Breeding movements and post-breeding dispersal of Black-fronted terns/Tarapirohe (*Chlidonias albostriatus*) in the Mackenzie Basin

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Black-fronted terns/Tarapirohe (*Chlidonias albostriatus*) are endemic to New Zealand, where they are currently listed as a nationally endangered species due to their small and declining population. They breed almost exclusively in braided rivers in the east of the South Island, where they are vulnerable to several threats, particularly introduced mammalian predators. Current conservation is focused almost exclusively on controlling mammalian predators around black-fronted tern colonies. Conservation actions away from breeding colonies are hindered by large knowledge gaps around habitat preferences while foraging, foraging range, and migration routes away from colony sites and significant wintering areas.

This study used GPS trackers to follow the movements of black-fronted terns, the first time this technology has been applied to this species. In November and December 2020, 34 black-fronted terns were caught and fitted with GPS devices in colonies in the Cass and Ohau rivers of the Mackenzie Basin. During the 2020/2021 breeding season, these terns primarily foraged in high-producing exotic grassland (irrigated paddocks) and avoided areas of low producing and depleted grassland. While foraging, the terns spent 87.6% of their time within 10 km of the breeding colonies and >99% of their time within 25 km of their breeding colonies. One individual black-fronted tern was tracked to 92.2 km from its breeding colony, visiting three major river systems in 24 hours. The mean GPS point distance from the breeding colony was significantly higher for terns from the Ohau compared to terns from the Cass, likely due to favoured foraging areas of high producing exotic grassland being further from the Ohau colony than this habitat is from the Cass colony. Terns from both colonies were found to have nocturnal roosting areas at river deltas near their respective colonies, the first evidence of breeding black-fronted terns roosting away from their breeding areas at night.

Following the breeding season, the terns left the Mackenzie Basin by flying overland to the lower Rangitata River or down the Waitaki River to its lower reaches. Before the GPS device batteries failed the terns spent time in and around the lower reaches of east coast braided rivers, particularly the lower Rangitata River. Further research is required to gain an understanding of black-fronted tern movements year-round, particularly during winter. The results of this study indicate that areas of high producing exotic grassland within 10 km of breeding colonies are important to breeding black-fronted terns, as are nocturnal roosts at nearby river deltas. These identified areas should be prioritised for new conservation actions.

Keywords: Black-fronted tern, *Chlidonias albostriatus*, GPS tracker, habitats use, foraging range, dispersal, Cass River, Ohau River, Mackenzie Basin

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Chapter 1

General Introduction

Adult black-fronted tern. Andrej Chudý, Flickr (CC BY-NC-SA 2.0).

New Zealand has an isolated geographical history, having been separated from other land masses for c. 80 million years (Keye, 2008). This isolation has meant that New Zealand's flora and fauna have evolved high levels of endemism (Duncan & Blackburn, 2004). In addition, several New Zealand ecosystems are considered internationally rare, one of which is the braided river system (Gray & Harding, 2007). Characterised by high levels of biodiversity (Tockner et al., 2006), braided rivers are complex and dynamic river systems that flow in multiple, mobile channels across a gravel floodplain (Gray & Harding, 2007). Although once widespread, most braided river systems around the world have been highly modified and today bear little resemblance to their highly dynamic natural state (Tockner et al., 2006). However, in New Zealand braided rivers remain largely unmodified and still support a diverse range of flora and fauna (O'Donnell & Hoare, 2011). Included in this diversity are six species of endemic birds in the order Charadriiformes that rely largely on braided river systems for breeding: black stilt (*Himantopus novaezelandiae*), wrybill – (*Anarhynchus frontalis*), South Island pied oystercatcher (*Haematopus finschi*), black-billed gull – (*Larus bulleri*), banded dotterel – (*Charadrius bicinctus*), and black-fronted tern – (*Chlidonias albostriatus*) (Bell, 2017; O'Donnell & Hoare, 2011; Sagar, 2013).

The first black-fronted tern description was based on a specimen collected in 1832 in Queen Charlotte Sound, Marlborough (Aidala & Hauber, 2011). This description was by Johann Reinhold Forster and used the name *Sterna antarctica*, which had already been used to describe Antarctic tern (now *Sterna vitatta*) the year before (Aidala & Hauber, 2011). The first valid description of a black-fronted tern came in 1845 when it was described as *Hydrochelidon albostriata* by George Robert Gray in an account of the zoology of the voyage of H.M.S Erebus & Terror (Gray et al., 1845). Following Gray, black-fronted terns were often placed in the genus *Sterna* ("white" terns) until a genetic study (Bridge et al., 2005) showed the species belonged to the genus *Chlidonias*, the marsh terns. This is reflected in the current binomial name of *Chlidonias albostriatus*. The specific name *albostriatus* (in Latin "albo" means white and "striatus" means lined) refers to the white primary feather shafts and white facial stripe in the breeding plumage of adults (Higgins & Davies, 1996). Other members of *Chlidonias* genus are the white-winged black tern (*Chlidonias leucopterus*), whiskered tern (*Chlidonias hybrida*) and black tern (*Chlidonias niger*) (Bridge et al., 2005). Of these only the black-fronted tern is endemic to New Zealand, the white-winged black tern is a rare migrant and the whiskered tern and black tern are vagrants (Allen & Gurney, 2021; Robertson et al., 2017).

Black-fronted terns are currently listed as Globally and Nationally Endangered due to their small and declining population (Birdlife International, 2021; Robertson et al., 2017). The most recent population estimate in 2011 puts the total black-fronted tern population at 8,325 (O'Donnell & Hoare, 2011), slightly lower than a previous estimate of approximately 10,000 in 2002 (Keedwell, 2002). However, these estimates are far from certain due to the difficulty of surveying black-fronted tern populations (Hamblin, 2017; O'Donnell & Hoare, 2011). Despite this difficulty in national surveying, population declines have been noted throughout the black-fronted tern breeding range (Taylor, 2000). This decline includes population decreases of 75% between the early 1980’s and early 1990’s at Farewell Spit and a reduction from over 750 individuals to fewer than 200 between 1981 and 1990 on the Ashburton River (Higgins & Davies, 1996; Taylor, 2000).

Black-fronted terns are medium-small terns with adults measuring 28-30 cm in length with a 65-72 cm wingspan and an average weight of 95 g (Higgins & Davies, 1996). The overall shape is that of a lightly-built tern, a short bill with a sharply decurved tip, very short legs and a moderately forked tail (Bell, 2013). Adults are slate grey above and light grey below with a distinctive black cap, white rump and bright orange bill, legs and feet (Higgins & Davies, 1996). When in full breeding plumage the black cap extends from the base of the bill to the nape of the neck with a white cheek line on the lower edge, while in non-breeding plumage the black cap recedes to the eyes and ears leaving the rest of the head a mottled grey (Bell, 2013). Breeding plumage is retained from June to November/December before transitioning into non-breeding plumage, which is retained from February to April before the transition back into breeding plumage which is completed by June (Higgins & Davies, 1996; Lalas, 1977). Juveniles and immatures resemble non-breeding adults but have a black, brown or dull orange bill, a more contrasting head pattern and speckling or streaking on the back and saddle area (Bell, 2013; Hamblin, 2017). Full adult plumage is attained by immatures in March of the second year with birds maturing at 1.5 years of age (Higgins & Davies, 1996; Lalas, 1977). Males and females are alike in plumage and show limited sexual dimorphism in size with males having greater head-bill length, bill depth and longer wings, however this is only noticeable in the hand and shows considerable overlap (Schlesselmann, 2018).

The most common call of black-fronted terns is a high-pitched staccato whistle that is most often given around breeding colonies (Higgins & Davies, 1996). The terns are generally silent while foraging, although they will utter a single high-pitched “ki” or “kit” when entering or leaving a foraging group or entering a roost (Lalas, 1977). A harsh “yark” or “kror” is uttered in annoyance at other terns or when dive-bombing intruders near a nest site (Higgins & Davies, 1996). Chicks produce a fast, repetitive begging call in response to the “fish call” (the fish call has not been formally described) of adults as they approach the nest site; females will also beg in response to their male partners “fish call” (Lalas, 1977). Chicks are able to distinguish the individual “fish calls” of their parents as they return with food (Lalas, 1977). Black-fronted terns are mainly insectivores but will also take small fish, and mainly feed over river channels (Hughey, 1986).

Black-fronted terns breed almost exclusively in colonies in braided river systems (Bell, 2017). The only exceptions to this are a very small number of records of nesting on river terraces adjacent to a braided river colony (R. Maloney, personal communication, November 17, 2020) (Hamblin, 2017). Most black-fronted tern breeding occurs in the eastern South Island with strongholds on braided river systems in the Canterbury, Southland and Marlborough regions (O'Donnell & Hoare, 2011). Outside the eastern South Island there are a few colonies with low numbers on rivers in the Grey, Buller and Nelson regions (Bell, 2017; Schlesselmann et al., 2017). Black-fronted terns may have previously nested on the volcanic plateau in the central North Island (Latham 1981) and breeding did formerly occur on the West Coast of the South Island more widely than it does today (O'Donnell and Moore, 1983).

Successful breeding colonies with high chick survival may be reused from year to year although, overall, black-fronted terns show relatively low site fidelity (Hamblin, 2019; Jones & Kress, 2012; Keedwell, 2005). Within colonies, nests are usually widely spaced at 5 – 100 m (Bell, 2013) on bare gravel and shingle substrates but can be near larger boulders for wind protection (Higgins & Davies, 1996; Robertson, 1983). Islands in riverbeds are preferred, as are areas with no vegetation, although nests can be present within partial vegetation cover (Higgins & Davies, 1996; Hughey, 1985). Nests are simple scrapes in sand or small stones, sometimes lined with twigs (Bell, 2013). Black-fronted terns lay their eggs from October to December and, occasionally, to January, where late eggs are thought to be replacement clutches (Bell, 2013; Higgins & Davies, 1996). Two eggs are laid per clutch, with the occasional three egg clutch laid by late nesting birds, and the incubation period lasts 22 to 24 days (Higgins & Davies, 1996; Lalas, 1977). Chicks are fed by both parents until they fledge one month after hatching (Lalas, 1977).

1.1 Threats to Black-fronted Terns

Black-fronted terns are globally endangered as they have a small population that has undergone rapid reductions at some wintering and breeding sites (these reductions are predicted to continue) (Birdlife International, 2021). Being endemic to New Zealand, they are also nationally endangered, with the most recent assessment of their status citing their dependence on conservation, being a data poor species, recruitment failure, and their sparse distribution as the reasons for this (Robertson et al., 2017). The main reason black-fronted terns are threatened with extinction, and the major cause of their recruitment failure, is predation by introduced mammals (Steffens et al., 2012). This is a recurring theme for New Zealand charadriiforms where predation is the primary cause of braided river bird mortality in New Zealand (Keedwell, 2002). Feral cats (*Felis catus*), Norway rats (*Rattus norvegicus*), European hedgehogs (*Erinaceus europaeus occidentalis*), mustelids (*Mustela* spp.), and mice (*Mus musculus*) have all been recorded predating black-fronted terns (Keedwell, 2005; Stein, 2010). The impacts of these predators on black-fronted terns are particularly serious as the terns have not evolved with mammalian predators and, as such, have very few effective defences against them (Norbury & Heyward, 2008).

Predation by introduced mammals often occurs at night when black-fronted terns are more vulnerable, with eggs, chicks and adult birds all being at risk (Keedwell, 2005; Sanders & Maloney, 2002). The terns will make no attempt to deter nocturnal predators and will temporarily or permanently desert eggs or chicks if disturbed at night, leading to egg and chick death (Keedwell, 2002). Nocturnal predation leads to the desertion of predated nests not directly involved in the predation event (Keedwell, 2005; Sanders & Maloney, 2002). In this way, just a single predator can destroy or cause the failure of an entire black-fronted tern colony (Keedwell, 2005; Steffens et al., 2012). At a colony in the Rangitata River a single feral cat caused 76% of the colony's nests to fail and killed 10% of the breeding adults in the colony (O'Donnell et al., 2010). Black-fronted terns will also abandon their nests when disturbed at night by seemingly innocuous species, such as rabbits (*Oryctolagus cuniculus*) (Keedwell, 2002), and have even been recorded abandoning their nests until dawn after being disturbed by a moth (Sanders & Maloney, 2002). Nocturnal desertion and catastrophic single predator events have been observed in other tern species, such as the least tern (*Sterna antillarum*) and common tern (*Sterna hirundo*) (Keedwell, 2005).

Rabbits are common around braided rivers and are a major food source for several mammalian predators, particularly ferrets (*Mustela furo*), stoats (*Mustela erminea*) and feral cats (Dowding & Murphy, 2001). Ferrets, stoats and feral cats are also major predators of black-fronted terns (Dowding et al., 2015; Sanders & Maloney, 2002). When rabbit numbers decline, then predators are forced to include higher proportions of other species in their diets (Dowding & Murphy, 2001). Black-fronted terns have been identified as one of the species vulnerable to this prey-switching (Aikman, 1997). Nest predation of banded dotterels significantly increases after periods of rabbit control (Norbury & Heyward, 2008), and the same is likely to be true of black-fronted terns. Adult birds are also at risk of increased predation, particularly from stoats and feral cats, both of which will kill more birds than they apparently need, to cache (Dowding et al., 2015; O'Donnell et al., 2010; Sanders & Maloney, 2002). The relationship between rabbit numbers and predation of braided river nesting birds is not well understood and needs further study to understand the specifics of this dynamic (Dowding & Murphy, 2001; Stein, 2010). However, mast events are known to increase mammalian predation of black-fronted terns, for example in 2014 predation by ships rats was significantly higher in the upper Clarence River following a beech and tussock masting event (Bell, 2017).

Avian predators are also known to prey on black-fronted tern eggs and chicks (Steffens et al., 2012). Australasian harriers (*Circus approximans*), southern black-backed gulls (*Larus dominicanus*), Australian magpies (*Gymnorhina tibicen*) and South Island pied oystercatchers have all been recorded predating black-fronted tern nests (Schlesselmann et al., 2018; Steffens et al., 2012; Stein, 2010), while black-billed gulls are a suspected occasional predator (Popenhagen, 2019). Australasian harriers and southern black-backed gulls, in particular, can be the main cause of chick and egg death in black-fronted tern colonies, particularly in lowland breeding areas (Schlesselmann et al., 2018; Stein, 2010). The populations of both Australasian harriers and black-backed gulls have increased since human arrival in New Zealand (Schlesselmann et al., 2018). Large gulls (*Larus* sp.) have been found to be a major threat to tern nests elsewhere; in a Canadian study they were responsible for 85% of common tern chick deaths (Guillemette & Brousseau, 2001). In New Zealand very high densities of southern black-backed gulls will completely exclude black-fronted terns from sections of river (O'Donnell & Moore, 1983). Despite this, avian predators are considered less of a threat to black-fronted terns than introduced mammals (Sanders & Maloney, 2002) as the terns have evolved effective countermeasures against these avian predators, such as mobbing behaviour and cryptic colouration of eggs and chicks (Higgins & Davies, 1996; Keedwell, 2002; O'Donnell & Moore, 1983).

Habitat loss/degradation is a threat to black-fronted terns, particularly that involving weed encroachment and changing flow rates in breeding rivers (O'Donnell & Moore, 1983; Taylor, 2000). Large-leaved and tree lupins (*Lupinus polyphyllus* and *L. arboreus*), gorse (*Ulex europaeus*), crack and grey willows (*Salix fragilis* and *S. cinerea*) and Scotch broom (*Cytisus scoparius*) are all major braided river weeds whose reduces the amount of breeding habitat available (O'Donnell et al., 2016; O'Donnell & Moore, 1983). Weeds stabilise channels and provide cover for mammalian predators (O'Donnell & Hoare, 2011). Breeding habitat is also destroyed through hydroelectric schemes and irrigation development (Higgins & Davies, 1996). This ever-increasing pressure on water resources often leads to lower flow rates, making breeding colonies more exposed to mammalian predators and the riverbed more open to the establishment of weeds (Gray & Harding, 2007; O'Donnell & Hoare, 2011). O'Donnell and Hoare (2011) found that declining black-fronted tern populations were most associated with rivers with lower flow rates, a relationship that is predicted to continue as more water is diverted from braided rivers for irrigation and dam impounds.

Climate change will worsen the problem. Rivers with low flow rates will reduce further, leading to increased predator access to breeding colonies (Caruso et al., 2017). Areas of high flow are predicted to rise higher still (Caruso et al., 2017; Tockner et al., 2006), increasing the risk of flooding which is already a major cause of nest failure (Higgins & Davies, 1996). The risk of flooding is further worsened by competition for other colonial nesting braided river birds (especially southern black-backed gulls) taking higher areas of riverbed and forcing black-fronted terns closer to flood zones (Robertson et al., 2013; Smith et al., 2020). Gravel extraction, as well as constant flood control work and its associated machinery, are also significant threats in terms of habitat destruction (O'Donnell & Moore, 1983; Taylor, 2000).

Terns in general are very vulnerable to disturbance, particularly frequent human disturbance, which commonly leads to colony abandonment (Palestis, 2014). Several studies have found large proportions of tern colonies destroyed by human disturbance, with one finding 35.7% of little tern (*Sternula albifrons*) nests destroyed by human activities (Medeiros et al., 2007) and human disturbance was responsible for over half the reproductive failures in least tern colonies (Burger, 1984). Black-fronted terns are probably just as vulnerable to human disturbance, and this is likely a major cause of nest failure (Hughey, 1985). Obvious signs of human activity have been found in and around failed colonies in several areas, including the Waimakariri River (Popenhagen, 2019). 4WD vehicles are increasingly the main human threat to birds breeding in braided rivers, as their activity displaces nesting birds and destroys nests, although fishing, hunting, walking, swimming and picnicking all cause disturbance (Taylor, 2000). Seemingly harmless activities, such as a fisherman walking slowly near a colony, can sometimes have a worse impact than vehicles as they disturb breeding birds for longer. For example, one angler was observed keeping birds off nests for 40 minutes (Smith et al., 2020). Increasing time off the nest increases the risk of abandonment and nest failure as eggs are not properly thermo-regulated (Smith et al., 2020). Wilful acts of destruction and domestic animals, such as dogs, sheep and cattle, have all been recorded damaging black-fronted tern colonies (Smith et al., 2020; Taylor, 2000). Black-fronted terns are also subject to human disturbance at coastal sites during the non-breeding season (Higgins & Davies, 1996).

1.2 Current Conservation of Black-fronted Terns

Black-fronted terns are currently dependent on conservation efforts for their survival (Robertson et al., 2017). These conservation efforts mainly consist of mammalian predator control around black-fronted tern breeding rivers targeting mustelids, cats, hedgehogs and rats (Hamblin, 2017; Smith et al., 2020). Avian predators, such as Australasian harriers and southern black-backed gulls, are also sometimes targeted through shooting, poisoning and nest destruction (Schlesselmann et al., 2018; Smith et al., 2020; Stein, 2010). Mammalian predator control (and control of prey items such as rabbits) comes in the form of trapping, poisoning and shooting, and is carried out at either a landscape-scale or localised around the tern's breeding colonies (Hamblin, 2017; Schlesselmann et al., 2018). Large-scale control is only partially effective (Cruz et al., 2013) although intensive landscape-scale control is considered best practice (O'Donnell et al., 2016). Colony scale control is effective when intensive, although this is difficult as black-fronted tern colony locations can vary from year to year based on available habitat (Hamblin, 2019; Schlesselmann et al., 2018). Where there is effective long-term predator control black-fronted tern populations increase and where there is none, they decrease (O'Donnell & Hoare, 2011). Examples of effective long-term control are the Eglinton and Ashley rivers, with local population increases between 1992 and 2008 in the

Eglinton and between 2000 and 2015 in the Ashley (O'Donnell & Hoare, 2011; Spurr & Ledgard, 2016).

