). Flooding caused only 1.4% of nest failures. Nest survival at colonies was not correlated with the number of nests laid at a colony (Figure 2).

Cats, ferrets and hedgehogs were responsible for 17 predation events involving eggs, recorded at 50 videoed nests (Table 4; see also Sanders and Maloney 2002). An additional nest was deserted after a cat approached and sniffed at, but did not eat, the eggs. Cats were videoed killing one adult and three chicks at the nest (see Chapter 5 for details). Video footage also showed non-fatal nocturnal desertion after terns were disturbed at night by hares, rabbits, hedgehogs, mice, possums and deer.

Of all eggs laid, 3.9% (73/1872) failed to hatch. Post-mortems on 33 of these indicated that 10 eggs died hatching (including four malpositioned chicks); six died partway through incubation; 14 eggs either died pre-incubation or were infertile; and the remaining egg had an overly porous shell that resulted in the egg contents dehydrating.

Table 3: Black-fronted tern egg and chick survival on the Ohau River, 1998-2000. Hatching success is the percentage of nests that hatched one or more eggs. Fledging success is the percentage of hatched chicks that survived through to fledging. Data tabulated are: % success, n – number of nests or chicks, CI – 95% binomial confidence interval, range – range in % hatching/fledging at individual colonies. Fledging success in 1999 and 2000 is presented as a minimum and maximum to account for chicks with unknown outcomes.

Hatching success				
Year	**%**	**n**	**CI**	**Range**
1998	44.5	247	38-51	17-67
1999	60.0	458	55-65	0-74
2000	40.4	317	35-46	0-71
Overall	50.2	1022	47-53	0-74
Fledging success				
Year	**%**	**n**	**CI**	**Range**
1998	27.4	190	21-34	0-36
1999	26.1-34.3	475	22-39	0-50
2000	31-36.6	232	25-43	15-45
Overall	27.6-33.4	897	25-37	0-50

Table 4: Egg predation events by predator species at black-fronted tern nests on the Ohau River, 1998-2000. Sample size is number of nests videoed in each year. Note that some of the nests videoed in 2000 were not randomly selected – several nests at one colony were targeted to determine the extent of hedgehog predation.

Year	**n**	**Cat**	**Hedgehog**	**Ferret**
1998	18	3	2	1
1999	15	2	2	0
2000	17	0	7	0
Total	50	5	11	1

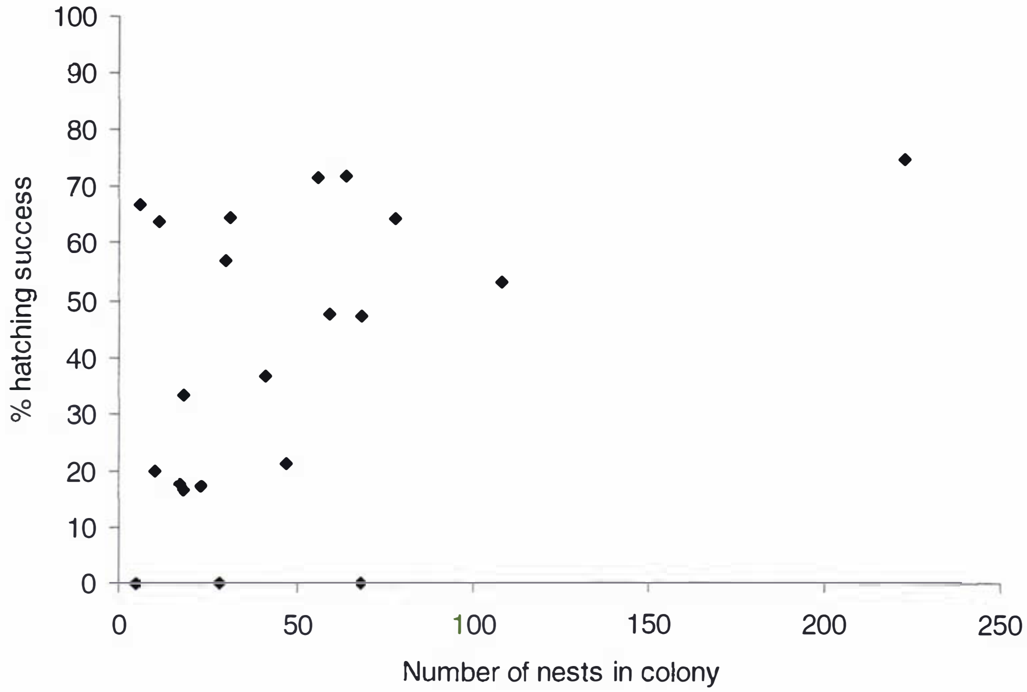

Figure 2: Black-fronted tern nest hatching success at colonies against number of nests in a colony on the Ohau River, 1998-2000.

Chick hatching and survival

Chick hatching was asynchronous with a mean of 18.7 ± 13.9 hours between chicks in a 2-egg clutch (range 4-49 hours; n = 18 videoed nests). Chicks used their nest bowl for 6 ± 2.6 days on average (range 3-13 days; n = 24 videoed nests), but after three days chicks used nests mainly at night. After leaving the nest, chicks often moved closer to the river and used the densely vegetated margin along the riverbank for cover. Chicks from one clutch would usually stay in one location until fledging but on at least six occasions I found that all the chicks in a colony had moved several hundred metres or crossed the river to a new location after intense predation had occurred within the colony.

Eight hundred and ninety-seven chicks were monitored through the three seasons and fledging success at colonies ranged from 0% to 50% (Table 3). Overall, a minimum of 28% of all hatched chicks survived to fledging. Of 232 chicks found dead, 29% showed evidence of predator feeding and 54% were found dead at the nest (but intact) within one week of hatching.

In 2000, early season nests had higher fledging success than late season (χ^2 = 11.46, P = 0.007, df = 1), but in 1999, early and late season nests fledging rates were similar ($\chi^2 = 0.05$, $P = 0.815$, df = 1). In the lower Ohau River, 6.4% of nests in 1999 and 18.5% in 2000 fledged one chick, and 1.3% in 1999 and 5.2% in 2000 fledged two chicks. No more than two fledglings were produced at any nest. The percentage of eggs that fledged chicks in 1999 was 14.9-19.5% (n = 835 eggs) and 12.6-14.9% (n = 570 eggs) in 2000. From DNA analysis, the sex ratio of 26 juveniles in 2000 was 10 females to 16 males.

Timing of predation events at colonies

In 1999 and 2000, several colonies appeared to rapidly decline in size through the loss of both eggs and chicks (Figure 3). This decline often coincided with the appearance of many depredated nests, the discovery of depredated chick carcasses or movement of the remaining chicks and adults across the river to a new island. The declines were not associated with severe weather or flooding, because the date of declines within individual colonies differed. Video footage and predator feeding sign provided evidence that an individual predator, such as a hedgehog or Norway rat, could potentially destroy an entire colony in a short space of time (see captions for Figures 3a and 3B). The only colony that had very low predation did not have any sudden decline in the number of active nests (Figure 3a: TI).

Nocturnal disturbance by unknown intruders potentially contributed to the loss of many chicks at one colony. At two videoed nests, nocturnal desertion resulted in the death from exposure of one chick at each nest. A further 19 chicks were found dead at the nest with no sign of predation and 17 of these were found within the same week that the chicks at the videoed nests died (Figure 3b: SF).

Juvenile movements

After fledging, 32% of the 50 juveniles with transmitters in 1999 and 2000 remained in their natal colony until the transmitter fell off (up to four weeks); 56% left the colony periodically or permanently 1-3 weeks after fledging; and 12% left the colony in the first week after fledging in response to large scale predation events within the colony. All juveniles continued to be fed by their parents throughout the monitoring period.

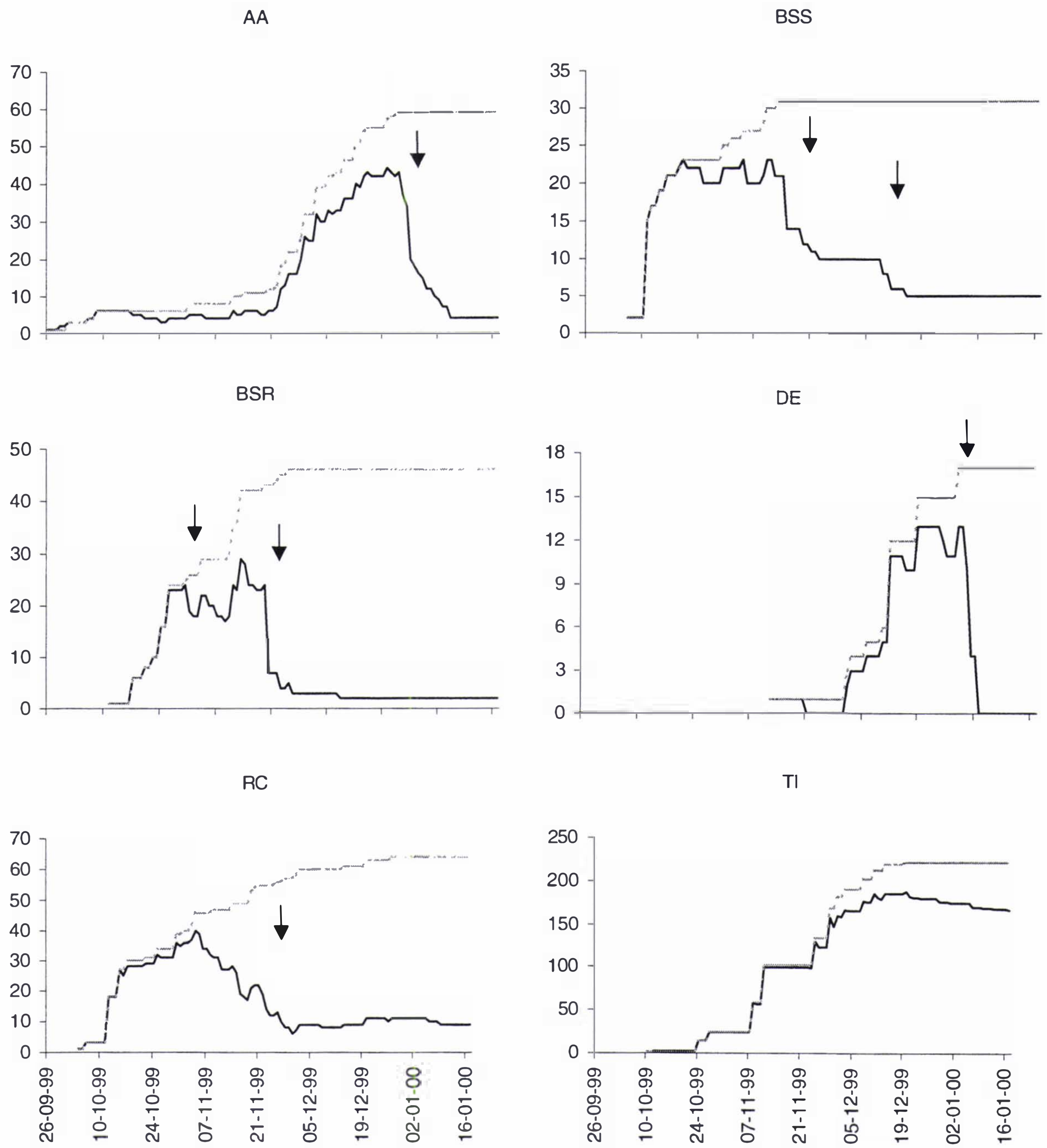

Figure 3a: Timing of declines in the number of active nests at black-fronted tern colonies in 1999. Grey line is the cumulative total of all nests laid in each colony; black line is the number of nests active at any point in time. Letters at the top of each figure represent colony location. Arrows indicate when evidence of predation was discovered. The timing of nest depredations, discovery of chick remains and videoed predations are listed by colony below. AA: 12 nests depredated 23-31 Dec; 21 chicks dead 21 Dec -5 Jan. BSS: seven chicks dead 20-29 Nov; 5 chicks dead 9-11 Nov. BSR: eight nests depredated 30 Oct – 4 Nov; 20 nests depredated 4-25 Nov and hedgehog filmed at two nests on 19 and 25 Nov. DE: eight nests depredated 31 Dec – 2 Jan. RC: eight chicks dead 24-29 Nov; remaining birds shifted across river 28 Nov. TI: only three nests preyed on; this figure records active nests through to hatching only.

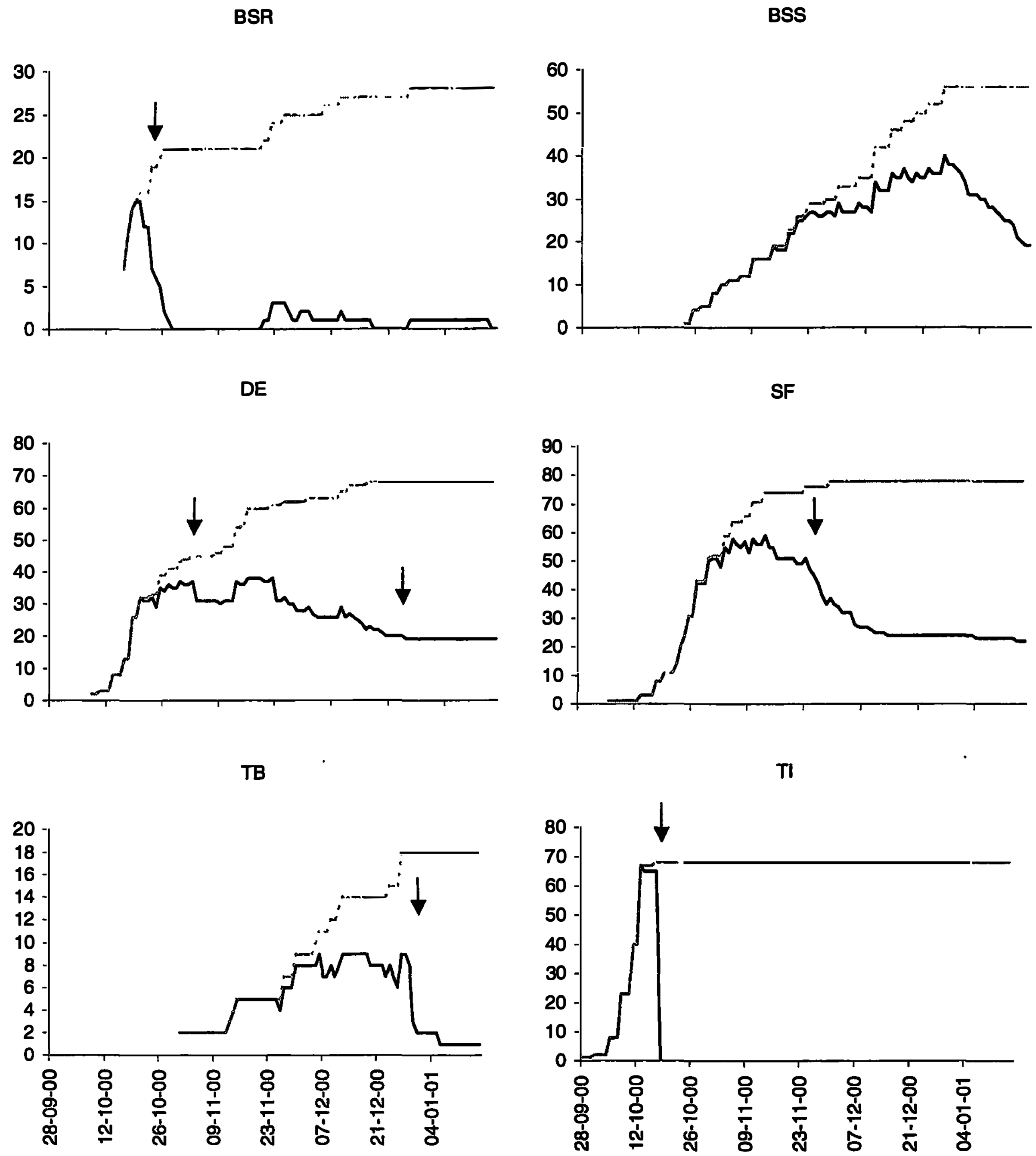

Figure 3b: Timing of declines in the number of active nests at black-fronted tern colonies in 2000. Grey line is the cumulative total of all nests laid in each colony; black line is the number of nests active at any point in time. Letters at the top of each figure represent colony location. Arrows indicate when evidence of predation was discovered. The timing of nest depredations, discovery of chick remains and videoed predations are listed by colony below. BSR: 20 nests depredated 19-27 Oct; hedgehogs filmed at four nests 19-25 Oct. DE: seven nests depredated 23-30 Oct; five nests depredated 2 Nov; eight chicks dead 24 Dec. SF: video footage shows nocturnal desertion kills two chicks 20 and 25 Nov. TB: six nests depredated 29 Dec. TI: 68 nests present 13 Oct, 67 nests depredated by next visit on 18 Oct; video camera at deserted nest records Norway rat eating eggs and eaten out eggs stashed in rat tunnels around perimeter of colony.

Immature survival and site fidelity

At least 233 banded black-fronted tern chicks survived to fledging, representing 19 different cohort band combinations from three years (Table 5). Two sources of error make it impossible to accurately assess survival rates: 1) underestimating survival because of dispersal from the Ohau River; and 2) overestimating survival by double counting (or more) of individuals. If each of the resightings in 2001 is assumed to be a separate individual, then 26% of fledglings from 1998 were resighted after three years.

Nine out of 168 birds banded as chicks were seen nesting two or more years after banding. Six of these were nesting at their natal colonies, one was still nesting on the Ohau River but was almost 10 km from its natal colony, and the remaining two birds were nesting on the Tekapo River over 20 km from their natal colonies.

Adult survival and site fidelity

Two models fitted well for estimating adult survival (Table 6). Both models held survival probabilities constant in each year $\{\phi\}$, but resighting probabilities either varied between 2001 and the previous two years $\{P_{1-2,3}\}$ or remained constant over all three years $\{P\}$. Annual adult survival (95% CI) was 0.92 (0.58-0.99) if the resighting probabilities are assumed constant, or 0.88 (0.57-0.98) if 2001 had a higher resighting probability.

In the first three seasons, I found four adults killed on the nest by predators, two adults died from unknown causes and two adults had broken a wing after hitting high-tension powerlines. All four adults killed on the nest were female.

Thirty-one banded adults were seen nesting in one or more years after banding. Only 19% were nesting at the original colony where they were banded, 58% were seen nesting at other colonies on the Ohau River and 23% were seen nesting in the adjacent Tekapo or Twizel Rivers. Banded black-fronted terns were most frequently seen in flocks or colonies located on the Ohau, Twizel and Tekapo Rivers and Ruataniwha Wetland (Figure 4). No banded birds were seen on distant rivers such as the Cass, Tasman or Waitaki.

Table 5: Resighting rates of banded black-fronted terns after fledging. Colour combinations were cohort combinations indicating the year and colony of fledging. Individual birds could not be identified, but the percentage resighted is estimated by assuming each sighting of a colour-banded bird was a separate individual. Additional sightings in 2000 were sightings made of colour combinations that were not subsequently seen in 2001.

	1998	**1999**	**2000**
Number colour combinations used	8	6	5
Number birds banded	46	122	55
Number seen in 2001	12	20	15
Additional sightings in 2000	3	1	-
% seen after three years	26.1	-	-
% seen after two years	32.6	16.4	-
% seen after one year	32.6	17.2	27.3

Table 6: Analysis of adult black-fronted tern survival rates, 1998-2001, using Program MARK 2.1. Models include survival (ϕ) and resighting (*P*) rates which may vary by time (*t*). Corrected Akaike Information Criterion ($\mathrm{AIC_c}$) is adjusted for overdispersion ($c = 2.01$). Δ $\mathrm{QAIC_c}$ is the difference in $\mathrm{QAIC_c}$ in the best model; weight indicates the relative support for the models.

Model	**$\mathrm{QAIC_c}$**	**Δ $\mathrm{QAIC_c}$**	**Weight**	**Number of parameters in model**
$\phi.P$	102.77	0.00	0.38	2
$\phi.P_{1-2,3}$	103.22	0.45	0.30	3
$\phi.P_t$	105.32	2.54	0.11	4
$\phi_t.P_{1-2,3}$	105.39	2.62	0.10	4
$\phi_t.P$	106.12	3.34	0.07	4
$\phi_t.P_t$	107.48	4.70	0.04	5

Renesting and productivity

Band resightings provided information on renesting attempts on only one occasion where a banded adult was observed courtship feeding and initiating a new nest 6 days after losing young chicks. Calculations based on the maximum number of adults with active nests at any one time in the lower Ohau River only, provide a crude estimate of renesting attempts. Based on the maximum number of nests active at any one time, approximately 20% (47/235) and 21% (50/249) of monitored nests in 1999 and 2000 respectively could have been renests. If this is correct, then the lower Ohau River black-fronted tern population was 386 adults in 1999 and 390 in 2000. Productivity estimates for the lower Ohau River population each year were 0.11 chicks/female in 1999, and 0.37-0.44 chicks/female in 2000.

Adult body measurements

Mass, tarsus length and bill depth provided the best model for predicting the sex of adults ($F_{3,34} = 13.82$, $P < 0.0001$). On average, males were lighter with longer tarsi and thicker bills (Table 7). The equation describing the linear discriminant function (LDF) using these measurements (LDF = -82.24 - 0.1294*mass + 3.57*tarsus + 2.72*bill depth) could accurately identify the sex of 80% of individuals. When all the birds of known sex were put into the equation, all 22 males were correctly identified (positive values), but only 10 out of 17 females were correctly identified (negative values). The remaining females produced positive values but all were less than 2. Seventy-seven percent of known males produced positive values greater than 2. Thus, using the LDF equation, a bird was definitely female if the value was negative, almost certainly male if the value was positive and greater than 2, but sex cannot be clearly identified if the value is between 0 and 2. Using the linear discriminant function equation, 17 of 33 unsexed birds were classified as females, eight as males and the outcomes were unclear for the remaining eight birds.

Table 7: Body measurements of adult black-fronted terns of known and unknown sex. Data tabulated are means ± 95% CI. 'All' includes 39 birds of known sex and 33 birds of unknown sex. For a description of each measurement, see Table 1.

Measurement	**Males**	**Females**	**All**
No. individuals	22	17	72
Mass (g)	92 ± 3	93 ± 4	92 ± 2
Wing chord (mm)	251 ± 2.	247 ± 4	251 ± 2
Tail tip (mm)	113 ± 4	108 ± 6	112 ± 2
Tail fork (mm)	74 ± 3	73 ± 4	75 ± 1
Tarsus (mm)	21.3 ± 0.2	20.3 ± 0.3	20.6 ± 0.2
Head and bill (mm)	65.9 ± 0.8	64.4 ± 0.9	65.0 ± 0.5
Bill length (mm)	22.4 ± 0.5	22.0 ± 0.5	22.2 ± 0.3
Bill width (mm)	6.1 ± 0.1	5.9 ± 0.1	6.0 ± 0.1
Bill depth (mm)	7.9 ± 0.2	7.4 ± 0.2	7.7 ± 0.1

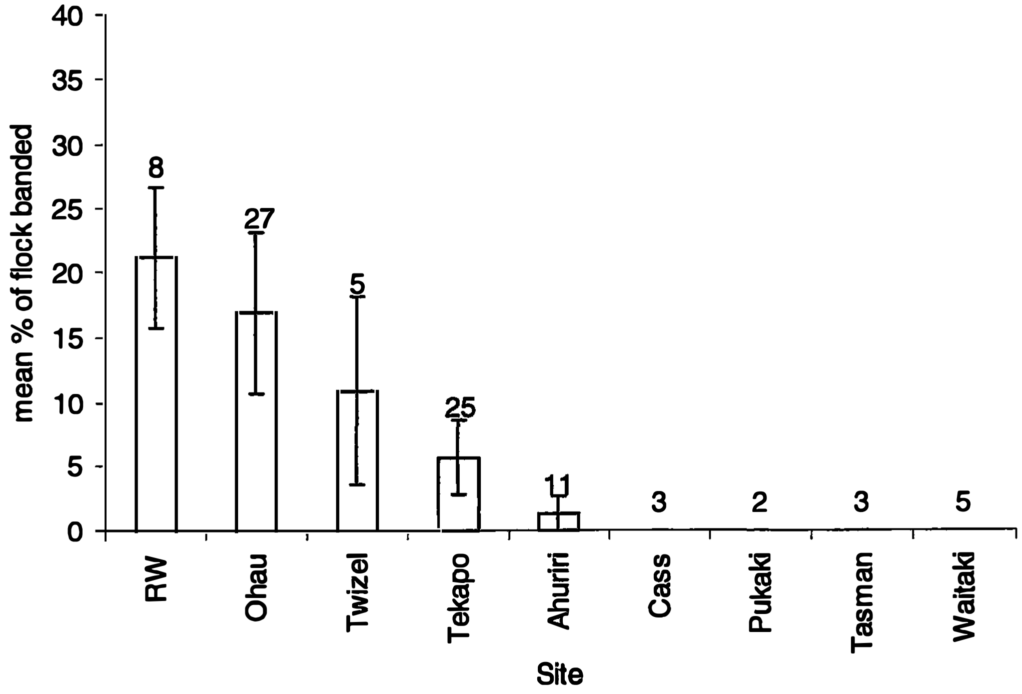

Figure 4: Mean percentage of banded black-fronted terns in flocks or colonies seen on rivers of the upper Waitaki Basin and at Ruataniwha Wetland (RW). Percentage was calculated as the number of banded birds/number of birds confirmed unbanded and banded (not total number of birds in flock). Numbers on top of bars represent the number of flocks examined. Error bars are 95% confidence limits.

Discussion

This study provides the first comprehensive account of black-fronted tern breeding biology and survival. The low survival rates and low productivity suggest that concerns about the species' survival (Taylor 2000) are well founded.

The data presented here provide valuable baseline information on black-fronted tern biology, and provide information on which to base management actions. Nevertheless, long-term studies in a range of locations need to be continued to improve many estimates of survival. For example, flooding had very little impact on breeding success, but success was only monitored on the Ohau River, which has a controlled flow. Earlier studies suggest flooding is a major cause of mortality (Stead 1932, Lalas 1977), and up to 11 out of 21 colonies were entirely or partially flooded on the Ahuriri River in 1982 (Robertson et al. 1983).

Although predation is probably the primary factor contributing to the low level of productivity in black-fronted terns, the variation in predation pressure from year to year is difficult to assess based on this study alone. In 2000, no adults were killed by predators and chick and juvenile survival rates were higher than in either of the previous two years. How frequently a low predation year like 2000 occurs will have a significant effect on long-term population trends. We need to understand variation in predation impacts among seasons. For this study, one cause may be the ongoing changes in the predator guild in the wake of the introduction of Rabbit Haemorrhagic Disease (RHD). The disease was illegally introduced to New Zealand in late 1997 to control rabbit populations on farmland. Initial declines in rabbit populations caused a shift in predator diet to braided river bird species (Norbury 2000), and a lag in the response of predator population sizes may be ongoing. Although neither rabbit nor predator abundance were formally monitored in this study, video cameras at braided river bird nests showed a possible change to the composition of the predator guild in 2000, with hedgehogs the only mammalian predators recorded. In previous years, cats were recorded on numerous occasions each season, and one or more mustelid predations were also recorded each season (Sanders and Maloney 2002).

Prior to the establishment of mammalian predators in New Zealand in the nineteenth century, coloniality in black-fronted terns would have been a useful defense against predation (Wittenberger and Hunt 1985). Black-fronted terns evolved with predators that were mostly diurnal and avian, and black-fronted terns will vigorously mob and chase any intruders, both avian and mammalian, entering the colony during the day. However, in the modified environment black-fronted terns now inhabit, coloniality may be detrimental to their survival. No avian predation of black-fronted terns was recorded in this study, despite previous records of Australian magpies and Australasian harriers preying on young of braided river bird species (Lalas 1977, Pierce and Maloney 1989, Keedwell and Sanders 1999). All videoed predations were by mammals at night. Black-fronted tern colonies are completely silent between dusk and dawn, and adults make absolutely no attempt to attack nocturnal intruders (pers. obs).