Control of avian predators, usually southern black-backed gulls, forms part of black-fronted tern conservation. Poisoning, shooting and egg/nest destruction have been successfully used to reduce gull numbers, although there can be issues, such as bait shyness and dogs consuming poison bait (Smith et al., 2020). Shooting operators must also be competent and distinguish southern black-backed gulls from the nationally critical black-billed gull to implement targeted and effective control (Robertson et al., 2017; Smith et al., 2020). Removal of weeds from riverbeds to create suitable breeding habitat is also a part of black-fronted tern conservation. Black-fronted terns respond to vegetation clearance by roosting and nesting on the resulting bare gravel (Schlesselmann et al., 2018) and the removal of crack willow has been shown to facilitate an increase in tern nesting and foraging (Maloney et al., 1999). As such, ongoing herbicide spraying and mechanical weed removal are important for creating breeding habitat in braided riverbeds (O'Donnell et al., 2016).

Islands in braided rivers have the potential to be “safe zones” for black-fronted terns if the surrounding river channels have a high enough flow (Duncan et al., 2008). Larger channels with higher flow deter mammalian predators from accessing the islands and predating the terns and their nests (O’Donnell et al., 2010; Pickerell, 2015). Modelling rivers and their flows makes it possible to predict which islands will be safest for tern colonies to establish on (Duncan et al., 2008). Islands smaller than 3.5 ha, clear of vegetation, more than 20 m from the mainland and separated by a channel with flow of more than 6 m^3s^{-1}, have been predicted to provide the best sites for breeding bird species, including black-fronted terns (Pickerell, 2015). Attempts to attract birds to breed on islands that replicate these conditions have been met with very limited success (Smith et al., 2020). Social attraction to particular breeding areas, in the form of decoys and audio playback shows some potential (Hamblin, 2017). Islands have also been enhanced (cleared of vegetation) to be more suitable for nesting, although black-fronted tern colonies were no more successful on these cleared islands than on vegetated ones due to predation by southern black-backed gulls (Schlesselmann et al., 2018). Despite this, with further research, artificially created nesting habitat has the potential to play an important role for black-fronted tern conservation (Schlesselmann et al., 2018).

There are several methods of conservation for black-fronted terns aimed at preventing human disturbance, almost all of which are focused at breeding colonies rather than at non-breeding sites. Smith et al. (2020) outlined techniques being used to limit disturbance around black-fronted tern colonies in the Waimakariri River. Large concrete blocks were placed around colonies to prevent vehicle access, often coupled with thick wire cables run through the blocks and attached to trees. Waratahs and electrical tape were also used as fencing around colonies. The public was advised of the presence of the birds and asked to keep clear with signage and some targeted ranger patrols. Away from the river there was public education in the form of brochures, school talks, an educational video, stickers for children and ranger interactions with members of the public. Raising public awareness has been shown to be hugely beneficial to nesting terns. Little tern nests are up to 34 times more likely to succeed when signage is present to protect a colony (Medeiros et al., 2007). Signage around black-fronted tern colonies is likely to be, at best, partially effective as signs are often seen to be ignored and obstructions deliberately removed by people using vehicles in the river bed (Smith et al., 2020). Even with signs around breeding colonies the terns are still vulnerable to disturbance at coastal wintering sites where there is no equivalent signage (Higgins & Davies, 1996).

There are several challenges that hinder black-fronted tern conservation. The birds are sparsely distributed and breed in a dynamic and often difficult to access environment, making actions, such as population counts, challenging (O'Donnell & Hoare, 2011; Robertson et al., 2017). The dynamic nature of braided rivers also makes investing in predator control or habitat enhancement risky. Terns may nest in very different places from year to year making work from the previous season redundant (Hamblin, 2017). Devices, such as predator traps, may be removed or damaged by flood events in the riverbed. Conservation actions, such as predator control, are currently focused around black-fronted tern breeding colonies, with little to no protection away from these areas. Black-fronted terns are also considered to be a data-poor species, with information that would be helpful for conservation (such as migration routes) currently unknown (Robertson et al., 2017). High profile conservation initiatives, such as Predator Free 2050, only target some of the mammalian predators that threaten black-fronted terns, leaving out key species, such as feral cats and hedgehogs (Murphy et al., 2019). Black-fronted tern conservation has had limited success as the overall population continues to decline and is predicted to continue to do so (Bell, 2013; Cruz et al., 2013; O'Donnell & Hoare, 2011).

1.3 Use of GPS for Tern Conservation

GPS (Global Positioning System) tracking devices have been used to track a wide range of bird species (Seward et al., 2021). Using a GPS system provides a method to track individual birds at low cost while maintaining a high level of spatial resolution with the collected data (Soanes et al., 2015). The number of studies that use GPS devices has increased since the first in 2001 but they have been constrained by the size of loggers, which are required to be below 3% of the adult body weight of the species in question (Vandenabeele et al., 2012). Recent advancements in technology has allowed progressively smaller species to be tracked effectively (Soanes et al., 2015). Precise data on foraging trip distance/duration, and habitat use are now easily retrievable without needing to recapture tagged birds (Maynard & Ronconi, 2018). With the recent advances in technology there has also been an increase in the use of GPS to track seabird and Charadriiform species (Seward et al., 2021).

Within Charadriiformes there have been many species tracked using GPS for the first time within the last ten years, including gulls and terns in the family Laridae (Maynard & Ronconi, 2018). A wide range of findings were made from the data collected in these studies, including home-range size of Arctic terns (*Sterna paradisaea*) (Seward et al., 2021) and migration routes of black terns (van der Winden et al., 2014). In the case of Sandwich tern (*Thalasseus sandvicenis*) and sooty tern (*Onychoprion fuscatus*), GPS trackers were used to determine how far and how long the terns travelled to forage (Fijn et al., 2017; Neumann et al., 2018; Soanes et al., 2015).

GPS has informed the conservation of wide-ranging seabird species through the identification/confirmation of foraging hotspots (Trebilco et al. 2008, Le Corre et al. 2012) and threats (Torres et al. 2011) and has similarly informed assessment of the effectiveness of marine protected areas (Trebilco et al. 2008). The spatial data gathered from tracking studies of tern species can be important for their conservation. In 2017, a Sandwich tern study identified that the species foraged up to 60 km from their breeding colonies (including up to 40 km out to sea), meaning conservation efforts need to reflect this, rather than being centred on the colony itself (Fijn et al., 2017). GPS data gathered from Forster's tern (*Sterna forsteri*) showed the species relies heavily on salt ponds for feeding and roosting (Ackerman et al., 2009). At the time, salt ponds were undergoing an 80% loss in the study area and this data highlighted the need for restoration of salt pond habitat to protect Forster's terns and other species that utilised the area (Ackerman et al., 2009). Tracking studies can also highlight issues that might hamper conservation efforts. For example, sooty terns were found to travel into the Exclusive Economic Zones of more than one country, meaning conservation efforts need to be coordinated between multiple countries (Neumann et al., 2018).

GPS trackers have never been used to study black-fronted terns although results from GPS research with other tern species indicate that it is a feasible option. The studies by Fijn et al. (2017) and Soanes et al. (2015) focusing on Sandwich and sooty terns respectively were the first times GPS had been used for either species. The use of GPS trackers on black terns (van der Winden et al., 2014) shows the technology can be successfully applied to a closely related species to the black-fronted tern (both in the genus *Chlidonias*).

Deploying GPS trackers on black-fronted tern will enable this study to record daily and seasonal movements of the species. Recording daily movements will identify habitat usage of breeding black-fronted terns, including areas around a black-fronted tern colony important for foraging and those requiring protection. Daily movements will also reveal how far from their breeding colonies that the terns forage. This will indicate the scale at which predator control and habitat protection will need to be implemented to be fully effective. Recording the seasonal movements of black-fronted terns will determine the migration routes of the species, as well as any major staging and wintering sites, which will allow for a year-round protection network to be introduced rather than the colony focused approach currently used.

1.4 Aims and Objectives

The aim of this study is to track black-fronted terns using GPS devices to determine their habitat use and migration routes. The objectives are:

I. Determine the habitat use of breeding black-fronted terns

II. Investigate the foraging range of breeding black-fronted terns

III. Determine the migration routes of black-fronted terns

Chapter 2

Breeding Movements

Black-fronted tern with attached GPS tracker visible (Adrian Paterson).

2.1 Introduction

Habitat is defined as “the resources and conditions present in an area that produce occupancy, including survival and reproduction, by a given organism” (Krausman, 1999). Animals use habitat in many ways, including foraging, nesting, cover and escape (Krausman, 1999). Different habitats may be selected by animals based on innate and learned behaviours as well as external factors, such as food availability, competition and predation (Hutto, 1985; Krausman, 1999). Among animals, no group has greater potential for habitat selection than the birds, many of which are known for their extreme mobility and wide-ranging behaviours (Cody, 1985). This mobility gives birds the ability to select habitats at fine and large scales. For example, belted kingfishers (*Megaceryle alcyon*) select fine scale areas of stream with high quality riffles, and vulture species (*Gyps* spp.) select large scale topographic conditions to optimise their soaring (Cody, 1985). Terns, like other seabirds, are typically highly mobile and usually associated with habitats centred on water bodies (Paiva et al., 2008). However, while breeding site selection in terns is well-known, their habitat selection while foraging is poorly understood (Paiva et al., 2008). This is true for black-fronted terns as there are few studies on black-fronted tern feeding ecology. In general, black-fronted terns favour habitat inland around braided rivers when breeding and at the coast when not breeding (Hughey, 1986).

The different reproductive and ecological roles of male and female birds frequently lead to differences in foraging behaviour (Ardia & Bildstein, 1997). These differences can cause males and females to use different habitats and feeding strategies. For instance, wintering female American kestrels (*Falco sparverius*) use more open areas with less woody vegetation than males (Ardia & Bildstein, 1997). This is also common among seabird species (Kasinsky et al., 2021), with male and female Christmas Island frigatebirds (*Fregata andrewsi*) differing in foraging habitat for parts of their breeding season. This sexual segregation is thought to allow for separation that enables each sex to optimise its foraging profitability (Hennicke et al., 2015). Differences in habitat use based on sex have often been attributed to sexual dimorphism, although differences are also observed in monomorphic species where the sexes have differing parental roles and nutritional requirements (Kasinsky et al., 2021). Larid species (gulls, noddies, skimmers and terns) often display different foraging behaviours and habit selection based on sex (Kasinsky et al., 2021; Ronald & Saskia, 1983). Most seabirds have wide breeding ranges, although their foraging range while breeding is limited by their need to return to their breeding colony (Christensen-Dalsgaard et al., 2017; Kasinsky et al., 2021). This limiting factor can mean different colonies have different habitats and prey species available (Christensen-Dalsgaard et al., 2017), which can lead to distinct environmental pressures on male and female individuals and geographical differences in sexual segregation (Kasinsky et al., 2021).

Tern species have been the subject of numerous studies involving habitat use. Roseate tern (*Sterna dougallii*) habitat selection has been found to be strongly linked to foraging of brown pelicans (*Pelecanus occidentalis*) and predatory fish, both of which improved access to roseate tern prey species (Shealer, 1996). Little terns were found to have higher foraging densities in estuarine lagoons than at sea, and at lower tides (Paiva et al., 2008). A habitat study focusing on gull-billed terns (*Gelochelidon nilotica*) found the species foraged mainly in areas of cereal crops, avoiding vineyards (the main land use around the colonies) and foraged an average of two km away from their colonies (Britto et al., 2018). In a study comparing the habitats where white-winged black terns and black terns located their breeding colonies, the former were three times more likely to nest in waterlogged fields and the latter three times more likely to nest on ox-bow lakes (Goławski et al., 2015). The same study also found a greater proportion of open habitats around the colonies of white-winged terns than around those of black terns (Goławski et al., 2015). Black terns also foraged more over larger wetland systems and bred more in wetlands with floating matted vegetation (Steen & Powell, 2012).

Habitat use in terns has been studied using GPS devices (Ackerman et al., 2009). GPS data collected from crested terns (*Sterna bergii*) showed that this species typically foraged in areas with water between 19 and 21° C, less than 20 m in depth and with relatively high levels of chlorophyll a (more than 0.5 mg m-3) (McLeay et al., 2010). A similar study conducted with Caspian terns (*Hydroprogne caspia*) found the species to select shallow waters between zero and five m in depth for foraging (Beal et al., 2021). Individual Caspian terns are faithful to foraging sites throughout the breeding season and individuals often show highly repeatable strategies regarding foraging site fidelity (Beal et al., 2021). GPS studies like these can be important for the conservation of the species as identifying key areas through spatial modelling tools can assist proper management, (Christensen-Dalsgaard et al., 2017).

2.1.1 Black-fronted tern habitat use

Breeding black-fronted terns use a variety of habitats, breeding in braided riverbeds and foraging over both running and standing water, grassland and ploughed land (Pierce, 1983). On fine days they generally forage over moving bodies of water (around 25% of their time is spent over land, including above forested slopes), concentrating over favoured sections of river and stream systems (Lalas, 1977). While feeding over moving water they will hold a temporary “territory” that they will defend while feeding, driving away other black-fronted terns that enter their section of river (Lalas, 1977). All life stages exhibit this behaviour and are all equally efficient at driving away intruders (Lalas, 1977). During December and January, black-fronted terns feed almost exclusively on insects on the surface of moving water, with the birds concentrating over the main river braids for several hours before dispersing throughout the river (Lalas, 1977; Pierce, 1983). When the weather is wetter the terns forage more over fields and grassland than over water (Latham, 1981). The terns also use different habitats depending on the time of day to take advantage of insect emergence (Pierce, 1983). Black-fronted terns roost on rock, gravel or sand near water, occasionally resting in ploughed fields but never on the water, snow or vegetation (Lalas, 1977).

When not breeding, a high proportion of the black-fronted tern population feeds at sea, particularly earlier in the non-breeding season when farmland feeding areas are drier (Lalas, 1977; Latham, 1981). The terns often feed off-shore, with several records of wintering birds feeding at Mayor Island in the Bay of Plenty, which is 35 km from the mainland, at its nearest point (Latham, 1981). At Aramoana in Otago, black-fronted terns feeding at sea were found to favour areas with strong tidal currents or upwellings, including shallower water above breakwaters where prey is concentrated nearer the surface (Lalas, 1977). Smaller proportions of the population feed in harbours, upstream of the coast and over neighbouring farmland (Lalas, 1977; Latham, 1981). Higher numbers of terns begin to feed over land as autumn and winter progress, and paddocks become wetter with the increased rain (Latham, 1981). As in the breeding season, non-breeding terns forage over different habitats depending on the weather, feeding mainly at sea on calm days and inland over paddocks during stormy and rainy days (never more than 3 km from the coast) (Lalas, 1977; Latham, 1981). On a calm day when farmland is sufficiently wet, and if paddocks are wet, the terns will feed over a mix of both, showing a preference for short sward (Latham, 1981). Black-fronted terns mainly use farmland during winter (Robertson, 1983). Overall, they spend more time feeding over moving water than other *Chlidonias* terns, which generally feed more over still water (Lalas, 1977). Roosting occurred on beaches, at river mouths, on fence posts and adjacent ground in farmland (Latham, 1981).

There have been very few studies looking at habitat use in black-fronted terns, with the main two being Lalas (1977) and Latham (1981). These studies were important but were based on human observations that are not able to provide as detailed or complete information as GPS data. Recent land use changes, including intensification of pastoral land, have made new local habitats available for black-fronted terns (Ministry for the Environment, 2021) which has possibly changed their habitat use since these previous studies. This is an important knowledge gap to fill for any species as conservation managers need to know the habitat preferences of the species they are working with (Britto et al., 2018). Habitat studies are commonly used to determine which habitats a species uses and at what scale, to rank habitats in order of relative use and to compare different groups, such as males and females (Aebischer et al., 1993; Morris, 1987). This is often done by overlaying movement or location information on habitat data, something that modern geographic information systems (GIS) have made relatively straightforward (Simpfendorfer & Heupel, 2004). This has not been attempted before for black-fronted terns. The aim of this chapter is to use GPS data to investigate black-fronted tern habitat use and foraging range during their breeding season. This may identify black-fronted tern habitat preferences while they are breeding and at what scale this habitat selection takes place, as well as any differences in habitat preference between different sexes and colonies. This information will lead to more effective management of this endangered species.

2.1.2 Research questions

- Which habitats are most important to foraging black-fronted terns during their breeding season?
- How far do black-fronted terns range from their breeding colonies while foraging?
- Is the habitat use and foraging range of breeding black-fronted terns influenced by sex and colony of origin?

2.2 Methods

2.2.1 Study sites

The Mackenzie Basin, also known as the upper Waitaki Basin, is a river basin in New Zealand’s South Island with an area of approximately 9490 km^2 situated east of the main divide in the Canterbury high country (Caruso, 2006). The basin has some of the largest braided river systems in the country and includes a significant proportion of the countries breeding braided river breeding habitat, making it a stronghold for black-fronted terns (Caruso, 2006; Maloney et al., 1999; O'Donnell & Hoare, 2011). The black-fronted terns caught and fitted with GPS devices were from two breeding colonies in the Mackenzie Basin. The first colony was located in the lower Cass River near Lake Tekapo (-43.875170, 170.480506), and the second colony was in the upper Ohau River between Lake Ohau and Lake Ruataniwha (-44.265508, 170.002858) (Figure 1). A third colony in the Tasman River near the confluence with the Jollie River was also going to be included but difficulties with locating this colony and sample sizes meant it was excluded. Access to the colony in the lower Cass River was via Godley Peaks Road and access to the colony in the upper Ohau River was over private land which was secured courtesy of the Department of Conservation.

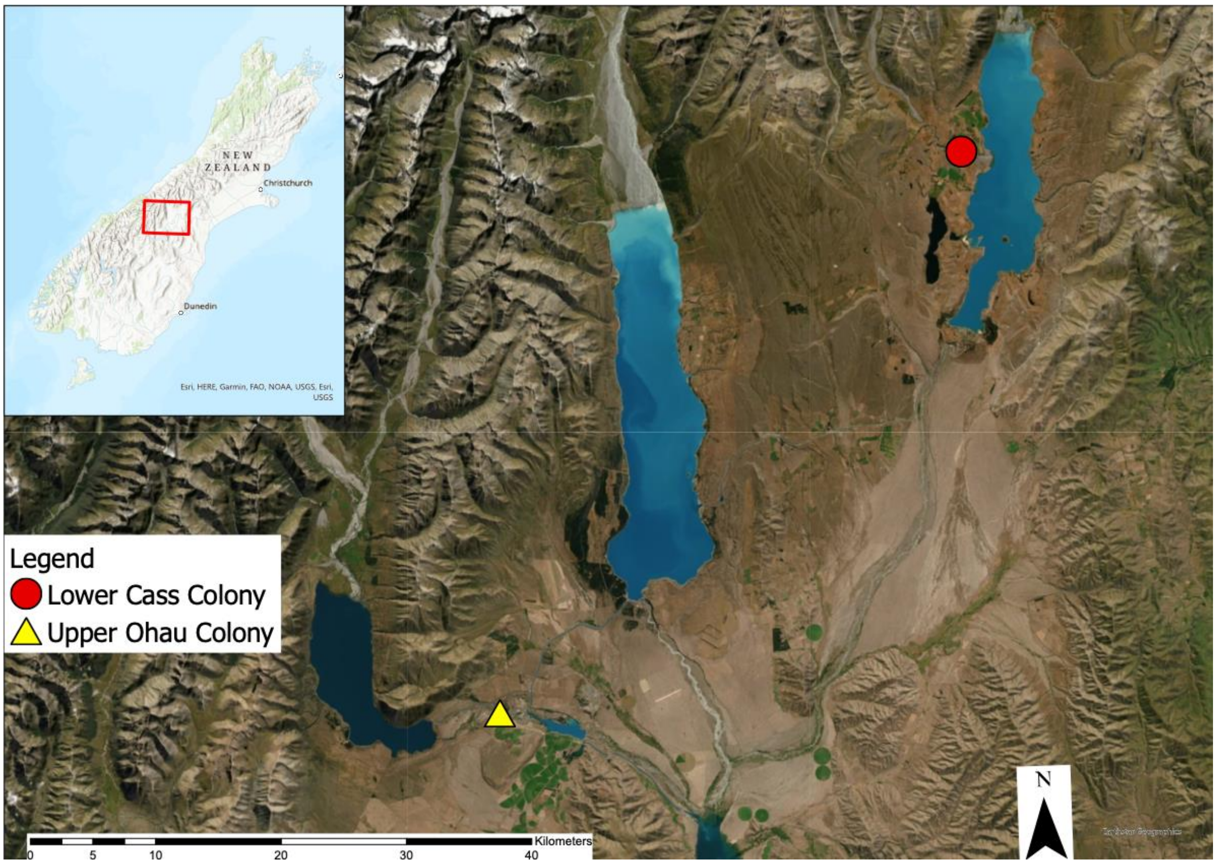

Figure 1: Map of part of the Mackenzie Basin showing the locations of the black-fronted tern breeding colonies in the lower Cass and upper Ohau rivers. The three large lakes are from left to right Lake Ohau, Lake Pukaki and Lake Tekapo. Created in ArcGIS Pro.