Colonies may provide an easily accessible and concentrated food source for individual predators. The sudden declines in numbers of active nests at colonies coinciding with videoed predation events and the appearance of chick carcasses suggest that predators such as hedgehogs and Norway rats use tern colonies as a constant food supply. Colonial nesting is probably detrimental to black-fronted tern survival also because adults will temporarily or permanently desert eggs or chicks if the colony is disturbed at night. The impact of single predators has also been observed at least tern

(*Sterna antillarum*) colonies, where red foxes (*Vulpes fulva*) destroyed the majority of nests at two or more colonies (Massey and Fancher 1989). In addition, nocturnal desertion has been documented at common tern (*S. hirundo*) colonies, which resulted in lower breeding success (Wendeln and Becker 1999).

There was no evidence in this study that bigger colonies were more successful. The exceptionally large colony recorded in 1999 had higher hatching and fledging success than any other colony, but whether very large colonies are more successful cannot be determined unless more colonies of a similar size can be monitored. Therefore, it is highly probable that any evolutionary advantages conferred by coloniality no longer hold for black-fronted tern survival in New Zealand. The impact of mammalian predators on black-fronted tern colonies suggests that coloniality may in fact be a disadvantage in the highly modified braided river environment.

Contrary to a widely held belief, monitoring black-fronted tern colonies does not result in colony-wide desertion of nests or chicks. Black-fronted terns do desert their eggs, along with many other tern species (Monaghan et al. 1992, Holt 1994, Arnold et al. 1998), but my study demonstrates that monitoring black-fronted tern breeding has a minimal impact on desertion rates. Black-fronted terns in this study readily deserted their eggs or young chicks for the rest of the night if disturbed by an animal as innocuous as a rabbit. In contrast, I spent over an hour a day in some colonies but adults would return to their nests as soon as I was at least 20 m away, even if they had been disturbed off the nest by the dog searching for chicks. Another colony survived with relatively low desertion levels despite being located on the main 4-wheel drive access route through the Ohau River, where up to 15 vehicles per day and foot traffic regularly disturbed the colony (Whiting 1999). Determining the relationship between predation and desertion rates within each colony was not possible. In colonies with high predation rates but apparently low desertion, it was entirely possible many nests were deserted and then were preyed upon before I could be certain the nests were deserted. Consistent with this, I often found deserted nests and subsequently noted depredation of the eggs. It is unlikely that monitoring black-fronted tern colonies reduces breeding success through causing desertion or increasing predation rates (Chapter 1). Instead, nocturnal disturbance and predators are more likely to be the primary causes of desertion.

It is difficult to accurately measure the survival of adult and immature black-fronted terns. Although they may be banded with coloured leg bands, only one band can fit per leg. In addition, black-fronted terns are usually either flying or on the nest, concealing their legs. Unless black-fronted tern fledglings can be banded with individual colour combinations or distance readable alphanumeric bands, it will be difficult to improve estimates of survival rates from fledging to maturity. Bands are more easily seen on roosting birds flocking at the start or end of the breeding season. Intensive surveys for bands are necessary if better data on survival rates are required.

The survival rates of adult black-fronted terns presented here have wide confidence intervals but are comparable to survival rates calculated from other more comprehensive studies (e.g., common tern 0.88-0.92 Nisbet (2002); roseate tern 0.78-0.89 Spendelow et al. (2002); least tern 0.88 Massey et al. (1992)). Survival rates of fledglings to first breeding for other species range from 0.16 to 0.68 (Nichols et al. 1990, Massey et al. 1992, Becker 1999, Spendelow et al. 2002). Because mortality of black-fronted terns is high in the immediate post-fledging period (Chapter 8), it is probable that survival from fledging through to first breeding is in the lower range of estimates published for other species.

Fewer resightings were made in 2001 of birds banded as fledglings (< 9%, with the optimistic assumption each sighting was a separate bird) than as adults (53%). Either survival of immatures is extremely low, or immatures disperse further afield to rivers outside of the central Waitaki Basin where I made little or no search effort. Alternatively, if only a small proportion of black-fronted terns breed at two years and full breeding is not observed until three or four years, the non-breeding birds may not have been present at the breeding areas as frequently as the breeding adults.

Using measures of black-fronted tern adult mass, bill depth and tarsus length provides a method for sexing at least 80% of birds of known sex. Previously, no method existed for sexing black-fronted terns, other than DNA analysis. The measurements I present here are similar to those presented elsewhere (Lalas and Heather 1980, Higgins and Davies 1996). However, this method of sexing adults needs validation because the birds whose sex I tested using the model were also used to build the model. Using the discriminant function analysis on measurements from an additional set of adult black-fronted terns of known sex will show whether this method is reliable.

The data I collected on adult and immature movements suggests that there is only limited dispersion to areas outside the original banding or hatching site. In addition, terns seemed to form colonies at several key locations each year, particularly if there was good breeding success, or large colonies, in the previous season. At some colonies where no or low predation was observed, hatching success and fledging success were much higher than average. Therefore, predator control around a colony would improve black-fronted tern productivity. If control was implemented at the main colony sites each year, ongoing control in a river such as the Ohau would most likely increase the population in that river and have a spill over effect into adjacent rivers.

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Chapter 5:

Causes of mortality of black-fronted terns (*Sterna albostriata*) on the Ohau River, South Island, New Zealand

Remains of two juvenile black-fronted terns

Abstract

We examined the carcasses of 148 black-fronted terns (*Sterna albostriata*) found during the 1998-2000 breeding seasons on the Ohau River, South Island, New Zealand. Predation was the primary cause of mortality of adults, juveniles and chicks, resulting in 47.3% of all deaths. Video footage showed feral cats (*Felis catus*) were responsible for 6% of all predator-caused deaths, and feeding sign linked cats to another 19% of predations. Feeding sign and other circumstantial evidence suggested Norway rats (*Rattus norvegicus*) and stoats (*Mustela erminea*) were responsible for 51% and 6% of predator-caused deaths, respectively. The feeding sign of the different predator species on black-fronted terns is described. Other causes of mortality included starvation (4%), power lines (1%), road traffic (1%) and various natural causes of mortality (5%). Causes of mortality could not be assigned to 41% of black-fronted terns, but most of these were young chicks that died at the nest soon after hatching. We suggest that predators are potentially the main cause of population decline in black-fronted terns and that predator control targeting cats and Norway rats during the breeding season should be trialled.

Introduction

The black-fronted tern is an endemic New Zealand species listed globally as endangered (BirdLife International 2000) and the population is probably in decline (Chapter 9, Taylor 2000). Black-fronted terns are colonial ground-nesting birds that breed only on the braided riverbeds of the South Island and their survival is threatened by loss of breeding habitat caused by hydro-electric development and weed invasion, and by increased mortality from introduced predators (Higgins and Davies 1996, Taylor 2000).

Recent research using remote video cameras has shown that predation is the main cause of egg loss (Sanders and Maloney 2002). However, because black-fronted tern chicks leave the nest soon after hatching, little is known about causes of mortality at the chick and juvenile life stages. Wildlife managers need to know the relative impacts of different causes of mortality at various life stages so that they can develop effective management strategies. If predation is important, as seems likely, it is helpful to know the relative impacts of different predator species.

Predation is a major cause of death in many species of New Zealand birds (Taylor 2000, Dowding and Murphy 2001, Sanders and Maloney 2002) yet only limited work has been done to positively identify sign left by different predator species on chicks or adults (Innes et al. 1994, Brown et al. 1996, Brown and Mudge 1999, Ratz et al. 1999, Lyver 2000). In this study, we identify predators that have preyed on black-fronted terns by clearly linking sign on the carcass to the predators responsible.

Study site

Black-fronted tern mortality was investigated as part of a three-year study into black-fronted tern breeding biology on the lower Ohau River, South Island, New Zealand (44°20'S, 170°11'E), from 1998 to 2000. The Ohau River is a braided river with large expanses of sparsely vegetated gravels, which are used by black-fronted terns and other bird species for breeding. The riverbed varies in width from 50 to 300 m. Most of the river water has been diverted to hydroelectric canals for power generation, leaving an average flow of <5 m^3sec^{-1}. Introduced predators, including cats (*Felis catus*), ferrets (*Mustela furo*), stoats (*M. erminea*), Norway rats (*Rattus norvegicus*) and hedgehogs (*Erinaceus europaeus*), and two native avian predators, southern black-backed gulls (*Larus dominicanus*) and Australasian harriers (*Circus approximans*), are found throughout the braided rivers of the South Island (Heather and Robertson 1996, Keedwell and Brown 2001).

Methods

Causes of mortality were assessed for 124 chicks, 16 juvenile and 8 adult black-fronted terns found dead on the Ohau riverbed. Tern carcasses were found during intensive searches of breeding colonies every 1-3 days (Chapter 4) or by monitoring radio-marked individuals daily (Chapter 8). Causes of adult and chick mortality were also recorded by video cameras at three nests; and by placing cameras at two carcasses found within 1 day of death (for details of the camera configuration, see Sanders and Maloney 2002). Birds were divided into three age categories: chicks – young of the season that had not fledged (mean age of first flight is 28 days); juveniles – newly fledged young of the season; and adults. All chicks and juveniles were metal-banded at hatching, which facilitated ageing and identifying recovered carcasses.

Carcasses that were recovered fresh were packed on ice and sent overnight to the Institute of Veterinary, Animal and Biomedical Sciences, Massey University where gross post-mortem examinations were undertaken. The birds were then fixed in 10% buffered formalin and selected tissues processed and embedded in paraffin for histopathology. Carcasses that were not found freshly dead or that were extensively eaten by predators were examined on site, feeding sign was recorded and the area around the carcass was checked for any further sign of predation, such as feathers, blood or predator scat.

Causes of death were divided into five categories:

1. Predation – evidence of predator feeding sign on the carcass, and/or the carcass was in a predator den site. The predator species responsible for each predation was either identified from video footage, or was inferred from the feeding sign left on the carcass (i.e., the parts of the carcass that were eaten, see Results for full descriptions), location of the carcass, presence of predator scat, or the distance between pairs of puncture wounds based on intercanine distances (Ratz et al. 1999, Lyver 2000). Feeding sign left after videoed predation events was used to infer probable predator identity at other predation events where similar feeding sign remained. Scavenging could not be distinguished from predation on the basis of feeding sign.
2. Starvation – no evidence of physical injury or other lesions. Examination of the intestinal tract showed it contained no or very little food; and there were no or few fat reserves remaining in the abdominal cavity or subcutaneous tissues.
3. Trauma – evidence of physical injury that was not linked to predator feeding sign. The location of the bird (e.g., on a road, under power lines) sometimes suggested the probable cause of the trauma.
4. Other – separate pathological conditions diagnosed through post-mortem examination.
5. Unknown – birds that showed no sign of physical trauma and/or the carcass was too autolysed for detailed post-mortem examination.

Results

Of the 148 carcasses found, we were able to determine the cause of mortality for 87 (Table 1). Cause of mortality could not be determined for 48% of chicks, whereas it was unknown for only 6% of juveniles and 12% of adults. For the 59 chicks that died from unknown causes, 83% were found dead at the nest at less than one week of age. Few of these chicks were recovered fresh enough for adequate post-mortem examination – their small carcasses deteriorated quickly in the hot weather.

Table 1: Causes of mortality for black-fronted tern chicks, juveniles and adults found dead on the Ohau riverbed, 1998-2000.

	Chicks		**Juveniles**		**Adults**		**Total**	
Cause of death	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**
Predation	52	42.2	13	76.5	5	62.5	70	47.3
Cat – definite	3	2.4			1	12.5	4	2.7
Cat – possible	5	4.1	6	35.3	2	25.0	13	8.8
Rat – possible	31	25.2	4	23.5	1	12.5	36	24.3
Stoat – possible	3	2.4	1	5.9			4	2.7
Unidentified	10	8.1	2	11.8	1	12.5	13	8.8
Starvation	5	4.1	1	5.9			6	4.1
Trauma			1	5.9	2	25.0	3	2.0
Road			1	5.9			1	0.7
Power lines					2	25.0	2	1.4
Other	7	5.7	1	5.9			8	5.4
Exposure	2	1.6					2	1.4
Asphyxiation	1	0.8					1	0.7
Hatching complications	2	1.6					2	1.4
Necrotising enteritis			1	5.9			1	0.7
Necrotising peritonitis	1	0.8					1	0.7
Respiratory failure	1	0.8					1	0.7
Unknown	59	48.0	1	5.9	1	12.5	61	41.2
Totals	**123**		**17**		**8**		**148**	

Predation

Predation was the major cause of mortality, accounting for 47.3% (70/148) of all recorded mortalities (Table 1). Proportionately more juvenile (75.1%) and adult (62.5%) mortalities were classified as predations, compared to only 42.6% of chick mortalities.

Cat predation

Cats were confirmed predators of 5.7% of terns that were preyed upon and were likely predators of a further 18.6% (Table 1). Video recordings showed a cat preying on three chicks at two nests and on one adult at another nest (Table 2). A cat also probably killed one other adult; a video camera was placed at a nest where an adult was found freshly killed and a cat was recorded visiting the carcass the following night. It is probable that this adult was killed by a cat because in 83% of 18 filmed nests of braided river birds where a predator returned to a depredated nest the night after a predation event, the nest predator and the visiting predator were the same species (Department of Conservation, unpubl. data). The feeding sign left on both these adult black-fronted terns was identical (Table 2).

Two sets of juvenile remains that were possibly from cat predations were left in place, and a subsequent check showed the remains were further eaten and the resulting sign was only a pile of feathers, which was different to the original sign documented. It is unclear whether this change was due to scavenging by the same or a different species of predator.

Rat predation

Norway rats were not directly observed killing terns. However, on four separate occasions over two-thirds of the chicks and some juveniles in a colony disappeared in less than a week, coinciding with the appearance of rat-eaten remains (Chapter 4). The remains of 36 terns were classified as possible rat predations based on the location of the carcass, the presence of Norway rat faecal pellets and feeding sign. The feeding sign was consistent with that recorded when a video camera was placed to record rat activity at a freshly killed adult (Table 2). All carcass remnants classified as rat predations were found in or next to tunnels burrowed into dense, low-growing vegetation bordering the river.

A video camera was placed at the remains of an adult that had been killed <1 day previously and was hidden in dense vegetation next to the river. The head, wings and dorsal surface of the bird were still intact but the ventral surface had been opened, the abdominal organs removed and flesh removed from both femurs. A Norway rat was filmed arriving at dusk and partly eating the carcass on the day the camera was set up. The rat (or rats) continued to eat the carcass over six of the next seven nights. During subsequent visits, the rat ate out the contents of the skull, and ate more of the body – severing the vertebrae and chewing the flesh from the bones. The legs were severed and the skin removed from the tarsi and then the metatarsi. The wings were the last body part to be eaten and the feathers were removed and the bones chewed clean. After a week, all that remained was a pile of feathers with jagged ends, a piece of mandible and clean pieces of bone with chewed ends.

Repeat visits to 16 chick and juvenile carcasses found in rat burrows 1-2 days after death showed that the remains were consumed in a similar sequence to that observed for the videoed adult remains. The head, body and proximal ends of the legs and wings were consumed first and the bones were chewed until all flesh was removed. The skin and flesh of the tarsi and subsequently metatarsi were then eaten, followed by de-feathering and dismantling of the wings. As with the videoed adult remains, feathers, chewed bones, pieces of mandible and rat scat were all that eventually remained.

On at least five occasions, remains were shifted and eaten at up to three different locations around the colony, but always within the vegetated margins of the river. On some occasions, the remains of 2-4 partially eaten individuals were found piled in the same burrow. Broken eggs and eggshell fragments were also found throughout the tunnels where the bird remains were located.

Table 2: Description of feeding sign left by predators on black-fronted tern adults (A), juveniles (J) and chicks (C). Where predator species is followed by '?' then predator identity was based on circumstantial evidence only. Remains were located at nest sites or on the nest; 'in open' – remains found on gravels or cobbles in the open riverbed; 'in tunnel' – remains found in well formed tunnels through dense vegetation adjacent to river channels, characteristic habitat of the Norway rat; 'dense vegetation' – remains stashed in dense vegetation adjacent to river channels but did not have clear tunnel systems.

Predator	Feeding sign or remains	Location	Evidence	Age	No. birds
Cat	Drops of blood and clumps of down.	At nest site	Video	C	2
Cat	Head missing, body intact.	At nest site	Video	C	1
Cat	Head and upper body missing, legs attached to rump, wings detached at mid-humerus.	On nest	Video	A	1
Cat?	Head and upper body missing, legs attached to rump, wings detached at mid-humerus.	On nest	Cat videoed at carcass	A	1
Cat?	Head missing, body intact.	On nest/in open	Similar to video sign	A J C	1 1 1
Cat?	Detached wings and fully or partially detached feet with a section of rump remain, in a pile of feathers. Piece of mandible present (1).	In open	Similar to video sign	J C	4 3
Cat?	Small chick with transmitter regurgitated in large pile of vomit – feet still attached to rump, wings detached.	In open	Probable cat vomit	C	1
Cat?	Body uneaten but localised haemorrhage and puncture holes 17 mm apart on neck.	In open	Tooth marks	J	1
Rat?	Chewed dried bones, pin feathers and leg band only remain.	In tunnel	Rat scat	C	9
Rat?	Pile of feathers, bill and legs, and a few	In tunnel	Rat scat	C	3

	chewed bones.				
Rat?	Body partially eaten with some of skeleton still intact: legs severed or chewed to top of tarsus; wings detached or chewed at proximal end only; parts of skull/mandible still attached to oesophagus and crop; if internal organs eaten, usually some intestines and crop remain; skull either intact or eaten out; neck often severed with vertebrae missing; flesh removed from ribs, pelvis, sternum and spine.	In tunnel	Rat scat and/or in rat tunnel. Rat videoed feeding on adult carcass.	A J C	1 3 15
Rat?	Body largely intact: skin and tissues removed from part of abdomen, thorax, neck and/or skull; brains missing (1) or intact (2); abdomen eaten out; ribs and sternum chewed. Leg missing (1).	In tunnel	In tunnel	J C	1 2
Rat?	Intact small chick but with three holes gouged into flesh on dorsal surface.	In tunnel	In rat tunnel	C	1
Rat?	Small chick with head and part of chest missing.	In tunnel	In rat tunnel and rat scat	C	1
Stoat?	Body uneaten but localised haemorrhage and puncture holes 4 mm apart to skull (1) and scapular (1).	In open	Tooth marks	J C	1 1
Stoat?	Body partially eaten: skin and tissues down one side of abdomen and chest removed, some of heart or liver eaten, severe haemorrhage around neck.	Dense vegetation	Location*	C	2
Cat/ferret?	Body uneaten but haemorrhage, dislocated wing and puncture holes 10 mm apart under wing.	In open	Tooth marks	C	1
Unknown	Body largely intact but abdominal area and head eaten out. Partially decomposed.	Dense vegetation	Nil	A	1
Unknown	Body uneaten but wound to neck (3) or pectoral area (1) with haemorrhage.	In open	Nil	J C	1 3
Unknown	Body intact but abdominal area eaten.	In open	Nil	C	3
Unknown	Body intact but upper mandible torn off.	Under bush	Nil	C	1
Unknown	Pile of feathers, bill tip (1) or one foot (1).	In open	Nil	J C	1 1
Unknown	Strewn out remains with feathers, head, one leg and partially eaten wings.	In open	Nil	C	1

* These two chicks were found freshly killed on the same day and within 50 m of the chick that had evidence of stoat tooth marks. Chicks were stashed in dense vegetation rather than tunnel systems.

Possible stoat predation

One chick and one juvenile had possible pairs of puncture wounds approximately 4 mm apart in the subcutaneous tissues of the skull or scapular, respectively (Table 2). Based on the intercanine distances, these individuals could have been killed by small stoats (Ratz et al. 1999). Another two freshly killed chicks were found partially eaten and hidden in dense vegetation. These remains were within 50 m of the chick that had possible stoat tooth marks in its skull. All three chicks died within the same day.

Predations by unidentified predators

Thirteen terns were found dead with predator feeding sign that did not match that observed for cats or rats (Table 2). One chick had a pair of puncture wounds that were 10 mm apart, but because both cats and ferrets can have intercanine distances matching this wound, predator identification was not conclusive.

Other causes of mortality

Four percent of terns (6/148) died of starvation and 2% died from non-predator related trauma injuries.

Eight chicks and juveniles (5.6%) died of miscellaneous causes. Two chicks died because of bacterial infections occurring shortly after hatching and another two chicks at videoed nests died from exposure after nocturnal desertion by the parents (Table 1).

Parasitism

Detailed post-mortem examinations were carried out on 25 black-fronted terns (1 adult, 5 juveniles and 19 chicks). Although four of these birds had internal parasites, these parasites did not appear to be linked to the death of the animal. A protozoal cyst was found in the myocardium of the adult; a trematode was found between the capsule and follicles of the bursa in one juvenile that died of starvation; one juvenile that died of necrotising enteritis also had intestinal nematodiasis; and a third juvenile that had been killed by a predator had mild intestinal parasitism.

Discussion

Importance of predation

This study provides the first comprehensive account of causes of nesting mortality in black-fronted tern chicks, juveniles and adults, and demonstrates that predators are an important cause of mortality of black-fronted terns. Predators were the primary cause of juvenile and adult deaths recorded here, and are the primary cause of death of black-fronted tern eggs in the nest (Chapter 4, Sanders and Maloney 2002). The species of predators identified in this study in the Ohau River are also found throughout the braided rivers of the upper Waitaki Basin (Keedwell and Brown 2001), an area that provides breeding habitat for at least 30% of the black-fronted tern population (Maloney et al. 1997). Existing information indicates that black-fronted tern populations are probably in decline throughout their range (Chapter 9) and we suggest that introduced predators are potentially the major cause of black-fronted tern population decline.

It is possible that some mortalities attributed to predation were actually cases where the carcasses were scavenged after death. However, this is unlikely because i) many depredated carcasses either had haemorrhage or obvious wounds inflicted by predators, or there were blood splatters nearby, indicating that the tern was alive when attacked, (ii) few uneaten adult or juvenile carcasses that died of natural causes were ever found, and (iii) large numbers of predations occurred within a short timeframe, indicating a widespread predation event throughout the colony. It is more likely that predation rates here are underestimated because many more terns were likely to have died than were found and were either carried away from the colony or remained undetected. The rates of chick predation are almost certainly underestimated because video footage showed chicks could easily be consumed whole by predators, and large predators such as cats were unlikely to leave any feeding sign after eating young chicks.

In this study we have presented some evidence of feeding sign from positively identified predators, but the large body of circumstantial evidence we have presented needs validating through further research. Previously, feeding sign at bird nests based on eggshell remains has been classified without direct observation (Moors 1983). The advent of video recording of predators at nests has shown how unreliable nest sign has been and how frequently it has been misclassified (Major 1991, Brown et al. 1998, Lariviere 1999). Similarly, with bird remains, it is important to either obtain direct observations to be able to classify feeding sign, or explicitly state the methods used to attribute the sign to a predator. One difficulty in classifying predator feeding sign is that the depredated remains may be further scavenged by other predator species. Even when carcasses have unmistakable predator sign around them, it does not mean that particular predator species was responsible for killing the prey. Captive feeding trials have proven to be an effective way of identifying feeding sign (Brown et al. 1996, Brown and Mudge 1999) and further trials should be used to validate the feeding sign of cats and rats documented in this study.

Overlap in feeding sign of stoats and rats

Although we have attributed a large proportion of the feeding sign to Norway rats, it is entirely possible that overlap in sign exists between stoats and rats. Stoats typically use the den sites of prey (G. Blackwell pers. comm., King 1990). Thus, stoats may cache the remains of terns in rat burrows, and rats subsequently scavenge the remains. However, Norway rats are known to kill adults and young from a wide range of species, including gulls, terns and shearwaters (Atkinson 1985). It is unlikely that all the rat-eaten remains were originally stoat kills because, i) rats are capable of killing black-fronted terns for themselves; ii) the timing of sudden and large scale losses of chicks from colonies followed by the appearance of rat eaten remains, suggest that rats would have had to be trailing stoats (a predator of rats) to be able to scavenge such a large number of remains; and iii) fresh rat scats regularly appeared next to the tern remains, but no stoat scat was ever found. In addition, stoats usually leave behind the head, wings and feet of birds (M. Potter, pers. comm., Dowding and Murphy 1996), which was dissimilar to the remains found in rat burrows.

Stoats are an important predator in New Zealand forest systems (King 1990), and have been implicated in high mortality rates of another braided river bird species, the wrybill plover (*Anarhynchus frontalis*) (J. Dowding, pers. comm.). Intensive predator trapping has previously shown that stoats were the least abundant predator on the Ohau River but were found in much higher densities on rivers such as the Tasman, Ahuriri and Godley Rivers (Keedwell and Brown 2001). Evidence from the Tasman River suggests stoats are important predators of both the wrybill and black-fronted tern (J. Dowding, pers. comm.). Although our results indicate that Norway rats are a more important predator of black-fronted terns in the Ohau River than are stoats, this result may not be true for all braided rivers.

No feeding sign was found to suggest that ferrets or avian predators such as harriers, black-backed gulls or Australian magpies (*Gymnorhina tibicen*) were significant predators of black-fronted terns. All three avian predators have been recorded preying on young chicks of braided river bird species, but either the chicks were carried off (Lalas 1977, Sanders and Maloney 2002) or no obvious sign remained after the event (Keedwell and Sanders 1999). Using the recovery of dead bodies from tern colonies alone as a measure of predation is therefore likely to under-represent the importance of those predators that carry their prey outside the tern colonies. However, further evidence will be required to indicate that ferrets or avian predators have a limiting influence on black-fronted tern populations.

Predator control to increase black-fronted tern survival

Effective predator control in the braided rivers is difficult because of high rates of immigration by predators into the trapped areas (Keedwell and Brown 2001), but narrowing the control regime to target two key species may prove easier than targeting all predator species combined. Cats clearly impact on black-fronted tern survival at the chick, juvenile and adult life stages, and are one of the major predators of black-fronted tern eggs (Sanders and Maloney 2002). Similarly, Norway rats are also important predators through a range of black-fronted tern life stages, whereas hedgehogs are probably only important at the egg stage. Although it is unclear the extent to which stoats play a role in black-fronted tern mortality, instigating a control programme that targets only cats and rats may be a simpler option because stoats can be difficult to target effectively (Dowding and Murphy 1996). Predator control targeting rats and cats needs to be trialled at black-fronted tern colonies to test whether controlling these predators alone can measurably alter black-fronted tern breeding success and survival.

Other causes of mortality

Starvation was the second highest cause of mortality after predation, although it only accounted for 4% of mortalities. Five young chicks died of starvation and many of the 59 chicks dead from unknown causes could also have died of starvation. Few black-fronted terns that rear their young to fledging succeed in fledging more than one chick from a clutch (Chapter 4). In years of limited food supply chick mortality may be naturally high, particularly among second-hatched chicks.

Rates and causes of mortality for adult and sub-adult black-fronted terns outside of their breeding season are unknown. Adults are probably more vulnerable to predation during the breeding season than at other times of the year, but both adults and sub-adults may be susceptible to injuries from power lines throughout the year. The upper Waitaki Basin is a major hydro-electricity production area and numerous power lines are strung throughout the breeding and feeding areas used by black-fronted terns. Surveys of areas beneath power lines are needed to determine whether power lines are a significant source of mortality for black-fronted terns. Because black-fronted terns are relatively long lived, loss of breeding adults relative to loss of young or eggs is more significant at the population level than for short-lived species. Thus, efforts should be made to identify and reduce causes of adult mortality.

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Chapter 6:

Characteristics of black-fronted tern eggs

Black-fronted tern nest

Abstract

This study provides the first detailed description of the characteristics of black-fronted tern (*Sterna albostriata*) eggs. Egg dimensions and changes in specific gravity of eggs are reported, and the rate and fraction of water loss throughout incubation are calculated. In clutches of two eggs, first laid eggs were significantly larger than second laid eggs. Specific gravity of eggs could not be used to precisely age black-fronted tern eggs. The characteristics of black-fronted tern eggs presented here follow similar patterns to those observed among other larid species elsewhere.

Introduction

Egg measurements are useful for a variety of purposes (as reviewed in O'Malley and Evans 1980) and in particular, the change in specific gravity of eggs throughout incubation has frequently been used to predict laying or hatching dates (Hays and LeCroy 1971, Suddaby and Ratcliffe 1997, Walter and Rusch 1997). The dimensions of black-fronted tern (*Sterna albostriata*) eggs have not been comprehensively reported, nor have changes in black-fronted tern eggs through time been investigated. This basic natural history information is useful for three reasons: i) black-fronted terns are considered globally endangered (BirdLife International 2000) and are probably in decline (Chapter 9), therefore information on incubation of black-fronted tern eggs is required now in case of the future need for intense management; ii) changes in specific gravity of eggs through time may provide a method for ageing black-fronted tern eggs in future studies; and iii) comparisons can be made between black-fronted terns and other related larid species. This study provides data on dimensions of black-fronted tern eggs, examines predicted rates of weight and water loss for black-fronted tern eggs, and examines whether the specific gravity can be used to accurately age black-fronted tern eggs.

Methods

Black-fronted tern eggs were examined as part of a larger study monitoring black-fronted tern breeding success in the lower Ohau River (44°20'S, 170°11'E), South Island, New Zealand, during 2000.

Egg dimensions

I measured the length and breadth of 283 eggs to the nearest 0.1 mm using Vernier calipers and took the mass of 28 freshly-laid eggs to the nearest 0.25 g using 30 g Pesola scales. Egg volume was calculated using the equation $V = K_v.\text{length}.\text{breadth}^2$ where the constant $K_v = 0.507$ (Hoyt 1979). This constant approaches 0.51 for a wide range of species (Hoyt 1979).

Specific gravity and water loss

I measured changes in specific gravity throughout incubation from a sample of 56 eggs from 33 nests to assess whether specific gravity could be used to predict hatching dates of eggs. Eggs were marked with a soft lead pencil on the pointed end and were weighed to the nearest 0.25 g every 2-4 days, but checked daily to determine the date the first star-fracture of the eggshell was evident. Specific gravity of eggs ($g.cm^{-3}$) was calculated as egg weight (g) divided by egg volume (cm^3).

Daily water loss (M_{H_2O}) for each egg was calculated as the difference in egg mass between the first weighing (range = 15-25 days before first star) and the last weighing (range = 2-5 days before first star) divided by the number of days between weighings. Fresh egg mass (W) was used to calculate the predicted mean daily water loss of unpipped eggs ($M_{H_2O} = 0.015W^{0.74}$) and the predicted incubation period (I) ($I = 12.03W^{0.22}$) (Rahn and Ar 1974). The fraction of water loss (F) of unpipped eggs during incubation was calculated as $F = M_{H_2O}.I/W$ (Rahn and Ar 1974). These equations have been applied to a wide range of species, and have changed little with the addition of new data (Ar and Rahn 1980, 1985).

Mean incubation period (24.9 ± 1.8 d) for black-fronted terns was derived from Chapter 4. Unless note otherwise, means are reported ± 1 standard deviation.

Results

Egg dimensions

Mean egg length and width were 40.7 ± 1.4 mm and 29.2 ± 0.8 mm respectively, and mean volume was 17.7 ± 1.3 cm^3 (Table 1). The mass of fresh eggs was 17.8 ± 1.2 g, which was 19.3% of mean adult body mass.

For fifty-three 2-egg nests, the length of first- and second-laid eggs was similar (paired t-test, $t = 0.167$, $P = 0.867$), but first-laid eggs were significantly wider than (t = 5.96, P <0.001) and had a greater volume (t = 3.86, P < 0.001) than second-laid eggs (Table 1). Although first-laid eggs were bigger than second-laid eggs on average, the volume of the second-laid egg was equal to or larger than that of the first-laid egg at 30% of nests.

Table 1: Mean length, width and volume of black-fronted tern eggs (± 1 SE). First- and second-laid eggs were pairs of eggs from the same 2-egg nest; single eggs were from 1-egg nests only.

	n	Length (mm)	Width (mm)	Volume (cm^3)
All eggs	283	40.7 ± 0.1	29.2 ± 0.1	17.6 ± 0.1
First-laid eggs	53	40.7 ± 0.2	29.4 ± 0.1	17.9 ± 0.2
Second-laid eggs	53	40.7 ± 0.2	29.0 ± 0.1	17.4 ± 0.2
Single eggs	21	41.0 ± 0.3	29.1 ± 0.1	17.6 ± 0.2

Specific gravity

The specific gravity of eggs decreased linearly through time (R^2 = 0.77; Figure 1). The density of individual eggs at any given point in the incubation period varied widely and could not be used to predict egg age with any accuracy. For example, using inverse predictions from the linear regression (Zar 1999), eggs with a density of 1.0 $g.cm^{-3}$ had a predicted age of 22.7 ± 14 days (± 95% CI). Eggs with a density of 0.9 $g.cm^{-3}$ had a predicted age of 6.9 ± 14.1 days. Eggs hatched 1-4 days after the first star-fracture of the shell was observed.

The measured rate of daily water loss was 0.113 ± 0.026 $g.day^{-1}$ and the fraction of water loss from laying to first star was 15.9%. These values differed slightly from the predicted values based on the mass of a freshly laid egg (Table 2).

Table 2: Measured and predicted values for daily water loss, incubation period and percent water loss for black-fronted tern eggs. Refer to text for details of equations used to calculate values. Measured values are means ± 1 SD.

Variable	Measured	Predicted
Daily water loss (M_{H_2O})	0.113 ± 0.026 $g.d^{-1}$	0.126 $g.d^{-1}$
Incubation period (I)	24.9 ± 1.8	22.7 d
Fraction of water loss prior to pipping (F)	15.9%	16.1%

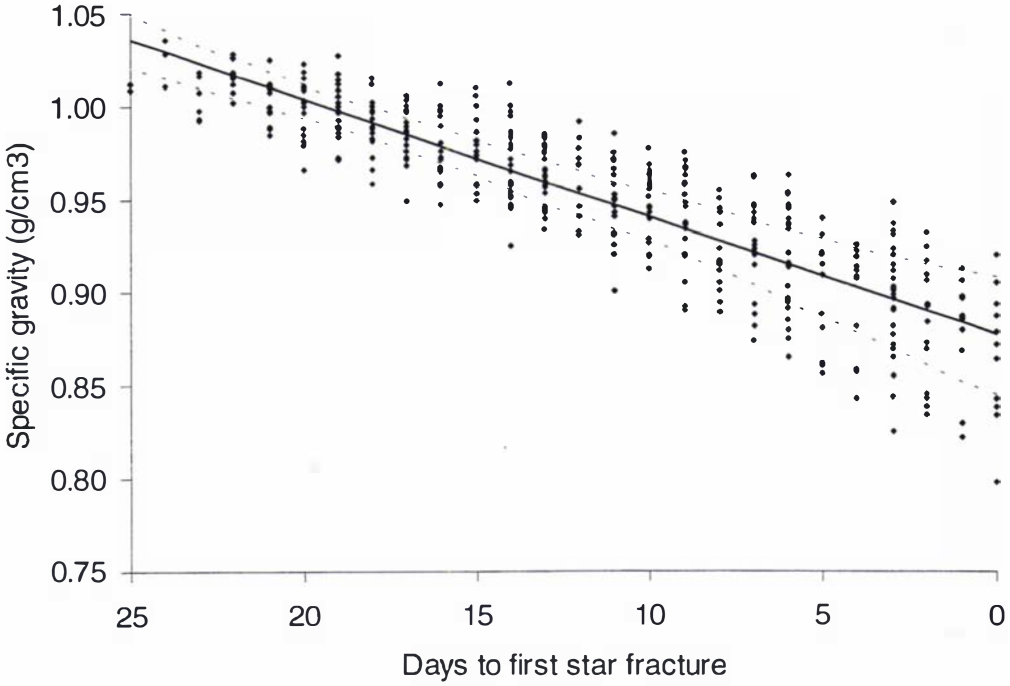

Figure 1: Change in specific gravity throughout incubation for 56 black-fronted tern eggs. Bold line is a linear regression of the mean specific gravity through time ($y=0.0064x+0.8759$). Dotted lines are 95% confidence intervals of the regression line.

Discussion

Changes in specific gravity have been used to predict hatching or laying dates for eggs from a range of species (Dunn et al. 1979, O'Malley and Evans 1980, Furness and Furness 1981). However, variation among individual eggs means the technique can only provide a rough estimate of incubation stage and is more robust when a range of eggs are used to predict the age of a colony of nests that were synchronously laid (O'Malley and Evans 1980, Collins and Gaston 1987). Egg-laying in black-fronted tern colonies is not highly synchronised (Chapter 4) therefore the technique can only be used to predict the age of specific eggs, not the entire colony. Using egg density to age individual black-fronted tern eggs provided no more information than could have been gained by using flotation of the eggs to identify incubation stage. Thus, specific gravity can only identify black-fronted tern eggs in either very early or late stage incubation, but it cannot be used to precisely age black-fronted tern eggs with any accuracy.

Sizes of black-fronted tern eggs are also similar to other larid species in that first-laid eggs were larger than second-laid eggs. Larger eggs often result in increased chick survival (Furness 1983, Quinn and Morris 1986), and although first-hatched chicks in black-fronted terns have higher survival than their sibling (Chapter 7) the exact relationships between egg size, hatching order and chick growth or survival were not tested here.

The fraction of water loss from avian eggs during incubation can range from 10-23% (Ar and Rahn 1980). For the eggs of seven species of terns, the mean fraction of water loss was 14%, and ranged from 12-16% (Rahn et al. 1976), and for 11 gull species ranged from 13-18% (as tabulated in Ar and Rahn 1980). Black-fronted tern eggs, with a water loss constant of 15.9%, closely follow the observed water loss in other larid species.

The observed rate of black-fronted tern egg water-loss was slightly lower than the rate predicted based on fresh egg mass, and the observed incubation period was longer than the predicted period (Rahn and Ar 1974). One possible explanation is that because eggs were measured with an accuracy of only 0.25 g, measurement error may account for any slight differences in observed and predicted values. Alternatively, the predicted value may not be appropriate for black-fronted tern eggs. Shell porosity and thickness were not measured, both of which could cause the rate of water loss or incubation period to differ from that predicted by the equation based on fresh egg mass alone (Martin and Arnold 1991). One further possibility is that many factors other than weight (such as seasonal variation, incubation temperature and predation pressure) can affect the length of the incubation period. The incubation period of black-fronted terns may be longer than expected because the species evolved in the absence of high predation, which would lessen selective pressures towards shorter incubation periods.

The dimensions of black-fronted tern eggs reported in this study provide more comprehensive and precise data than other existing sources (Heather and Robertson 1996, Higgins and Davies 1996). These egg dimension data combined with documentation of changes in black-fronted tern eggs through time provide baseline data that will be useful if intensive management of black-fronted tern eggs is ever required.

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Chapter 7:

Aspects of chick growth and survival in the black-fronted tern (*Sterna albostriata*)

Six-day-old black-fronted tern chick

Abstract

I measured growth and survival of black-fronted tern (*Sterna albostriata*) chicks in 1999 and 2000 on the Ohau River, New Zealand, to determine whether growth rates and hatching asynchrony affect chick survival. Chicks were banded at hatching and monitored every 1-3 days until fledging. In each year, chicks were weighed and had their wing chord measured every 2-6 days. Chicks with higher growth rates had lower mortality rates and tended to fledge at a younger age than chicks with slower growth rates. Chicks from broods of one and first-hatched chicks from broods of two had higher rates of growth and survival than second-hatched chicks. There was some evidence that chick growth was linked to parental quality. The large variation in growth rates among chicks meant weight or wing measures could not be used to age chicks accurately. Age or growth rates alone were not good indicators of fledging success because of high predation rates. This study provides the first assessment of black-fronted tern chick growth and survival and indicates that the effects of growth and hatching asynchrony on survival in black-fronted terns are similar to those observed in other tern species.

Introduction

The black-fronted tern (*Sterna albostriata*) is endemic to New Zealand and has not been widely studied. The species' breeding range has declined since Europeans arrived in New Zealand 200 years ago, and the population is probably still in decline (Chapter 9). Little is known about this species yet there are potential threats to the survival of the New Zealand population. As a result, the national conservation status of black-fronted terns has recently been upgraded to chronically threatened (Hitchmough in press, Molloy et al. in press) and the global conservation status has been raised from threatened to endangered (BirdLife International 2000). Much more research into the natural history and breeding ecology is needed on this species to better understand productivity, survival rates and population trends.

One aspect of the breeding ecology of black-fronted terns that is unknown is the growth and survival rates of chicks. Chick survival in many other terns (*Sterna* spp.) is well documented (Langham 1972, Scolaro et al. 1996, Eyler et al. 1999) and the best methods of monitoring survival in these precocial and often difficult to monitor species are well established (Nisbet et al. 1990). Chick growth rates have also been well studied and can provide valuable information for helping to assess survival rates (Ewins 1985, Nisbet et al. 1999), ageing chicks when their hatch date is unknown (Sanchez-Guzman and Munoz Del Viejo 1998), and assessing the effects of parental quality

(Pugesek 1993, Nisbet et al. 1998). In addition, in tern species that have more than one chick per brood, chick survival is often affected by asynchronous hatching and sibling competition (Bollinger 1994, Eyler et al. 1999, Nisbet et al. 1999). Understanding how growth rates and hatching asynchrony in black-fronted terns affect chick survival, particularly in the current highly modified environment where the primary cause of mortality is predation by introduced mammals (Chapter 5, Sanders and Maloney 2002), will help in assessing how different management techniques can increase chick survival and productivity.

In this study, I measured growth and survival of black-fronted tern chicks to examine whether growth rates are related to survival, and whether growth rates or survival are affected by hatching asynchrony. I also assessed whether initial rates of chick survival can predict eventual fledging success for individuals, and whether black-fronted tern chicks can be accurately aged based on body measurements. Finally, I assessed how growth rates of black-fronted terns compared with growth rates in other terns.

Study area

I studied black-fronted tern chick growth and survival in breeding colonies on the lower Ohau River, South Island, New Zealand (44°20'S, 170°11'E), in 1999 and 2000. The lower Ohau River is a braided riverbed that is approximately 11 km long, with large expanses of sparsely vegetated gravels that are used by black-fronted terns and other bird species for breeding. The riverbed varies in width from 50 m to 300 m. Most of the river water has been diverted to canals for power generation, leaving an average flow of $<5\ m^3.sec^{-1}$. Introduced predators, including cats (*Felis catus*), ferrets (*Mustela furo*), stoats (*M. erminea*), Norway rats (*Rattus norvegicus*) and hedgehogs (*Erinaceus europaeus*), and two native avian predators, southern black-backed gulls (*Larus dominicanus*) and Australasian harriers (*Circus approximans*), are found throughout the braided rivers of the South Island (Heather and Robertson 1996, Keedwell and Brown 2001).

Methods

I monitored chicks at six colonies in 1999 and four colonies in 2000 from early September until January of each season. Colonies ranged in size from 10 to 78 nests. Nests were marked with a small rock cairn 1-3 m away and I visited each colony every

1-3 days to check marked nests and search for new nests. After hatching, I banded each chick at 2 or 3 days of age with a numbered metal band. Because black-fronted tern chicks move throughout the colony and abandon the nest site within a week of hatching, it was not possible to use enclosures to keep chicks at nest sites to facilitate measuring growth and survival. Instead, I searched for chicks in each colony every 1-3 days by walking through the colony and catching any visible chicks, or by sitting back and waiting until chicks called to incoming adult birds carrying food. A trained dog was also used to locate chicks, but use of the dog was confined to areas of the colony where there were few adults incubating eggs so as to avoid any risk of nest desertion.

Hatch date for each chick was assigned to within a day. However, the age of some chicks may have been overestimated by 1 day if the length of time between the last visit before hatching was greater than two days. Day of hatching was designated as day 0.

Chick survival

To determine survival rates, I recorded the band numbers of all chicks captured during each visit. Chicks that survived to fledging were usually captured on every visit, or at least every second visit. Chicks were released within 2 m of where they were caught. I recorded the bands of any dead chicks found, and placed rocks over any unbanded dead chicks to avoid counting them twice. Chick outcomes were classified as: ‘fledged’ – the chick was seen flying or it had a wing length greater than 140 mm when last seen (see below for details); ‘dead’ – the carcass was recovered; or ‘presumed dead’ – the chick was no longer found during regular searches, or all chicks in the colony disappeared after a predation event. For 12 chicks at one colony in 2000, the outcome was recorded as ‘unknown’ because, although the chicks were last seen at up to 15 days of age, the large size of the colony meant I was not confident that I had caught all chicks present. Fledging success was calculated as the percentage of hatched chicks that survived to fledge. Differences in survival rates between years were compared using contingency table analysis.

In both years, a sample of chicks was radio-marked 1-10 days prior to fledging as part of a separate study monitoring post-fledging survival (full details of transmitter attachment are presented in Chapter 8). I used this sample of radio-marked chicks to assess causes of mortality in the period before fledging. I monitored all radio-marked chicks daily either until fledging was confirmed or until the bird was found dead. The criteria for determining whether predation was the cause of mortality for recovered radio-marked chicks are presented in Chapter 5. Differences in the proportion of chicks that died from predation in each year were compared using contingency table analysis.

Chick growth

I examined the growth rates of chicks from hatching until fledging at five colonies in 1999 and three colonies in 2000. At the remaining two colonies, I took growth measurements from only radio-marked chicks from the time of transmitter attachment until fledging. For each chick, I measured its mass and wing length every time it was captured. All chicks were weighed using Pesola spring balances. Small chicks were weighed on a 30 g balance, larger chicks on 100 g or 200 g balances. Chicks were weighed to the nearest 0.25 g when less than 30 g, to the nearest 0.5 g for chicks less than 80 g and to the nearest 1 g for chicks over 80 g. Balances were calibrated at least once per season and were tared at regular intervals. Once the primaries emerged, I measured the wing length from the bend of the wing to the tip of the longest primary using a stopped rule.

Too few chicks were found on a daily basis to construct complete growth curves for each chick. Instead, a linear growth rate was calculated for each chick by fitting a regression line to the mass data collected during the quasi-linear period of growth (Nisbet et al. 1995). The period of linear growth of chick mass (LGR) was for days 1-13, but the linear growth rate was calculated only for those chicks with at least four data points within this period, and where the regression equation had an R^2 greater than 0.9. The growth rate of the wing chord was linear throughout the monitoring period. Thus, I calculated the wing growth rate for all chicks that had three or more wing measurements taken and where the regression equation had an R^2 greater than 0.9. I also calculated the asymptotic mass (AM) (Nisbet et al. 1995), which is the mean of all masses taken during the period of near-constant mass (days 18-30). Only those chicks with two or more data points within the specified period were included. I also calculated the mass of chicks at day 5 (mass_5), which was either the actual measurement (if the chick was measured on day 5) or extrapolated from the linear regression equation calculated from the period of quasi-linear growth. Age at fledging was recorded as either the first day a radio-marked bird was seen to fly, or the regression equation of wing growth was used to determine chick age once its wing length reached 155 mm (the shortest wing length at which fledging was observed).

I used analysis of variance (ANOVA) to test whether each growth parameter was affected by year and/or fate. Each parameter was analysed separately. Where an ANOVA showed significant effects, Tukey's T-test was used to assess the statistical significance of differences among categories. Residuals were checked for normality, and Levene's test was used to check variances for homogeneity.

I used forward stepwise multiple linear regression to examine the dependence of fledging age on wing growth rate, $mass_5$, and asymptotic mass for those birds that reached fledging.

I calculated the proportion of chicks that reached 5, 10, 15 and 20 days that subsequently survived to fledging in each year, and used this to assess whether chick survival to a certain age gave an accurate estimate of fledging success. I used logistic regression to examine whether combining growth rates with survival to a given age could give a more accurate estimate of the subsequent probability of fledging. I constructed separate logistic regression models for chicks that reached 5, 10 and 15 days using predictor variables $mass_5$, LGR and wing growth individually, as well as for LGR and wing growth combined. I used the best fitting model to determine probabilities of fledging for chicks that reached a given age with a given growth rate. Data from both years were pooled after initial analyses indicated models fitted better with years pooled rather than separated.

Growth and survival rates were not examined by individual colony because colony sizes and locations changed each year, and because of the small sample size of some colonies.

Predicting age from growth data

I examined growth curves of known age chicks to assess whether wing length or body mass could be used to accurately age chicks. Mass growth curves proved too erratic to use, but wing length growth curves were approximately linear over the range of the data, with little variation around a fitted straight line. Using wing length data from 92 chicks whose ages were known exactly, I fitted a model using Markov Chain Monte Carlo (MCMC) techniques (Gelfland et al. 1990), using the package BUGS (Gilks et al. 1995). From the model, I attempted to estimate ages of chicks with wing lengths that varied from 40 to 140 mm.

Effects of hatch order

Where known, each chick was classified at hatching into one of four hatch order categories: A_1 – chick from a single egg clutch or from a 2-egg clutch where one egg failed to hatch, A_2 – first hatched chick from a clutch of two eggs, B – second hatched chick from a clutch of two or three eggs. Only four broods of three chicks were found, but because all the third hatched chicks died within 2 days of hatching they were excluded from further analyses. For broods of two chicks, I marked the first hatched chick with ink on the white down of its belly to ensure the chicks were distinguishable until they were old enough to be metal banded. The hatching interval between two eggs ranges from 4-48 hours (Chapter 4) but the exact interval for each brood in this study was not determined.

I used Kaplan-Meier survival analysis to examine the survival rates of A- and B-chicks. Chicks that were found dead were assumed to have died at the midpoint between visits. Chicks that disappeared and were presumed dead were assumed to have died the day after the last visit during which they were seen alive. Chicks that disappeared after day 15, and the fate of which I was uncertain, were censored from the model on the last day they were seen alive. Differences in survival rates between A- and B-chicks in each year were tested using a log-rank test. A_1 and A_2 chicks were combined into a single category because there were too few A_1 chicks to analyse separately, and the proportions of A_1 and A_2 chicks that survived to fledge in each year were similar.

I used ANOVA to examine the relationship of each growth parameter with year and hatch order (where A_1 and A_2 chicks were combined into a single category). Pearson product-moment correlations were used to assess correlations of each growth parameter between A and B chicks in the same brood.

Slow-growing chicks

In 1999 and 2000, a number of chicks appeared to have markedly slower growth than average. These chicks either put on weight very slowly or were much smaller in appearance than other chicks the same age, and they took longer to fledge. To investigate whether slow-growing chicks were predominantly disadvantaged B-chicks or whether there was evidence that some pairs were poor quality parents and both chicks in one brood were slow-growers, I used the growth parameters to identify which chicks were slow-growers. I identified the median value for three growth rate parameters

(LGR, AM and wing growth). Any chick that ranked below the median value for at least two of the three parameters was classified as a slow-grower. An additional seven chicks where data were only available for one growth parameter, but the chicks fell in the bottom 10% of values for this parameter, were also classified as slow growers.

To assess whether slow-growing chicks tended to occur within the same brood, indicating differences in parental qualities, I used chi-square analysis to compare the observed distribution of growth patterns among pairs of chicks with the expected distribution. For all pairs of chicks where I had some growth data, I identified how many A_2- and B-chicks had normal growth, slow growth or died before adequate growth data could be gathered, and constructed the observed and expected distributions.

Statistical analyses were performed using STATISTICA (StatSoft 1998) software. Unless otherwise noted, means are presented ± 1 SD.

Results

Mean chick weight at hatching was 12.7 ± 1.8 g (n = 43) and at fledging was 81.5 ± 12.7 g (n = 68). Fledging age ranged from 20-34 days with a mean of 27.7 ± 3.2 days (n = 75), excluding one chick with deformed wings that did not fledge until 40 days. Chicks fledged when their wings reached 65 % of adult wing length on average. Mean length at fledging was 163.4 ± 7.3 mm (n = 69).

Survival rates

I monitored the survival of 192 chicks in 1999 and 232 chicks in 2000. Fledging success in 2000 (32%, unknown outcomes excluded) was higher than in 1999 (11%; $\chi^2 = 25.69$, $P < 0.0001$, df = 1). Predation was the major cause of mortality of radio-marked chicks; 17 of 18 radio-marked chick mortalities were attributable to predation. Significantly fewer radio marked birds died from predation in 2000 (10.8%, n = 37) than in 1999 (41.9%, n = 31; $\chi^2 = 7.13$, $P = 0.008$, df = 1).

Chick growth

I gathered growth mass data from 246 chicks, with an average of 6 (± 4) measurements per chick and 6 (± 3) wing measurements from 151 chicks (Figure 1). Chicks that survived had significantly higher values for all four growth parameters than chicks that died (Table 1). Year had no effect except that chicks had a lower AM in 2000 than in 1999 ($F_{1,86} = 8.423$, $P = 0.005$).

The fledging age of chicks in 2000 (28.0 ± 3.5 days) was not significantly different from fledging age in 1999 (26.8 ± 2.3 days; Mann Whitney z = 1.026, P = 0.309). A multiple regression of fledging age by wing growth, AM and mass_5 showed that chicks with a higher mass_5 and faster wing growth tended to fledge earlier but AM had no effect ($R^2 = 0.593$, $P < 0.0001$).

The proportions of chicks surviving through to 5, 10, 15, or 20 days were not good predictors of the proportions of chicks surviving to fledging, particularly in the high predation year of 1999 (Table 2). However, linear growth rate combined with survival to 15 days of age could predict subsequent survival to fledging ($\chi^2 = 18.51$, $P <$ 0.0001, df = 1; Table 3).

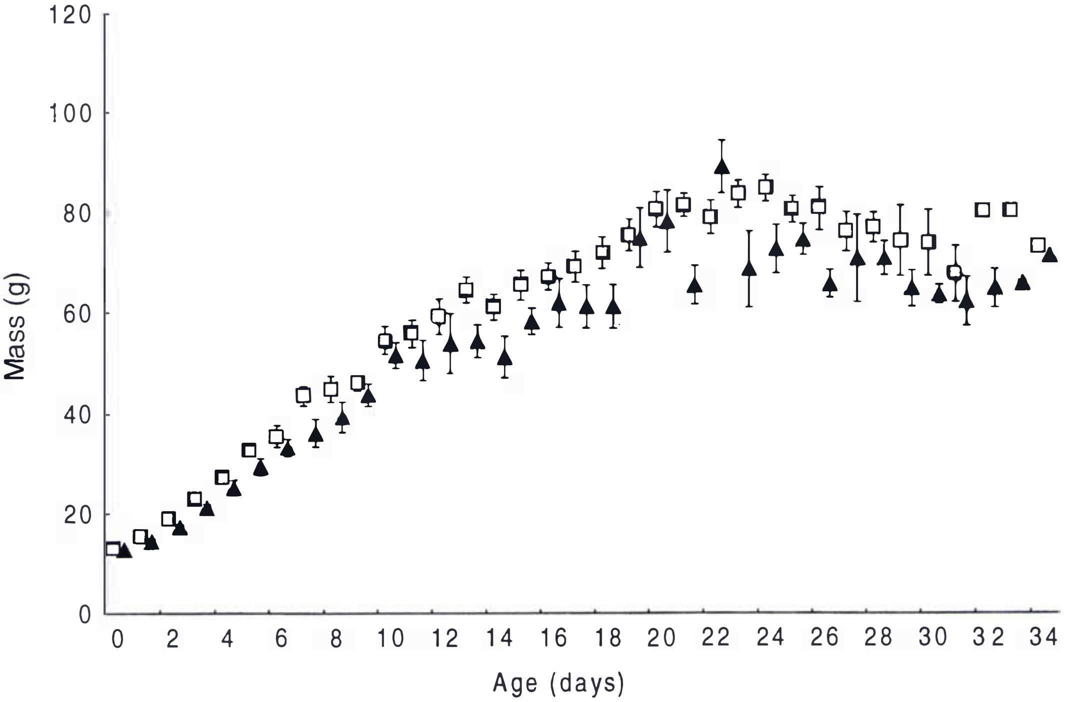
Table 1: Mean growth parameters of black-fronted tern chicks that survived through to fledging and those that died before fledging, in 1999 and 2000. Values tabulated are mean ± SD (sample size). Significant effects on fate of growth parameters are marked on the bottom row (see text for test details).

Year	Fate	Linear growth rate (g/day)	Mass_5 (g)	Wing growth (mm/day)	Asymptotic mass (g)
1999	Dead	3.72 ± 0.91 (29)	30.1 ± 6.3 (47)	5.36 ± 1.39 (28)	73.1 ± 14.0 (16)
	Fledge	4.68 ± 1.05 (9)	34.8 ± 6.7 (13)	6.93 ± 0.38 (17)	87.4 ± 7.5 (18)
2000	Dead	3.04 ± 1.08 (8)	28.2 ± 5.0 (30)	5.29 ± 1.34 (15)	59.5 ± 23.6 (6)
	Fledge	4.62 ± 0.97 (11)	33.3 ± 4.9 (34)	6.27 ± 1.14 (52)	79.3 ± 13.6 (50)
Over-all	Dead	3.57 ± 0.97 (37)	29.4 ± 5.9 (77)	5.34 ± 1.36 (43)	69.4 ± 17.7 (22)
	Fledge	4.65 ± 0.98 (20)	33.7 ± 5.4 (47)	6.44 ± 1.04 (69)	81.5 ± 12.7 (68)
		$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$

Table 2: Proportion of black-fronted tern chicks reaching different ages that subsequently survived through to fledging in 1999 and 2000. '# alive' is the number of chicks known to be alive at a given age, '% fledge' is the percentage of these chicks alive that survived through to fledging.