The first colony in the lower Cass is in a braided riverbed approximately 2 km upstream of Lake Tekapo, in a section where the riverbed is approximately 600 m wide. The colony itself is a loose association of nests that runs for at least 500 m downstream and 100 m across the river, near the central braids. In the area of the colony, the land surrounding the river is made up of gently undulating hills covered by low producing and depleted grassland with intermixed high-producing exotic grassland (irrigated paddocks) (Landcare Research New Zealand, 2020). The colony sits at around 730 m above sea level. The second colony in the upper Ohau (often referred to as "Tern Island") is on an island in a river channel 100 m wide, approximately 7.5 km downstream of Lake Ohau and 6.65 km upstream of Lake Ruataniwha. This island is 300 m long and 60 m wide at its widest with the black-fronted tern colony spread across the entire island. The land surrounding the island is low producing and depleted grassland with a pine plantation to the east/north-east (Landcare Research New Zealand, 2020). The Ohau Canal is approximately 750 m north of the colony. The colony sits just below 500 m above sea level and is surrounded by steep river terraces, including a >50 m cliff directly to the north. Both the lower Cass and upper Ohau colonies lie in the rain shadow of the Southern Alps (Caruso, 2006) and receive around 700 mm of rain annually (Ministry for the Environment, 2017).

The upper Ohau colony island has been artificially stabilised since 1991, allowing the terns to return to the same spot year after year and prolonging the use of the colony for breeding beyond that of one on a naturally occurring braided river island (Hamblin, 2019). The artificial stabilisation of the river reduces flow fluctuation and the severity and frequency of flooding events, meaning black-fronted terns have been able to nest there for more than 10 (and possibly up to 25) successive breeding seasons prior to 2017 (Hamblin, 2019). Vegetation has also been removed from Tern Island with a bulldozer to reduce potential cover for mammalian predators (R. Maloney, personal communication, 13/11/2021). Since 2009, intensive predator trapping has taken place in a one km radius around the upper Ohau colony as part of Project River Recovery. This intensive management has allowed the black-fronted tern colony to grow from ~220 birds in 2010 to at least 696 birds in 2014/2015 (Hamblin, 2017; Rebergen & Woolmore, 2016; Schlesselmann et al., 2017). The lower Cass colony is also a part of Project River Recovery as well as another conservation project named Te Manahuna Aoraki that launched in 2018. The second year of monitoring saw hatching success of 49% for black-fronted terns in the lower Cass Colony during the 2019/2020 breeding season (Te Manahuna Aoraki, 2020).

2.2.2 GPS devices used

The devices used in this study were Debut NANOs manufactured by Druid Technology Co., Ltd., China. These devices weigh 2.8 g each, which is 2.85% of the average body weight (95g) of an adult black-fronted tern (Bell, 2013). This is within the recommended “3%-of-body-weight-rule” that minimises energetic cost to a bird fitted with a transmitter (Vandenabeele et al., 2012). The Debut NANO devices were chosen based on Department of Conservation guidelines for this study which specified the devices used must have remote download capabilities, comply with the “3%-of-body-weight-rule” for ethics and be within the $20,000 budget provided by the Department.

The Debut NANOs include a GPS system, battery and solar panels to maintain battery and a Bluetooth system to transmit data. Because of their low weight the NANO devices cannot house a system to transmit data directly to a satellite or phone network, they instead use Bluetooth to transmit to a receiving unit (Debut HUB – also manufactured by Druid Technology Co., Ltd., China). The receiving unit then uses the cellphone network to upload data to an online data management centre provided by Druid Tech. The Bluetooth system can transmit data from the NANO tracking devices to the HUB receiving unit at up to 1 km with a clear line of sight. Alternatively, a cellphone with the Druid Tech app installed can collect data directly from the NANOs or from the HUB at up to 100 m with a clear line of site. Once data has been transmitted from the NANO to the HUB it is cleared from the NANO, freeing up storage for further data to be collected. The NANO devices have enough memory space to hold a year’s worth of data if the GPS collection interval is set to one hour.

The NANO devices collect several different types of data, the most significant for this study being the GPS points. Each GPS fix records the coordinates, the altitude of the point, how fast the bird was travelling, the light intensity and temperature, the date and time it was collected, when it was transmitted and how long the transmission took. The devices are also capable of collecting behavioural data (ODBA – overall dynamic body acceleration), although this function was turned off as the behavioural data often has a higher volume of data than the GPS points and consumes more battery to transmit. The interval at which the NANOs took GPS fixes was set at one hour for 28 of the birds, with the remaining six (three from each colony) set at five minutes to capture more fine-scale data. Each device also had a setting called BOOST which takes GPS fixes at a higher rate when the device detects high levels of sunlight on the solar panel combined with high battery levels. The BOOST setting was turned off on 17/12/2020 for the devices deployed during the first round of attachment and 21/12/2020 for devices deployed during the second round of attachment. This was done to save storage space and battery power on the devices as the terns moved away from their breeding colonies (and out of range of the HUB devices) and the days became shorter with fewer hours of sunlight. The device settings are applied when the NANOs are turned on in preparation for deployment, but the settings can be updated at any time from the Druid online data centre. The updated settings are then applied to the NANOs when they come into range of a HUB device.

2.2.3 Capture and attachment

34 NANO devices were used in this study, 10 in the lower Cass colony and 24 in the upper Ohau colony. This uneven split was caused by the colony in the lower Cass being more advanced in the breeding cycle, meaning suitable nests for capture (nests containing two eggs) were more common in the upper Ohau colony. The Cass colony also had fewer breeding pairs and were more dispersed than at the Ohau colony, making locating nests more difficult. Only nests with two eggs were targeted for catching adults to avoid early abandonment (terns with one egg are less settled and more likely to abandon the nest) and prevent stress to newly hatched chicks. Capture and attachment took place in two rounds, dictated by the arrival of the tracking devices in two shipments. The first round took place on 04/11/2020 (Cass) and 05/11/2020 (Ohau) and the second on 07/12/2020 (Ohau), 10/12/2020 (Cass and Ohau) and 11/12/2020 (Ohau). During the first round of attachment the HUB devices were set up with one at each colony, at -43.873805, 170.482269 in the Cass and at -44.266173, 170.003452 in the Ohau. Each HUB was secured with zip ties to a waratah approximately one m off the ground with the HUB's solar panel attachment facing north.

To catch the black-fronted terns and attach the GPS trackers, a Moundry TSB30N tent spring trap was used. This trap has base dimensions of 30 x 30 cm and is filled in with a mesh netting which contains a large hole designed to go over a nest. When sprung, the trap forms a mesh tent 15 cm high (no part of the trapped bird is gripped or entangled), with the hole over the nest used to extract the bird. The trap is set by pulling one edge of the square base back to meet the opposite, folding down the tent and securing it with the trip wire. When set, the trap was placed over a tern nest with the hole in the mesh base over the nest and the tripwire directly over the eggs. While set the corners were pegged down with sticks and the mesh base was covered with sand and pebbles. All trapping and bird manipulation was carried out during daylight hours and none were carried out in the rain to avoid eggs being exposed to wet or cold while the adult was being processed.

Nests were found by walking slowly through the colony and watching where the terns flushed from or landed after mobbing the searchers. When a nest was located the trap was set with one person waiting a short distance away to collect the trapped bird and another readying the equipment to process the bird. Once caught, the tern was placed in a catch bag and carried a short distance to the edge of the colony where the bird was processed without disturbing the rest of the colony. The catch bag was then weighed with the caught bird inside using a PESOLA Medio Line 600 g spring scale. The weight of the bag (65 grams) was subtracted from the total weight of each measurement. Following this, each bird was removed from the bag and fitted with a metal c-band on the right tarsus using Porzana banding pliers. Feather samples were then extracted from the underwing near the carpal joint using sterile tweezers with three pin feathers taken from each bird.

As this is the first time a GPS device has been fitted to a black-fronted tern (and the first use of this model of device in New Zealand) there was not a set methodology for attachment. However, DOC has fitted other devices to similar sized birds, which creates a general guideline, based on the leg-loop harness method in Rappole and Tipton (1991). The activated NANO device was then attached using 270 mm lengths of 0.5 x 1.5 mm silicone tubing sourced from Druid Tech, with two green felt pen marks 170 mm apart and two blue felt marks 150 mm apart. This leaves a green mark and a blue mark at each end of the length of silicone with the marks at each end 10 mm apart. One length of silicon was used to attach each NANO device, with the silicone passed once through the first attachment hole on the device and twice through the second. This creates two leg loops to place on the bird that were tightened with the green (larger birds) and blue (smaller birds) marks as a size guide as per DOC best practice before being tied off and the excess silicone trimmed with scissors. To reduce the handling time of the terns, the NANO devices were pre-fitted with the silicone up to the point of being tightened per each bird’s size before being tied off and trimmed. Two pairs of terns (two individuals caught in the same nest) were caught and fitted with tracking devices, one pair at the Cass colony and one at the Ohau colony.

Before the terns were released, several welfare checks were undertaken to ensure that: a) no flight feathers were caught underneath the silicon or NANO device; b) the wings and legs of each bird functioned normally and were not impeded in any way; and c) all parts of the processing had been completed. The birds were then released and observed for between one to five minutes to ensure that they were flying and behaving normally. The whole process from when a tern was caught until it was released was timed and recorded to ensure no individuals were handled for too long (15-20 minutes) and to inform ethics committee follow ups. Had any bird being handled begun to show heightened levels of stress, e.g. sustained panting, the manipulation would have been abandoned and the bird immediately released. A week after device attachment, trips to both colonies were undertaken to resight birds and make sure there were no issues with the harnesses or transmitters (no issues were observed).

2.2.4 Sex determinatation

Male and female black-fronted terns are not able to be differentiated in the field or in the hand and as such molecular techniques are needed to distinguish the sexes (Schlesselmann & Robertson, 2017). The feather samples from the 34 black-fronted terns fitted with GPS devices were used to determine the sex of each bird. After collection, the three pin feathers from each bird were labelled T1-T34 and placed in storage, initially at 4° and then at -20°. The molecular work was carried out and reported on by Matthew Janssen and Cor Vink, both of Lincoln University. To extract DNA the tip of each feather was cut and inserted into a collection tube included in a DNEasy Blood and Tissue Kit. Following the instructions provided with the DNeasy Blood & Tissue Kit, a 50 µl buffer was added when repeating the final step rather than the full 200 µl amount. With the extracted DNA a polymerase chain reaction (PCR) was performed in three primary batches (T1-T10, T11-T18 and T19-T34) to create a 20 µl reaction including one µl of template from the extracted DNA. Each reaction included 10 µl of dream Taq, one µl of forward primer P8 (5'-CTCCCAAGGATGAGRAAYTG-3'), one µl of reverse primer M5 (5'-YTYMCTTCAYTTCCATTAAAGC-3'), seven µl of H_2O, and a one µl template. A previously tested DNA template (BC44) was used as a positive control and water was used as the template in a negative control. The primers used amplified two fragments of slightly different lengths (~250 bp and ~260 bp) in females and a single ~250 bp fragment in males. A four percent agarose gel running at 60 V for 180 minutes was used to view results, which were used as part of the data analysis.

2.2.5 Data analysis

GPS data from the 2020/2021 breeding season was downloaded from the Druid data centre on 29/07/2021, encompassing all GPS points collected by the NANO devices from when they were first attached to birds until they left the area of the colonies (and went out of range of the HUBs) at the end of the breeding season. These data were stored in CSV (comma-separated values) files with one file per bird. Prior to any analysis, failed or obviously erroneous and irrelevant GPS points were removed from the dataset. The failed points all showed coordinates of 200, 200. In contrast, the obviously erroneous points were hundreds or thousands of km from the previous or next points in the bird's flight path with insufficient time between the points for this to be accurate. GPS points recorded during device tests were also removed.

The CSV files were then imported into ArcGIS Pro (Version 2.7.0). A layer for habitat type was added (LCDB v5.0 – Land Cover Database version 5.0, Mainland New Zealand) and the "Summarise Within" tool was used for each tern to retrieve the number of GPS points in each habitat/land cover type. Each tern's resulting land cover summary then had the land cover polygons with no GPS points in them removed through their respective attribute tables by selecting and deleting all polygons with the attribute "count" equal to zero. The land cover summary attribute tables for each tern were exported as Microsoft Excel files using the "Table to Excel" tool. Once exported, these attribute tables were edited to combine the multiple rows for each habitat type to create a count for each habitat type and each tern. The counts were then fed into a final summary table (habitat dataset) of tern habitat use for further analysis. Habitat types were removed from further analysis if they had fewer than 50 GPS points across all of the terns (less than 0.05% of the total dataset).

For a habitat comparison, the habitats used by the terns were compared with the actual available habitat (the habitats surrounding each breeding colony). In ArcGIS, Pro polygons were created around each breeding colony with a radius equal to the third quartile of the GPS distance from the relevant colony (covered later in this section 2.2.5 Data Analysis). The Land Cover Database layer was then clipped by each of these polygons with the "Clip" tool with the result summarised by the Summarise Within" tool to find the area of each habitat type within the specified distance of each colony. This information was converted to percentages of available habitat to compare with tern habitat usage. The available habitat percentages were separated into six tab-delimited text files (three files per colony), with each file comparing the available habitat of a colony with the habitat used for all terns from that colony, females from that colony and males from that colony. The six subsets for each colony were, all terns, all males, all females, terns from that specific colony, males from that specific colony and females from that specific colony.

In ArcGIS Pro both breeding colonies were marked as points in the centre of each colony area. The distance of the furthest GPS point from either colony was recorded to inform the extent of the "Multiple Ring Buffer" tool, which was used on the GPS dataset for each tern originally imported into ArcGIS Pro. Within the "Multiple Ring Buffer" tool each buffer ring around each colony was 5 km across. The "Summarise Within" tool was then used for each tern to determine the number of points in each 5 km buffer ring and produce a distance summary. The attribute tables from each tern's distance summary were exported as Microsoft Excel files using the "Table to Excel" tool. Once exported, the data from these attribute tables was then used to make a summary table of the distance each tern travelled from its breeding colony. In ArcGIS Pro the "merge" tool was used to create two separate data layers, one with all the GPS points from birds in the Cass colony and one with all the GPS points from the Ohau Colony. The "near" tool was used to retrieve the distance of each GPS point from the relevant colony. This data was then exported using the "table to excel" tool. The exported data was merged into one excel file (distance dataset) containing every GPS point, and the distance from the relevant breeding colony for further analysis.

Data analysis was carried out in R version 4.1.3 (2022-03-10) "One Push-Up" via RStudio 2022.02.1 build 461 "Prairie Trillium". Packages used were "lme4" (version 1.1-29), "emmeans" (version 1.7.3), "rlang" (version 1.0.2), "ggplot2" (version 3.3.5) and "MASS" (version 7.3-55). The habitat and distance datasets were imported into R. For the habitat dataset, the colony of origin, sex and individual ID of each tern were added as factors. The first run was a generalised linear model (GLM) with binomial error distribution and location (Ohau or Cass colony), sex (male or female) and habitat (depleted grassland, high producing exotic grassland, gravel or rock, lake or pond, low producing grassland and river) as the three fixed effects. The significance of the fixed effects (and their interactions) was assessed using function 'drop 1' with a chi-squared test. Next was a generalised linear mixed model (GLMM) with binomial error distribution. Location (Ohau or Cass colony), sex (male or female), and habitat (depleted grassland, high producing exotic grassland, gravel or rock, lake or pond, low producing grassland and river) were the three fixed effects and name (the ID of each individual tern) was the random effect. Again, the significance of the fixed effects (and their interactions) was assessed using function 'drop 1' with a chi-squared test. Tern ID was added as the GLM model was over-dispersed and had a poor fit.

At this point, only six habitat types had greater than 5% of the total GPS points within them, so the rest were excluded, and the analysis was run again. Where statistical significance was indicated, pairwise tests were run using the package emmeans. Emmeans was also used to estimate the proportion of GPS points in each habitat for each sex, split by colony. Joint tests were used to test the significance of sex, colony and sex, and colony on the number of GPS points in the six habitat types. To compare the habitat available and the habitat used by the terns (expected habitat use vs observed habitat use) the six tab-delimited text files for each habitat type were loaded into R and analysed one by one. Each file compared the expected and observed habitats with a Pearson's Chi-squared test, and the residuals and contributions of each of the six main habitat types were extracted.

Within the GPS dataset it is likely that not all the GPS fixes are from terns using a habitat, some will be of terns in transition between (overflying) the areas of habitat that they are actually interacting with. To account for this, GPS points with a speed of greater than 10 m per second (m/s) were removed from the dataset before running the habitat analysis again. These higher speed GPS points were removed as terns in flight travel faster when moving between foraging and colony areas compared to when they are foraging (Fijn & Gyimesi, 2018). Faster speeds should be from transitory rather than feeding GPS fixes. Sandwich terns have a mean foraging speed of 8.31 m/s (Fijn & Gyimesi, 2018) and Arctic, common, Sandwich and little terns together have a mean foraging speed of 8.72 m/s (Hedenström & Åkesson). A basic visual inspection of a map of the black-fronted tern GPS points collected in this study revealed the majority of transitory points (consecutive fixes in a straight line) to be greater than 10 m/s. The mean foraging speeds of other species and the observed speeds of the black-fronted tern GPS fixes make it highly likely that removing GPS points over 10 m/s will exclude the majority of transitory GPS fixes. Once these points had been removed the data was analysed the same way (see above) and compared to the previous habitat dataset which included all GPS (all speeds).

For the distance dataset, the colony of origin, sex and individual ID of each tern were added as fixed effects. Histograms were created to visualise the distribution of the data, with the distance of the GPS points from the relevant breeding colony as a continuous variable. The next run was a GLM with negative binomial error distribution (NB) as the data was not normally distributed (right-skewed). The significance of the fixed effects (and their interactions) was assessed using function 'drop 1' with a chi-squared test. Emmeans was used again to test the paired difference of GPS point distance between the sexes, split by colony location. Emmeans was then used to estimate the GPS point mean distance from the breeding colony for each sex at each colony.

Finally, boxplots of the distance of the GPS points from the relevant breeding colonies were created to ascertain the median and the third quartile of GPS point distance for part of the habitat analysis. The majority of outlying GPS points in the distance dataset were from one tern (a male from the Cass colony); the above manipulation of the distance dataset was run again without this individual to see if this significantly changed the outcome.

2.3 Results

During the 2020/2021 black-fronted tern breeding season, 112,852 GPS points were collected across the 34 terns fitted with transmitters. One device failed to collect any data. The most GPS points collected by a single device was 22,583 and the fewest 134, with an average of 3,419.76 points per bird. These points ranged in date from 04/11/2020 when the first trackers were deployed, until 14/03/2021 when the last tern stopped returning to its breeding colony and went out of range of the

HUB. Of the devices that transmitted data, the longest transmission period was 94 days and the shortest two days, with an average transmission length of 33.39 days of data per bird.