Age (d)	1999		2000	
	# alive	% fledge	# alive	% fledge
5	99	21	116	61
10	69	30	102	70
15	49	43	90	79
20	39	54	79	90

A



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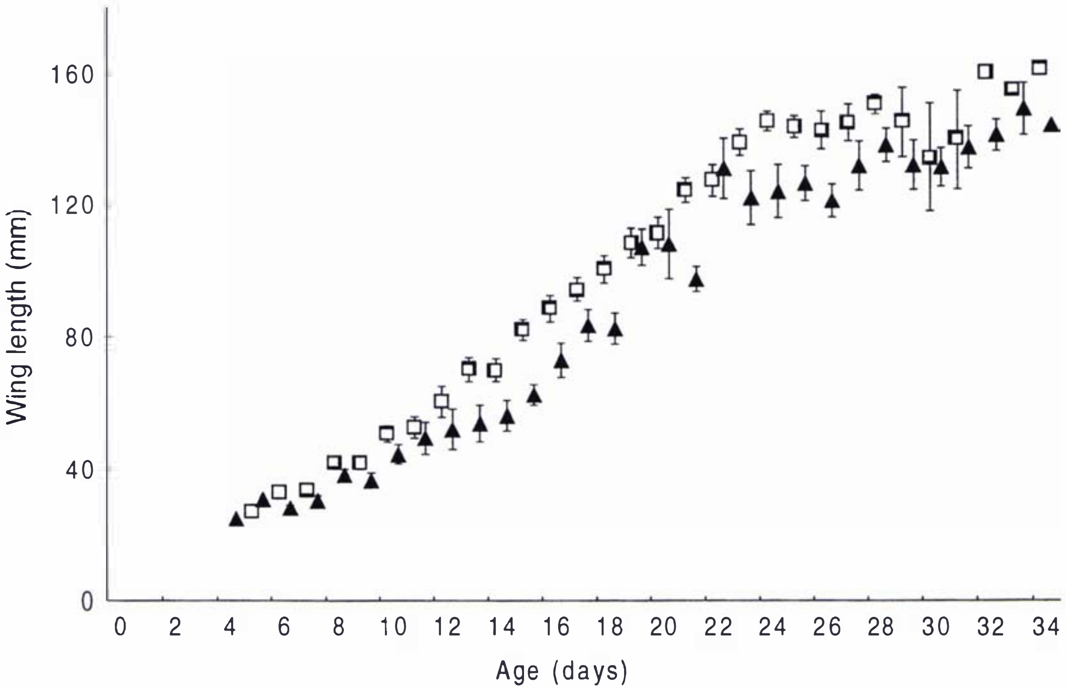

Figure 1: Composite growth data for black-fronted tern chicks. (A) mass of chicks by age for A-chicks (n = 132; squares) and B-chicks (n = 80; triangles); and (B) wing chord length by age for A-chicks (n = 84; squares) and B-chicks (n = 44; triangles). Data presented are mean ± 1 standard error, both years are pooled.

Table 3: Minimum linear growth rate (LGR) for different fledging probabilities, for black-fronted tern chicks that survive to at least 15 days. Probabilities based on the logistic regression equation: -6.9926 + 1.7809(LGR) = log(P/(1-P)), where *P* is the probability of surviving to fledging.

Probability of surviving to fledging	Minimum LGR (g/day)
0.5	3.93
0.6	4.03
0.7	4.13
0.8	4.26
0.9	4.46

Predicting age of unknown chicks

Black-fronted tern chick age could be approximately estimated with the equation $x = 0.165Y + 2.25$; where x is chick age in days, and Y is wing length in mm. However, there was considerable variation in growth rates between chicks, which made it impossible to accurately estimate chick age from only one measurement of wing length (Table 4).

A- and B-chicks

Hatch order was determined for 83% of chicks. Within each year, survival rates of A_1- and A_2-chicks were similar, and were higher than that of B-chicks (Table 5). Although survival differed between years, A-chick survival was consistently higher than B-chick survival and the difference appeared to establish from day 5 onwards (Figure 2; 1999: log-rank statistic = -2.481, $P = 0.013$, 2000: log-rank statistic = -2.124, $P = 0.034$).

All four growth parameters were higher for A-chicks than B-chicks (Table 6) and this did not vary between years, except that B-chicks had a lighter asymptotic mass than A-chicks in 2000 but not 1999 ($F_{1,70} = 5.036$, $P = 0.028$). A-chicks fledged at a significantly lower age than B-chicks (Table 6; Mann Whitney $z = 2.558$, $P = 0.011$). Among 47 pairs of chicks from the same brood, A_2- and B-chick parameters were correlated for 5-day mass ($r_{34} = 0.55$, $P < 0.001$), and for asymptotic mass ($r_{16} = 0.66$, $P = 0.003$), but there was no correlation for LGR ($r_6 = 0.62$, $P = 0.10$) or for wing growth rate ($r_{22} = 0.25$, $P = 0.244$).

Table 4: Estimates of black-fronted tern chick age based on measurements of wing length.

Wing length (mm)	Estimated age (days)	95% confidence interval
40	9.2	(4.9, 15.1)
60	12.9	(8.2, 20.1)
80	16.6	(11.3, 25.6)
100	20.3	(14.0, 31.5)
120	23.7	(22.9, 36.8)
140	27.3	(26.3, 41.7)

Table 5: Percentage of chicks surviving through to fledging in each year, grouped by hatch order. 95% binomial confidence intervals are given in parentheses.

Hatch order	1999		2000	
	%	n	%	n
A$_1$	15	26	37	30
	(4-35)		(20-56)	
A$_2$	18	74	37	68
	(10-28)		(25-49)	
B	4	74	19	67
	(1-11)		(11-31)	

Table 6: Mean growth parameters and fledging age of black-fronted tern A- and B-chicks in 1999 and 2000. Values tabulated are mean ± SD (sample size). Significant effects of hatch order on growth parameters and fledging age are marked on bottom row (see text for test details).

Year	Chick	Linear growth rate (g/day)	Mass$_5$ (g)	Wing growth (mm/day)	Asymptotic mass (g)	Fledge age (days)
1999	A	4.06 ± 0.97 (28)	31.9 ± 7.2 (35)	6.04 ± 1.32 (29)	80.4 ± 13.7 (24)	26.7 ± 2.2 (16)
	B	3.31 ± 1.02 (8)	29.5 ± 5.9 (22)	5.76 ± 1.47 (15)	80.3 ± 12.4 (9)	25.7 ± 2.1 (3)
2000	A	4.44 ± 1.21 (13)	32.5 ± 6.1 (33)	6.28 ± 1.25 (37)	82.9 ± 15.5 (28)	26.5 ± 2.6 (35)
	B	2.7 ± 0.29 (3)	28.7 ± 4.5 (15)	5.14 ± 1.18 (13)	66.1 ± 14.5 (13)	30.4 ± 3.2 (11)
Over-all	A	4.18 ± 1.05 (41)	32.2 ± 6.6 (68)	6.17 ± 1.28 (66)	81.7 ± 14.6 (52)	26.5 ± 2.5 (51)
	B	3.15 ± 0.91 (11)	29.1 ± 5.4 (37)	5.47 ± 1.36 (28)	71.9 ± 15.1 (22)	29.4 ± 3.5 (14)
		$P < 0.01$	$P < 0.05$	$P < 0.01$	$P < 0.05$	$P < 0.05$

Slow-growing chicks

Fifty chicks were classified as slow-growers, of which 44 were from 2-chick broods, two were from single chick broods and four were from separate two chick broods but of unknown hatch order. Of the 44 slow-growing chicks that were from 2-chick broods and whose hatch order was known, 73% were either from the same clutch where both chicks were slow-growers (n = 28) or were A_2-chicks where the B-chick died early before adequate growth data could be collected (n = 4). The remaining 12 chicks were either slow-growing B-chicks whose older sibling had normal growth rates (n = 9) or slow-growing A_2-chicks whose younger siblings had normal growth (n = 3). Only one (6%) of the 18 slow-growing chicks from 1999 survived through to fledging, but 63% of 32 slow-growing chicks from 2000 fledged successfully. The higher proportion of slow-growing chicks fledging in 2000 contributed to the lower asymptotic mass in 2000.

Examination of the observed versus expected distribution of growth patterns within 73 pairs, showed that chicks with similar growth patterns tended to occur within pairs, and slow-growing chicks tended to be B-chicks rather than A_2-chicks (Table 7; $\chi^2 = 22.86$, $P < 0.001$, df = 4).

Table 7: *Observed* and **expected** frequencies of growth patterns within 76 pairs of black-fronted tern chicks. Growth of A_2- and B-chicks within each pair are classified as 'normal' – growth rate normal, 'slow' – chicks identified as slow-growing (see methods), or 'dead' – chick died before adequate growth data could be gathered.

			B-chick	
		Normal	Slow	Dead
	Normal	*13* **9**	*14* **15**	*20* **23**
A2-chick	Slow	*0* **3**	*11* **6**	*6* **8**
	Dead	*1* **2**	*0* **4**	*11* **6**

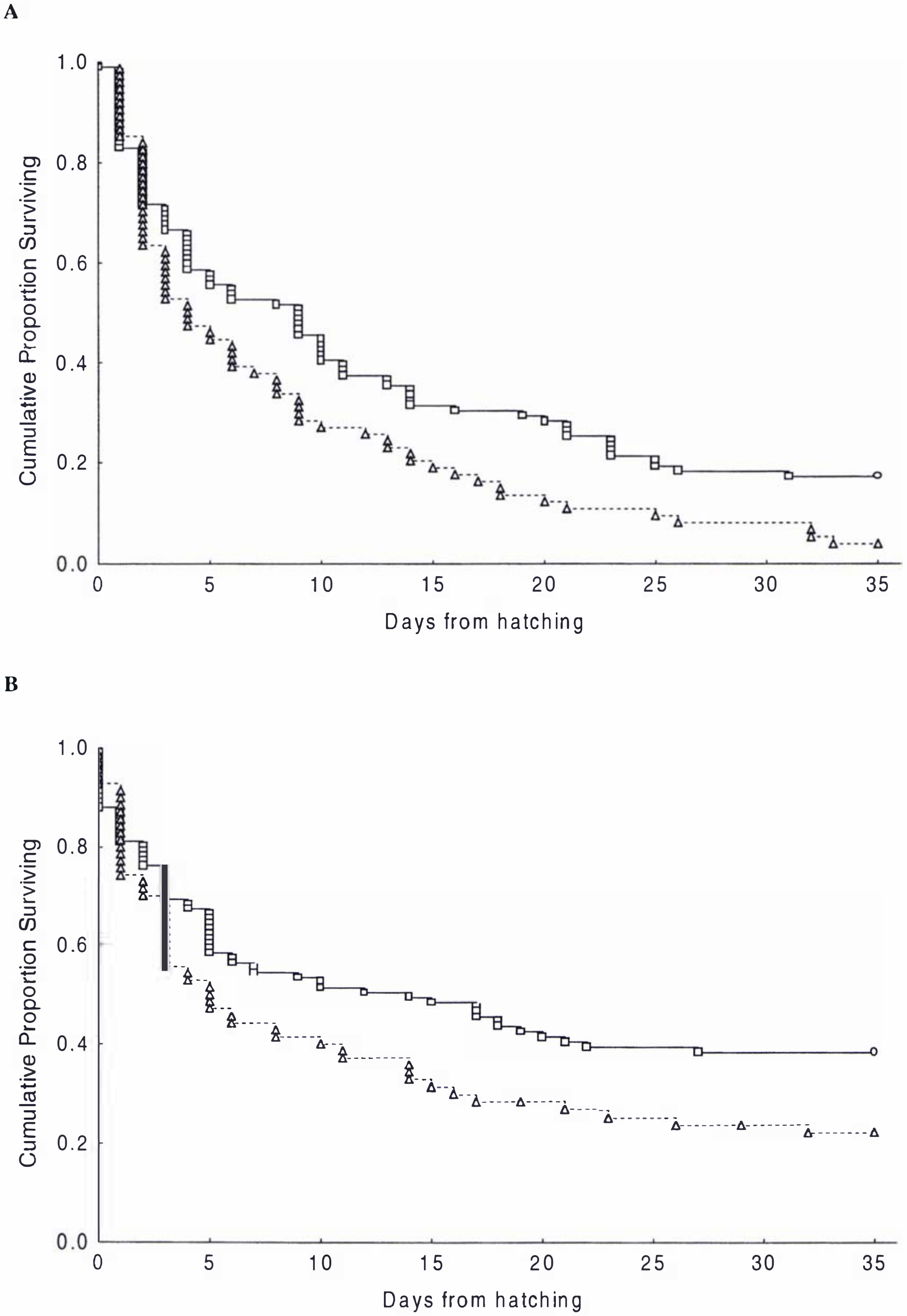

Figure 2: Kaplan-Meier survival curves for black-fronted tern A-chicks (solid line) and B-chicks (dotted line) in 1999 (A) and 2000 (B).

Discussion

Hatching asynchrony in black-fronted terns leads to a distinct survival advantage of A_2-chicks over B-chicks from hatching to fledging. Numerous studies have documented hatching asynchrony in terns and other larid species (Bradbury and Griffiths 1999, Royle 2000) and the adaptive or functional significance of incubation before clutch completion that leads to hatching asynchrony and the subsequent survival advantage of first-hatched chicks have been tested experimentally (Bollinger et al. 1990). For some species, hatching asynchrony does not maximize clutch survival, even in years of low food abundance, and the effects of asynchrony may be a trade-off against early incubation to increase protection of eggs immediately after laying (Bollinger et al. 1990). For black-fronted terns, the onset of incubation prior to clutch completion fits the 'egg protection hypothesis' (Parsons 1976) where incubation may lessen the chances of predation. In addition, earlier incubation reduces the overall time an egg and subsequently the chick is vulnerable to predation. Black-fronted terns evolved in an environment with only avian predators, and incubating the eggs as early as possible would have provided a degree of protection from predation. However, in the current environment where introduced, primarily nocturnal, mammalian predators are the major cause of egg mortality (Sanders and Maloney 2002), early incubation provides no additional protection and the resulting hatching asynchrony appears to lower reproductive output in black-fronted terns.

Second-hatched black-fronted tern chicks do not appear to act as 'insurance' (Graves et al. 1984) against loss of an older sibling. Only on one occasion did a B-chick survive through to fledging after the death of the A_2-chick. The overall difference in survival between A- and B-chicks appeared to establish by five days after hatching, where a greater proportion of B-chicks die in the first five days than A-chicks. This pattern of increased survival in A-chicks over later hatched chicks is well documented in other terns (Langham 1972, Nisbet et al. 1995, Eyler et al. 1999) and high rates of early mortality in both A- and B-chicks are also common (LeCroy and Collins 1972, Ewins 1985, Bollinger et al. 1990). Although I collected few data on the first five days of growth, B-chicks are likely to be more vulnerable in the early post-hatching stage because the growth data presented here show that B-chicks were generally smaller and had slower growth rates. Black-fronted terns also tended to lay larger A-eggs than B-eggs (Chapter 6), suggesting that the survival advantage of A_2-chicks is established prior to hatching (Bolton 1991).

Over 15% of black-fronted tern nesting attempts have only one egg, yet from this study chicks from a single-egg clutch do not have any advantage over chicks from larger broods. Because B-chicks do not appear to operate merely as insurance against loss of the older sibling, pairs that lay two eggs have a higher chance of producing more young. Moreover, given that 4% of eggs either fail to hatch, or have hatching problems (Chapter 4), pairs with two eggs do have an insurance policy at the egg stage. Black-fronted terns that lay three eggs would similarly have an advantage. However, because none of the four 3-egg clutches had C-chicks that survived past two days, the extra investment required to produce a third egg is highly unlikely to result in increased productivity.

Age and experience of breeding terns can significantly influence breeding success, with older or more experienced breeders producing larger clutches, bigger eggs and bigger chicks, and better provisioning their chicks (Pugesek 1993, Bollinger 1994, Nisbet et al. 1998). Because black-fronted terns have not been intensively studied, few of the adults in this study were banded and the history of the breeding pairs, such as age and experience, was unknown. The presence of a number of slow growing chicks in each year, most of which were from 2-chick broods where both chicks were poor quality, suggests that there may be some effect of parental quality influencing the survival of chicks in black-fronted terns. These slower-growing chicks also had less chance of reaching fledging than better quality chicks when predation pressure was high. Exactly why the poorer quality chicks were more susceptible to predators was not clear. It is possible that slow-growing chicks were going to die anyway and were subsequently eaten by predators or were easier targets than bigger, faster-growing chicks. Alternatively, it may have been that simply because chicks with lower growth rates took longer to fledge, and were therefore at risk to predators for a longer period.

In the absence of high predation rates, the growth and survival of black-fronted tern chicks may well be determined primarily by parental quality, as has been demonstrated for roseate terns (*Sterna dougallii*, Nisbet et al. 1998). However, the impact of predation on black-fronted tern chick survival obscures what the natural rates of mortality would have been at different ages. As a result, to accurately monitor black-fronted tern chick survival, chicks need to be monitored through to fledging rather than to a given age such as five or 10 days, as with other tern species (Bollinger 1994, Nisbet et al. 1999). Even using growth rates to help predict which chicks had a greater chance of survival, black-fronted tern chicks would still need to be monitored through to at least 15 days to get an accurate estimate of fledging rates.

Because black-fronted terns evolved in a largely predator free environment, the growth rates of chicks may be different to those of terns that evolved with higher levels of predation. A comparison with the growth rates of other tern species (Table 8) indicates that for its size, black-fronted terns do have comparatively slow growth rates. The black-fronted tern has a lower rate of mass and wing growth than other terns of a similar size, with the occasional exception of more tropical species such as the bridled (*Sterna anaethetus*) and black-naped (*S. sumatrana*) terns. Given such slow growth rates, black-fronted terns are poorly equipped to deal with the current environment of high predation.

This study was carried out over only two years but the survival rates of chicks differed significantly between years. There was no difference in growth rates between years, which suggests that food was not a factor limiting survival in 1999 compared with 2000. The lower proportion of radio-marked birds that died from predation in 2000 instead provides evidence that a change in predation pressure was responsible for the altered survival rates. One possible explanation for greater chick survival in 2000 than 1999 may be that cat numbers declined. Cats are the major predator of black-fronted tern eggs, chicks, juveniles and breeding adults (Chapter 5). In 2000, cats were not responsible for any videoed nest predation events (Chapters 1 and 4) whereas cats were the primary predator recorded at 60 predation events in the previous six years of video records (Sanders and Maloney 2002). The relationships between rabbit abundance, the abundance of different predator species and predator impacts on braided river birds are not well understood. Clearly, further research into predator guilds on the braided rivers is needed to fully explain why variations in predation occur for black-fronted terns and what the implications are for managing the species.

Despite this difference in predation pressure between years, the survival rates of A- and B-chicks differed by a similar amount in both years. Thus, although predation is probably the primary cause of mortality for black-fronted tern chicks older than one week (Chapter 5), it is unlikely that the difference in survival is a result of different predation rates on A and B chicks.

Table 8: Mass and wing growth in tern (*Sterna* spp. and *Chlidonias* spp.) chicks. Data were collected from all published accounts of chick growth. Where more than one datum was available for a growth rate, the mean of all available data was used. Because not all studies reported all growth parameters, there may be discrepancies between growth measurements within species due to results from different locations and different years. Linear growth rate (LGR) is the daily increase in mass during the linear phase of growth; adj. LGR = LGR/adult mass*100; adj. wing = wing growth/adult wing*100; *K* is the growth constant from the logistic equation (see Ricklefs 1967); t_{90} is the time taken to reach 90% of the asymptotic mass (AM).

Species*	**Adult mass (g)**	**Adult wing (mm)**	**Fledge age (d)**	**LGR (g/day)**	**Adj. LGR**	**Wing growth (mm/day)**	**Adj. wing**	***K***	t_{90} **(d)**	**AM (g)**
Least	45		20					0.290	14	39
Black	63		25	5.7	9			0.365	12	
Black-fronted	92	251	23-29	3.9	4.2	6.0	2.4	0.231	16	81
Arctic	109	275	22	6.9	6.3	7.9	2.9	0.287	15	115
Black-naped	110	225	24	4.2	3.8	6.7	3.0	0.288	15	100
Roseate	115	232	22	6.0	5.2	5.9	2.5	0.247	17	102
Common	123	263	23	7.0	5.7	7.0	2.7	0.268	16	113
Forster's	123		24	8.1	6.6			0.280	16	129
Bridled	130	268	55-63	3.1	2.4	4.8	1.8	0.114	37	125
Antarctic	150		27	7.2	4.8			0.216	19	133
Gull-billed	170	333	28-30	7.1	4.2	7.8	2.3			
South American	194		27					0.234	18	181
Sandwich	235		26	9.8	4.2			0.250	20	204
Crested	350	340	35-41	6.9	2.0	5.1	1.5	0.106	37	284
Caspian	672	414	35	27.1	4	8.3	2.0	0.200	22	566

*Sources of data on each species: least (*Sterna antillarum*) – Schew et al. 1994; black (*Chlidonias niger*) – Dunn 1979; black-fronted (*S. albostriata*) – this study, logistic growth calculated from complete growth curves of 37 chicks; Arctic (*S. paradisaea*) – Pearson 1968, Ricklefs 1973, Coulson and Horobin 1976, Langham 1983, Ewins 1985, Klaassen 1994, Suddaby and Ratcliffe 1997, Robinson et al. 2002; black-naped (*S. sumatrana*) – Langham 1983, Hulsman and Smith 1988; roseate (*S. dougallii*) – LeCroy and Collins 1972, Ricklefs 1973, Langham 1983, Schew et al. 1994; common (*S. hirundo*) – Pearson 1968, LeCroy and Collins 1972, Ricklefs 1973, LeCroy and LeCroy 1974, Langham 1983, Klaassen 1994, Nisbet et al. 1995, Robinson et al. 2002; Forster's (*S. forsterii*) – Schew et al. 1994; bridled (*S. anaethetus*) – Langham 1983, Hulsman and Langham 1985, Garavanta and Wooller 2000; Antarctic (*S. vittata*) – Klaassen 1994, Higgins and Davies 1996; gull-billed (*S. nilotica*) – Erwin et al. 1999; South American (*S. hirundinacea*) – Scolaro et al. 1996; sandwich (*S. sandvicensis*) – Pearson 1968, Ricklefs 1973, Langham 1983, Klaassen 1994; crested (*S. bergii*) – Langham 1983, Langham and Hulsman 1986; and Caspian (*S. caspia*) – Dunn 1979, Schew et al. 1994.

Predator control cannot eliminate all chick mortality, because many deaths of younger chicks are probably not predator-related. Food availability and rates of feeding were not measured in this study, and both 1999 and 2000 may have had low food availability that resulted in the many slow-growing chicks in each year. Further studies of chick growth both on the Ohau River where water flows are controlled, and on other uncontrolled rivers where black-fronted terns breed are necessary to determine whether food supplies are playing a role in population decline. Even if food supply does influence survival, if predator control can simulate the difference in chick survival between 1999 and 2000 where survival rates almost tripled, then managing predation will probably be the most effective action in mitigating population decline in the species.

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Chapter 8:

Does fledging equal success? Post-fledging mortality in the black-fronted tern

Banding a black-fronted tern chick close to fledging. Photo: Mark Sanders

Abstract

Fledging success is widely used as an index of reproductive success in avian studies, but survival of young after fledging is not widely studied. In this study, I used radio-telemetry to measure rates and causes of mortality of 63 black-fronted terns (*Sterna albostriata*) in the immediate post-fledging period on the lower Ohau River, South Island, New Zealand in 1998-2000. Juvenile survival (± 95% CI) through the first four weeks after fledging was 0.795 ± 0.108. Mean daily survival increased from 0.972 ± 0.010 in the first week after fledging, to 0.995 ± 0.005 in the second week and 1.00 for the third and fourth weeks. Introduced predators such as feral cats (*Felis catus*) and Norway rats (*Rattus norvegicus*) were responsible for a minimum of 9 out of 12 deaths and all except one death occurred at the natal colony prior to dispersal. Larger, heavier juveniles that fledged at a younger age tended to have higher survival post-fledging but survival could not be accurately predicted based on measurements of growth. These results indicate that the post-fledging period can be an important source of mortality in young birds, and that survival until dispersal from the natal colony is the best measure of black-fronted tern reproductive success currently available.

Introduction

Fledging success is widely used as an index of reproductive success in avian studies (Van Riper 1995, LaHaye et al. 1997, Poulsen et al. 1998, Magrath 1999, Weatherhead and Dufour 2000). Measuring chick survival through to fledging is relatively simple in most species and is commonly used, but measuring survival from fledging through to breeding age is more difficult and usually relies on banding studies. Banding studies can provide measures of survival over the period between fledging and breeding but cannot give detail on changes of mortality rates throughout that period. Mortality rates of eggs and chicks of some species of terns are high (Langham and Hulsman 1986, Scolaro et al. 1996, Quintana and Yorio 1997, Eyler et al. 1999), and assessing whether mortality rates remain high after fledging may provide important information for management of threatened or endangered species. In addition, if immediate post-fledging survival is low, estimates of the number of young fledged per pair typically reported in reproductive studies are poor estimates of reproductive success.

In some species, banding records cannot be used to measure post-fledging survival and recruitment because few individuals are banded or the population has not been intensively studied. This is the case for an endemic New Zealand species, the black-fronted tern (*Sterna albostriata*). Black-fronted terns are considered globally endangered (BirdLife International 2000) and the population is probably in decline (Chapter 9). Population decline is primarily due to predation by introduced mammals (Chapter 5, Higgins and Davies 1996, Sanders and Maloney 2002). To accurately model the black-fronted tern population and determine appropriate management strategies, it is necessary to improve estimates of post-fledging survival and to assess causes of mortality.

Post-fledging survival in some species is positively correlated with chick mass and age at fledging or with chick growth rates (Hedgren 1981, Sagar and Horning 1990, Gaston 1997) but this relationship does not hold true for all species (as reviewed in Magrath 1991). If aspects of black-fronted tern chick growth prior to fledging are correlated with post-fledging survival, then measuring chick growth may provide one method of estimating post-fledging survival. In this study, I attached radio transmitters to black-fronted tern juveniles to: 1) determine survival rates of newly fledged young; 2) assess whether predation remains the main cause of mortality after fledging; and 3) examine whether post-fledging survival is correlated with body size prior to fledging and age at fledging.

Study area

I studied black-fronted tern survival on the Ohau River, South Island, New Zealand (44°20'S, 170°11'E) from October to January, 1998-2000. The Ohau River is a braided riverbed with large expanses of sparsely vegetated gravels. It varies in width from 50 to 300 m. Most of the river water has been diverted to hydroelectric canals for power generation, leaving an average flow of <5 m^3sec^{-1}. Introduced predators, including cats (*Felis catus*), ferrets (*Mustela furo*), stoats (*M. erminea*), Norway rats (*Rattus norvegicus*) and Australian magpies (*Gymnorhina tibicen*), and two native avian predators, black-backed gulls (*Larus dominicanus*) and Australasian harriers (*Circus approximans*), are found throughout the braided rivers (Heather and Robertson 1996, Keedwell and Brown 2001).

Methods

I caught 63 tern chicks 1-10 days prior to fledging and fitted them with single-stage transmitters, which weighed 1.3 g, had a 12.5 cm whip antenna and a battery life of up to nine weeks (HOLOHIL Systems Ltd., Canada). I attached a piece of chiffon that was slightly larger in area than the transmitter to the bottom of each transmitter with cyanoacrylate glue. The transmitter and chiffon package were glued to a patch of skin between the scapulars trimmed clean of down and feathers. I attached transmitters to the skin with a latex-based surgical adhesive (Skin-Bond) in 1998, but changed to using a contact adhesive (Ados F2) in 1999 and 2000 to improve transmitter retention times (mean ± SE days retention time for transmitters were: 1998, 9.1 ± 1.2; 1999, 18 ± 1.8; 2000, 23.6 ± 2.7). The transmitter package represented 2% or less of chick body mass.

Chicks were banded with a numbered metal band at hatching as part of a larger study investigating black-fronted tern breeding success (Chapters 4 and 7). A hood was placed over the heads of the chicks throughout the handling period and chicks were returned to where they were found within 15 minutes of capture.

I monitored radio-marked birds daily with a handheld three-element Yagi antenna and Merlin 12 receiver. Black-fronted terns usually fledge at 23-32 days of age (Chapter 4), and I considered a bird fledged on the first visit that it could fly well enough to avoid capture by me. After fledging, I monitored juveniles daily until they shed their transmitter, were found dead, or the signal disappeared (indicating either dispersal from natal colony or transmitter failure).

When a radio-marked juvenile was found dead, the area up to 5 m around the bird was checked for any signs of predation (scats, footprints, blood or feathers). Cause of mortality was assessed from the location of and evidence on the carcass according to the criteria described in Chapter 5. If the carcass was found fresh, it was packed in ice and sent overnight to the Institute of Veterinary, Animal and Biomedical Sciences, Massey University, New Zealand for post-mortem examination. These carcasses were given a complete pathological examination and selected histopathological tests.

Survivorship through time was examined using the Kaplan-Meier estimator (SAS Institute 1996). Juveniles whose survival was uncertain (dropped transmitter or lost signal) were included but were right-censored from the model on the last day they were seen alive. I assumed juveniles were randomly sampled from the colonies; survival times for individuals were independent; survival of right-censored individuals was equal to animals remaining in the monitored population; and capture, radio-marking and monitoring did not affect survival rates (White and Garrott 1990). Too few terns were radio-marked in 1998 (n = 13) or 1999 (n = 18) to allow for meaningful analysis, thus survival analyses were based on all three years pooled. Daily survival rates (S_D) were calculated for each day as $S_D = (x-y)/x$, where x was the number of birds alive with functioning transmitters, and y was the number of birds that were found dead (from Trent and Rongstad 1974). Daily survival rates were averaged to give mean daily survival rates for each of the four weeks after fledging.

For radio-marked juveniles in 1999 and 2000, I tested whether age at fledging or body size prior to fledging affected post-fledging survival. I measured the mass and wing chord of known aged birds every 1-2 days from approximately 20 days of age until fledging. The relaxed wing chord (mm) was measured with a stopped rule from the bend of the wing to the tip of the longest primary.

Because not all birds were measured on the day of fledging, and 23 days was the youngest age at which a radio-marked bird fledged, I used body measurements taken at 22 days of age to assess the relationship between chick body size and post-fledging survival. Wing growth in black-fronted tern chicks is linear (Chapter 7). Thus, for chicks that were not measured at 22 days, the wing length at 22 days was extrapolated from the measurements taken either side of day 22. Mass of black-fronted tern chicks tends to level out asymptotically after 18 days (Chapter 7), and I averaged all masses taken from day 21 to day 25 for each chick to provide an indication of mass at day 22. An index of body condition was calculated by dividing mass by wing chord at 22 days.

I tested whether wing length, mass, age at fledging and body condition were related to survival after fledging using canonical discriminant analysis (SAS Institute 1996). Five juveniles that dropped their transmitter or disappeared within one week of fledging were excluded from these analyses.

Results

I monitored 63 radio-marked juveniles for 750 radio-telemetry days and detected 12 mortalities. Predators were responsible for at least nine (75%) juvenile mortalities: five possibly by cats, two by rats, and two by unidentified predators. Of the remaining three juveniles found dead, one died of necrotising enteritis, one from starvation, and the cause of death could not be confirmed for the remaining juvenile because although the carcass had been partially eaten, it was not recovered fresh enough to determine whether the bird had been preyed upon or scavenged after death.

The survival rate (± 95% CI) of juvenile terns in the first four weeks after fledging was 0.795 ± 0.108. All deaths (except the one unknown cause of death) occurred in the first week after fledging (Figure 1) and happened at the natal colony prior to dispersal.

Mean daily survival rates increased from 0.972 ± 0.010 in the first week after fledging, to 0.995 ± 0.005 in the second week, and 1.00 for the third and fourth weeks.

On at least four occasions, I recorded a bird as fledged then on a subsequent visit found it hiding on the ground where it was easily caught. These birds flew when released into the air after capture. For these birds, the original fledging date was used in the survival analyses.

Larger, heavier chicks that fledged earlier tended to have better survival post-fledging than smaller, lighter chicks that fledged later ($F_{4,39} = 2.84$, $P = 0.037$; Table 1). Mass, wing length and fledging age, but not condition, were all strongly correlated ($r > 0.8$) with the linear discriminant function. However, juveniles that survived the post-fledging period could not be accurately predicted based on these variables alone (Figure 2).

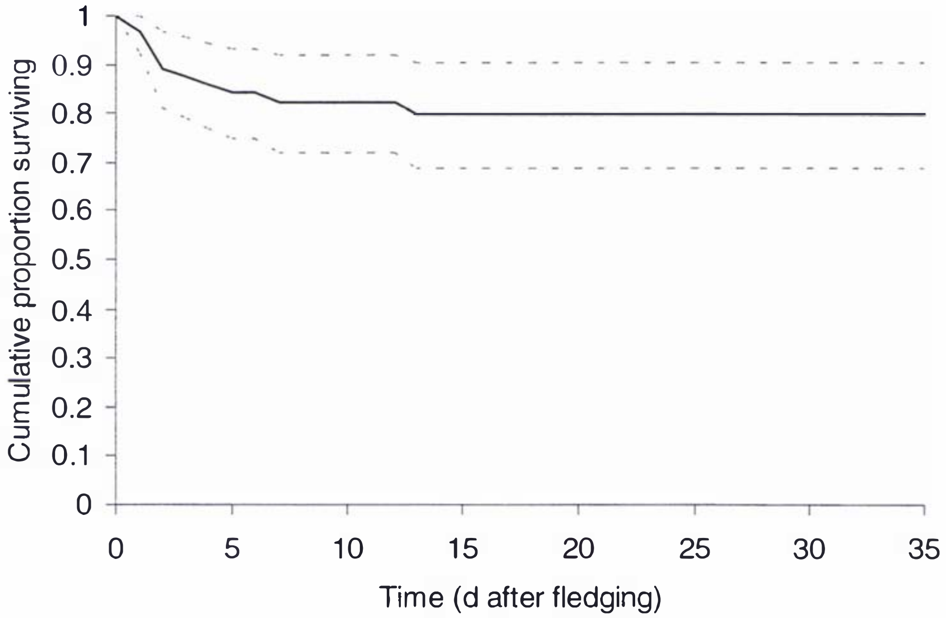

Figure 1: Cumulative proportion of 63 juvenile black-fronted terns surviving in the first month after fledging, based on the Kaplan-Meier estimator. Dotted lines are 95% confidence intervals.

Table 1: Pre-fledging body measurements and age of fledging for black-fronted terns that died after fledging (n=8) versus those that survived one or more weeks after fledging (n=36). Data are means with 95% confidence intervals in *italics*. Mass and wing length were measured at 22 days of age; condition was calculated as mass divided by wing length at 22 days

	Died	**Survived**
Mass (g)	73.6 62.5-84.7	85.9 81.6-90.2
Wing length (mm)	121.1 105.75-136.5	136.4 131.4-141.4
Condition (g/mm)	0.608 0.547-0.668	0.631 0.605-0.657
Fledge age (d)	30.1* 25.7-34.5	26.7 25.7-27.7

*Includes one bird that did not fledge until 41 days because of a slight wing deformity; without this individual, mean fledge age is 28.7 days (25.2-32.2)

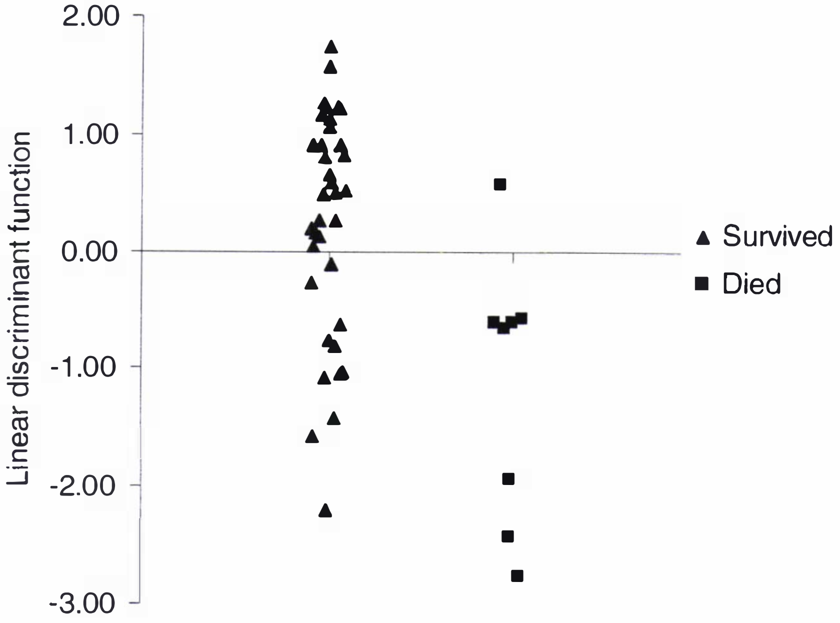

Figure 2: Linear discriminant function for juvenile black-fronted terns that survived one or more weeks after fledging (n=36) versus those that died (n=8). The discriminant function was based on wing length and weight at 22 days of age, condition, and age at fledging, according to the following equation: LDF = 0.298 * (mass-mean(mass)) - 0.149 * (wing-mean(wing)) - 32.94 * (condition-mean(condition)) - 0.175*(fledge age-mean(fledge age)).

Discussion

Juvenile survival and recruitment in terns is one of the most difficult parameters to measure accurately, even when based on long-term banding studies (Spendelow 1991, Massey et al. 1992, Kirsch 1996, Bacon and Rotella 1998). For black-fronted terns, until there are further studies using banding records to provide improved estimates of survival or recruitment, the results of this study suggest that measuring juvenile survival through to dispersal rather than fledging will give better estimates of reproductive success. Fledging success on the lower Ohau River was 21% (n = 522 hatched chicks) over the three years. If only 79.5% of these fledglings survive to dispersal, then the proportion of successfully fledged young is closer to 16.8%. Using fledging success alone to estimate reproductive success of black-fronted terns annually would have provided overestimates and failed to identify an important stage of high mortality. Although there are no current estimates of black-fronted tern survival between fledging and age of first breeding (two years), it is possible that during that period the rate of mortality is highest immediately after fledging when the newly fledged young are still vulnerable to predators.

All deaths caused by predators occurred in the first week after fledging. This early mortality, coupled with the observations of how supposedly 'fledged' birds were hiding on the ground to avoid capture, suggests that newly fledged juveniles take several days to rely on flight as their primary mechanism of escape from predators. Poor flying abilities in the immediate post-fledging period has resulted in high mortality due to predation in a range of other species (Anders et al. 1997, Zelenak et al. 1997, Green and Cockburn 2001, Naef-Daenzer et al. 2001). A black-fronted tern juvenile that had been fledged for at least one week was easily captured by hand within the colony at night (pers. obs.). Given that almost all recorded predation events in the Ohau River occurred at night (Sanders and Maloney 2002), juveniles probably remain highly vulnerable to mammalian predators for several weeks after fledging.

Although heavier black-fronted tern chicks tended to have higher survival post-fledging than their lighter counterparts, the relationship was not strong enough to confidently predict outcomes for juveniles based on pre-fledging information alone. The two birds that died of non-predator related causes did so in 1998 when pre-fledging body size was not monitored, which prevents any comparison of pre-fledging body size between juveniles that died from predation versus other causes. Although the high rates of predation may have obscured any strong effects of pre-fledging condition on post-fledging survival, these data suggest that the smaller, slower growing chicks could be more susceptible to predators after fledging. Monitoring recruitment rates of the surviving juveniles to the breeding population in subsequent years would indicate whether there is any longer term relationship between pre-fledging condition and survival, as has been shown elsewhere (Sagar and Horning 1990, Olsson 1997).

In this study, it was not possible to follow unmarked birds in order to make a comparison of survival against the radio-marked birds. There was no evidence, however, that the transmitters affected the fate of the radio-marked juveniles. A concurrent study in the Ohau River where chick growth was monitored daily showed no difference in fledging age, or chick weight and wing length 1-2 days before fledging between radio-marked and unmarked chicks (unpubl. data). Transmitters were completely preened under the feathers after attachment and only the antenna was visible protruding past the end of the tail feathers. The survival rates reported here are probably maximum estimates because juveniles that went missing or that dropped their transmitters early on may have subsequently died.

Identifying predation as the major factor affecting black-fronted tern survival after fledging, and that the majority of this mortality occurs before dispersal, emphasises the need for effective predator control at black-fronted tern colonies. Mammalian predators are also the major cause of black-fronted tern egg mortality (Sanders and Maloney 2002), chick mortality and mortality of breeding adults (Chapter 5). Together, these results indicate that control of mammalian predators during the breeding season will be the most effective way of increasing black-fronted tern breeding success. Moreover, any management actions such as predator control at black-fronted tern colonies needs to be continued until juvenile dispersal from colonies to provide protection from predators through the vulnerable early post-fledging period. The immediate post-fledging period may also be an important source of mortality for other threatened and endangered species, therefore should be considered in future studies examining reproductive success.

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Chapter 9:

Estimating population sizes and trends of black-fronted terns from historical data

Black-fronted tern landing at nest. Photo: Department of Conservation

Abstract

Black-fronted terns are an endemic New Zealand species listed as chronically threatened. Although black-fronted terns face many threats from introduced predators and habitat loss, and the population is suspected to be in decline, exact population size and trends are unclear. In this study, I collated all historical data to assess whether existing data can provide accurate information on black-fronted tern population sizes and whether the population is in decline. Data from 54 South Island rivers were compiled and indicate that the population probably numbers fewer than 10 000 individuals but too few data are available to provide an accurate estimate. Existing datasets from regular river surveys and winter flock counts do not provide clear evidence of population trends. This study highlights how data on the black-fronted tern population are scarce and incomplete. There is an urgent need for nationwide surveys to estimate population size and for ongoing surveys in key locations to estimate population trends.

Introduction

Black-fronted terns are an endemic New Zealand species that breeds only on the wide, sparsely vegetated riverbeds of the braided rivers of the South Island. Once more widespread, there is growing concern that black-fronted tern populations may be in decline (O'Donnell 1992, Higgins and Davies 1996, Maloney 1999). Reduction in quantity and quality of available braided river habitat through development of hydroelectric dams and canals has also reduced the availability of adequate feeding and breeding habitat for black-fronted terns. Increased weed invasion in the riverbeds has provided favourable habitat for the introduced European rabbit (*Oryctolagus cunniculus*) and its associated predators, which, in turn, prey on black-fronted terns (Balneaves and Hughey 1989, Taylor 2000, Sanders and Maloney 2002). Recently reclassified as a species in 'serious decline' in New Zealand (Hitchmough in press, Molloy et al. in press), the global conservation status of black-fronted terns was also upgraded from threatened to endangered (BirdLife International 2000).

Black-fronted terns have been identified as a New Zealand species in urgent need of further research and conservation effort (Taylor 2000). Existing published estimates of population size range from 2000 to 20 000 individuals (Robertson and Bell 1984, del Hoyo et al. 1996, Heather and Robertson 1996), but no nationwide census has been conducted. Despite the growing concerns that the population is in decline, until recently the only comprehensive study on the species focussed on feeding ecology (Lalas 1977).

Accurate measures of population size, population trends and distribution are urgently needed to better manage the species.

In this study, I have collated all existing data on black-fronted tern population sizes to address three aims:

1) to estimate current population size and compare this with existing published estimates;
2) to assess whether existing data provide clear evidence of population trends; and
3) to put all black-fronted tern population data into one accessible location to provide baseline information against which to compare any future surveys.

Methods

I collated black-fronted tern population data from all the published and unpublished sources that I could locate. Available data were based on surveys or observations of breeding populations on South Island rivers, and on regular winter flock counts from coastal areas of both the North and South Islands.

I collated and reviewed all available data from South Island river surveys to assess whether the data could provide a viable measure of black-fronted tern population size. River survey data on black-fronted terns were usually collected as part of general surveys for all river bird species. Surveys were normally carried out in spring following a standard methodology. Experienced observers were spread evenly across the riverbed and walked downstream at a constant rate recording all birds that moved upstream of the observer. On some of the larger rivers, jet boats were used to enable accurate counts of black-fronted terns nesting on otherwise inaccessible islands. Full descriptions of survey methods are detailed in O'Donnell and Moore (1983) and Maloney et al. (1999). Where necessary, I collated data based on sightings of single colonies, if comprehensive survey data for a river were not available.

I looked for evidence of population trends in data from river surveys where similar sections of rivers were re-surveyed in subsequent years, and from winter flock counts. Counts from wintering black-fronted tern flocks were only collated from coastal locations where there were regular counts within winters and carried out for more than ten years. For each year and location, winter flock counts are based on the highest count of black-fronted terns seen on one day, after frequent repeat counts throughout each winter. For three winter flock count datasets and long-term survey data from the Ashburton River, I log-transformed the data and then fitted a series of polynomial regressions (constant, linear, quadratic and cubic) to each set of data, both with and without auto-correlation between successive errors, using SAS Proc Mixed (SAS Institute 1996). For each dataset, the best model describing the population trend was chosen on the basis of the Akaike Information Criterion (AIC).

Results

Population size

I located black-fronted tern survey data from 54 South Island rivers, with 9130 birds counted (Table 1). Because many of these data are from surveys carried out over fifteen years ago, I also calculated a more conservative estimate of minimum population size based on all black-fronted terns counted in surveys since 1990 only. These recent surveys total 6815 black-fronted terns (Table 1). However, several major rivers such as the Waimakariri, Rakaia, Hurunui and Oreti Rivers have not been surveyed recently and these rivers could potentially contribute a further 1500 individuals based on data from earlier surveys.

Population change

Annual surveys of the Ashburton River from 1981-1990 (O'Donnell 1992) and 1997-1999 (C. O'Donnell, unpubl. data) provide one of the most comprehensive datasets on changes in black-fronted tern populations through time. Population trends on the Ashburton are best described by a quadratic curve with no correlation of counts between years, indicating a decline through the 1980s and early 1990s with a slight recovery in the late 1990s (Figure 1). Winter flock counts from the Bay of Plenty (P. Latham, unpubl. data, Latham 1981) show a similar trend (Figure 2) but autocorrelation between years show years with high counts tend to be followed by years with lower counts. Winter counts from Farewell Spit (OSNZ Nelson-Golden Bay region, unpubl. data) and from Hawke's Bay (M. & W. Twydle, unpubl. data; Figure 3) did not show any change in numbers through time.

Table 1: Black-fronted tern population counts on braided rivers of the South Island, New Zealand during spring. Counts are presented from the most recent surveys available from each river. Where the data are from surveys that were carried out annually for several consecutive years, the count is the average of those years shown. Descriptions of the sections of each river covered are available in the original source.

Region	River	Count	Year	Source
Canterbury	Ahuriri (lower)	368	1998, 2001	Wells and Sanders (1999), Keedwell and Sanders (2002)
	Ahuriri (upper)	288	1991-1994	Maloney et al. (1997)#
	Ashburton	251	1997-1999	C. O'Donnell, pers. comm.
	Ashley (lower)	79	2000	OSNZ, Tony Crocker pers. comm.
	Ashley (upper)	139	1981	O'Donnell and Moore (1983)
	Cass	88	1991-1994	Maloney et al. (1997)#
	Conway*	30	1980	Cowie (1981)
	Dobson	53	1992-1994	Maloney et al. (1997)#
	Godley	98	1992-1994	Maloney et al. (1997)#
	Hakataramea	66	1983	Robertson et al. (1984)
	Harper-Avoca	11	1978	O'Donnell and Moore (1983)
	Hopkins	71	1992-1994	Maloney et al. (1997)#
	Hurunui	338	1978	O'Donnell and Moore (1983)
	Kakanui	0	1983	Robertson et al. (1984)
	MacAulay	37	1992-1994	Maloney et al. (1997)#
	Maerewhenua	1	1983	Robertson et al. (1984)
	Ohau (lower)	295	1991-1994	Maloney et al. (1997)#
	Ohau (upper)	137	1991-1994	Maloney et al. (1997)#
	Opihi	50	1994	Schweigman (1994)
	Orari	3	1994	Schweigman (1994)
	Pukaki	18	1991-1994	Maloney et al. (1997)#
	Rakaia (lower)	267	1983	Robertson et al. (1984)
	Rakaia (mid)	120	1979	O'Donnell and Moore (1983)
	Rakaia (upper)	403	1978	O'Donnell and Moore (1983)
	Rangitata	804	2000	C. O'Donnell, pers. comm. Butcher (2001)
	Tasman	120	1992-1994	Maloney et al. (1997)#
	Tekapo	501	1991-1994	Maloney et al. (1997)#
	Twizel*	44	2001	RJK, pers. obs.
	Waiau	217	1975	O'Donnell and Moore (1983)
	Waimakakariri (lower)	74	1981	O'Donnell and Moore (1983)
	Waimakakariri (upper)	69	1980	O'Donnell and Moore (1983)
	Waitaki	632	2001	Boffa Miskell Ltd (2002)
	Wilberforce	87	1978	O'Donnell and Moore (1983)
Nelson/Marlborough	Awatere (lower)	20	1997	Clayton-Greene (1999)
	Awatere (upper)	30	1996	Clerke (1996)

	Clarence	147	1992	Hallas (2002)
	Hapuku	0	2000	Barber (2001)
	Kahutara	15	2000	Barber (2001)
	Kowhai	0	2000	Barber (2001)
	Maruia*	9	1986	Gaze (1988)
	Matakitaki	13	1999	Ure (1999)
	Motueka*	14	1987	O'Donnell and West (1989)
	Waima (Ure)	0	1997	Clayton-Greene (1999)
	Wairau (lower)	635	1993	Clerke (1993b)
	Wairau (mid)	495	1995	Clerke (1993a)
	Wairau (upper)	293	1996	Clerke (1996)
	Wairau/Rainbow	90	1999	Ure (1999)
Otago	Colourburn*	50	1986	Child (1986)
	Dart	221	1994	McKinlay (1995)
	Hunter	183	2000	McKinlay (1993)
	Makarora	0	1991	McKinlay (1992)
	Manuherikia	0	1989	McKinlay (1990)
	Matukituki	276	1996	McKinlay (1997)
	Nevis*	32	1969	Child (1975)
	Rees	17	1994	McKinlay (1995)
	Shotover (lower)	0	1993	McKinlay (1994)
Southland	Aparima*	200	1995	W. Cooper, pers. comm.
	Clutha	12	1985	Hughey et al. (1986)
	Eglinton*	90	2001	C. O'Donnell, pers. comm.
	Mararoa*	78	1986	Gaze (1988)
	Mataura*	130	2001	W Cooper, pers. comm.
	Oreti*	298	1986	Gaze (1988)
West Coast	Howard/Buller	23	1995	Ure (1995)
	Taramakau	0	1985	Moore (1986)
Overall Total		**9130**		
Recent Total (surveys from 1990 onwards)		**6815**		

*Denotes a single colony count only or an incomplete river survey.
#Figures reported here for rivers surveyed by Maloney et al. (1997) are the means of all four surveys, rather than the single highest count from one year as reported in Maloney et al. (1997).

Maloney (1999) provides an analysis of black-fronted tern population changes in nine braided rivers in the upper Waitaki Basin over a thirty-year period. He concludes that although the majority of rivers had lower counts in the 1990s than 1960s, this decline was significant in only the Cass River. Data for the lower Ahuriri from Maloney (1999) and more recent counts (Wells and Sanders 1999, Keedwell and Sanders 2002) also show there has been no apparent decline in the Ahuriri from 1962-2001 (Table 2).

Limited repeat survey data exist for at least another 10 rivers (Table 2), but only three of these rivers show a decline, and two potentially show an increase in population size.

Regular winter counts have also been carried out at the Manawatu Estuary since 1976, and at intermittent intervals from 1954-1974, but because fewer than 10 black-fronted terns were present in all except two years (Moore 1998), it is not possible to determine trends from this dataset. Other count data from winter flocks from around the country are reported in the classified summarized notes in *Notornis* each year, but unless winter counts were performed frequently within each season to positively identify the maximum flock size, little information could be gained from the counts.

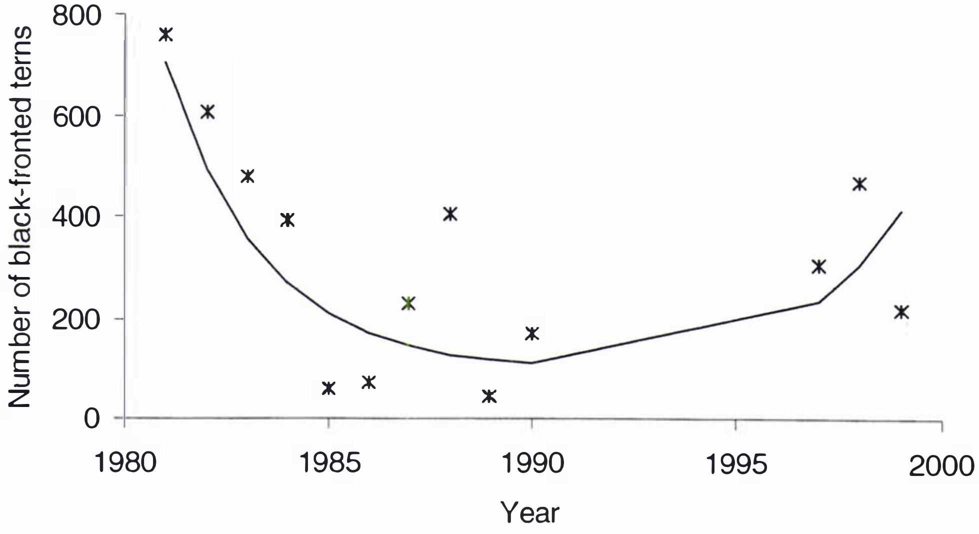

Figure 1: Black-fronted tern population counts on the Ashburton River, during spring 1981-2001 (C. O'Donnell unpubl. data, O'Donnell 1992). Curve is a fitted quadratic regression with no auto correlation, of the equation: Log(Count) = 165.04 - 3.533*Year since 1900 + 0.02*Year^2, error variance = 0.679.

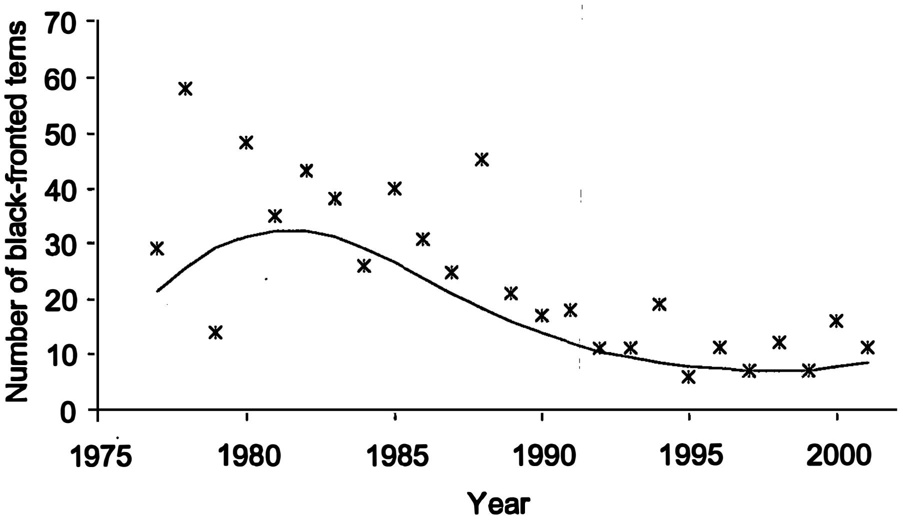

Figure 2: Winter flock counts of black-fronted terns in the Bay of Plenty, 1977-2001 (P. Latham unpubl. data, Latham 1981). Each count represents the maximum number of terns seen in one day during winter. Counts were made at the Tarawera and Rangataiki River mouths. Curve is a fitted cubic regression with negative auto-correlation, of the equation: Log(Count) = -504.3 + 17.3*Year since 1900) - 0.2*Year^2) + 0.001*Year^3), error variance = 0.342, correlation between successive errors = -0.053.