Around the Cass colony, the third quartile of 3,032.93 m (GPS point distance from breeding colony - covered in a later section 2.3.2 Foraging range) gave an area of 2,887.13 hectares in which 75% of the GPS points from terns from the Cass colony were recorded. Within the area, 94.72% of the habitat was one of the six main types. Depleted grassland made up 6.2%, gravel or rock 8.39%, exotic high producing grassland 27.47%, lake or pond 14.84%, low producing grassland 35.37% and river 2.46%.

Around the Ohau colony, the third quartile of 7,856.02 m (GPS point distance from breeding colony - covered in a later section 2.3.2 Foraging range) gave an area of 19,363.366 hectares in which 75% of the GPS points from terns from the Ohau colony were recorded. Within the area, 78.68% of the habitat was one of the six main types. Depleted grassland made up 18.73%, gravel or rock 0.43%, exotic high producing grassland 29.68%, lake or pond 4.97%, low producing grassland 23.97% and river 0.91%. Tall tussock grassland made up 13.45% of this area but was not one of the major habitat types in which GPS points were recorded, making up less than 4% of the overall and Ohau datasets.

The PCRs revealed that of the 34 birds in this study, 15 were female, and 19 were male. There were no obvious differences in the recorded weights between the sexes. Of the 112,852 GPS points, 40,023 (35.47%) were from female terns and 72,829 (64.53%) were from male, while of the same total 33,180 (29.4) were from birds caught in the Cass Colony and 79,672 (70.6) were from birds caught in the Ohau colony (Table1).

Table 1: The counts and percentages of the male, female, Cass colony and Ohau colony subsets of the 2020/2021 breeding season black-fronted tern GPS points dataset. Female points + male points and Cass points + Ohau points both = 100% as they are both discrete subsets of the total number of GPS points.

	Female Points *n*=40,023	**Male Points** *n*=7,286	**Cass Points** *n*=33,180	**Ohau Points** *n*=79,672	**% of Total Points**
Female Cass *n*=12,056	30.12%	-	36.33%	-	10.68%
Female Ohau *n*=27,967	69.88%	-	-	35.1%	24.78%
Male Cass *n*=21,124	-	29.01%	63.67%	-	18.72%
Male Ohau *n*=51,705	-	70.99%	-	64.9%	45.82%
% of Total Points	35.47%	64.53%	29.4%	70.6%	

2.3.1 Habitat use

Black-fronted terns recorded GPS points in 23 different habitat types based on LCDB v5.0 habitat classifications during the 2020/2021 breeding season. Of these 23 habitat types, nine had fewer than 50 GPS points across all birds with devices and were not considered significant enough to be analysed further. These habitats were alpine grass/herb field, broadleaved indigenous hardwoods, built-up area, gorse and/or broom, indigenous forest, landslide, short-rotation cropland, short-rotation shrubland and urban parkland/open space (the "Other" category, Table 2). Of the 14 remaining habitat types, six made up 92.49% of all the GPS points. These six habitats were depleted grassland, gravel or rock, high producing exotic grassland, lake or pond, low producing grassland and river. High producing exotic grassland was the habitat most used by the terns, with 39,493 GPS points, 34.97% of the total GPS point (Table 2). Other habitats which had more than 5% of the total GPS points were low producing grassland (15443 points, 34.1%), river (15812 points, 14.01%), lake or pond (12617 points, 11.18%), gravel or rock (10741 points, 9.52%) and depleted grassland (10267 points, 9.1%) (Table 2).

Table 2: The number of GPS points and the percentage of the total GPS points in each habitat for breeding black-fronted terns in the Mackenzie Basin.

Habitat Type	Number of GPS Points	% of Total GPS Points (2dp)
Deciduous Hardwoods	209	0.19
Depleted Grassland	10,267	9.1
Exotic Forest	1143	1.01
Gravel or Rock	10,741	9.52
Herbaceous Freshwater Vegetation	729	0.65
High Producing Exotic Grassland	39,493	35
Lake or Pond	12,617	11.2
Low Producing Grassland	15,443	13.68
Manuka and/or Kanuka	224	0.2
Matagouri or Grey Scrub	521	0.46
Mixed Exotic Shrubland	108	0.1
Orchard, Vineyard or Other Perennial Crop	552	0.49
River	15,812	14.01
Tall Tussock Grassland	4,896	4.34
Other	97	0.09

The GLMM found that habitat, sex and colony location had a significant three-way interaction (X^2=2918; P <0.001). Female black-fronted terns from the Cass colony spent 4.29% of their time in depleted grassland, 39.02% in high producing exotic grassland, 36.43% in gravel or rock, 3.07% in low producing grassland, 6.67% in lake or pond and 5.2% in river (Figure 2). This means they spent 75.45% of their time in just two habitat types – high producing exotic grassland and gravel and rock.

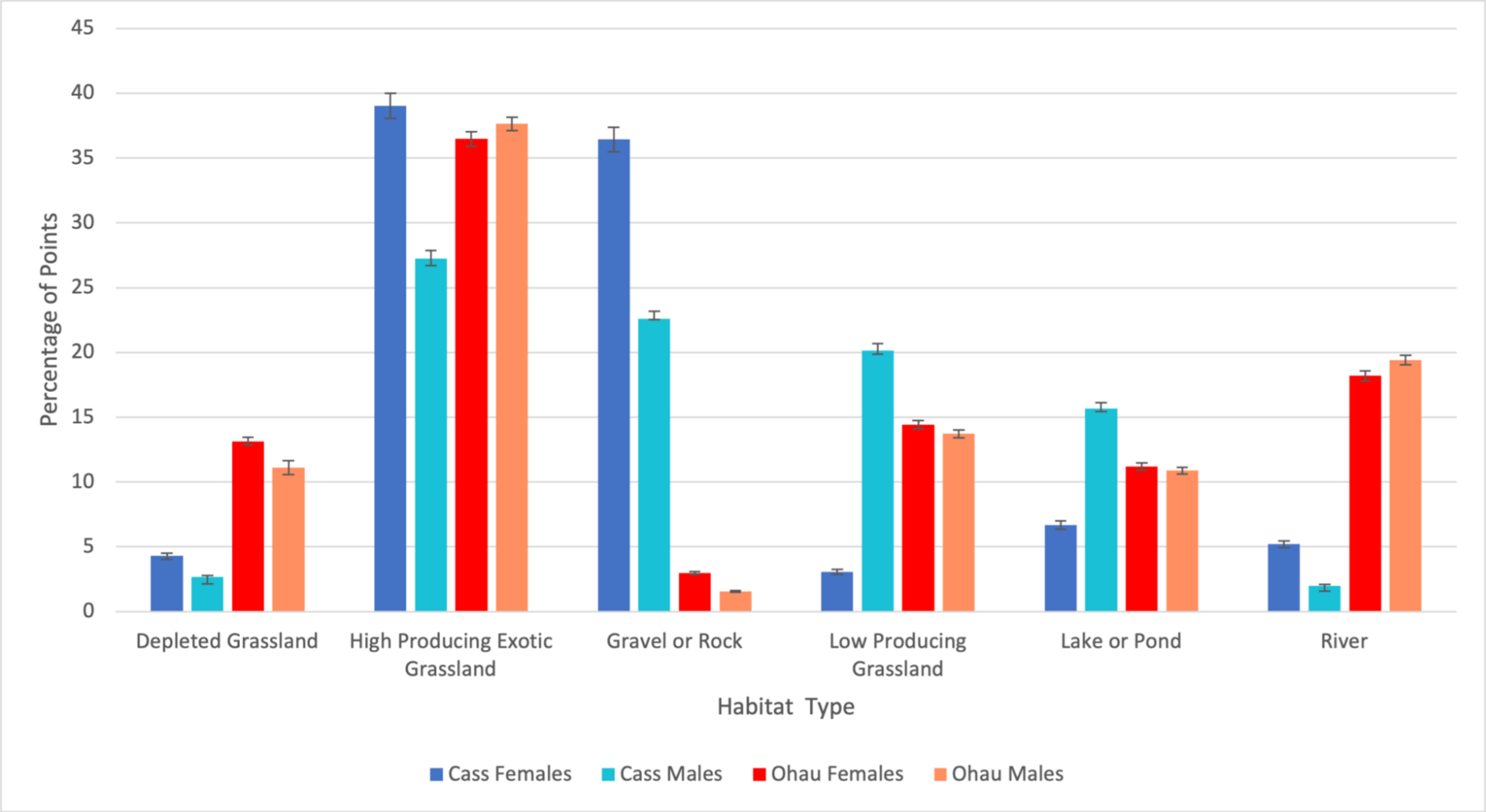

Figure 2: The percentage of GPS points in six habitats for Cass female, Cass male, Ohau female and Ohau male black-fronted terns in the Mackenzie Basin (with standard error bars).

Female black-fronted terns from the Ohau colony spent 13.15% of their time in depleted grassland, 36.48% in high producing exotic grassland, 2.99% in gravel or rock, 14.43% in low producing grassland, 11.2% in lake or pond and 18.19% in river (Figure 2). Male black-fronted terns from the Cass colony spent 2.66% of their time in depleted grassland, 27.23% in high producing exotic grassland, 22.61% in gravel or rock, 20.14% in low producing grassland, 15.68% in lake or pond and 1.97% in river (Figure 2). Male black-fronted terns from the Ohau colony spent 11.1% of their time in depleted grassland, 37.64% in high producing exotic grassland, 1.57% in gravel or rock, 13.72% in low producing grassland, 10.87% in lake or pond and 19.43% in river (Figure 2).

Ignoring sex, black-fronted terns from the Cass colony spent 3.38% of their time in depleted grassland, 32.86% in high producing exotic grassland, 29.04% in gravel or rock, 8.21% in low producing grassland, 10.33% in lake or pond and 3.22% in river (Figure 3).

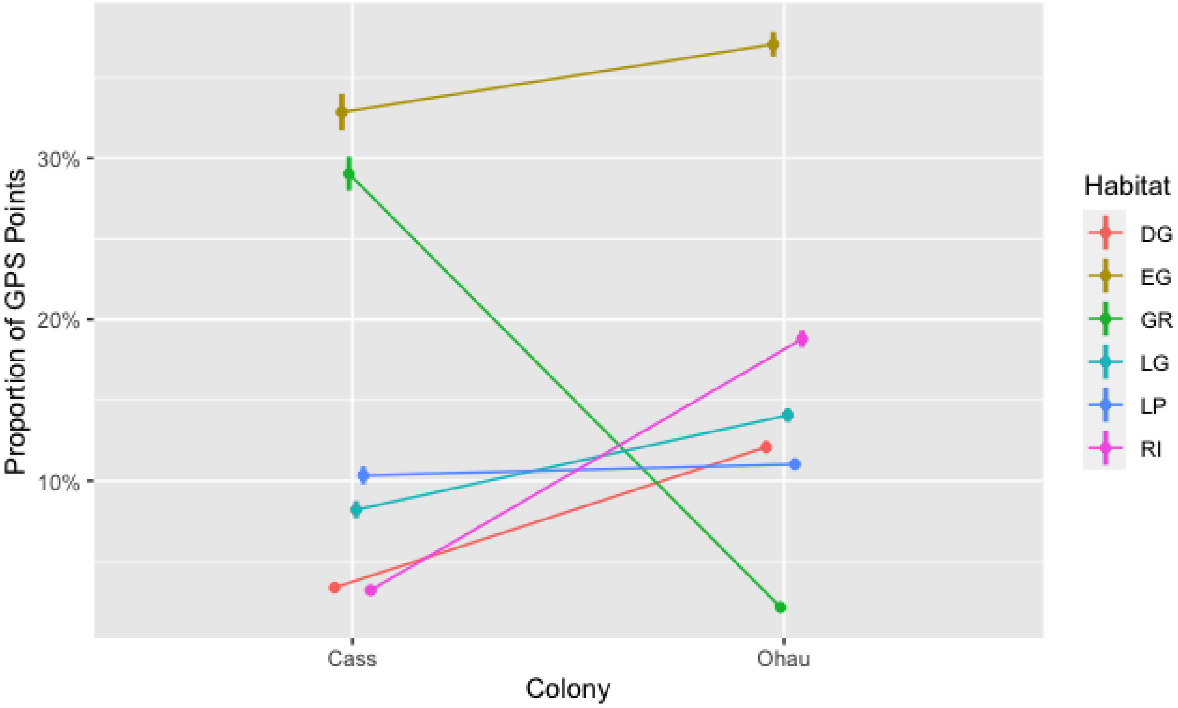

Figure 3: The effect of colony location on the proportion of GPS points of breeding black-fronted terns in six habitat types (Interaction plot with standard error). DG = depleted grassland, EG = high producing exotic grassland, GR = gravel or rock, LG = low producing grassland, RI = river.

Terns from the Cass colony spent 61.9% of their time in just two habitat types, high producing exotic grassland and gravel or rock. Again, ignoring sex, black-fronted terns from the Ohau colony spent 12.09% of their time in depleted grassland, 37.06% in high producing exotic grassland, 2.17% in gravel or rock, 14.07% in low producing grassland, 11.03% in lake or pond and 18.8% in river (Figure 3). The most used habitat for terns from both colonies was high producing exotic grassland, with the least used of the six main habitats was river for terns from the Cass colony and gravel and rock for birds from the Ohau colony. The main differences between the colonies were the proportion of time spent in the gravel or rock and river habitat types. Gravel or rock was the second most used habitat for Cass bird but the least used for Ohau birds with a difference of 25.87%. Conversely, river was the second most used for Ohau birds but the least used for Cass birds with a difference of 15.58%. Due to the three-way interaction of habitat, colony location and sex, results concerning colony location which exclude the effects of sex can potentially be misleading, as sex is a significant part of this relationship.

Ignoring the effect of colony location, female black-fronted terns spent 7.61% of their time in depleted grassland, 37.74% in high producing exotic grassland, 11.73% in gravel or rock, 6.81% in low producing grassland, 8.67% in lake or pond and 9.95% in river (Figure 4).

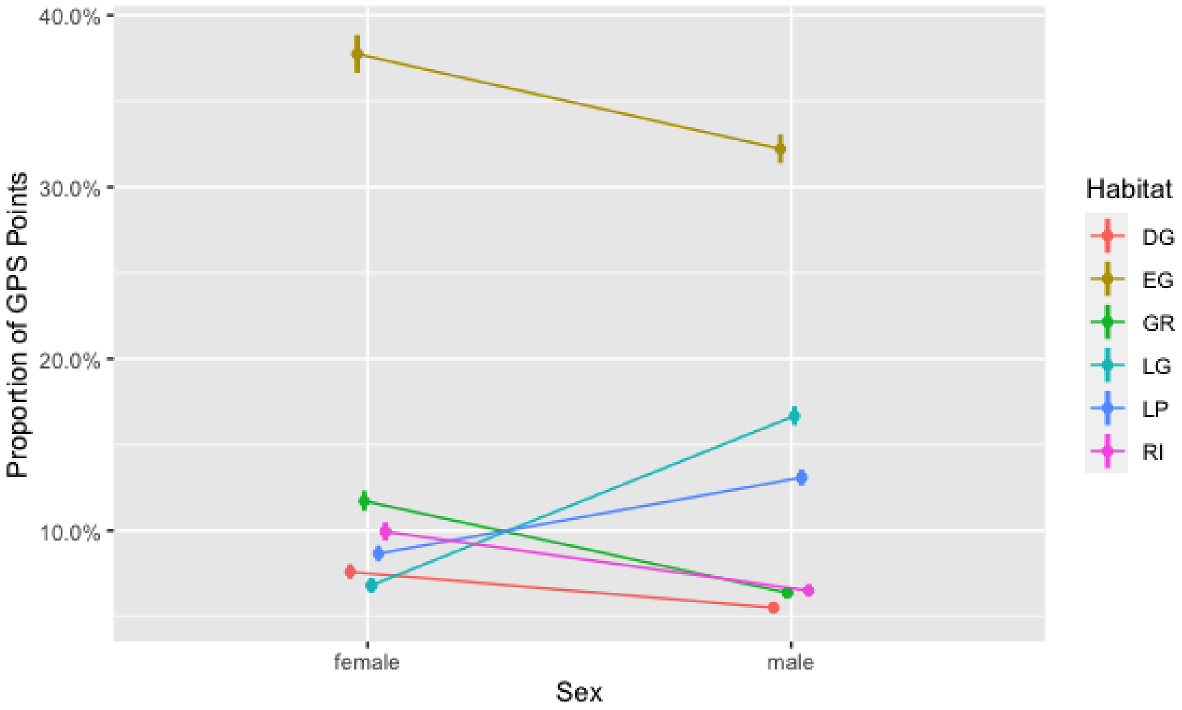

Figure 4: The effect of sex on the proportion of GPS points of breeding black-fronted terns in six habitat types (Interaction plot with standard error). DG = depleted grassland, EG = high producing exotic grassland, GR = gravel or rock, LG = low producing grassland, RI = river.

Again, ignoring the effect of colony location, male black-fronted terns spent 5.52% of their time in depleted grassland, 32.21% in high producing exotic grassland, 6.39% in gravel or rock, 16.69% in low producing grassland, 13.09% in lake or pond and 6.51% in river (Figure 4). The most used habitat type for both sexes was high producing exotic grassland, while the least used for females was low producing grassland and the least used for males was depleted grassland. The main difference between the sexes was the use of low producing grassland, the least used habitat for females but the second most used for males which was used 9.88% more by males than females. Due to the three-way interaction of habitat, colony location and sex, results concerning sex that exclude the effects of colony location can potentially be misleading, as colony location is a significant part of this relationship.

There is a strong (X^2=2918; P<0.001) three-way interaction between habitat, colony location and sex. The number of GPS points in each of the six main habitat types was significantly affected by colony location, sex and colony location and sex together. The only exception to this was in the habitat gravel and rock, which was not significantly affected by colony location and sex together. The effect of colony location on lake or pond was, while statistically significant (F=4.12; P=0.0424), not as strong as the other interactions which were all P<0.001. Across both sexes and both colony locations, high producing exotic grassland was the habitat with the highest number of GPS points (Figure 5).

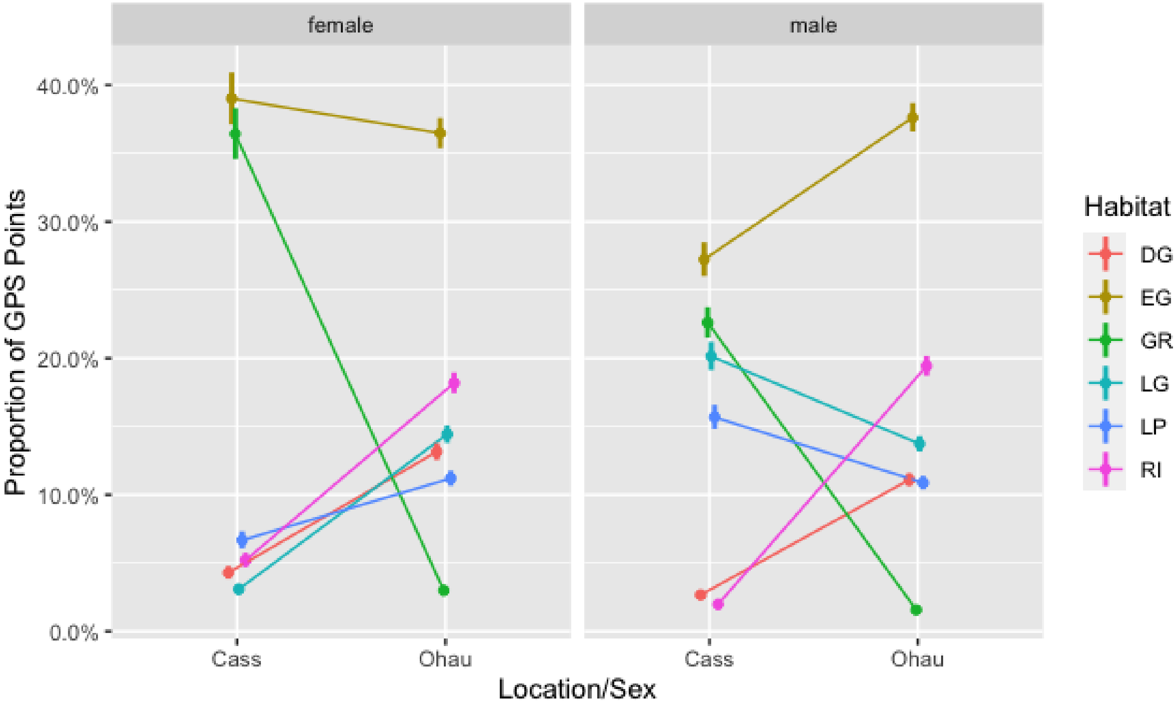

Figure 5: The proportion of GPS points of breeding black-fronted terns in six habitats split by sex and colony location (interaction plot with standard error). DG = depleted grassland, EG = high producing exotic grassland, GR = gravel or rock, LG = low producing grassland, RI = river.

Both sexes from the Cass colony used gravel or rock more than both sexes from the Ohau colony, where it was the habitat with the lowest number of observed points (Figure 5). Both sexes from the Ohau colony used depleted grassland and river more than both sexes from the Cass Colony (Figure 5). Males from the Cass Colony used low producing grassland and lake or pond than males from the Ohau colony, however, females from Ohau colony used these two habitats more than females from the Cass colony (Figure 5). Within the Cass Colony, females used exotic high-producing grassland and gravel or rock significantly more than males, while males used low producing grassland and lake or pond more than females (Figure 5). Within the Cass colony, the use of depleted grassland and river were relatively similar (Figure 5). Within the Ohau colony, habitat use was very similar between the sexes across all six main habitats (Figure 5).

There was a significant difference (X^2=41.04; P<0.001) between the available habitat around the Cass colony and the habitat used by terns from the Cass colony. The main differences were the Cass terns having 29.04% of their GPS points in gravel or rock when that habitat type represented 8.39% of the available habitat and having 8.21% of their GPS points in low producing grassland when that habitat represented 35.37% of the available habitat. There was a significant (X^2=53.89; P<0.001) difference between the available habitat around the Cass colony and the habitat used by female terns from the Cass colony. The main differences were the Cass females having 36.43% of their GPS points in gravel or rock when that habitat type represented 8.35% of the available habitat and having 3.07% of their GPS points in low producing grassland when that habitat represented 35.37% of the available habitat. There was a significant (X^2=17.43; P=0.004) difference between the available habitat around the Cass and the habitat used by male terns from the Cass colony. The main differences were the Cass males having 22.61% of their GPS points in gravel or rock when that habitat type represented 8.39% of the available habitat and having 20.14% of their GPS points in low producing grassland when that habitat represented 35.37% of the available habitat.

There was a significant (X^2=28.73; P<0.001) difference between the habitat available around the Ohau colony and the habitat used by terns from the Ohau colony. The main differences were the Ohau terns having 18.8% of their GPS points in river when that habitat type represented 0.91% of the available habitat and having 14.07% of their GPS points in low producing exotic grassland when that habitat represented 23.97% of the available habitat. There was a significant (X^2=29.92; P<0.001) difference between the habitat available around the Ohau colony and the habitat used by female terns from the Ohau colony. The main differences were the Ohau terns having 18.19% of their GPS points in river when that habitat type represented 0.91% of the available habitat and having 14.43% of their GPS points in low producing grassland when that habitat takes up 23.97% of the available habitat. There was a significant (X^2=28.07; P<0.001) difference between the habitat available around the Ohau colony and the habitat used by male terns from the Ohau colony. The main differences were the Ohau terns having 19.43% of their GPS points in river when that habitat type represented 0.91% of the available habitat and having 13.72% of their GPS points in low producing grassland when that habitat takes up 23.98% of the available habitat.

For both colonies, and both sexes at both colonies, the proportion of GPS points in low producing grassland was significantly lower than the proportion of available habitat represented by low producing grassland. For both colonies, both sexes at the Ohau and females at the Cass, the proportion of GPS points in exotic high producing grassland was significantly higher than the proportion of available habitat represented by exotic high producing grassland. For males from the Cass colony, the proportion of GPS points in exotic high producing grassland of 27.23% was very similar to the proportion of available habitat represented by exotic high producing grassland 0f 27.47%. For both colonies, and both sexes at both colonies, depleted grassland was used proportionately less than it was available. All terns from the Ohau and both sexes from the Ohau used lake or pond proportionately more than it was available.

Running the habitat analysis again after removing GPS points with speeds greater than 10 m/s changed very few of the results. The proportion of GPS points in depleted grassland was no longer significantly affected by colony location and sex together (F=2.88; P=0.0895), while the proportion of GPS points in gravel and rock changed to be significantly affected by colony location and sex together (F=10.47; P=0.0012). Removing the GPS points with speeds greater than 10 m/s did not change the significance of any results when comparing the available habitat around each breeding colony to the habitat the terns used. The biggest differences in available and used habitat for each habitat type (across both sexes and colony locations) were the same as when GPS points of all speeds were included. One minor change was that male terns from the Cass colony now used exotic high producing grassland a little more than it was proportionally available (28.4% vs 27.47%). This meant that terns from both colonies, and both sexes from both colonies, now used exotic high producing grassland more than it was proportionally available at either colony.

2.3.2 Foraging range

During the 2020/2021 breeding season, black-fronted terns from the Cass colony had a mean GPS distance from the colony of 3,780.23 m, with a first quartile of 467.2 m and a third quartile of 3,032.93 m (Figure 6). The furthest point from the Cass colony was 92,195.11 m away. Terns from the Ohau colony had a mean GPS distance from the colony of 5,982.91 m, with the first quartile of 1,039.41 m and the third quartile of 7,856.02 m (Figure 7). The furthest point from the Ohau colony was 41,897.76 m away.

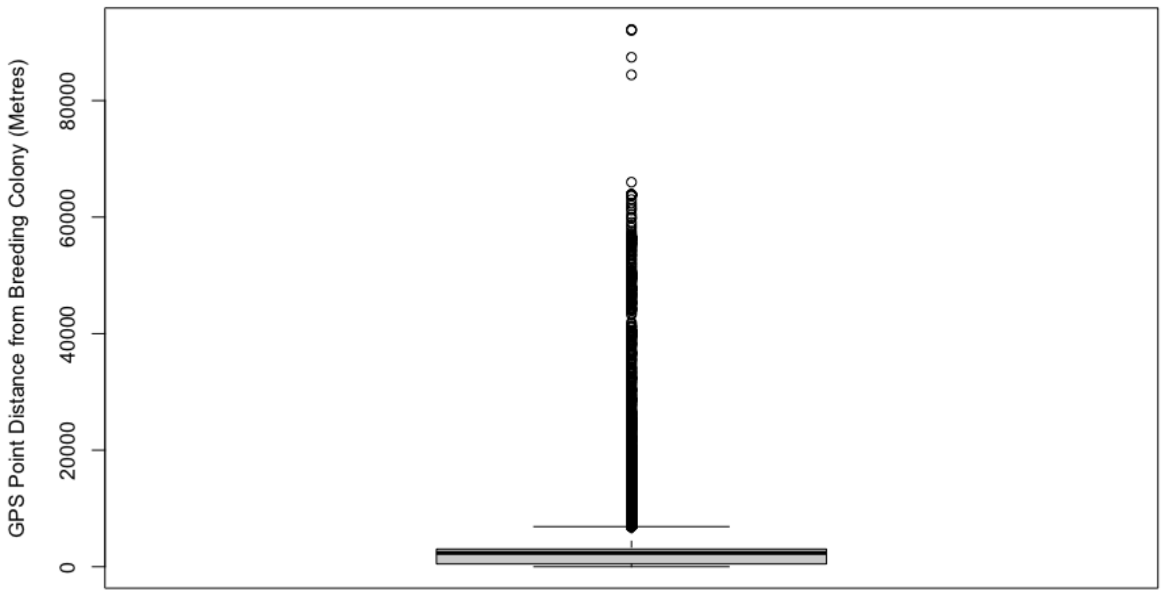

Figure 6: Black-fronted tern GPS point distances from Cass breeding colony. A box plot showing the median (thick black horizontal line) and first and third quartiles (thin black horizontal lines).

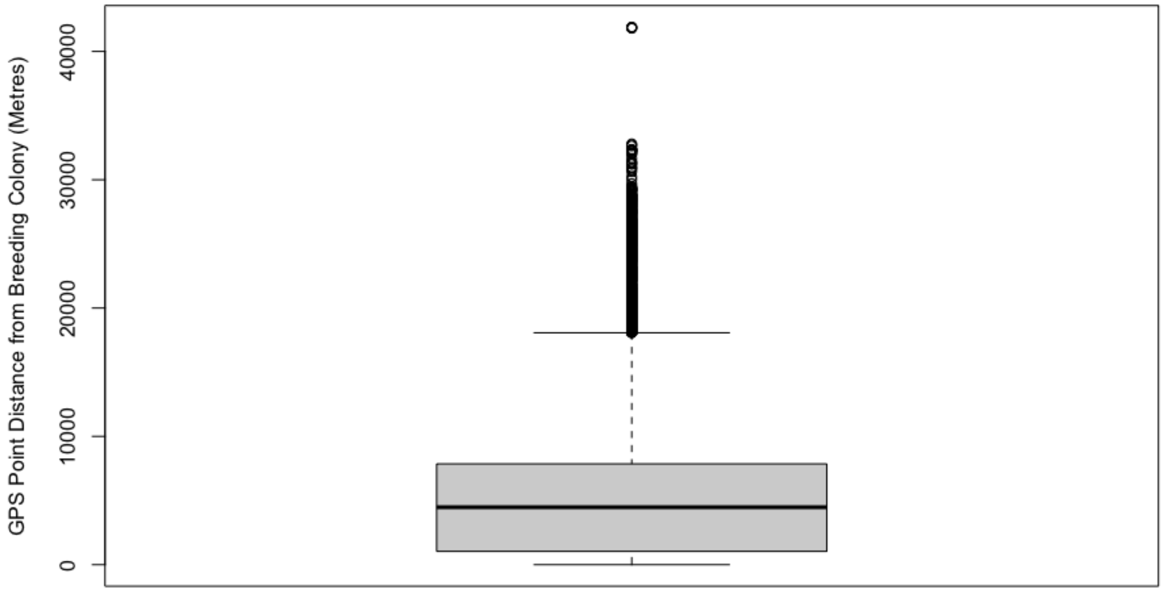

Figure 7: Black-fronted tern GPS point distances from Ohau breeding colony. A box plot showing the median (thick black horizontal line) and first and third quartiles (thin black horizontal lines).

The distance of GPS points from a breeding colony was significantly different (X^2=3642; P<0.001) between colonies, dependent on the sex. The mean distance of female GPS fixes was 1,921 m from the Cass colony and 6,565 m from the Ohau colony (Figure 8). The mean distance of male GPS fixes from the Cass colony was 4,841 m and 5,668 m from the Ohau colony (Figure 8). Both males and females from the Ohau colony had higher mean GPS point distance from breeding colony than males and females from the Cass colony (Figure 8). This is consistent with the higher mean GPS point distance from the breeding colony for terns from the Ohau overall (5,982.91 m) compared to terns from the Cass overall (3,780.23 m).

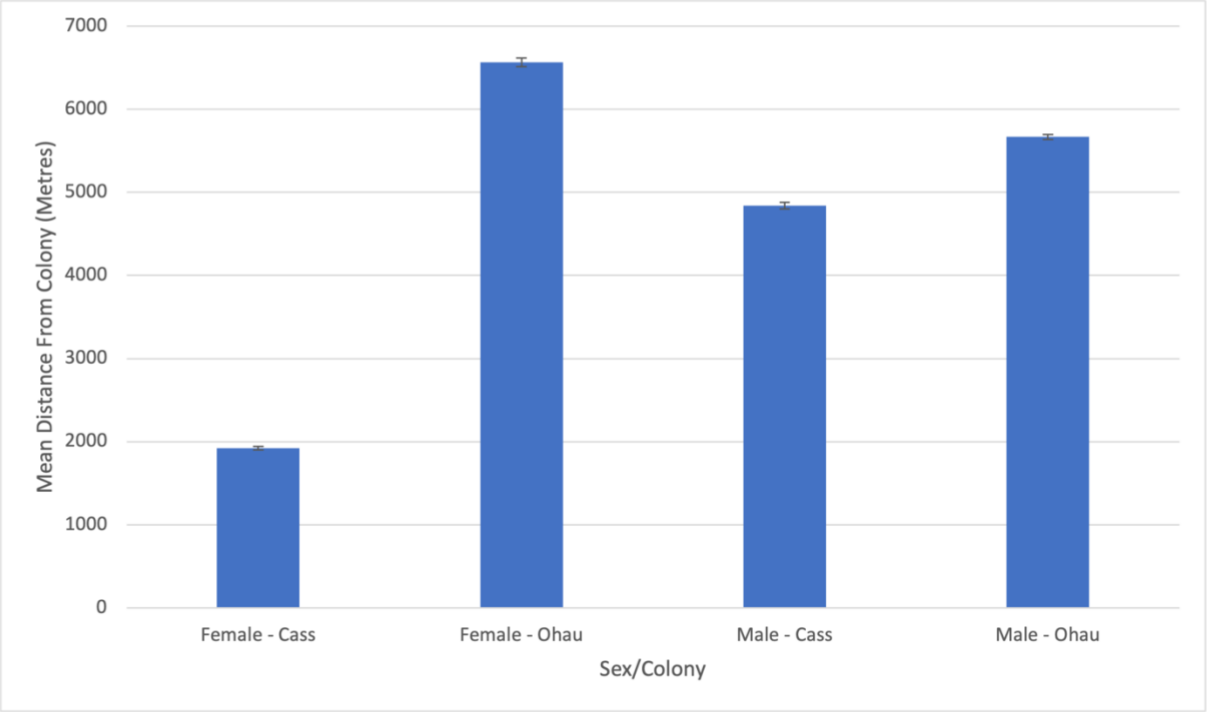

Figure 8: Mean distance of black-fronted tern GPS points from their breeding colonies, split by sex and colony location (with standard error).

All four groups (Cass females, Ohau females, Cass males and Ohau males) had significantly different mean GPS point distances from their breeding colonies compared with each other (Figure 8). For female terns there was a significant (Z=-89.05; P<0.001) difference between the Cass and Ohau in mean GPS point distance from breeding colony. Male terns also showed a significant (Z=-15.24; P <0.001) difference between the Cass and Ohau in mean GPS point distance from breeding colony. For terns from the Cass colony there was a significant (Z=-63.94; P<0.001) difference between males and females in mean GPS point distance from breeding colony. Terns from the Ohau colony also showed a significant (Z=15.64; P<0.001) difference between males and females in mean GPS point distance from breeding colony.

The farthest GPS points from either breeding colony were all from one tern, a male from the Cass colony with the individual ID of “Tern2”. Terns2’s farthest point was 92.2 km from the Cass colony in the Rakaia Riverbed, with 146.3 km between its two farthest apart GPS points. The GPS point 92.2 km away was part of a sequence of points that saw Tern2 reach this farthest point and return to the area of the Cass colony within a 24-hour period (Figure 9). The two GPS points 146.3 km apart were collected within 31 hours of each other. Tern2 was the only individual to travel more than approximately 35 km from either breeding colony and, as such, biases the mean GPS distance from breeding colony for male terns from the Cass. Excluding Tern2 from the dataset and running the distance analyses again significantly changed the mean GPS point distance from breeding colony for Cass males, reducing from 4,841 m to 3,006 m (Figure 10).

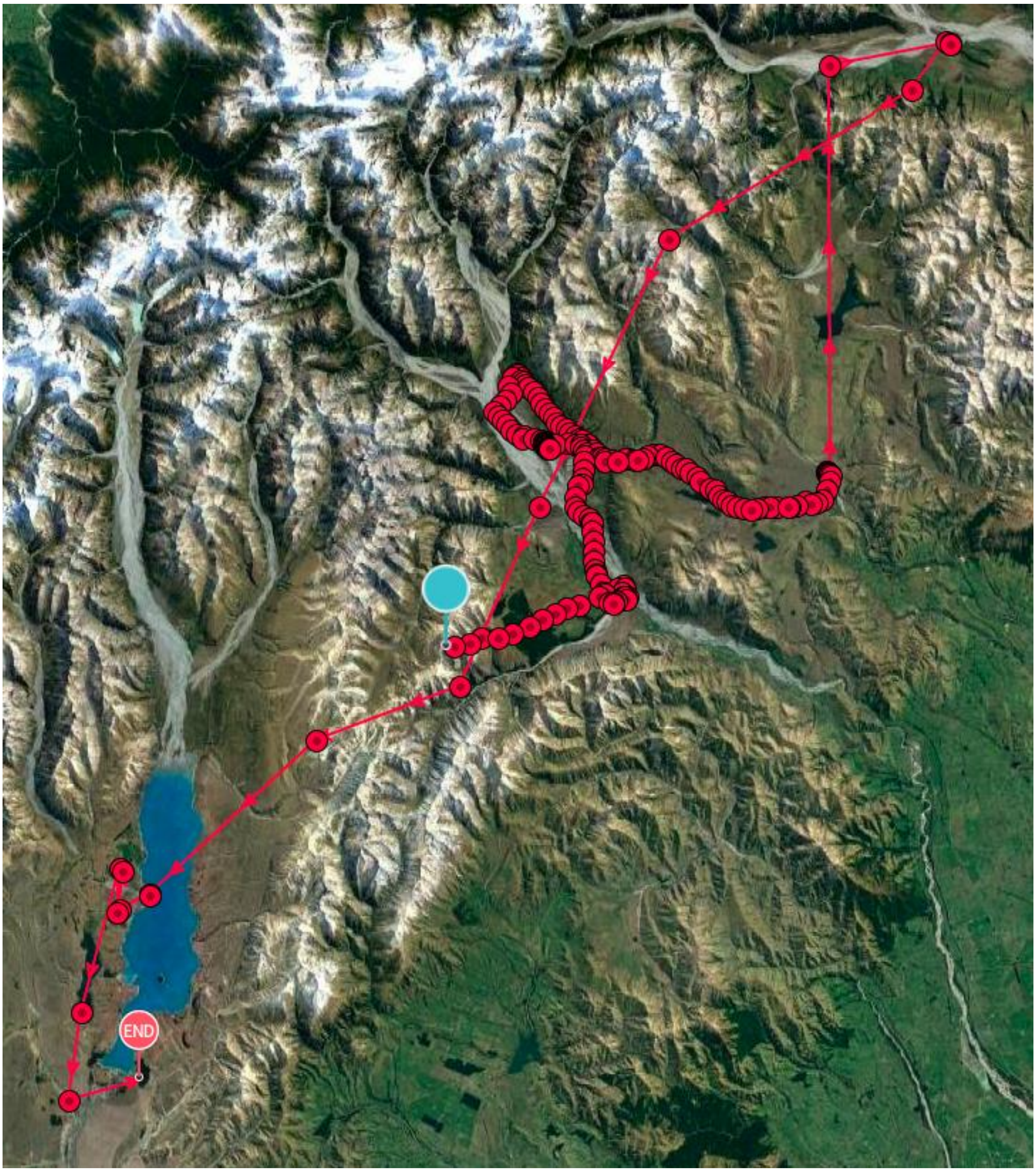

Figure 9: The movements of black-fronted tern “Tern2” over a 22-hour period with red dots for GPS fixes and the red line with direction arrows for the predicted path. The large blue dot is the first GPS fix for the time period (2pm 19/11/2020) and the large red point labelled “end” is the last in the time period (12pm 20/11/2020). The Cass colony is on the western shore of Lake Tekapo in the bottom left of the map and the farthest away GPS point in the Rakaia Riverbed in the top right of the map. Created in Druid Tech. online data centre.