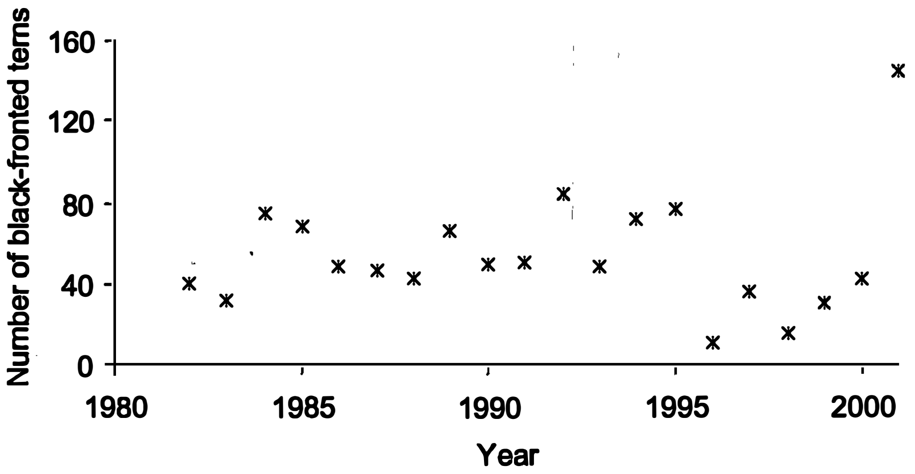

Figure 3: Winter flock counts of black-fronted terns in Hawke's Bay, 1982-2001 (M & W Twydle unpubl. data; 2001 count by J. Sheen). Each count represents the maximum number of terns seen in one day during winter. Counts were made from Marine Parade (Napier) to Waitangi River mouth.

Table 2: Changes in black-fronted tern population counts through time. All counts were carried out during spring. Ahuriri River data are presented from Longslip Creek to Benmore Delta, all other descriptions of sections of each river covered are available in the original sources.

Region	River	Year	Count	Source
Marlborough	Wairau	1985	1359+	Hallas (2002)
		1990s	1423	(See Table 1 for sources)
Canterbury	Ahuriri	1962	308	B. D. Bell, unpubl. data
		1963	368	
		1964	239	
		1982	536	Robertson et al. (1983)
		1991	307	Maloney (1999)
		1992	238	
		1993	249	
		1994	373	
		1998	408	Wells and Sanders (1999)
		2001	342	Keedwell and Sanders (2002)
	Opihi	1983	133	Robertson et al. (1984)
		1985	79	Schweigman (1994)
		1987	127	
		1994	50	
	Orari	1983	0	Robertson et al. (1984)
		1985	38	Schweigman (1994)
		1987	162	
		1994	3	
	Waitaki	1974	597	Wildlife Service, unpubl. data
		2001	632	Boffa Miskell Ltd (2002)
Otago	Hunter	1969	38	McKinlay (1993)
		1982	118	
		1992	132	
		2000	183	
	Makarora	1966	35	McKinlay (1992)
		1972	49	
		1980	24	
		1984	38	
		1991	0	
	Manuherikia	1967	71	Child (1975)
		1986	18	McKinlay (1990)
		1989	0	
	Matukituki	1971	137	McKinlay (1997)
		1984	184	
		1993	76	
		1996	276	
	Rees/Dart	1967	147	McKinlay (1995)
		1982	108	
		1984	166	
		1990	203	
		1991	44	
		1994	238	
	Shotover (lower)	1968	126	McKinlay (1994)
		1993	0	
Southland	Oreti	1974	317	W. Cooper, pers. comm.
		1986	298	Gaze (1988)

Discussion

The existing historical data on black-fronted terns cannot be used to effectively estimate population size or population trends. Although the data presented in Table 1 are the most comprehensive population data currently available and provide counts from 54 rivers, there are many limitations in using these data to estimate population size. The data from over 39% of rivers are more than 10 years old and data from 18% of rivers were based on informal sightings of single colonies or incomplete surveys. There are at least a further 5-10 rivers in the South Island that may contain populations of black-fronted terns but either have not been surveyed, or I could not locate any information. In addition, pooling data together from different years and different rivers or sections of rivers assumes there is little movement between populations and years. Limited data from studies of black-fronted tern population dynamics suggest black-fronted terns have relatively high site fidelity to localities, but not necessarily to individual rivers within and between breeding seasons (Chapter 4). Therefore, collating counts from adjacent rivers carried out in separate years does incur a risk of double-counting individuals.

Differences in survey methods, observer ability, and both within- and between-season variation in counts all increase the error margin on the population estimates and further show that the population estimates provided here are only 'ballpark' figures at best. Despite these limitations, the data presented in Table 1 suggest that the black-fronted tern population is unlikely to number fewer than 5000 individuals as has been published elsewhere, but is probably within the range of 6000 - 10 000 individuals.

Clearly, it is necessary to get a better minimum estimate of black-fronted tern population size. In 1982, the Ornithological Society of New Zealand (OSNZ) attempted a census of wintering terns, which resulted in population estimates of fewer than 2300 birds (P. Sagar/OSNZ, unpubl. data), but winter population counts are probably the least accurate method of carrying out a census of black-fronted terns (see below). Relatively accurate population censuses have been carried out for other braided river birds such as black-billed gulls (*Larus bulleri*) and white-fronted terns (*Sterna striata*, Powlesland 1998), because breeding colonies can easily be located by surveying with light aircraft, and for wrybills (*Anarhynchus frontalis*), which can be censussed on their wintering grounds (Sagar et al. 1999).

Getting an accurate census of the black-fronted tern population is more difficult because: (i) colony locations change frequently both within and between years; (ii) colonies are not easily visible from the air therefore cannot be quickly located for counting; (iii) over the winter, black-fronted terns are scattered widely over the coastlines of both the North and South Islands, inland and out to sea, covering too large an area to allow an accurate census; and (iv) river survey data provide only an index of abundance and the relationship between the number counted and the real population size on a river has not been determined. The best method available to estimate population size accurately is to implement nationwide surveys during the breeding season, where all rivers with black-fronted tern populations are surveyed within a two-month period. In addition, calibrating the number of terns counted with the absolute number of terns nesting on a river will indicate the proportion of the population counted during a river survey. Regular repeat surveys for black-fronted terns either nationwide or at key rivers will increase the available data for use in examining population changes.

Although it is clear the population has declined historically, it is unclear whether the population is still in decline. Black-fronted tern populations have declined since European settlement (Higgins and Davies 1996) and their range has also decreased. Black-fronted terns once bred on the Central Plateau of the North Island (Stead 1932) and on the rivers of the west coast of the South Island (as quoted in Morse 1981) but are now restricted primarily to the braided rivers of the east coast of the South Island, from Marlborough to Southland. The historical data presented in this study provide ambiguous results, with two long-term data sets suggesting the population has recently declined, and the other two indicating no trend. Published accounts suggest the population is in decline (Higgins and Davies 1996, Taylor 2000) but these accounts rely on counts from only two sites (Farewell Spit and the Ashburton River). Higgins (1996) reports a decline of 75% at Farewell Spit but this is based on the erroneous comparison of one unusually high count in 1982 with the subsequent more stable counts. Accurate analysis of all data from Farewell Spit instead indicates the counts are erratic but stable (OSNZ Nelson-Golden Bay, unpubl. data; my analysis).

Other data, however, suggest the population may well be in decline. Black-fronted terns have declined or disappeared from some rivers. In other rivers, such as the Manuherikia and Shotover, there is evidence that a lack of either weed-free or disturbance free habitat has lead to the decline (McKinlay 1990, 1994).

Black-fronted terns currently have low productivity in some rivers (Chapter 4), which is primarily caused introduced predators. Computer simulations suggest that with the current rates of productivity the population is probably in decline (Chapter 10). If predation is the major limiting factor on the population, there is little evidence to suggest historical declines in black-fronted tern numbers will cease given that predators are established nationally. Therefore, it is essential to continue monitoring black-fronted tern populations where long-term data sets already exist to ensure trends can be detected.

All the river survey data presented here, except for 1998 and 2001 from the Ahuriri, are based on a single count in each year. The variation within and between seasons can be large because surveys vary in timing, weather conditions, and food availability. For example, the 2001 Ahuriri River survey was based on the mean of four counts carried out throughout the same breeding season and these varied from 287 to 395 black-fronted terns (Keedwell and Sanders 2002). Variation between years is even greater, where the yearly counts from 1991-1994 in the Mackenzie Basin (based on raw data from Maloney et al. 1997) ranged from decreases of over 80% (Hopkins River: 129 to 24 individuals) to 16-fold increases (Cass River: 14 to 236 individuals). The colonial nature of black-fronted terns can cause huge variation in counts because the presence or absence of a single colony on a river at the time of surveying can lead to large differences in total counts for each survey.

Power analyses indicate that a single river survey of black-fronted terns carried out each year for four years and compared with a later similar data set could only detect a minimum decline of 80% (Sanders 1999). Thus, the population could decline by over 50% in some rivers but the current survey methods would not be able to detect it. Much of the between year variation in black-fronted tern population counts at each river is probably because of within-season variation (Sanders 1999). Yearly estimates of black-fronted tern population size in a river should have improved accuracy if repeat surveys are carried out within each year. Failing that, surveys consistently need to be carried out every year over a time frame of 10 years or more to detect any trends beyond the annual and seasonal variation.

Despite the apparent problems with using the existing historical data to estimate population size, collating black-fronted tern data in this manner has provided information on which rivers are most important to the population. If the black-fronted tern population is approximately 8 000 birds or more, the following rivers each provide breeding habitat for at least 5% of the population: the Wairau, Ahuriri, Waitaki, Rangitata, Tekapo, Ohau and Rakaia Rivers. It is also apparent that Southland rivers have been poorly surveyed. Given that black-billed gulls have shown declines of at least 30% in Southland rivers (Taylor 2000) and black-fronted terns are thought to number fewer than 1000 individuals and declining (W. Cooper, pers. comm.), it is essential to increase the baseline information in Southland.

Because few black-fronted terns have been banded, little is known about their movements outside of the breeding season, and whether they have any degree of site attachment to overwintering locations. Winter flock counts are highly variable because of weather, and flocks can be extremely large after southerly storms (Fleming and Fleming 1985). As a result of this variation and the large area of coastline and the numbers feeding out to sea, winter censuses are not an accurate way of determining total population, as shown by the OSNZ surveys in the early 1980s. However, if counts are made regularly throughout each winter and continued for periods of ten years or more, this method may provide a measure of population trends.

Conclusions

The difficulty in accurately determining sizes and trends in black-fronted tern populations in this study highlights how scarce and incomplete existing knowledge is. There is an urgent need for a nationwide survey of black-fronted terns during the breeding season. Although I suggest the population is not as low as has been previously estimated, the population probably numbers fewer than 10 000 individuals, which, given our lack of knowledge about the species and lack of adequate monitoring, is cause for concern. This study also highlights how difficult it is to determine population trends based on available information. The colonial nature of black-fronted terns makes them very difficult to monitor accurately, but repeat surveys within a season would help lessen some of the variation observed between years. Winter counts need to be carried out at a range of sites, rather than just two or three, because without knowing about site fidelity of terns to winter sites, winter counts may be a reflection of weather patterns or food availability influencing distribution rather than an indication of population change.

Despite the lack of strong evidence for a decline in black-fronted tern populations, the possibility that the population is in decline needs to be taken seriously. Given the inability to detect slow declines using current methodology, the declines recorded in some locations, the past decline in the species range, the low productivity in the only comprehensively studied black-fronted tern population, and that declines are ongoing in other New Zealand shorebirds (Dowding and Murphy 2001), a precautionary approach data sources on black-fronted tern populations against which future surveys can be compared.

Further research and monitoring of black-fronted tern populations is urgently needed, and I recommend that:

1) A nationwide survey of all rivers where black-fronted terns occur is carried out during the breeding season to estimate minimum population size.
2) Annual or biennial counts during spring are continued on the Ahuriri and Ashburton Rivers, and are initiated on the Wairau and Waitaki Rivers and on other rivers with large black-fronted tern populations. Where possible, repeat surveys within a season should be completed.
3) Regular winter flock counts at Farewell Spit, Hawke's Bay and Bay of Plenty are continued, and regular counts are instigated at three more South Island locations (for example, Ashley Estuary, Lake Grassmere and Aramoana).
4) Counts from river surveys are calibrated with the number of birds actually breeding on the river.

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Chapter 10:

Comparative population viability analysis of black-fronted terns and banded dotterels on braided rivers

Black-fronted tern and banded dotterel nesting habitat on the lower Ohau river

Abstract

Black-fronted terns (*Sterna albostriata*) and banded dotterels (*Charadrius bicinctus*) both breed on the braided rivers of the South Island, New Zealand, and suffer high predation by introduced mammals. Black-fronted tern populations are probably in decline whereas banded dotterel populations are relatively stable. We used population viability analysis to explore the population dynamics of black-fronted terns and to model potential management actions. We also compared projected population outcomes of black-fronted terns with those of banded dotterels. Even using optimistic estimates of black-fronted tern survival rates, the projected population growth remained negative. This is consistent with observations of a decline in the black-fronted tern population. Further research is needed to accurately determine rates of adult and sub-adult survival, and to assess the temporal and spatial variation in egg and chick survival. If the parameters used in the model are accurate, predator control that protects at least half the black-fronted tern population during breeding is required to reverse the population decline. Simulation models for banded dotterels indicate the population is unlikely to be in decline, despite using low estimates for most parameters. We suggest that in a high predation environment, the higher reproductive output, shorter generation time and shorter evolutionary isolation of banded dotterels, rather than any behavioural differences, provide a survival advantage over black-fronted terns.

Introduction

The avifauna of New Zealand has been severely depleted since Polynesian arrival around 750 AD and European arrival in the late 18th century. Habitat destruction, disease and competition have all played a part in population declines and extinctions, but predation by introduced mammals has probably had the greatest impact (King 1984, Atkinson 1989, Gill and Martinson 1991). The link between introduced predators and ongoing declines in New Zealand forest bird populations is widely accepted (Innes and Hay 1991, Brown et al. 1998). More recently, this link has been extended to the declines in ground-nesting shorebird populations (Dowding and Murphy 2001). The effect of predators on ground-nesting birds has varied among species. For example, the shore plover (*Thinornis novaeseelandiae*) disappeared from mainland New Zealand after the arrival of cats (*Felis catus*) and Norway rats (*Rattus norvegicus*) but prior to the arrival of mustelids (Davis 1994). In comparison, species such as the New Zealand dotterel (*Charadrius obscurus*) and banded dotterel (*C. bicinctus*) still occur on the mainland, although with differing degrees of success (Dowding and Murphy 2001).

In braided rivers of the South Island, many ground-nesting bird species suffer high levels of predation (Sanders and Maloney 2002). Four out of the five endemic bird species that breed primarily or exclusively in braided river habitat (Maloney 1999), have conservation rankings ranging from vulnerable to critically endangered (BirdLife International 2000). Comparisons of survival, reproductive success and natural history between the critically endangered black stilt (*Himantopus novaeseelandiae*) and the more common native pied stilt (*H. himantopus leucocephalus*) on the braided rivers suggest that the pied stilt has anti-predator behaviours that enhance survival (Pierce 1982).

Despite the impact of predation on the survival of many braided river bird species, the biology of some species and the influence of predation on their survival have not been well studied. The black-fronted tern (*Sterna albostriata*) is a braided river species listed as endangered (BirdLife International 2000) but its population dynamics are poorly understood. The population numbers fewer than 10 000 individuals and is probably in decline (Chapter 9). There is an urgent need to assess factors impacting on the species' survival and to evaluate management options.

Further, the black-fronted tern shares the same habitat type within braided rivers as the banded dotterel, and has similar nesting habits. Despite these similarities, the banded dotterel is common and widespread, and does not appear to be in decline. Evaluating differences between the two species in their response to high predation levels may help determine factors that have led to the decline of the black-fronted tern and help to identify management to mitigate the decline.

Use of population viability analysis (PVA) can be helpful in assessing population trends and determining the relative importance of different management scenarios (Beissinger and Westphal 1998, Beissinger 2002). Although it is often near impossible to gather precise data for developing PVA models, preliminary models can be useful in endangered species management by assembling all known information on the species and identifying knowledge gaps (Brook and Kikkawa 1998). Preliminary models are also highly useful in identifying which parameters are most critical to population growth and determining which parameters can be changed to influence population growth (Mills and Lindberg 2002). Despite the limitations involved in using PVA (Coulson et al. 2001), if the relative model outputs rather than the explicit quantitative predictions are used, valuable information on species management can be gained (Brook et al. 2002).

Accordingly, in this study we use PVA to assess the probable population trends of black-fronted terns given the current data, identify the most important gaps in our knowledge of black-fronted terns, and evaluate potential management options. We also compare the survival of black-fronted terns and banded dotterels by using sensitivity analyses of parameters commonly measured in reproductive studies.

Methods

We reviewed the published literature for any accounts on reproductive and survival estimates for black-fronted terns and banded dotterels, and for other closely related species. A stochastic age-structured model was constructed using the modelling software Stella v.7.0.1 (High Performance Systems 2001). The models for each species had the following assumptions: 1) equal sex ratios, 2) equal reproductive success and survival for adult age classes, 3) no immigration or emigration, 4) population growth and mortality was density-independent, and 5) no inbreeding depression or other deleterious genetic effects. We omitted the effects of catastrophic events such as flooding or severe weather because there were insufficient data to explicitly model the effects of such a parameter and the effects were already incorporated in the input data values. In addition, the variation in reproductive success was modelled with an arbitrary standard deviation of 0.1, which would account for annual variation in survival due to spatial and environmental effects. The input values for each model are detailed below.

Both black-fronted tern and banded dotterel models were run for 50 years and the mean final population size from 50 simulations was assessed.

Black-fronted terns

All input data for black-fronted terns were gathered from research in the Upper Waitaki Basin (this thesis) or extrapolated from other tern studies to fill gaps in parameter estimates (Table 1). The model structure and equations are presented in Appendix 2.

Initial simulations using the mean survival rates measured from 1998-2000 for egg and chick survival (Chapter 4) and post-fledging survival to four weeks (Chapter 8) resulted in the modelled population declining to extinction in under 50 years. Consequently, we selected the highest value recorded for each of the three parameters in any one year. Annual survival rates for each of these three parameters were varied based on a normal distribution, with a standard deviation of 0.1.

Re-nesting attempts were factored into the model by assuming the rate of production of replacement eggs was proportional to egg and chick survival. On average, black-fronted terns lay 1.86 eggs per nest (Chapter 4). The average rate of renesting in the model assumed 37% of females laid a replacement nest, which resulted in each female laying 2.5 eggs per year on average. The actual rate of renesting varied in each year with up to 60% of females renesting when egg survival was 0, and the percentage of females renesting decreased linearly until egg survival was 1 and renesting was zero. A similar relationship was established for replacement eggs after chick failure (see Appendix 2). Black-fronted terns cannot successfully raise more than

Table 1: Parameters used in population simulations for black-fronted terns. 'Range' is the maximum and minimum values recorded each year during 1998-2000 on the Ohau River. Egg, chick and 4 week post-fledging survival rates taken from a normal distribution with a mean of the tabulated value and standard deviation of 0.1.

Parameter	**Value**	**Range**	**Source**
No. eggs laid per female	1.86	1-3	Chapter 4
Egg hatch rate	0.6	0.404-0.60	Chapter 4
Chick fledge rate	0.3661	0.261-0.366	Chapter 4
Proportion renests after egg or chick failure	Function proportional to egg and chick survival		Estimated from Chapter 4, see Appendix 2
Survival 4 weeks post-fledging	0.87	0.69-0.87	Chapter 8
Survival from 4 weeks post-fledging to year 1	0.54		Estimated from other tern species (Becker 1999, Nisbet 2002, Spendelow et al. 2002)
Annual survival from year 1 to year 2	0.85		Estimated
Annual adult survival (from year 2 onwards)	0.88	0.88-0.92	Chapter 4
Maximum adult age	26		Estimated from other terns species of similar body size (del Hoyo et al. 1996)
Proportion breeding at 2 years	0.25		Based on records from other tern species (del Hoyo et al. 1996)
Proportion breeding at 3 years	0.75		Based on records from other tern species (del Hoyo et al. 1996)
Proportion adults breeding	1		Based on records from other tern species (del Hoyo et al. 1996)
Starting population size (adults)	2100		Upper Waitaki Basin population (Chapter 9)

one brood in a season. In black terns (*Chlidonias chlidonias niger*), no replacement clutches were laid by adults that lost clutches after approximately the midpoint of incubation or in the last one-third of the breeding season (as reported in Servello 2000). Black-fronted terns probably follow a similar pattern, thus fewer than half of adults whose nests fail are likely to lay replacement clutches.

No data exist on mortality of black-fronted terns from four weeks post-fledging through to recruitment age. Estimates of survival for common terns (*Sterna hirundo*) from fledging to two years range from 0.22-0.46, with a mean of 0.33 (Becker 1999). Assuming annual survival increases after year one, and given that average annual survival of 2-5 year old common terns is 0.81 (calculated based on data in Wendeln and Becker 1998), then common tern juvenile survival (from fledging to year one) is 0.41. Initial simulations indicated this value was too low for the black-fronted tern model, therefore we used the approximate midpoint of survival to two years reported in Becker (1999), setting juvenile survival at 0.47. If post-fledging survival to four weeks in black-fronted terns is 0.87, then a first year survival of 0.47 is equivalent to 0.54 survival from four weeks post-fledging to year one.

Additional data exist for roseate terns (*S. dougallii*), where survival from fledging to first breeding ranges from 0.33-0.68 (Spendelow et al. 2002) or 0.156 (Nichols et al. 1990), and 0.16 for least terns (S. antillarum, Massey et al. 1992). However, the data in Becker (1999) are probably more accurate because they come from birds individually marked with transponders.

Annual survival from year one to year two was estimated at 0.85, assuming that survival of immatures was lower than that of adults.

Annual adult survival (year two onwards) for black-fronted terns ranged from 0.88-0.92, based on mark-recapture modelling (Chapter 4). Annual survival of 0.88 is probably the most accurate estimate because it accounts for the unequal search effort among years, and the subsequent re-sighting bias (Chapter 4). Annual survival rates reported for other terns are similar to black-fronted tern estimates: Arctic (*S. paradisaea*) 0.87-0.88, least (*S. antillarum*) 0.85-0.92, and Caspian (*S. caspia*) 0.85-0.91 (all reported in del Hoyo et al. 1996); common 0.88-0.92 (Nisbet 2002) and roseate terns 0.78-0.89 (Spendelow et al. 2002).

We set maximum adult age to 26 years. An Arctic tern was recorded at 34 years old (del Hoyo et al. 1996) and is probably the record for longevity in terns. At least five other species also have recorded longevities of over 20 years.

Black-fronted terns can breed at two years (RJK pers. obs.) but it is likely that most do not begin breeding until older. Some common terns breed by year two, most by year three and a few for the first time at year four (Nisbet 2002). There is also little evidence of adult common terns ‘skipping’ years once they have begun breeding (Nisbet 2002). Accordingly, we estimated 25% of 2-year-old birds, 75% of 3-year-olds, and all adults aged 4 years or more breed each year.

The simulations were run with a starting population of 2100 adults, the estimated size of the Upper Waitaki Basin black-fronted tern population (up to 30% of the entire population, Chapter 9), and assumed a stable age distribution.

Banded dotterels

Input data for banded dotterels were gathered from research in the Upper Waitaki Basin (this thesis) and other braided rivers, or extrapolated from other plover species from New Zealand and elsewhere (Table 2). The model structure and equations are presented in Appendix 3.

We set egg survival at 0.57, which is the Mayfield egg survival rate over three years on the Ohau River (Chapter 3). Chick survival was set to 0.381, based on a mean of all recorded accounts of individual banded dotterel chick survival (A. Rebergen, unpubl. data, Sanders and Brown 2000, 2001, Keedwell and Sanders 2002). Egg and chick survival rates in each year of simulations were sampled from a normal distribution with a standard deviation of 0.1. The number of eggs laid per female was 2.9 (Chapter 3), and renesting attempts (proportional to egg and chick survival rates, see Appendix 3) increased egg-laying rates to 4.6 eggs per female per year.

No comprehensive data are available on juvenile survival (fledging to year one) in banded dotterels. Resighting rates of birds banded as chicks on the Cass River 1977-1984, indicate juvenile survival could be between 30-56% (R. Pierce, pers. comm.), but these data have not been formally analysed. Larson et al. (2000) provide an estimate of piping plover (*Charadrius melodus*) juvenile survival and report comparable survival rates from three other studies. For the banded dotterel simulations, we used the mean of the four survival rates presented (0.46).

Despite extensive banding records for banded dotterels, there are no comprehensive estimates of annual adult survival rates. Survival rates of adults studied on the Cass River were estimated at 0.82 (R. Pierce, pers. comm.) but this was based on resighting rates only. We used the mean of all adult survival rates reported for North

American plover species (Larson et al. 2000) and for the New Zealand dotterel (Marchant and Higgins 1993). These ranged from 0.69 to 0.92, with a mean of 0.77. Because this mean survival rate was calculated from many threatened or endangered plover populations, we assumed 0.77 survival from year one to year two, and increased survival to 0.8 for adults (two years or older).

The oldest colour-banded banded dotterel is 12 years (NZ Banding Office, unpubl. data), but a New Zealand dotterel has been recorded at 41 years, with others regularly surviving 15-19 years (Marchant and Higgins 1993). Maximum ages recorded for other plover species ranges from 12-21 years (Marchant and Higgins 1993). Accordingly, we set maximum adult age at 20.

Table 2: Parameters used in population simulations for banded dotterels. 'Range' represents the minimum and maximum values from the set of all values used to determine the final parameter value. Egg and chick survival rates were taken from a normal distribution with a mean of the tabulated value and a standard deviation of 0.1.

Parameter	**Value**	**Range**	**Source**
No. eggs laid per female	2.9	1-3	Chapter 3
Egg hatch rate	0.57	0.52-0.65	Chapter 3
Chick fledge rate	0.381	0.23-0.54	(A. Rebergen, unpubl. data, Sanders and Brown 2000, 2001, Keedwell and Sanders 2002)
Proportion renesting	Function proportional to egg and chick survival		Estimated based on accounts of productivity (A. Rebergen, unpubl. data, Sanders and Brown 2000, 2001, Keedwell and Sanders 2002)
Survival from fledging to year 1	0.46	0.32-0.57	Estimated from other plovers (Larson et al. 2000)
Annual survival from year 1 to year 2	0.77		Estimated
Annual adult survival (from year 2 onwards)	0.8	0.69-0.92	Estimated from other plovers (Marchant and Higgins 1993, Larson et al. 2000)
Maximum adult age	20		Estimated from other plover species (Marchant and Higgins 1993)
Proportion breeding at 1 year	0.75		Estimated from Pierce (1983) and other plover species
Proportion adults breeding	1		Estimated from other plover species
Starting population size (adults)	3300		Upper Waitaki Basin population size (Maloney et al. 1997)

Most banded dotterels breed at one year, with a few not breeding until their second year (Pierce 1989). We assumed 75% of first-year birds and all adults bred each year. The simulations were run with a starting population of 3300 adults (size of the upper Waitaki Basin, Maloney et al. 1997), based on a stable age distribution.

Sensitivity analyses

For both models, each parameter was varied by ±10% of its original value while all other parameters remained unchanged. We ran 50 simulations over a 50-year period and recorded mean population size. The effect of each parameter on mean population growth rate and final population size was ranked.

Predator control simulations

We simulated the effects of predator control at black-fronted tern colonies by simultaneously reducing a proportion of egg, chick, post-fledging and adult mortality. We assumed that egg and chick survival in the presence of predator control were 0.72 and 0.5 respectively, which was equivalent to the rates of survival observed in one colony in 1999 where there was almost no predation. We assumed predator control increased post-fledging survival to 0.93, and adult survival to 0.89.

Assuming 30% of the upper Waitaki Basin black-fronted tern population could be protected (equivalent to 5-6 large colonies that could feasibly be protected by one person working full-time), we ran simulations to determine how frequently this level of control needed to be implemented to increase the population growth rate. Because the presence of only one predator can potentially cause the failure of an entire colony (Chapter 4), we assumed predator control consisted of the maximum possible effort at a colony to reduce impacts of predation as far as possible.