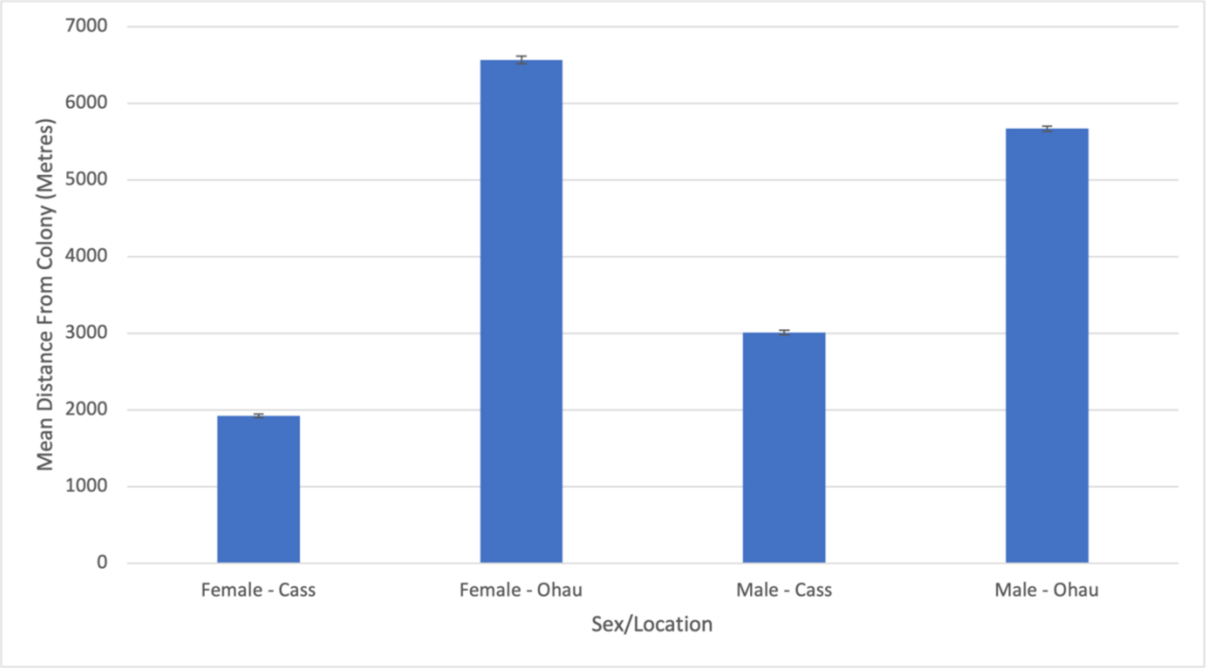

Figure 10: Mean distance of black-fronted tern GPS points (excluding the far-ranging individual "Tern2") from their breeding colonies, split by sex and colony location (with standard error).

The mean GPS point distance from breeding colony for Cass terns overall reduced from 3,780.23 m to 2,541.725 m, the first quartile from 467.2 m to 305.93 m and the third quartile from 3,032.9 m to 2,708.717 m. All other results remained the same in terms of significance.

Of the total GPS dataset, 47,876 of the points were at one of the two breeding colonies (Figure 11). Of the GPS points from birds from the Cass colony, 18,737 points were at the Cass colony itself and of the GPS points from birds from the Ohau colony, 29,139 points were at the Ohau colony itself (Figure 11). This equates to 42.42% of the total GPS points being at one of the two breeding colonies, with 56.41% at the breeding colony for Cass birds and 36.57% at the breeding colony for Ohau birds.

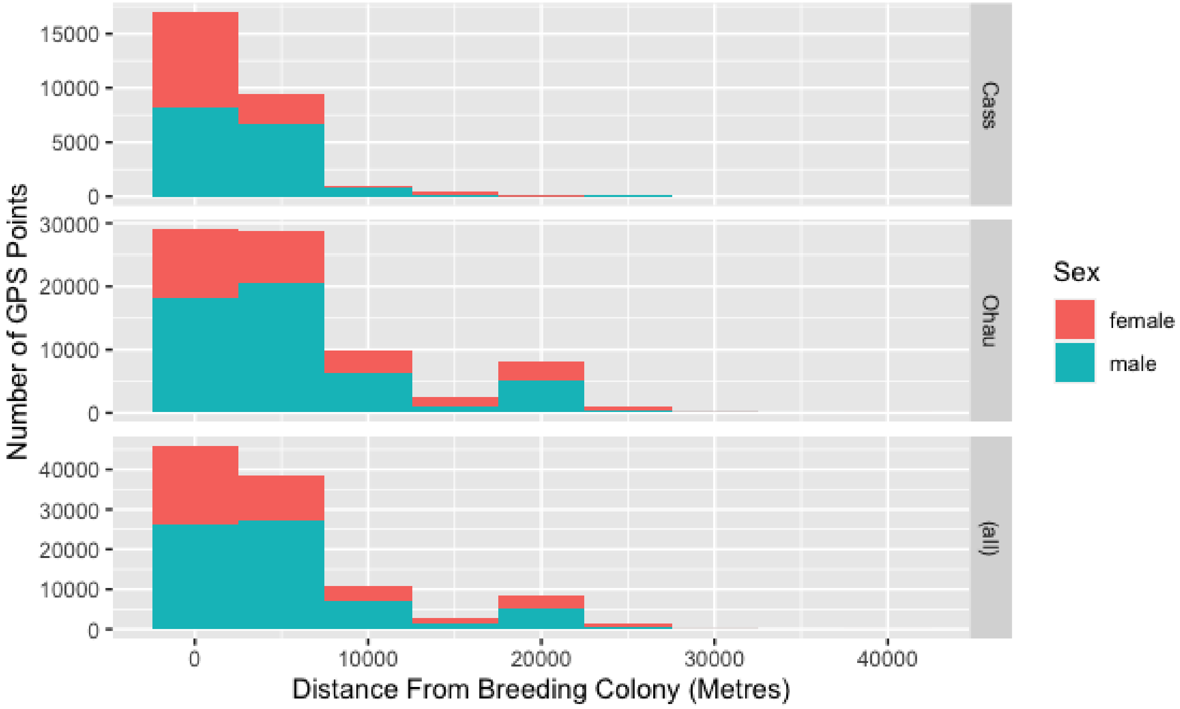

Figure 11: Number of black-fronted tern GPS points (without Tern2) in nine distance bins (0, 5000, 10,000, 15,000, 20,000 25,000 30,000, 35,000, and 40,000 m) representing distance from breeding colony.

Of the total GPS dataset, 39,260 (34.79%) of the points were within 5,000 m of either breeding colony and 11,457 (10.15%) were 5,000 to 10,000 m from either breeding colony (Figure 11). Cass birds had 10,535 points (31.75%) within 5,000 m and 17,08 points (5.15%) between 5,000 and 10,000 m away from the Cass colony, while Ohau birds had 28,723 points (36.05) within 5,000 m and 9,755 points (12.24%) between 5,000 and 10,000 m away from the Ohau colony (Figure 11). This means 87.37% of the total GPS points were within 10 km of a breeding colony, with 93.37% within 10 km of the Cass colony and 84.87% within 10 km of the Ohau colony. Terns from the Ohau colony had 10.31% of their points between 15,000 and 20,000 m away from the Ohau colony while terns from the Cass colony had <1% of their points between 15,000 and 20,000 m away from the Cass colony. Almost all (>99%) of all the GPS points were within 25 km of either breeding colony, a relationship that held true for birds from the Cass colony and birds from the Ohau colony. For birds from the Cass colony, this dropped to 96.77% when Tern2 was included. Heat maps of where the terns from each colony were travelling in relation to their breeding colonies can be seen below in Figure 12 and Figure 13. Representative terns of each sex from each colony with similar numbers of GPS points can be seen below in Figure 14, Figure 15, Figure 16 and Figure 17.

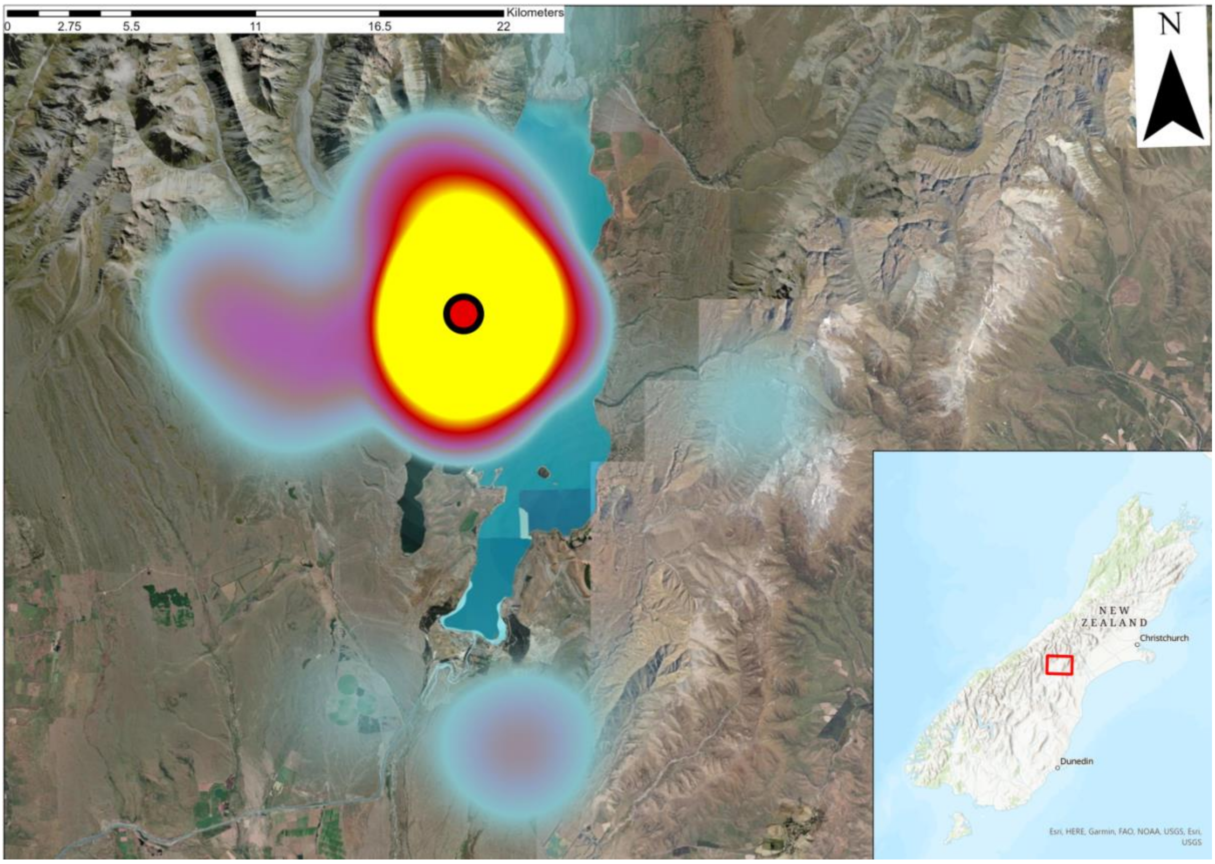

Figure 12: Heat map showing the density of GPS points from black-fronted terns from the Cass Colony. The colours indicating density go from blue through to yellow, with blue being low density and yellow high density. The solid red circle is the Cass colony. Note the secondary areas of activity to the south and east. Note the three areas of activity around irrigated farms to the south. Created in ArcGIS Pro.

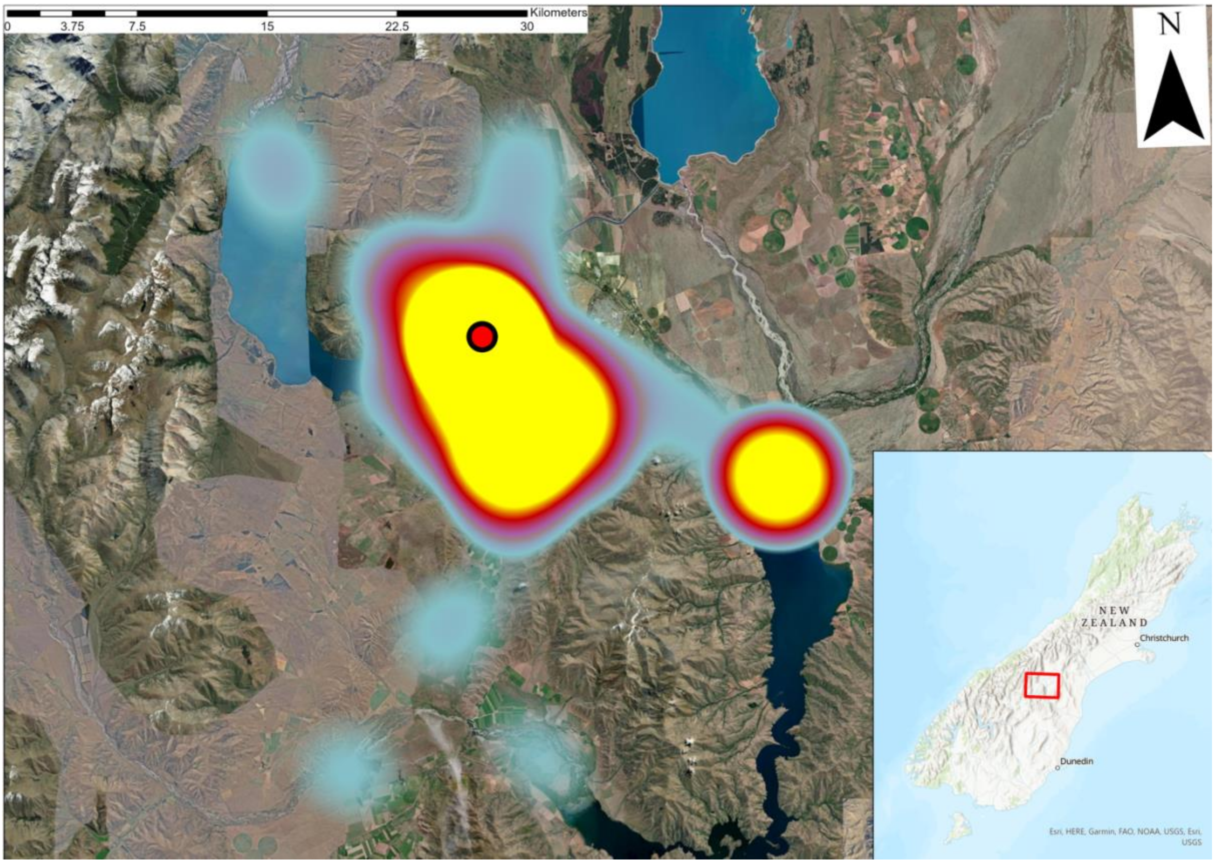

Figure 13: Heat map showing the density of GPS points from black-fronted terns from the Ohau Colony. The colours indicating density go from blue through to yellow, with blue being low density and yellow high density. The solid red circle is the Ohau colony, the right hand yellow cluster of high density GPS points is the roost at the Tekapo delta. Created in ArcGIS Pro.

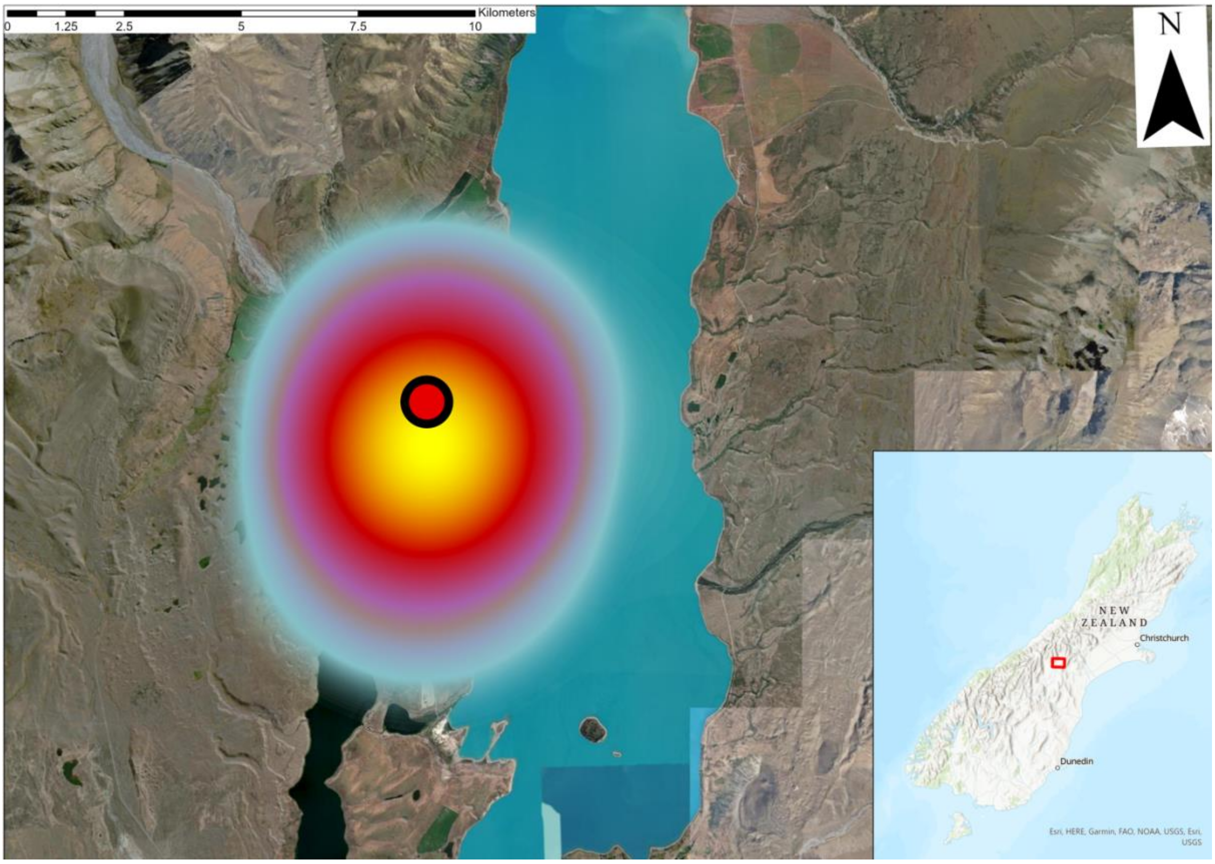

Figure 14: Heat map showing the density of GPS points from Tern1, a female black-fronted tern from the Cass Colony. The colours indicating density go from blue through to yellow, with blue being low density and yellow high density. The solid red circle is the Cass colony. Created in ArcGIS Pro.

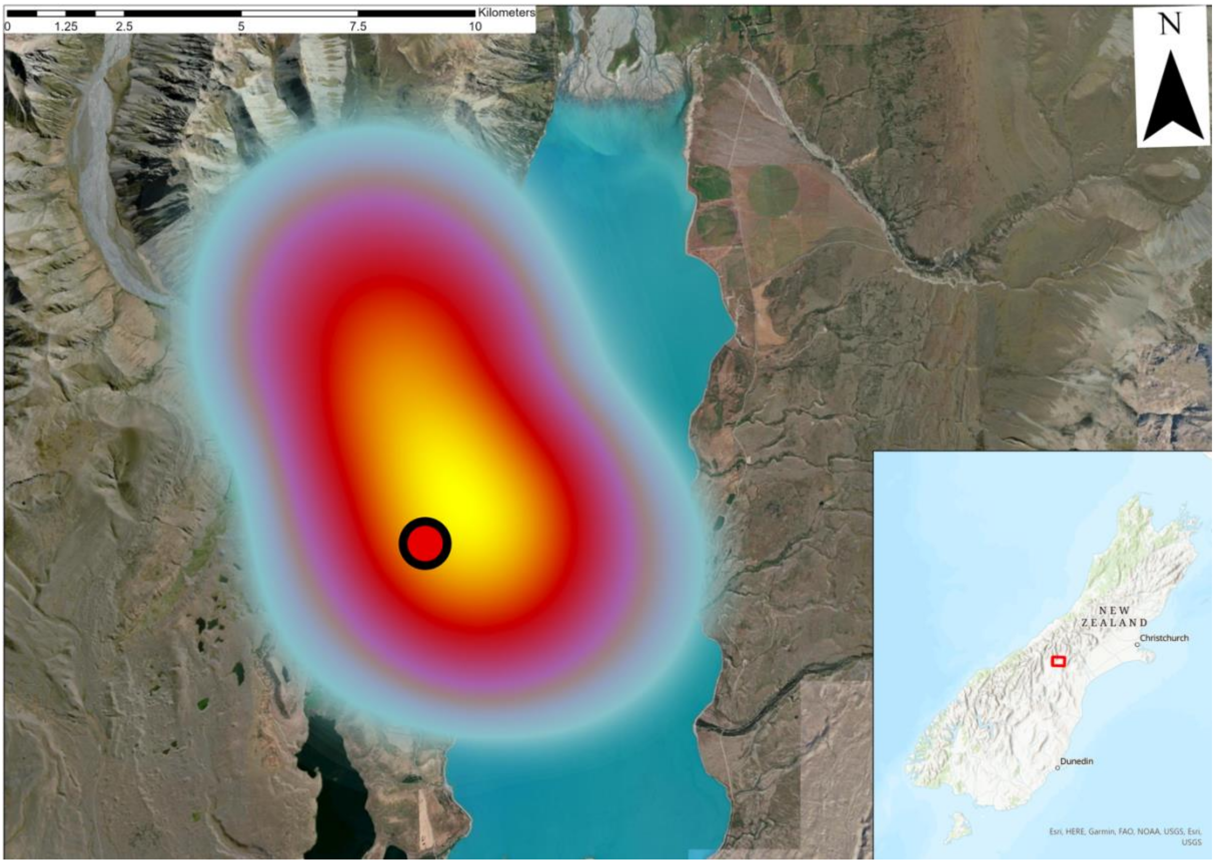

Figure 15: Heat map showing the density of GPS points from Tern5, a male black-fronted tern from the Cass Colony. The colours indicating density go from blue through to yellow, with blue being low density and yellow high density. The solid red circle is the Cass colony. Created in ArcGIS Pro.