Comparison of natural histories between species

We tabulated data on black-fronted tern and banded dotterel natural history, based on published accounts and personal observations during three years of research on the Ohau River (Chapters 2-8). We examined the differences in natural histories of the two species with respect to population model predictions.

Results

Black-fronted terns

Even using the highest egg, chick and post-fledging survival estimates, the simulated black-fronted tern population rapidly decreased with an annual population growth rate of 0.974 (Figure 1).

The growth rate was most sensitive to changes in adult mortality (Table 3). Survival from post-fledging to year one, chick survival and the percentage of adults breeding also had strong influences on population growth rate (Table 3). Survival from post-fledging to year one had an important effect on the model yet this parameter was based solely on information from other terns. However, additional simulations showed that this parameter must be increased from the current value of 0.54 to at least 0.72 to result in a stable population.

Maximum adult age, percent of year two and three birds breeding and mortality from year one to year two had little effect on the model.

Predator control simulations indicated that protecting 30% of the population annually increased the growth rate to 0.988 but was not sufficient to stabilise the population (Figure 2). Predator control of at least 48% of the breeding population annually was required to get a stable or increasing population. If the estimated value for survival from post-fledging to year one was increased to 0.6, only 36% of the population needed protection in order to reverse the decline.

Banded dotterels

The banded dotterel population model predicted an annual population growth rate of 1.006 over 50 years (Figure 1). Juvenile survival had the most influence on the model and a decrease in this parameter by 0.05 resulted in negative population growth (Table 4). Chick and adult survival rates were also important parameters.

Renesting rates had only a small impact on population growth if decreased by 10%, but if increased by 10% this parameter had the biggest effect on population growth rate. To examine the effect of renesting rate on the model predictions, we reset banded dotterel renesting rates from 59% to only 37% (equivalent to the renesting rate in the black-fronted tern model). The resulting population growth rate was 0.978.

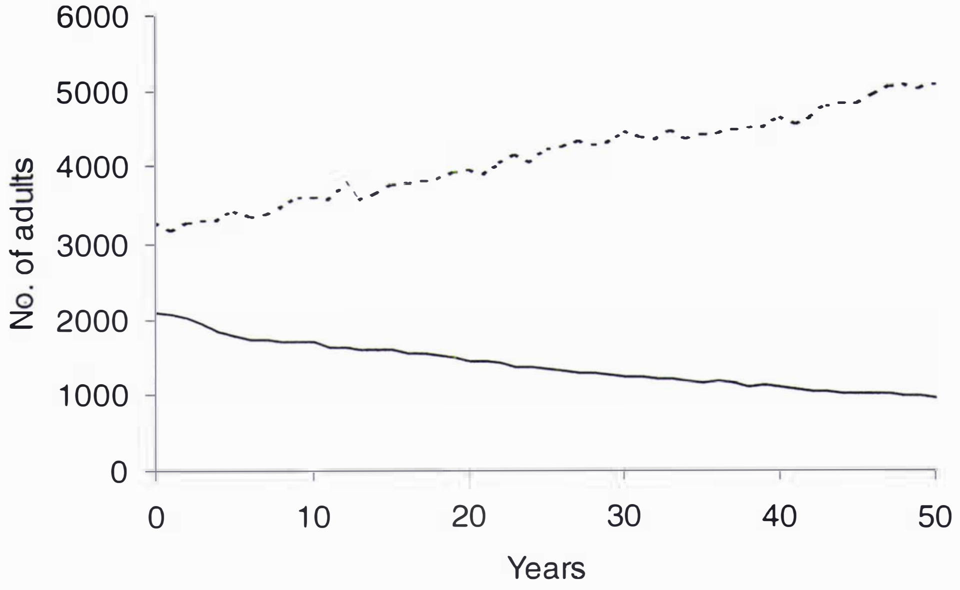

Figure 1: Simulation results for banded dotterel (dotted line) and black-fronted tern (solid line) population models over fifty years.

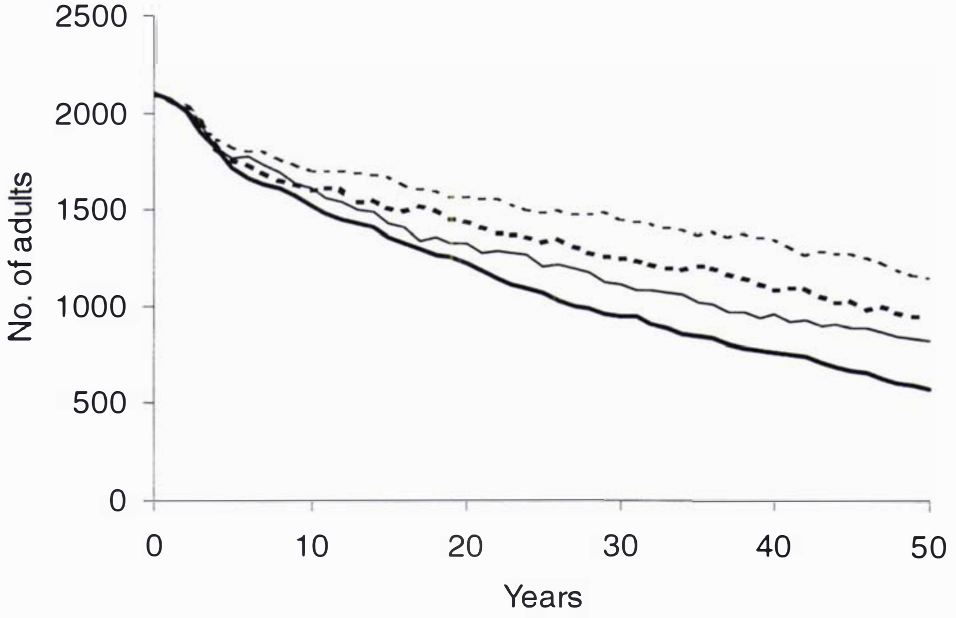

Figure 2: Black-fronted tern population growth where 30% of the population is protected from predators: annually (fine dotted line, $r = 0.988$), two out of three years (bold dotted line, $r = 0.984$), every second year (thin line, $r = 0.981$) and no control (bold line, $r = 0.974$).

Table 3: Sensitivity analysis results for black-fronted tern population model. Starting population size was 2100 adults. Data presented are the base and new value for each parameter varied, mean and standard deviation (SD) of ending population size after 50 years over 50 simulations, population growth rate *r*, and percent change in *r* from the base model. Where survival rates are greater than 0.5, the 10% change is based on 10% of (1-survival rate). Year 1, 2 and 3 age groups are abbreviated as Y1, Y2 and Y3.

Parameter	**Base value**	**New value**	**Mean**	**SD**	***r***	**% change *r***
Decrease adult survival 10%	0.88	0.87	352	66	0.965	-0.93
Decrease survival post-fledge to Y1	0.54	0.49	366	89	0.966	-0.85
Reduce % adults breeding	1	0.9	370	72	0.966	-0.83
Decrease chick survival 10%	0.37	0.33	374	79	0.966	-0.81
Decrease renesting 10%	2.3*	2.5*	395	70	0.967	0.70
Decrease egg survival 10%	0.60	0.56	433	81	0.969	-0.52
Decrease post-fledge survival 10%	0.87	0.86	494	90	0.971	-0.25
Decrease Y1-2 survival 10%	0.85	0.83	513	87	0.972	-0.18
Reduce adult age	26	24	523	97	0.973	-0.14
Increase chick survival SD	0.1	0.15	526	146	0.973	-0.13
Increase post-fledge survival SD	0.1	0.15	532	116	0.973	-0.10
Decrease % Y3 breeders 10%	0.75	0.73	550	122	0.974	-0.03
Decrease post-fledge survival SD	0.1	0.05	550	109	0.974	-0.03
No change			**560**	**121**	**0.974**	**0**
Increase egg survival SD	0.1	0.15	566	127	0.974	0.02
Decrease % Y2 breeders 10%	0.25	0.23	567	99	0.974	0.03
Increase % Y3 breeders 10%	0.75	0.77	568	121	0.974	0.03
Decrease chick survival SD	0.1	0.05	572	81	0.974	0.04
Decrease egg survival SD	0.1	0.05	579	112	0.975	0.07
Increase % Y2 breeders 10%	0.25	0.28	583	110	0.975	0.08
Increase post-fledge survival 10%	0.87	0.88	583	113	0.975	0.08
Increase Y1-2 survival 10%	0.85	0.86	597	136	0.975	0.13
Increase adult age	26	28	606	125	0.975	0.16
Increase egg survival 10%	0.60	0.64	688	115	0.978	0.41
Increase renesting 10%	2.3*	2.7*	772	165	0.980	0.64
Increase survival post-fledge to Y1	0.54	0.59	821	177	0.981	0.77
Increase chick survival 10%	0.37	0.40	850	174	0.982	0.84
Increase adult survival 10%	0.88	0.89	864	144	0.982	0.87

*renesting rate is a function of egg and chick survival and is expressed here as number of eggs laid/female/year.

Table 4: Sensitivity analysis results for banded dotterel population model. Starting population size was 3300 adults. Data presented are the base and new value for each parameter varied, mean and standard deviation (SD) of ending population size after 50 years over 50 simulations, population growth rate *r*, and percent change in *r* from the base model. Where survival rates are greater than 0.5, the 10% change is based on 10% of (1-survival rate). Year 1 and Year 2 age groups are abbreviated as Y1 and Y2.

Parameter	**Base value**	**New value**	**Mean**	**SD**	***r***	**% change *r***
Decrease juvenile survival 10%	0.46	0.41	1,831	784	0.988	-1.80
Decrease chick survival 10%	0.38	0.34	2,168	693	0.992	-1.46
Decrease adult survival 10%	0.80	0.78	2,324	692	0.993	-1.33
Reduce % adults breeding	1	0.9	2,408	810	0.994	-1.26
Decrease egg survival 10%	0.57	0.53	2,568	981	0.995	-1.13
Decrease renesting 10%	4.6*	4.2*	3,224	1,123	1.000	-0.68
Decrease Y1-2 survival 10%	0.77	0.74	3,795	1,426	1.003	-0.36
Decrease % Y1 breeders 10%	0.75	0.68	3,932	1,221	1.004	-0.28
Reduce adult age	20	18	4,440	1,944	1.006	-0.04
No change			**4,531**	**1,640**	**1.006**	**0**
Increase adult age	20	22	4,869	1,390	1.008	0.14
Increase % Y1 breeders 10%	0.75	0.83	5,304	2,212	1.010	0.32
Decrease egg survival SD	0.1	0.05	5,738	1,839	1.011	0.47
Increase Y1-2 survival 10%	0.77	0.79	5,792	1,751	1.011	0.49
Increase egg survival SD	0.1	0.15	5,889	2,471	1.012	0.53
Increase chick survival SD	0.1	0.15	6,113	3,354	1.012	0.60
Decrease chick survival SD	0.1	0.05	6,374	1,718	1.013	0.69
Increase egg survival 10%	0.57	0.61	7,415	2,320	1.016	0.99
Increase adult survival 10%	0.8	0.82	8,765	2,898	1.020	1.33
Increase chick survival 10%	0.38	0.42	9,518	2,902	1.021	1.50
Increase juvenile survival 10%	0.46	0.51	10,759	3,796	1.024	1.74
Increase renesting 10%	4.6*	5.0*	10,902	3,272	1.024	1.77

*renesting rate is a function of egg and chick survival and is expressed here as number of eggs laid/female/year.

Sensitivity analyses indicated little effect on growth rate for most parameters that were estimated, such as maximum adult age, proportion of first year birds breeding or mortality from year one to year two (Table 4).

Natural history characteristics

The natural history characteristics of both species are summarised in Table 5. Black-fronted terns have shorter incubation and chick-rearing periods than do banded dotterels, which decreases the time breeding black-fronted tern adults are vulnerable to predation. However, banded dotterel annual productivity is far higher than that of black-fronted terns because their offspring are fully independent at fledging, they produce more young per nesting attempt, have a longer breeding season and can successfully raise a second clutch in one season.

Behaviourally, banded dotterels attempt to avoid detection when nesting and have better nest camouflage. In comparison, black-fronted terns remain on their nests for longer and rely on colony-based mobbing of intruders after they are disturbed off their nests (Table 5).

Discussion

Comparisons of survival

Our model for black-fronted terns predicts negative population growth even when optimistic estimates of most parameters are used and when predator control is incorporated. Although our model is based on imperfect estimates of many parameters, the model outputs are consistent with concerns about declines in the black-fronted tern population (Chapter 9). Our model indicates that two of the most critical determinants of population growth rate are adult mortality and survival to year one. In comparison, the banded dotterel model predicted a stable to increasing population.

Despite the higher projected growth rates for the banded dotterel population, the model had lower estimates of egg, juvenile, adult and sub-adult survival and maximum adult age than for black-fronted terns. The predation rates at nests of banded dotterels and black-fronted terns in the Ohau river were almost identical (Chapters 3 and 4), but black-fronted terns suffer slightly higher levels of chick predation than banded dotterels. However, in the models, chick survival was very similar for both species. The simulations suggest that when the two species are subject to the same level of predation pressure, in the same habitat, the banded dotterels survive better.

The higher rate of renesting in the banded dotterel model is probably the primary reason for the difference in predicted growth rates for the two species. Reducing renesting in the banded dotterel model to equivalent of that in the black-fronted tern model resulted in similar growth rate predictions. Banded dotterels do have a higher capacity for renesting than black-fronted terns (Table 5), and the differential renesting rates in the models was designed to reflect this capacity. The ability to renest, produce more young and a shorter generation time are critical factors in allowing banded

Table 5: Natural history characteristics of black-fronted terns and banded dotterels. All descriptions from data in Chapters 3,4,6 & 8, or personal observations. Descriptions marked with * from Marchant and Higgins (1993).

Characteristic	Black-fronted terns	Banded dotterels
Mean # eggs per nest	1.9	2.9
Incubation period	24 days	28 days
Fledge age	3-4 weeks	5-7 weeks
Age at independence	9+ weeks	5+ weeks
Care of young post-fledging	Feeds and defends young	None
Number of replacement nests in a season	Unclear, but can lay at least one replacement nest	Up to 3 replacement nests per season
Maximum number broods raised per season	1	2
Productivity	0.11-0.44 chicks/female/year	0.55-1.72 chicks/female/year
Breeding season	Late September to January	Late August to January
Mean egg size	40.7 x 29.2 mm	34.3 x 24.9 mm*
Breeding habitat	Braided riverbeds of the South Island, sometimes on river terraces	Braided riverbeds, pasture, beaches and estuaries
Egg description	Eggs obvious. Brown or olive-green with black markings.	Eggs well camouflaged. Blue-green to olive-green in colour with black markings.
Nest description	Ranges from no obvious nest to a depression lined with twigs.	Scrape in ground, lined with smalls stones and vegetable matter, eggs often partially covered.
Nest site	Sand, gravel, cobbles or next to boulders, sparsely vegetated.	Sand, gravel or small cobbles, sparsely vegetated.
Use of nest site	Remain at nest for 3-13 days after hatching, defecates at nest site	Leave nest permanently within 48h of hatching
Inter-nest distance	1-100 m apart, in loose colonies	> 40 m
Nest desertion	Abandons eggs permanently; will desert eggs or chicks nocturnally, particularly in response to nocturnal disturbance. Will not return to nest site after predation.	Desertion of eggs or chicks uncommon, will continue incubating at nest after partial-clutch predation.
Chicks	Semi-precocial	Precocial
Hatching interval	Asynchronous hatching, poorer survival in second-hatched chick	Asynchronous hatching, no evidence of differential survival among chicks.
Chick defensive behaviour	At adult alarm call will run slowly then freeze, may hide under vegetation or rocks, will take to water	At adult alarm call, freezes or runs very quickly, will occasionally take to water
Age at first breeding	2	1
Adult weight	92 g	58 g*
Adult defence of eggs	Remains on nest until intruder is < 20 m away, then vigorously dive-bombs, defecates on and loudly calls at intruder. Usually joined by neighbouring terns.	Leaves nest when intruder is > 50 m away. Remains silent and keeps well away from nest until threat has gone.

Adult defence of chicks	Vigorously dive-bombs, defecates on and harshly calls at intruder . Attacks are most vigorous when chicks are youngest. Usually joined by neighbouring terns.	Flies calling loudly from when intruder is > 50 m away and continues until threat has gone. Broken-wing and distraction displays with newly hatched chicks.
Role of female	Shares incubation, brooding and chick-feeding with male	Incubates eggs during the day, shares brooding and guarding chicks with male
Role of male	Shares incubation, brooding and chick-feeding with male	Incubates eggs at night, shares brooding and guarding chicks with male
Wintering grounds	Coastal South Island, some in North Island	Coastal areas of both main islands, also Australia
Diet	Insects, crustaceans, fish and worms	Molluscs, insects, crustaceans, seeds and fruit

dotterels to survive well in the same environment where black-fronted terns are doing poorly.

For New Zealand forest birds, Innes and Hay (1991) suggest that some species have made behavioural adaptations since the arrival of mammalian predators and these changed predator response behaviours have enhanced survival. Pierce (1986) argues that inherent behavioural differences between pied stilts and black stilts are, in part, responsible for the greater relative breeding success of pied stilts. Black-fronted terns and banded dotterels exhibit different behavioural responses to predators. Black-fronted terns rely on dive-bombing and mobbing to drive off predators, a strategy that is effective for deterring avian predators (Sordahl 1981) but is probably less effective against mammalian predators. In comparison, banded dotterels attempt to avoid detection when nesting, and use broken wing displays to lure predators away from newly hatched chicks. We suggest, however, that the behavioural differences between banded dotterels and black-fronted terns contribute very little to the differential survival rates observed on the Ohau River. At nests of braided river birds, all except one of 65 videoed predations by mammals occurred at night (Sanders and Maloney 2002). Black-fronted terns show no response to intruders at night (RJK pers. obs.) and video records indicate that banded dotterels probably respond similarly. Therefore, despite anti-predator behavioural differences, it is more likely that the higher productivity of banded dotterels is the primary factor leading to higher banded dotterel survival.

Comparisons of survival between black and pied stilts found that predation rates were higher at black rather than pied stilt nests (Pierce 1986). This was partly attributed to different nesting habitats of the two species within the braided river systems, because predators were found at higher densities in the habitat type selected by black stilts. Banded dotterels and black-fronted terns nest in very similar habitats, and nests of the two species can be interspersed. The similar rates of nest predation suggest these two species are exposed to the same intensity of predation. Pierce (1986) also suggested that the shorter fledging period and colonial behaviour of pied stilts increased the survival of pied over black stilts. In comparison, black-fronted terns have a shorter fledging period and colonial behaviour yet have lower survival than banded dotterels. Colonial breeding in black-fronted terns probably results in higher mortality rates. Black-fronted terns are prone to deserting eggs and occasionally chicks, and presence of a predator in a colony may cause this desertion (Chapter 4). In addition, video studies and intensive nest monitoring suggest that, once a predator discovers a black-fronted tern colony, it may keep coming back until all the nests are destroyed (Chapter 4). Solitary nesting banded dotterels are not affected by what happens at neighbouring nests.

Conversely, colonial breeding provides an advantage for managing black-fronted tern populations. Localised predator control at a colony is logistically easier, and probably offers a higher degree of protection, than attempting to control predators along the entire length of a river.

The difference in survival between banded dotterels and black-fronted terns is consistent with analyses of extinction-risk factors. Species with higher productivity, shorter generation time, smaller body size and shorter evolutionary age are more likely to have lower extinction risk (Blackburn et al. 1996, Bennett and Owens 1997, Gaston and Blackburn 1997) or are better at establishing in new locations (Veltman et al. 1996, Cassey 2001). The majority of banded dotterels migrate to Australia annually (Pierce 1999) and possibly have a less isolated evolutionary history than black-fronted terns (Dowding and Murphy 2001).

Identifying research needs

The black-fronted tern model was most sensitive to adult survival rates. The rate used in the model was estimated from only four years of mark-recapture study but was similar to rates reported for other long-term and more comprehensive studies of terns

(Spendelow and Nichols 1989, Nisbet 2002, Spendelow et al. 2002). The model was also sensitive to changes in juvenile mortality, a parameter for which we have no data. Nichols et al. (1990) estimated that annualised survival of roseate terns from fledging to first breeding was only 40% of annual adult survival rates. The estimates we have used here from fledging to first breeding, when converted to annual survival rates, are equivalent to over 65% of adult survival rates. This suggests our estimates of survival used in the model are probably optimistic.

Reading bands on black-fronted terns is notoriously difficult, and distance-readable metal bands need to be trialled in order to have enough combinations to band each bird individually. In the absence of this, further work following up the currently banded population would enhance the existing adult survival estimates.

The black-fronted tern model was also sensitive to egg and chick survival rates. These vital rates can be increased by reducing predation, which is the major cause of mortality over a range of life stages (Chapters 4, 5 and 8). Thus, the most effective management action to reverse any population decline would be to implement predator control. The predator control modelled here showed that even protecting a logistically possible proportion of breeding birds would not stabilise the population. However, if the data on which the model parameters were based were in any way underestimates of black-fronted tern survival, predator control may have a stronger effect on population survival than modelled here.

The effects of predator control on black-fronted tern breeding success or survival have not been tested. Implementation of any control programme needs to use an adaptive management approach to facilitate continuous improvement of management (Walters 1986, Lancia et al. 1996). Trapping is the most commonly used method in braided river systems but there is debate over its effectiveness at increasing breeding success (Keedwell et al. 2002). Implementing predator control at some black-fronted tern colonies in a replicated, experimental fashion, and comparing subsequent breeding success with that of uncontrolled colonies is one of the first steps necessary to begin effective management of black-fronted tern populations.

The contribution of renesting to black-fronted tern annual productivity needs to be better understood. Renesting had a relatively strong effect on predicted growth rate but our model used only an estimate of renesting impact. Improved understanding of renesting in least terns led to better estimates of productivity and population dynamics (Massey and Fancher 1989). Aspects of renesting, such as the renesting rate, frequency of attempts within a season, success of replacement nests compared to first nests, probability of renesting in relation to timing of chick or egg loss and temporal changes in success are not known for black-fronted terns but may have a substantial influence on estimates of annual productivity.

Both adult and juvenile mortality for banded dotterels had to be estimated from other species because of a lack of data. Several thousand banded dotterels have been colour-banded since the 1970s (Pierce 1989, Marchant and Higgins 1993, Pierce 1999), and some of these data have been extensively analysed to determine population movements (Pierce 1999). However, none of this banding work has been used to estimate rates of juvenile or adult survival. Analysis of these data should be a first step to developing better models of banded dotterel survival.

This study has not examined how other factors such as habitat availability, water flows and food supply affect survival rates of banded dotterel and black-fronted tern populations. Black-fronted terns are a more specialised species that depend solely on braided riverbeds for nesting habitat and primarily on braided rivers for food. Specialist species are more likely to be affected by habitat changes than are generalists (Owens and Bennett 2000). For example, the wrybill (*Anarhynchus frontalis*) is a plover species with similar biology to that of the banded dotterel but is entirely reliant on the braided river habitat. Wrybills are classified as vulnerable (BirdLife International 2000) and declines in the population may be linked to reduction in their specific breeding and feeding habitat requirements, as well as the impacts of predation (Dowding and Murphy 2001). Future studies on black-fronted terns and banded dotterels need to take into account the effects of how changing the water regime and habitat affects survival rates, particularly of black-fronted terns. There is some indication that removal of weed infestations can increase habitat availability for both black-fronted terns and banded dotterels (Maloney et al. 1999), but how current levels of habitat change affect population survival are not clear.

The strengths of population viability analysis are in assessing relative outcomes of simulations, rather than making quantitative predictions of population sizes and trends (Beissinger and Westphal 1998, Reed et al. 2002), particularly for preliminary models where the data are scarce (Akcakaya and Sjogren-Gulve 2000). These models are far from comprehensive, but even these preliminary models provide guidance on the future direction of research and management efforts. We suggest that black-fronted terns urgently require further research, and development of effective predator control techniques is the first step to ensuring the continued survival of black-fronted terns and other braided river bird species.

Acknowledgements

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Concluding remarks

Black-fronted tern in flight

Concluding remarks

This thesis originally arose in response to the lack of information about rates and causes of chick mortality in braided river systems. It evolved into a study that addresses this issue but also one that addresses the urgent knowledge gap on black-fronted terns and assesses the impacts of predators on braided river birds. Below, I highlight some of the major findings from my work and make a series of recommendations for further research and management on the braided rivers.

Banded dotterels are one of the most widely studied braided river bird species, but this study highlights aspects of its survival that need further research. We do not have good estimates of adult annual survival, or of survival from fledging to first breeding. Formal analysis of the existing colour-banding and band resighting data, using a mark-recapture programme such as MARK, would improve current estimates.

The impact of predators on banded dotterel chicks is also poorly understood. In Chapter 2, use of harness-attached radio-transmitters indicated predators are an important cause of mortality, but the rates of mortality of chicks due to predation and the relative impact of different predator species could not be clearly determined using this method. Predators, particularly cats, are a major cause of mortality for black-fronted tern chicks (Chapter 5) and cats have been videoed eating banded dotterel chicks (Sanders and Maloney 2002). In addition, the pattern of increased fledging success in 2000 for both banded dotterels and black-fronted terns (Chapters 3 and 4) suggests that the impacts of predation on both species are similar. Future studies looking at banded dotterel breeding success need to monitor survival through to fledging, not just hatching, if the full effect of predation on banded dotterel survival and productivity is to be accurately measured.

Use of video cameras provided evidence that monitoring banded dotterel nests does not affect survival. Although predators are the main cause of mortality of nesting attempts on the braided rivers, they are unlikely to use human scent trails to locate the nests. Accordingly, I suggest that continued monitoring of all species of braided river bird nests is safe and does not appreciably affect survival rates. This study also illustrates how use of video cameras does not affect nest survival either. Video cameras provide an invaluable tool for unambiguously identifying predators and measuring predation rates and should continue to be part of management and research on the braided rivers.

Although our knowledge of black-fronted terns remains far from complete, my research has provided valuable information on many aspects of black-fronted tern biology. Chapters 4, 6 and 7 detail the first comprehensive study investigating rates of egg and chick survival. Aspects of natural history such as egg sizes, changes in egg density through time, chick weights at hatching and fledging, incubation period and fledging period have been comprehensively documented. I have also provided the first estimates of adult survival rates in black-fronted terns, and a preliminary method for sexing adult terns.

This research quantifies the impact of predators on black-fronted tern survival and provides strong evidence that the species is indeed in decline. In the Ohau river, Norway rats, feral cats and to a lesser degree hedgehogs significantly impact on survival of black-fronted terns. Predators continued to have an impact on survival after fledging, with newly fledged juveniles suffering high predation, and a number of adults killed on the nest. Stoats were less important as predators in the Ohau River but they are found at higher densities in other rivers (Keedwell and Brown 2001). There is evidence that that the relative importance of different predators on the Ohau may be different from that on other braided rivers (J. Dowding, pers. comm.). Further research is urgently needed to determine whether the rates of productivity I report here are similar across other rivers and years. If my estimates of productivity are representative of nationwide reproductive success, and the population viability analysis simulations are realistic, then black-fronted terns will require management to prevent continuing decline and possible extinction in the near future. Until further research confirms my results, a conservative approach should be taken and the species ought to be managed assuming the population is in decline.

This research highlights how different endemic species can have vastly different survival outcomes when faced with the same pressures. Black-fronted terns are poorly equipped to cope with the high predation environment of the braided rivers. In Chapters 6 and 7, I suggest black-fronted terns show signs of having evolved in a low predation environment, with potentially longer incubation periods and slower chick growth than in other comparable tern species. Additional disadvantages are that colonial nesting leads to higher mortality and hatching asynchrony leads to differential chick survival. Finally, the anti-predator behaviours of the terns are not effective against mammals. Banded dotterels, in comparison, still suffer high predation but have higher productivity because of breeding strategies that are more suited to cope with frequent egg and chick loss. The comparative approach used in Chapter 10 allows better understanding of how differences in biology affect the response of a population to high predation rates.

This study shows that concern over the ongoing survival of black-fronted terns is well founded (Maloney et al. 1997, Taylor 2000). Predator control is probably the most effective management tool for increasing productivity and survival, and it will increase survival of other species of braided river birds. Additional funding and research effort is needed to better understand the dynamics of braided river communities. Reducing predation rates will be beneficial to river bird species, but until the relationships between rabbit abundance, predator abundance, predator guild and nest predation rates are better understood, developing the most cost-effective and efficient predator control strategy will be hindered. A broad scale approach is also necessary to assess the ongoing effects of rabbit haemorrhagic disease on braided river fauna (Chapter 4).