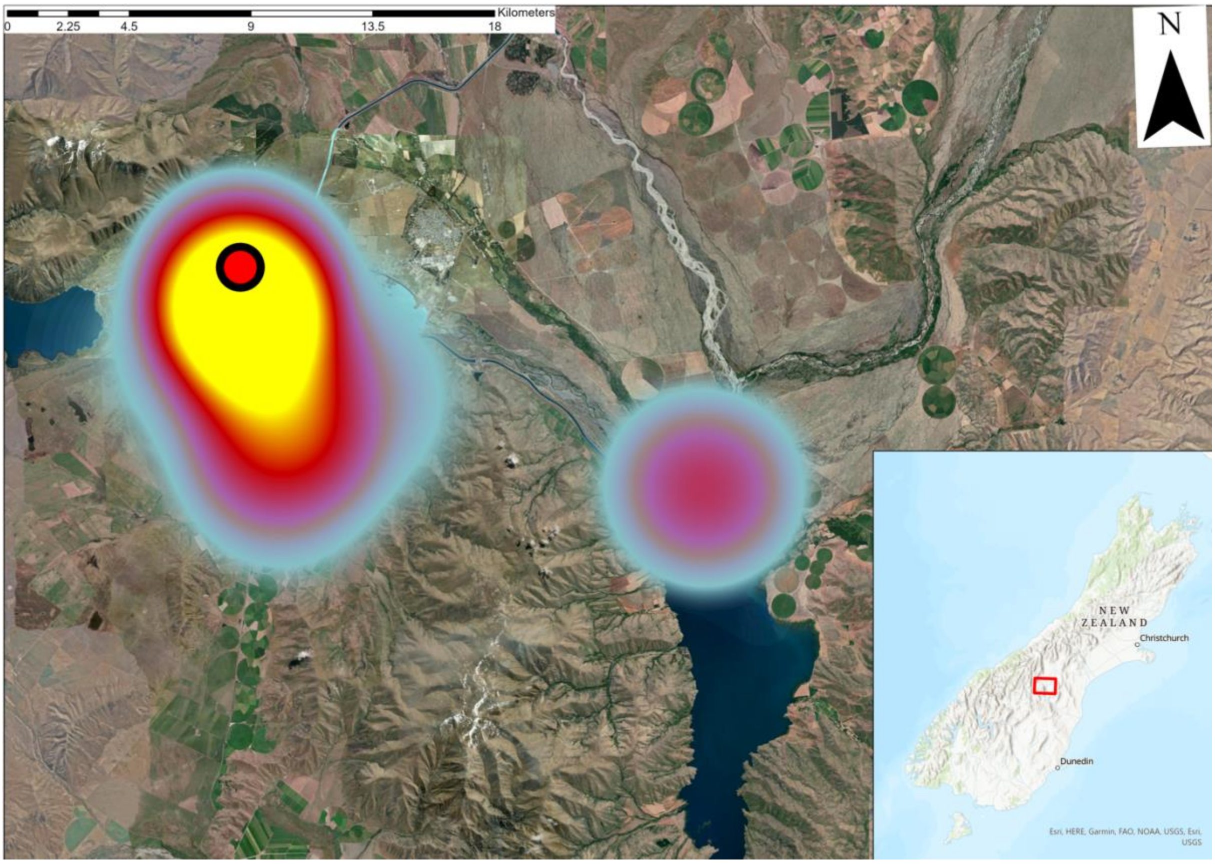

Figure 16: Heat map showing the density of GPS points from Tern13, a female black-fronted tern from the Ohau Colony. The colours indicating density go from blue through to yellow, with blue being low density and yellow high density. The solid red circle is the Ohau colony, the right hand circular cluster of GPS points is the roost at the Tekapo delta. Created in ArcGIS Pro.

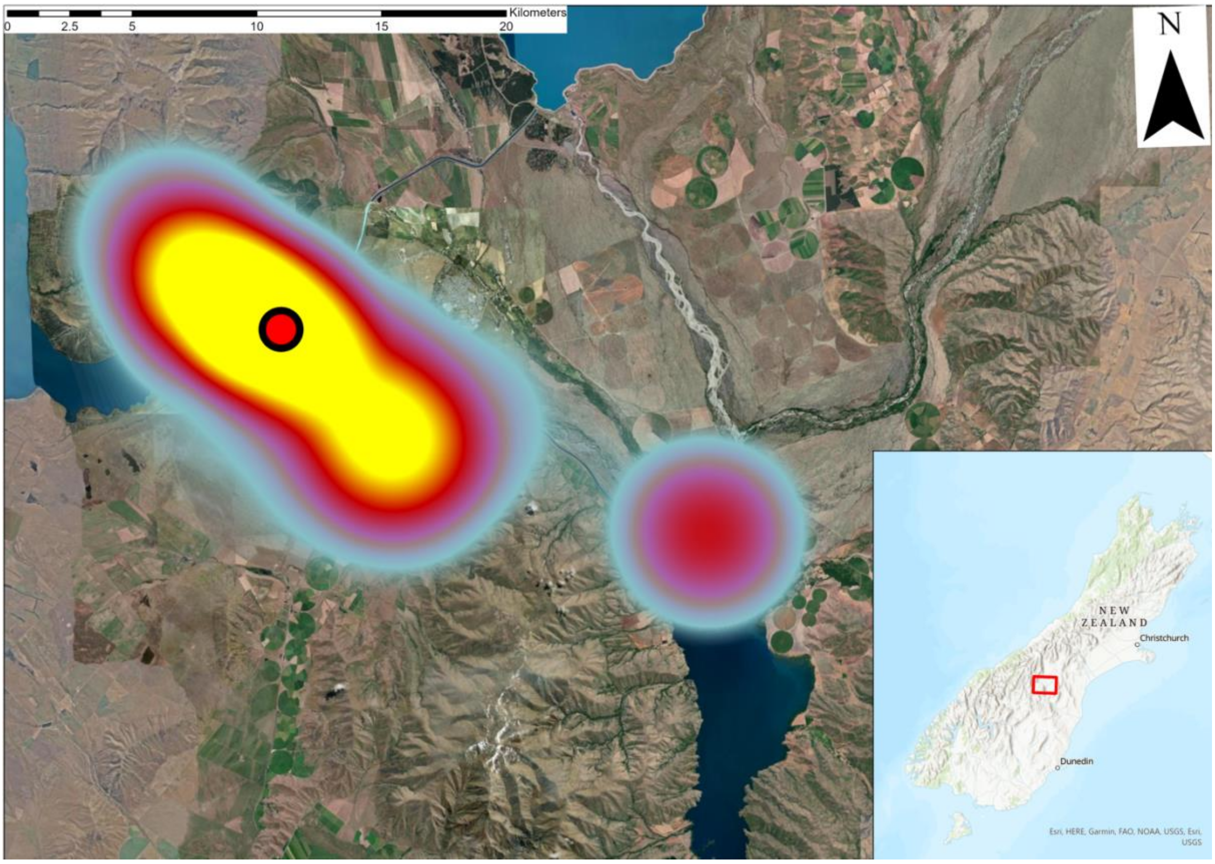

Figure 17: Heat map showing the density of GPS points from Tern12, a male black-fronted tern from the Ohau Colony. The colours indicating density go from blue through to yellow, with blue being low density and yellow high density. The solid red circle is the Ohau colony, the right hand circular cluster of GPS points is the roost at the Tekapo delta. Created in ArcGIS Pro.

When viewing the GPS points on the Druid online database, several terns were noticed with clusters of points at the Tekapo River delta at the northern end of Lake Benmore. These GPS points were recorded between 05/11/2020 and 27/02/2021 and were all during hours of darkness. In total, there were 7,147 GPS points from 23 terns at this river delta, with 22 of the terns from the Ohau colony (every Ohau bird in the study bar two) and one from the Cass (the Cass bird was the wide-ranging Tern2 that only recorded 33 GPS points here). Of the 7,147 GPS points at the Tekapo delta, 4,538 (63.5%) were from male terns and 2,609 (36.5%) were from females. Across the birds from the Ohau that used this site there were fairly consistent routes between the Ohau breeding colony and the Tekapo delta roost. From the Ohau breeding colony, the terns generally travelled east to join up with the Ohau River downstream of the colony and follow the river to Lake Ruataniwha. From here they flew east across the lake then southeast down the lower Ohau River to Lake Benmore and the Tekapo delta. The Tekapo delta is 18.87 km from the Ohau breeding colony in a straight line. Near the Cass colony, the Cass River delta also had large and tightly spaced clusters of nocturnal GPS points, all from terns from the Cass colony. All 10 Cass terns (Tern1 – Tern7 and Tern26 – Tern28) had GPS points at night from the Cass delta. Here, there were many diurnal GPS points in the same vicinity as the nocturnal ones, however the tight clusters of points recorded during hours of darkness indicated that Cass terns were roosting there at night. The Cass delta is approximately two km downstream from the Cass colony, on the western shore of Lake Tekapo.

2.4 Discussion

The most important habitats for black-fronted terns from the Cass and Ohau colonies in the Mackenzie Basin appear to be high producing exotic grassland, depleted grassland, gravel or rock, lake or pond, low producing grassland and river. The terns spent more than 92% of their time in these habitats, making them by far the most important in terms of proportion of time used. Of these six habitats, high producing exotic grassland was the most prominent. Terns used it proportionally more than it was available around either colony. This grassland was the most used habitat for male and female terns from both colonies. This preference for high producing exotic grassland was maintained after transitional GPS points were removed from the data. The main use of high producing exotic grassland was irrigated paddocks, with very large clusters of GPS points in irrigated paddocks directly north and south of the Cass colony and directly to the south/southeast of the Ohau colony. It has been well documented that black-fronted terns forage over farmland/grassland, especially in winter (Lalas, 1977; Latham, 1981; Robertson, 1983), but this is the first direct evidence that this habitat type can be the primary habitat used by breeding black-fronted terns where it is available.

This study did not investigate why black-fronted terns may spend time in certain habitats over others, but there are potential reasons why the terns showed this preference for high producing exotic grassland. This grassland (in the form of irrigated fields) made up approximately one quarter of the available habitat around both breeding colonies, it was the second most common habitat around the Cass colony and the most common habitat around the Ohau colony. As such it was always likely for the terns to record a relatively high number of GPS points in high producing exotic grassland. However, the fact that the proportion of time the terns spent in this habitat was higher than the proportion of available habitat it represented (at both colonies) means black-fronted terns were actively showing a preference for it. It has been noted that black-fronted terns primarily feed on grass grubs and earthworms when feeding in pastures, with grass grub adults being particularly important during November and December (Lalas, 1977). This coincides with when the most GPS points were being collected (Nov-Dec, immediately after device deployment) and could go some way to explaining the high number of GPS points in high producing exotic grassland. Given that agriculture has been identified as the largest global extinction threat to birds (Green et al., 2005), it is perhaps surprising but positive that an endangered species like that black-fronted tern seems to gain some benefit from an agricultural land use.

As irrigated paddocks did not exist in New Zealand before human arrival, any black-fronted tern preference for high producing exotic grassland is likely an exaptation rather than an adaptation. Human activity has almost completely transformed the vegetation in the Mackenzie Basin cover (McGlone & Moar, 1998), with there previously being much more woody vegetation and tussock grassland (Connor & Vucetich, 1964; Williams et al., 2012). The high proportion of farmland around both colonies in this study is not a natural setting for a black-fronted tern colony, making the results of this study not entirely representative of a natural system (but typical of the majority of current black-fronted tern breeding areas). As such, there are potential negative consequences for black-fronted terns becoming dependent, or partly dependent, on irrigated farmland. Irrigated paddocks can have lower invertebrate diversity than more natural land uses (Bowie et al., 2016; Schon et al., 2012), which has been linked to lower bird diversity and abundance in grassland birds in Britain (Vickery et al., 2001). Insecticides used on irrigated farmland can also have negative consequences for birds, both through reducing invertebrate prey and thus breeding productivity (Hart et al., 2006), and through both fatal and sub-lethal secondary poisoning (Stanton et al., 2018). Changes in a farming or watering regime are also likely to change the amount of available invertebrate prey, although black-fronted terns are less likely to be affected by this given their opportunistic foraging strategy (Pierce, 1983) and the dynamic nature of the braided rivers they depend on for breeding.

Being able to determine the sex of the individuals fitted with GPS devices was extremely valuable and added another layer to the study. Significant differences in habitat use between male and female terns were only seen at the Cass colony, where the main difference was that males spent over four times as much time in low-producing grassland than females. Sex-based differences in habitat use in birds have been linked to morphological differences between sexes, with the different morphologies allowing the sexes to make use of different habitats or the larger sex able to exclude the smaller from areas of favourable habitat (Ardia & Bildstein, 1997). This is unlikely to be the case for black-fronted terns, which are a monomorphic species (Schlesselmann, 2018). Female birds have higher energy requirements than males early in the breeding season while they are forming eggs (Perrins, 1996). Females may, therefore, be more selective in their habitat use, avoiding low quality habitats in favour of high quality ones (Lintott et al., 2014). Males may be less selective as they have lower energy requirements (Lintott et al., 2014). Low producing grassland is a lower quality habitat than the high producing exotic grassland preferred by black-fronted terns in this study (Landcare Research New Zealand, 2020), so males using low producing grassland more than females may be due to higher female selectivity. However, the GPS devices in this study were attached to the terns after laying had occurred, meaning any differences in selectivity due to energy requirements are a hangover from the female egg formation phase or caused by another factor. Sex-based differences in habitat selection, as well as any habitat selection seen in this study, may be due to adaptive value or occur out of constraints (Kolts & McRae, 2017). Constraints may be factors such as terns being excluded from an area (through competition and predation) (Pasinelli et al., 2016) or a temporary or permanent lack of resources in what is usually a productive habitat.

Between the Cass and Ohau colonies the big differences were how much the terns used the gravel and rock habitat (29.04% vs 2.17%) and the river habitat (3.22% vs 18.8%). This difference is likely due to the differences between the Cass and Ohau rivers where the black-fronted tern colonies are located. Near the Cass colony the Cass River is a very wide braided river with multiple channels and large areas of exposed gravel, while at the Ohau colony the Ohau River is much narrower with far less exposed gravel and a single channel either side of the colony island. Because of this, the Land Cover Database classification of the Cass colony is mostly gravel and rock with a small area of river, while the Ohau colony is classified as just river. This means most GPS points from the Cass colony return a habitat reading of gravel and rock, while every GPS point from the Ohau colony returns a habitat value of river. If gravel and rock and river are treated as a single habitat (24.58% for Cass, 21% for Ohau), the difference between the two colonies is less than 4% and doesn’t indicate any habitat preference. The other difference between the two colonies is depleted grassland, which was used more by terns from the Ohau colony than terns from the Cass colony. Again, this difference is likely because there is proportionately more depleted grassland habitat around the Ohau colony than the Cass colony.

Black-fronted terns selected some habitats over others, as evidenced by the significant statistical differences (<0.001 for both colonies) between the habitat that was available around the breeding colonies and the habitat the terns actually used**.** The drivers of this relationship were Cass terns using gravel and rock proportionately more than it was available, Ohau terns using river proportionately more than it was available and both colonies using low producing grassland proportionately less than it was available. Low producing and depleted grassland are characterised as having lower fertility soil than high producing exotic grassland, which the terns favoured, resulting in fewer and poorer quality, less vigorous plants (Landcare Research New Zealand, 2020). Depleted grassland areas have also been degraded by extensive grazing, leading to sparse plant cover and areas of bare ground (Landcare Research New Zealand, 2020). These poorer areas of grassland likely support a lower diversity and amount of prey species for black-fronted terns, resulting in them selecting against these habitats. Other bird species, such as Eurasian skylark (*Alauda arvensis*) and yellowhammer (*Emberiza citrinella*), are known to favour grassland with large populations of seeding grasses, while tern species, such as the closely related black tern, have also been shown to avoid areas of grassland in favour of wetter areas (Naugle et al., 2000).

Overall, the habitats in which breeding black-fronted terns in the Mackenzie Basin spend their time depends on their sex, their colony, and which sex from which colony. The most significant difference between the sexes within one colony was at the Cass, where females used high producing exotic grassland and gravel and rock proportionally more than males. Females spent over three quarters (75.45%) of their time in one of these two habitats, i.e. they spent three quarters of their time at the breeding colony or foraging over irrigated paddocks. This was the highest proportion of time spent in just two habitat types for any combination of sex and colony location. This use of high producing exotic grassland and gravel or rock was balanced by Cass males who used low producing grassland and lake or pond significantly more than Cass females. In contrast, there was little difference in habitat use between the sexes at the Ohau colony. Depleted grassland was the only habitat that was not affected by sex and location together, possibly indicating that both sexes at both colonies select against it equally.

Black-fronted terns breeding at the Cass and Ohau spent >99% of their time within 25 km of their breeding colonies. Within this 25 km foraging range, the terns spent 87.37% of their time within 10 km of their breeding colony. This is a smaller foraging range than has been reported for several other tern species. Bridled terns (*Onychoprion anaethetus*) can forage up to 160 km from their breeding colony (Dunlop, 1997) and sooty terns were recorded up to 139 km (Soanes et al., 2015) and up to 865 km away (Neumann et al., 2018) from their breeding colonies. For the black-fronted terns, the average distance of GPS points from the breeding colony was 3.78 km for the Cass colony (2.54 km when excluding Tern2) and 5.98 km for the Ohau colony. Again, these averages are lower than mean foraging ranges seen in other terns, such as the Sandwich tern (average foraging range 27 km) (Fijn & Gyimesi, 2018). The distance terns travel from their breeding colony when foraging depends on the location of their preferred foraging habitats (Fasola & Bogliani, 1990), so black-fronted terns may have foraging habitat closer to their colonies than these other species. This seems likely as the black-fronted terns in this study had major clusters of GPS points over irrigated paddocks up to 3.5 km from the Cass colony and up to 10 km from the Ohau colony. The other species mentioned above forage almost exclusively in marine environments where foraging habitat ,such as shelf breaks, may be much further away (Dunlop, 1997; Fijn et al., 2017; Neumann et al., 2018; Soanes et al., 2015).