Based on the results of my research, I recommend the following priorities for future research and management:

1) **Implement a nationwide survey of the black-fronted tern population during the breeding season to estimate minimum population size.** See Chapter 10.
2) **Continued monitoring of key locations (winter and summer counts) to monitor changes in the black-fronted tern population size.** See Chapter 10.
3) **Implement a controlled experiment monitoring the effects of predator control on breeding success at black-fronted tern colonies.** Use a replicated experimental design, for example: select four colonies on each of the Ohau, Tekapo and Ahuriri Rivers. Apply predator control to half the colonies on each river and measure egg and chick success at each colony. Continue for at least three years. A structured experiment such as this provides the option to trial and compare different predator control methods.
4) **Implement a broad scale collaborative research programme examining inter-relationships between predator abundance, rabbit abundance and nest predation rates, and the impacts of changes to rabbit abundance and predator guild composition.** Such a project is crucial to better understanding the dynamics of the braided river communities. This project requires collaboration between a number of organisations, such as the Department of Conservation, Landcare Research, universities and other research organisations.
5) **Continue to improve estimates of black-fronted tern adult and immature survival rates.** Continue recording sightings of black-fronted terns that are

currently banded. Trial the use of distance readable alphanumeric bands or similar bands, and if applicable, band more fledglings to increase estimates of sub-adult survival.

6) **Test the accuracy of using adult body measurements for sexing black-fronted terns.** More adults need to be measured and definitely sexed to validate the method suggested in Chapter 4.
7) **Use existing banding records and resightings to improve estimates of banded dotterel adult and sub-adult survival.**

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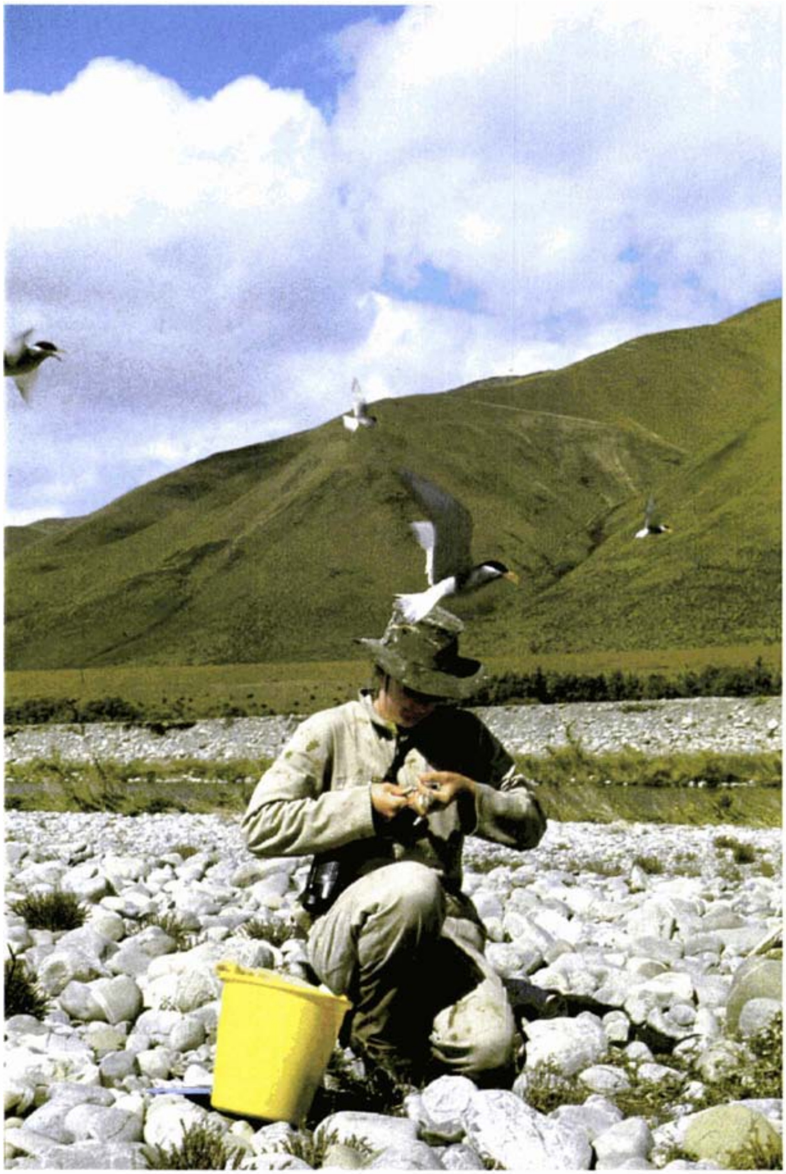
Appendices



Getting dive-bombed by black-fronted terns

Appendix 1: Locations and breeding success of black-fronted tern colonies on the Ohau River

Colony locations

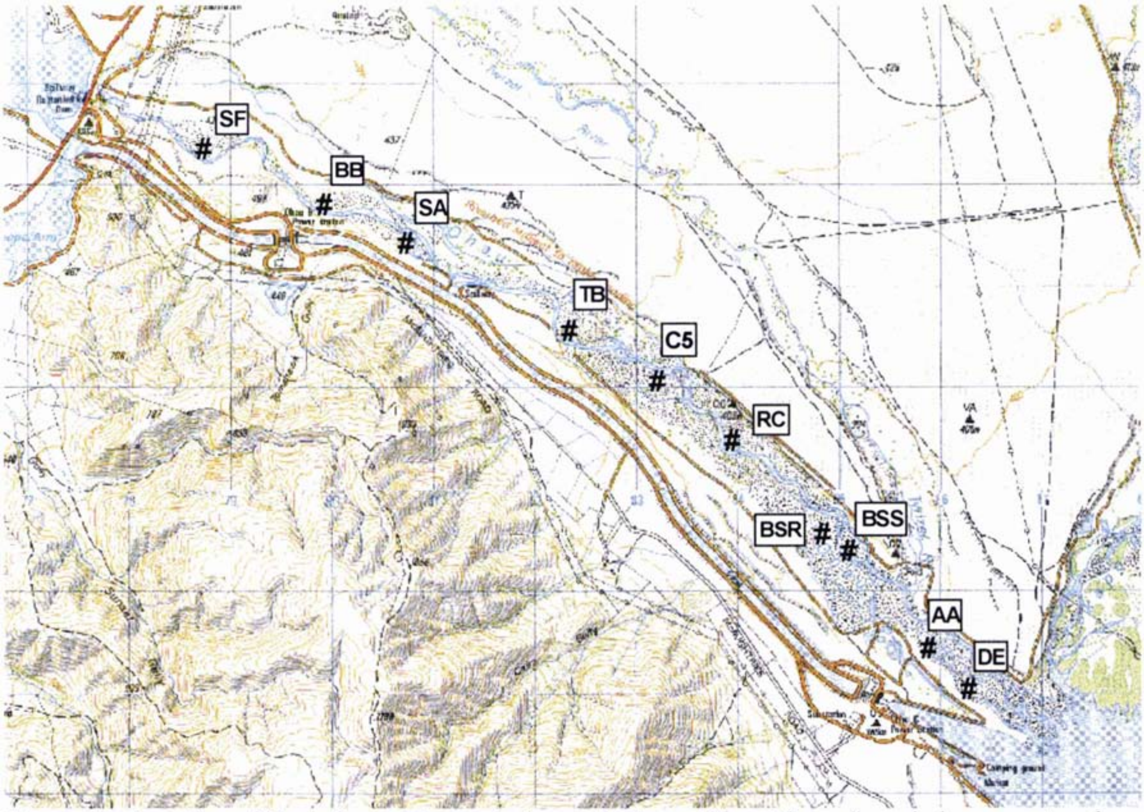


Figure 1: Location of black-fronted tern colonies on the lower Ohau River. # symbol represents colony location, colony code in box adjacent to symbol. Map is from 1:50 000 topographic maps H38 and H39.

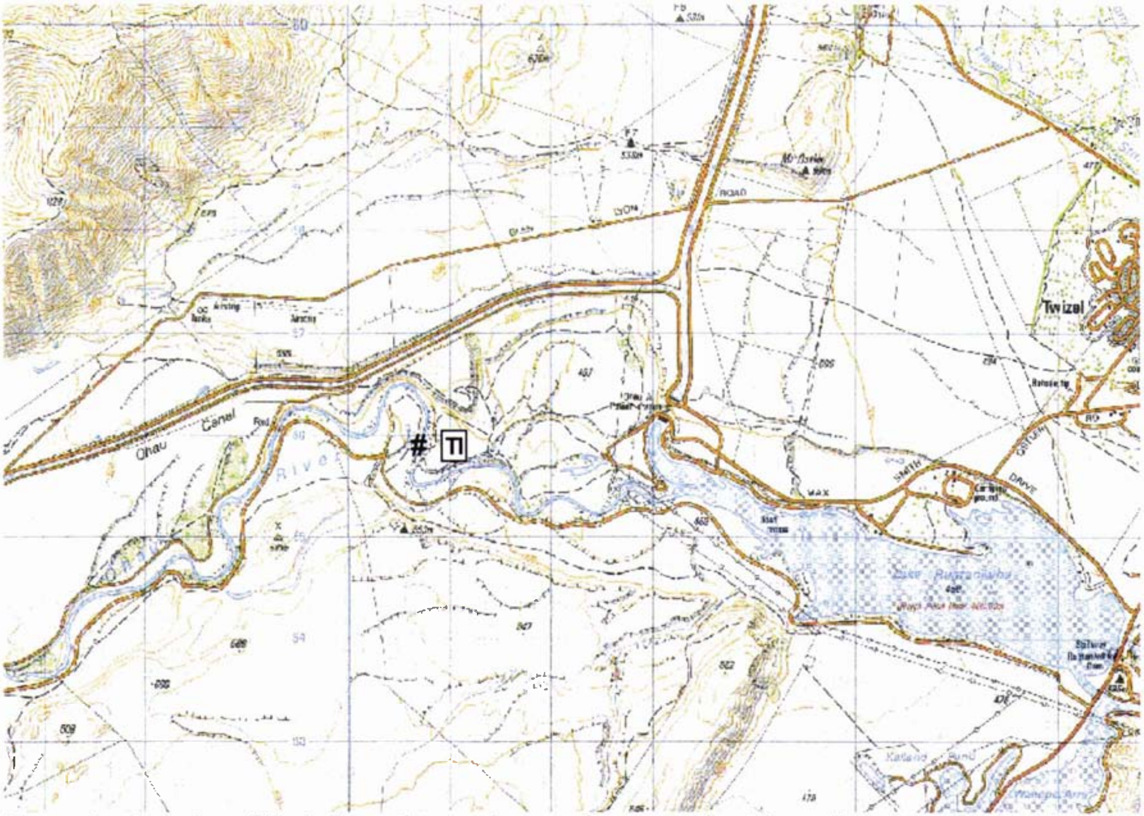


Figure 2: Location of black-fronted tern colony on the upper Ohau River. # symbol represents colony location, colony code in box adjacent to symbol. Map is from 1:50 000 topographic map H38.

Hatching and fledging success at black-fronted tern colonies, 1998-2000

Table 1: Hatching success at black-fronted tern colonies on the Ohau River, 1998-2000. Codes in top row are colony locations. Fate categories are: n – number of nests; H – % nests hatching one or more eggs; P – % depredated nests that failed to hatch any eggs; D – % nests deserted; O – % nests that failed to hatch due to flooding or other causes, or nest fate was undetermined. Note that solitary nests are not included in the table. In 1998, some colonies were found not found until partway through the season (BSR, RC). As a result, hatching success could not be calculated for the entire colony and these colony outcomes are not included in the table.

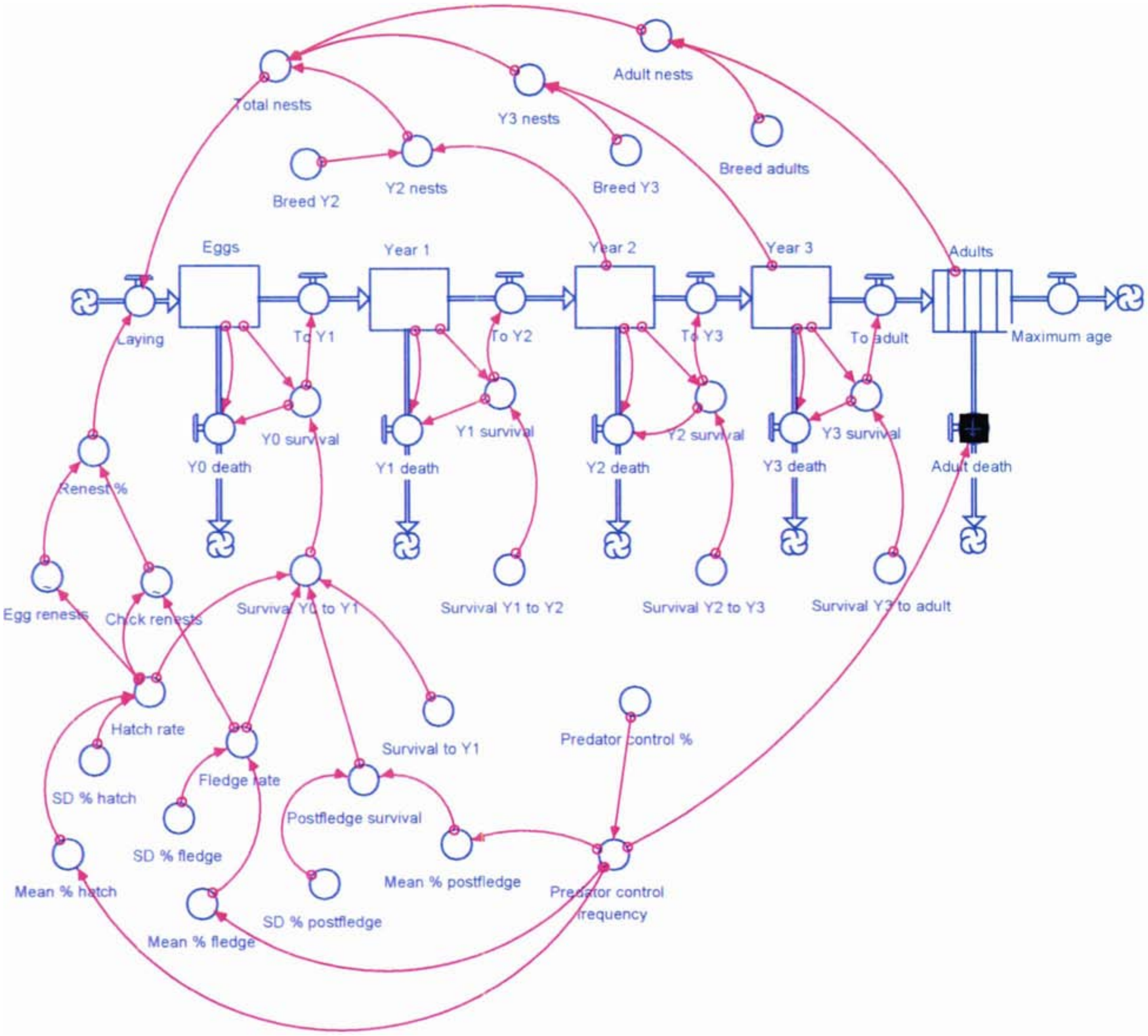
Year	Fate	AA	BB	BSR	BSS	C5	DE	RC	SA	SF	TB	TI
1998	n	23	11	-	-	6	30	-	-	41	18	108
	H	17.4	63.6	-	-	66.7	56.7	-	-	36.6	16.7	52.8
	P	47.8	9.1	-	-	33.3	16.7	-	-	53.7	33.3	16.7
	D	34.8	27.3	-	-	0	26.7	-	-	9.8	50.0	20.4
	O	0	0	-	-	0	0	-	-	0	0	10.2
1999	n	59	5	47	31	-	17	64	10	-	-	223
	H	47.5	0.0	21.3	64.5	-	17.6	71.9	20.0	-	-	74.4
	P	25.4	60.0	59.6	6.5	-	47.1	3.1	50.0	-	-	1.3
	D	23.7	40.0	17.0	29.0	-	35.3	18.8	20.0	-	-	17.9
	O	3.4	0	2.1		-	0	6.2	10.0	-	-	6.3
2000	n	-	-	28	56	-	68	-	-	78	18	68
	H	-	-	0	71.4	-	47.1	-	-	64.1	33.3	0
	P	-	-	96.4	10.7	-	14.7	-	-	1.3	55.6	97.1
	D	-	-	3.6	17.9	-	36.8	-	-	32.1	11.1	2.9
	O	-	-	0	0	-	1.5	-	-	2.6	0	0

Table 2: Fledging success at black-fronted tern colonies on the Ohau River, 1998-2000. Codes in top row are colony locations. Fate categories are: n – number of chicks hatched; F – % chicks fledged. Where some chick fates were unknown, fledging success is shown as a range.

Year	Fate	AA	BB	BSR	BSS	C5	DE	RC	SA	SF	TB	TI
1998	n	8	13	-	-	8	30	-	-	28	6	97
	F	0	0	-	-	50	0	-	-	36	50	36
1999	n	49	0	19	34	-	5	82	3	-	-	283
	F	10	-	11	15	-	0	9	67	-	-	36-50
2000	n	-	-	0	69	-	57	-	-	93	13	0
	F	-	-	-	29	-	46	-	-	26-40	15	-

Appendix 2: Black-fronted tern population model

Stella model map



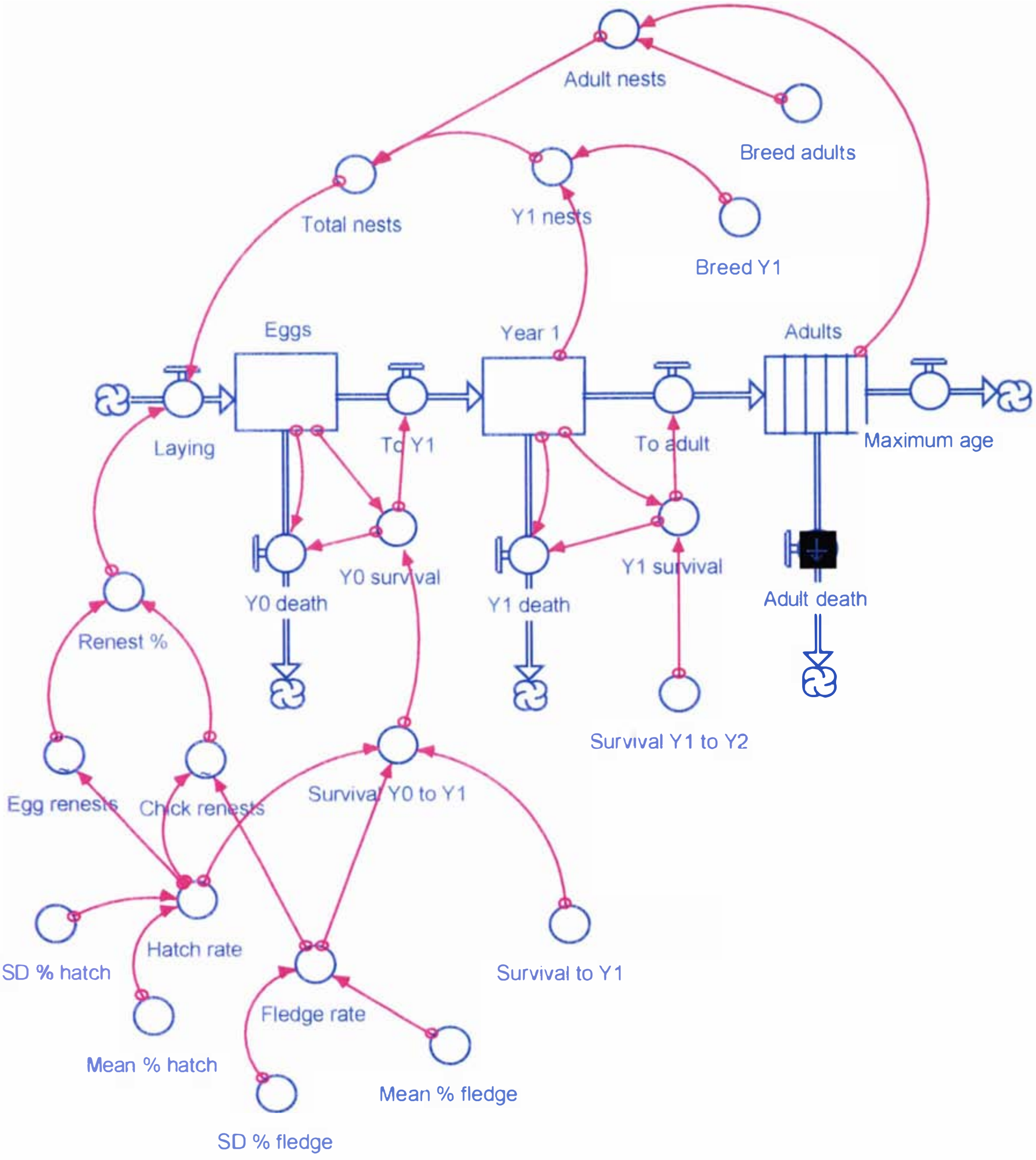
Stella model equations

```
Adults(t) = Adults(t - dt) + (To_adult - Maximum_age - Adult_death) * dt
INIT Adults = 11, 12, 14, 16, 18, 20, 23, 26, 30, 34, 38, 44, 50, 56, 64, 73, 83, 94, 107, 121,
        138, 157, 178, 202, 230, 261
        TRANSIT TIME = 26
        INFLOW LIMIT = ∞
        CAPACITY = ∞
INFLOWS:
        To_adult = Y3_survival
OUTFLOWS:
        Maximum_age = CONVEYOR OUTFLOW
        Adult_death = LEAKAGE OUTFLOW
        LEAKAGE FRACTION = 0.12*(1-Predator_control_frequency) + 0.11 *
        Predator_control_frequency
        NO-LEAK ZONE = 0
Eggs(t) = Eggs(t - dt) + (Laying - To_Y1 - Y0_death) * dt
INIT Eggs = 823
INFLOWS:
        Laying = Total_nests*1.86*(1+Renest_%)
OUTFLOWS:
        To_Y1 = Y0_survival
        Y0_death = Eggs-Y0_survival
Year_1(t) = Year_1(t - dt) + (To_Y1 - To_Y2 - Y1_death) * dt
INIT Year_1 = 261
INFLOWS:
        To_Y1 = Y0_survival
OUTFLOWS:
        To_Y2 = Y1_survival
        Y1_death = Year_1-Y1_survival
Year_2(t) = Year_2(t - dt) + (To_Y2 - To_Y3 - Y2_death) * dt
INIT Year_2 = 261
INFLOWS:
        To_Y2 = Y1_survival
OUTFLOWS:
        To_Y3 = Y2_survival
        Y2_death = Year_2-Y2_survival
Year_3(t) = Year_3(t - dt) + (To_Y3 - To_adult - Y3_death) * dt
INIT Year_3 = 261
INFLOWS:
        To_Y3 = Y2_survival
OUTFLOWS:
        To_adult = Y3_survival
        Y3_death = Year_3-Y3_survival
Adult_nests = Adults*Breed_adults*0.5
Breed_adults = 1
Breed_Y2 = 0.25
Breed_Y3 = 0.75
Fledge_rate = NORMAL(Mean_%_fledge,SD_%_fledge)
Hatch_rate = NORMAL(Mean_%_hatch,SD_%_hatch)
Mean_%_fledge = 0.366*(1-Predator_control_frequency) + 0.5 * Predator_control_frequency
Mean_%_hatch = 0.6*(1-Predator_control_frequency) + 0.72 * Predator_control_frequency
Mean_%_postfledge = 0.87*(1-Predator_control_frequency) + 0.93 Predator_control_frequency
Postfledge_survival = NORMAL(Mean_%_postfledge,SD_%_postfledge)
Predator_control_% = 0
```

Predator_control_frequency = if(Time/1=int(time/1)) then Predator_control_% else 0
Renest_% = Chick_renests+Egg_renests
SD_%_fledge = 0.1
SD_%_hatch = 0.1
SD_%_postfledge = 0.1
Survival_to_Y1 = 0.54
Survival_Y0_to_Y1 = Fledge_rate*Hatch_rate*Postfledge_survival*Survival_to_Y1
Survival_Y1_to_Y2 = 0.85
Survival_Y2_to_Y3 = 0.88
Survival_Y3_to_adult = 0.88
Total_nests = Adult_nests+Y2_nests+Y3_nests
Y0_survival = INT(Eggs*Survival_Y0_to_Y1)
Y1_survival = INT(Year_1*Survival_Y1_to_Y2)
Y2_nests = Year_2*Breed_Y2*0.5
Y2_survival = INT(Year_2*Survival_Y2_to_Y3)
Y3_nests = Year_3*Breed_Y3*0.5
Y3_survival = INT(Year_3*Survival_Y3_to_adult)
Chick_renests = GRAPH(Hatch_rate*(1-Fledge_rate))
    (0.00, 0.002), (0.1, 0.03), (0.2, 0.055), (0.3, 0.075), (0.4, 0.095), (0.5, 0.12), (0.6, 0.14), (0.7, 0.165), (0.8, 0.185), (0.9, 0.205), (1, 0.23)
Egg_renests = GRAPH(Hatch_rate)
    (0.00, 0.605), (0.1, 0.545), (0.2, 0.49), (0.3, 0.43), (0.4, 0.365), (0.5, 0.295), (0.6, 0.24), (0.7, 0.175), (0.8, 0.11), (0.9, 0.06), (1, 0.00)

Appendix 3: Banded dotterel population model

Stella model map



Stella model equations

```
Adults(t) = Adults(t - dt) + (To_adult - Maximum_age - Adult_death) * dt
INIT Adults = 5,7,9,1215,20,26,33,43,56,73,94,122,159,207,268,348,452,588,763
        TRANSIT TIME = 20
        INFLOW LIMIT = ∞
        CAPACITY = ∞
INFLOWS:
        To_adult = Y1_survival
OUTFLOWS:
        Maximum_age = CONVEYOR OUTFLOW
        Adult_death = LEAKAGE OUTFLOW
        LEAKAGE FRACTION = 0.2
        NO-LEAK ZONE = 0
Eggs(t) = Eggs(t - dt) + (Laying - To_Y1 - Y0_death) * dt
INIT Eggs = 9359
INFLOWS:
        Laying = Total_nests*2.9*(1+Renest_%)
OUTFLOWS:
        To_Y1 = Y0_survival
        Y0_death = Eggs-Y0_survival
Year_1(t) = Year_1(t - dt) + (To_Y1 - Y1_death - To_adult) * dt
INIT Year_1 = 726
INFLOWS:
        To_Y1 = Y0_survival
OUTFLOWS:
        Y1_death = Year_1-Y1_survival
        To_adult = Y1_survival
Adult_nests = Adults*Breed_adults*0.5
Breed_adults = 1
Breed_Y1 = 0.75
Fledge_rate = NORMAL(Mean_%_fledge,SD_%_fledge)
Hatch_rate = NORMAL(Mean_%_hatch,SD_%_hatch)
Mean_%_fledge = 0.381
Mean_%_hatch = .57
Renest_% = Chick_renests+Egg_renests
SD_%_fledge = 0.1
SD_%_hatch = 0.1
Survival_to_Y1 = 0.46
Survival_Y0_to_Y1 = Fledge_rate*Hatch_rate*Survival_to_Y1
Survival_Y1_to_Y2 = 0.77
Total_nests = Adult_nests+Y1_nests
Y0_survival = INT(Eggs*Survival_Y0_to_Y1)
Y1_nests = Year_1*Breed_Y1*0.5
Y1_survival = INT(Year_1*Survival_Y1_to_Y2)
Chick_renests = GRAPH(Hatch_rate*(1-Fledge_rate))
        (0.00, 0.035), (0.1, 0.07), (0.2, 0.115), (0.3, 0.169), (0.4, 0.215), (0.5, 0.27), (0.6, 0.325),
        (0.7, 0.38), (0.8, 0.45), (0.9, 0.515), (1, 0.6)
Egg_renests = GRAPH(Hatch_rate)
        (0.00, 0.9), (0.1, 0.805), (0.2, 0.71), (0.3, 0.62), (0.4, 0.535), (0.5, 0.455), (0.6, 0.365),
        (0.7, 0.275), (0.8, 0.18), (0.9, 0.095), (1, 0.00)
```