Both female and male terns from the Ohau travelled further on average than males and females from the Cass. This difference could be driven by the distance from the respective colonies of the terns main foraging habitat, high producing exotic grassland. As previously mentioned, irrigated fields with high clusters of GPS points were only 3.5 km from the Cass colony but up to 10 km from the Ohau colony, meaning Ohau terns potentially have to travel further to reach these areas. Cass females, Cass males, Ohau females and Ohau males all had significantly different mean GPS point distance from breeding colony ($P<0.001$). This means that overall, the foraging range of Black-fronted terns from the Cass and Ohau colonies depends on their sex, their colony location and which sex from which colony.

One individual tern, Tern2, was a male from the Cass colony and was the source of nearly all the outlying GPS points in terms of distance from the breeding colony. Tern2 was by far the widest ranging tern in this study, with the next widest ranging travelling a maximum of 41.91 km from its breeding colony (compared with a maximum of 92.2 km for Tern2). Removing Tern2 from the analysis lowered the mean distance of GPS points from the Cass colony by over a km but didn't change the significance of any of the results when comparing the sexes or colony locations. The outlying GPS points were collected in one 24-hour period where Tern2 travelled as far as the upper Rakaia River, over 92 km away in a straight line. During this 24-hour period, Tern2 also spent time in the upper Rangitata River, meaning Tern2 was present in three distinct river catchments within a single day (Cass, Rangitata and Rakaia). This is likely the first direct evidence of such mobility in black-fronted terns in such a short timeframe and highlights the potential difficulty of conducting population counts for the species. Had a population census been conducted on the day this bird travelled so far, Tern2 could potentially have been counted three times.

Between the two breeding colonies, black-fronted terns spent 42.42% of their time at one of the colonies (56.41% for the Cass, 36.57% for the Ohau). This is relatively similar to what has been found for other tern species, with Forster's terns spending 51% (incubation period) and 41% (chick rearing) of their time at their breeding colony and Caspian terns also spending 51% of their time at their breeding colony (Ackerman et al., 2009). As a general rule for the Cass and Ohau colonies, as the distance from the breeding colonies increased there were fewer GPS points. Between the two colonies black-fronted terns spent 34.79% of their time within five km of either colony and 10.15% of their time between five and 10 km of either colony. This was the same with terns from the Cass and Ohau colonies separately, with fewer and fewer GPS points in the distance bins as the distance from the colony increased. This is the same as what has been observed in terns elsewhere; the density of both gull-billed and little terns decreases as the distance from the breeding colony increases (Fasola & Bogliani, 1990). The exception to this was between 15 and 20 km away, where terns from the Ohau had far more points than terns from the Cass (10.31% vs <1%).

The higher number of GPS points between 15 km and 20 km from the breeding colony for Ohau terns is likely due to the cluster of points at the Tekapo River delta at the north end of Lake Benmore, 18.87 km from the Ohau colony. This cluster of points was from a nocturnal roost for terns from the Ohau colony, the first evidence of breeding black-fronted terns roosting away from their breeding colony at night. The ratio that male and female terns were using this roost (63.5% male, 36.5% female) is extremely similar to the male and female ratio of GPS points from the Ohau colony (64.9%

male, 35.1% female), suggesting this roost was being used equally by males and females. The even use between males and females coupled with the fact that the terns did not spend every night at the Tekapo delta roost indicates parental pairs may be alternating between incubation or chick guarding and roosting at the delta. Terns from the Cass colony also appeared to be roosting away from the colony at night, with nocturnal GPS points from Cass terns approximately two km downstream at the Cass River delta. The Cass delta is much closer to the Cass colony than the Tekapo delta is to the Ohau colony, meaning there were more diurnal GPS points around the nocturnal ones at the Cass delta. The night roost for the Ohau colony being further away also likely contributes to terns from the Ohau colony having a greater average GPS point distance from the breeding colony than Cass terns.

Black-fronted terns often roost on islands in river systems as they afford good visibility of the surrounding area (Lalas, 1977). River deltas usually contain multiple islands (Hoitink et al., 2017), making them an attractive place for black-fronted terns to roost. The Tekapo and Cass deltas were likely chosen as roost sites as the closest river deltas to the Ohau and Cass colonies, respectively. Excluding the breeding colonies themselves, the two deltas are also the closest major roosting areas to the areas of irrigated fields favoured as foraging areas by the respective colonies. Again, this makes the deltas likely roost sites as black-fronted tern roosts are often near feeding sites (Lalas, 1977). The terns from the Ohau colony that used the Tekapo delta as a night roost could have some life history link to the delta, such as previously nesting in either the Pukaki or Tasman rivers. Both of these rivers feed into the Tekapo delta (the confluence is approximately four km upstream of the delta) and in previous breeding seasons both have had black-fronted tern colonies (Richard Maloney, personal communication, 11/05/2022). In some river systems black-fronted terns may return to the same general area across multiple years (Hamblin, 2017; Pierce, 1983), so previously nesting in this river system may draw them back even if there are no current breeding colonies. Regardless of the reason why, river deltas appear to be an important area for breeding black-fronted terns in the Mackenzie Basin.

The GPS dataset for 2020/2021 black-fronted tern breeding season is data rich, with 112,852 GPS points spanning 129 days. However, there were several limitations to the data and how it was analysed. There are skews in the data favouring male terns and terns from the Ohau colony, with 64.53% of the GPS points from male terns and 70.6% from Ohau terns. This bias is the same within both sexes and colonies, both males and females GPS points are primarily from the Ohau and both Cass and Ohau GPS points are primarily male. This potentially may have masked some of the differences between the sexes and colonies. Another potential bias was the large variation in how many GPS points from individual terns were collected, ranging from 134 to 22,583 points (the individual with 22,583 points made up over 20% of the entire dataset). This disparity potentially hid variation between individuals.

The habitat type of tall tussock grassland contained 4.34% of the dataset but was excluded from most of the analysis as it was significantly lower than the next lowest habitat type at 9.10%, which was depleted grassland. However, tall tussock grassland contained significantly more of the dataset than all of the other habitat types that weren't included, with the next highest being exotic forest at 1.01%. Excluding tall tussock grassland may have removed the effects that this habitat type had on black-fronted tern habitat selection. Findings from this study are highly relevant, but only cover one breeding season. This study was also conducted solely on black-fronted terns in the Mackenzie Basin; findings may differ elsewhere in New Zealand (or even within the Mackenzie Basin).

In conclusion, the most important habitat for all black-fronted terns during the breeding season was high producing exotic grassland. In contrast, both low-producing and depleted grassland were selected against by the terns in this study. Black-fronted terns ranged up to 92 km from their breeding colonies, but 99% of their time was spent within 25 km of their colonies. This study also provided the first evidence of breeding black-fronted terns roosting away from their breeding colonies at night, identifying river deltas near both breeding colonies as important areas for these terns. Both the habitats used, and the distances ranged from breeding colonies of black-fronted terns, were influenced by sex and colony location. There was a significant three-way interaction between habitat, sex, and colony location and the mean distance from breeding colony was significantly different across both sexes and colony locations. This chapter provides a picture of black-fronted tern habitat use in the Mackenzie Basin and at what scale this occurs. The next steps are to investigate the reasons for these differences and compare these results with black-fronted tern colonies outside the Mackenzie Basin.

Chapter 3

Post-breeding Dispersal

A black-fronted tern being released after having its GPS tracker attached (Jo Monks).

3.1 Introduction

Animal migration is defined as the relatively long-distance movement of individuals, usually on a seasonal basis and with a return journey in the same year (Chan, 2001; Li et al., 2013). As a behavioural phenomenon, migration in animals has been intensively studied (Li et al., 2013), and has many different causes, involves different modes of locomotion, and is found in all major animal groups (Bauer & Klaassen, 2013; Li et al., 2013). Although migration is evident in many animal groups, it is nowhere more widespread or well developed than in birds (Newton & Brockie, 2007). Birds are incredibly mobile and far-ranging, are accomplished navigators, and can travel quickly and economically over almost any environment (Newton & Brockie, 2007). This conspicuous ability to migrate is likely why the classic image of animal migration is of birds flying south for the winter (Li et al., 2013). As of 2015, nearly 20% of the estimated 10,000+ extant bird species were thought to be migratory (Somveille et al., 2015). The scale of migration can vary greatly between different bird taxa, with some, such as bar-tailed godwit (*Limosa lapponica*), flying over 11,000 km (Battley et al., 2012) and others, such as white-ruffed manakin (*Corapipo altera*), travelling fewer than 550 m along an altitudinal gradient (Rosselli, 1994).

Terns are generally a wide-ranging group of birds that are capable of travelling large distances. The Arctic tern performs the longest annual migration of any animal, moving between polar regions (Egevang et al., 2010). The marsh terns (genus *Chlidonias*) are also long-distance migrants, with significant parts of the population of both the black tern and the white-winged black tern migrate between breeding grounds in the far northern hemisphere and wintering areas in Africa (Van Der Winden & Nesterenko, 2003). Whiskered terns are known to travel long distances as they are relatively regularly recorded in New Zealand despite the closest breeding grounds being in Australia (Southey, 2013). Black-fronted terns are also a migratory species, travelling back and forth between their braided river breeding colonies and non-breeding wintering grounds (Latham, 1981; O'Donnell & Hoare, 2011). Although they are able to take advantage of their highly specialised breeding habitat, black-fronted terns are thought to migrate away from their inland braided river breeding grounds to avoid harsh winters when there is little food available (Martin & Fahrig, 2018; O'Donnell & Moore, 1983).

By definition, part of a migration is returning to the same or adjacent area (Chan, 2001; Newton & Brockie, 2007), where individuals show specific breeding site fidelity, season after season. Breeding sites or colonies in habitats with greater stability usually have higher return rates than breeding sites in habitats with lower stability (Hamblin, 2017). Marsh terns generally have low site fidelity due to their dynamic nesting environment in freshwater wetland systems (Palestis, 2014). Black-fronted terns differ from other marsh terns as they breed in braided rivers rather than on floating vegetation in wetlands (Lalas, 1977), although braided rivers are just as dynamic (and potentially more so) than freshwater wetlands (Gray & Harding, 2007; Tockner et al., 2006). As such, black-fronted terns show low site fidelity although, they can exhibit high site fidelity to specific sites that remain suitable year to year (Hamblin, 2017).

Post-breeding, most black-fronted terns leave their breeding colonies by March, although some begin leaving in December and the last birds possibly leave in May (Higgins & Davies, 1996; Lalas, 1979). Some birds will move from breeding colonies to other non-coastal areas before continuing to the coast (Lalas, 1979). Once at the coast, there is a general movement northwards with some birds overwintering in the North Island (Hamblin, 2017), possibly migrating up the east coast, once across Cook Strait (Latham, 1981). In the Bay of Plenty and Hawkes Bay, Latham (1981) found that black-fronted terns arrived in March/early April and left in the last week of July/first week of August, which matches the timing of departure and return to breeding rivers in the South Island found by Lalas (1979). The last to leave the North Island are immature non-breeding birds, with some recorded still in the North Island during October/November (the height of the breeding season), indicating a small number of birds may spend their first summer there (Latham, 1981). Birds begin arriving back at their breeding colonies in mid-August with a peak in numbers in October, suggesting their migration from wintering grounds back to breeding colonies is faster and more synchronised than the post-breeding migration (Lalas, 1979; Latham, 1981; Pierce, 1983). Black-fronted terns return slightly later to higher altitude breeding colonies (Pierce, 1983), presumably to avoid lingering harsher winter conditions.

Following post-breeding migration, black-fronted terns are present in coastal areas from January until the end of July (Lalas, 1979). During this time they are mainly present on the eastern, southern and northern coasts of the South Island, rarely being found west of the Southern Alps (Higgins & Davies, 1996; Lalas, 1979). Around the South Island they range as far south as Stewart Island (O'Donnell & Moore, 1983), with a single record from the Snares Islands and a doubtful record from the Chatham Islands (Higgins & Davies, 1996; Oliver, 1955). In the North Island most black-fronted tern records are from southern and south-western areas, ranging as far north as Hawkes Bay and Bay of Plenty where they are found in varying numbers every autumn and winter (Latham, 1981). They are sporadically recorded farther north to the Kaipara with two isolated records from Northland (Higgins & Davies, 1996; Watola, 2021). Black-fronted terns were formerly a far more common migrant to the North Island during autumn and winter and their decline in the north likely reflects the decline in the overall population (Latham, 1981). Small numbers remain in the upper reaches of the South Island breeding rivers throughout the year, although they are rare here between mid-May and mid-August, particularly in higher elevation areas (Pierce, 1983).

There has been only one record of a black-fronted tern away from New Zealand (pending official acceptance); a recent sighting in Fort Scratchley, New South Wales, Australia on 20/06/2021 (Kearns, 2021; Spicer-Bell, 2021). There is a possible record of a black-fronted tern collected from Norfolk Island (Australia) in c. 1894 but a lack of detail precludes formal acceptance of this record, which would otherwise be the first outside New Zealand (McAllan, 2000). The lack of records outside New Zealand is potentially unusual given the migratory nature of black-fronted terns. South Island pied oystercatchers have a similar migration to black-fronted terns (breeding on South Island braided rivers and moving to the coast and towards the North Island in winter) and are a regular vagrant to areas of south-eastern Australia (McAllan, 2000; Sagar, 2013). Banded dotterels and white-fronted terns (*Sterna striata*) both migrate annually between Australia and New Zealand (Mills, 2020; O'Donnell & Monks, 2020) and a black-fronted tern migrating northwards could easily become "caught up" in a flock of either species (especially white-fronted terns). This scenario could go some way to explaining the one Australian black-fronted tern record. However, wrybill also have a similar migration pattern to black-fronted terns (Dowding, 2017) and they have never been recorded away from New Zealand.

The timing of black-fronted tern migration is relatively well known, however there is currently little known about the migration routes they take between breeding colonies and their wintering grounds. This is a knowledge gap that needs to be filled as understanding migration routes is essential for the conservation of migratory species (Bauer & Klaassen, 2013). It is also important to identify stopover and staging sites along migration routes as migratory species rely heavily on these sites while migrating (Lyons et al., 2018). Migration routes and stopover sites often act as population funnels, with large proportions of the population using the same sites (Fuller, 2016). Black-fronted tern conservation currently focuses on predator control at breeding colonies, with little to no work done in areas they use when not breeding. This is of concern as conservation efforts for migratory species may fail if they are focused on a single site (Rueda-Uribe et al., 2021). Other tern species, such as roseate terns, are threatened by various human disturbances at their non-breeding grounds, while bridled terns migrate through the exclusive economic zones of several countries making multi-site conservation extremely difficult (Surman et al., 2018). Black-fronted terns may face similar threats so the research to determine this and adjust conservation accordingly is a priority for the species.

In recent times the advent of lightweight data loggers has revolutionised migration studies, massively contributing to understanding seabird movements away from their breeding colonies (Nisbet et al., 2011). However, the use of GPS trackers on birds in migration studies is still a relatively new phenomenon and a developing field. GPS trackers have been used to discover migration routes, wintering areas and breeding/wintering site fidelity, a study on black-crowned night-herons (*Nycticorax nycticorax*) being one example (Scarpignato et al., 2021). Gull-billed terns have also had their migrations tracked with GPS, revealing strong fidelity to specific routes and wintering sites (Goodenough & Patton, 2019). This study on black-fronted terns will be a species first and has similar aims, as well as acting as a pilot study to test the feasibility of using GPS trackers on black-fronted terns and other small braided river birds. This chapter aims to use GPS devices to reveal the migration routes of black-fronted terns travelling between their breeding colonies and wintering sites. This chapter also aims to reveal any key migration stopover or staging sites and key wintering areas. The results of this work could lead to a more complete, year-round conservation network for black-fronted terns and provide a base for future migration and GPS studies for the species(Hamblin, 2019).

3.1.1 Research questions

- Which migration routes do black-fronted terns take when travelling between their inland breeding grounds and coastal non-breeding areas?
- Do individual black-fronted terns return to the same breeding colony for consecutive seasons?

3.2 Methods

The methodology for this chapter is a continuation of that from the previous chapter, with the same devices on the same birds. As the black-fronted terns fitted with the NANO GPS devices enter their post-breeding phase they stop returning to their breeding colonies and stop transmitting data to the HUB receivers. If their batteries have power, the NANO devices continue to collect data, which is stored on the device until it comes into range of a HUB receiver again. In this way the devices should collect data over the black-fronted tern non-breeding season and will be transmitted if/when the birds return for the next breeding season. In order to maximise the battery life of the NANO devices the BOOST function (which takes more GPS fixes if the device's solar panels are exposed to prolonged/strong sunlight) was turned off for all devices. The 14 devices from the first round of attachment had the BOOST function turned off on 17/12/2020 and the 20 devices from the second round of attachment had it turned off on 21/12/2020. To further maximise battery life, any devices set to take GPS fixes at five-minute intervals were updated to one-hour intervals.

During their non-breeding season in the austral autumn and winter, black-fronted terns are often seen at river mouths and lagoons along the east coast of the South Island (Bell, 2013). Following the 2020/2021 black-fronted tern breeding season, searches for terns fitted with NANO devices were carried out along the Canterbury coast south of Banks Peninsula. The goal of these searches was to collect data from wintering birds with GPS devices, in case these birds didn't return to their breeding colonies during the next breeding season, the NANO lost battery power or otherwise failed.

In preparation for searching for wintering terns and their NANO devices, two tests were carried out on the NANO and HUB devices to assess the range at which the NANOs could be detected. The first test used a Debut QUEST, a Druid Tech device which boosts the Bluetooth signal of a cellphone, increasing the phone's chance of connecting with a NANO. A spare NANO was activated and held at chest height by a person on the side of a one km stretch of straight road, while a QUEST and cellphone with the Druid Tech app were held by an observer in the passenger seat of a car travelling 100 km per hour. The distance at which the Druid app detected the NANO was recorded. The second test of the range that a NANO device can be detected used a HUB to assess the feasibility of searching for NANOs with a mobile HUB. This test was carried out with an activated NANO on a car roof of the ground and a HUB and cellphone with the Druid app held by a person in the passenger seat of the cockpit of a Cessna 185 light aircraft. The aircraft made several passes above the car at varying altitudes, horizontal distances and speeds. The altitude and horizontal distance at which the Druid app detected the NANO was recorded.

In June 2021 the two HUB devices were retrieved from the Cass and Ohau breeding colonies to be used in the winter searching. This was three months after the last breeding season data had been transmitted on 14/03/2021. The searches were then made from 22/06/2021 to 26/06/2021, a period of time before black-fronted terns leave the coast to return to their breeding colonies at the end of July (Higgins & Davies, 1996; Lalas, 1979). Sites where HUBs were deployed and searches were undertaken were chosen based on concentrations of black-fronted tern sightings on eBird and the presence of a significant hydrological feature, such as a lagoon or river mouth. In each location a HUB device was left to detect birds and collect data over a 24-hour period. A visual one-hour search for black-fronted terns was also carried out when setting up the HUB on the first day and when retrieving it 24-hours later on the second day. Any NANO devices seen would be attempted to be connected with using either a HUB or QUEST device (the QUEST would be used if the HUB had already been set up and was out of range of the observer).

Starting on 22/06/2021, the HUBs were placed at the Waitaki River mouth (-44.941860, 171.145192) and at Wainono Lagoon (-44.711458, 171.167183). On 23/06/2021 they were moved to Washdyke Lagoon (-44.363875, 171.252544) and the Opihi River mouth (-44.277688, 171.348549). On 24/06/2021 they were moved to the Rangitata River mouth (-44.189354, 171.508423) and Ashburton River mouth (-44.053839, 171.802654). On 25/06/2021 they were moved to the Rakaia River mouth (-43.900884, 172.206498) and Coopers Lagoon (-43.868993, 172.306058) before being collected on 26/06/2021. The Orari River mouth (-44.241927, 171.408685) and nearby Rhodes Lagoon (-44.236851, 171.415110) were also visually searched for black-fronted tern on 24/06/2021. On 11/08/2021 a HUB was placed on the shore of Lake Waitaki (-44.680733, 170.401706) to try and detect signals from any terns that may have been migrating back up the Waitaki River to the

Mackenzie Basin from the coast. This HUB was retrieved on 15/09/2021. The locations mentioned above can be seen in relation to the lower Cass and upper Ohau breeding colonies below in Figure 18.

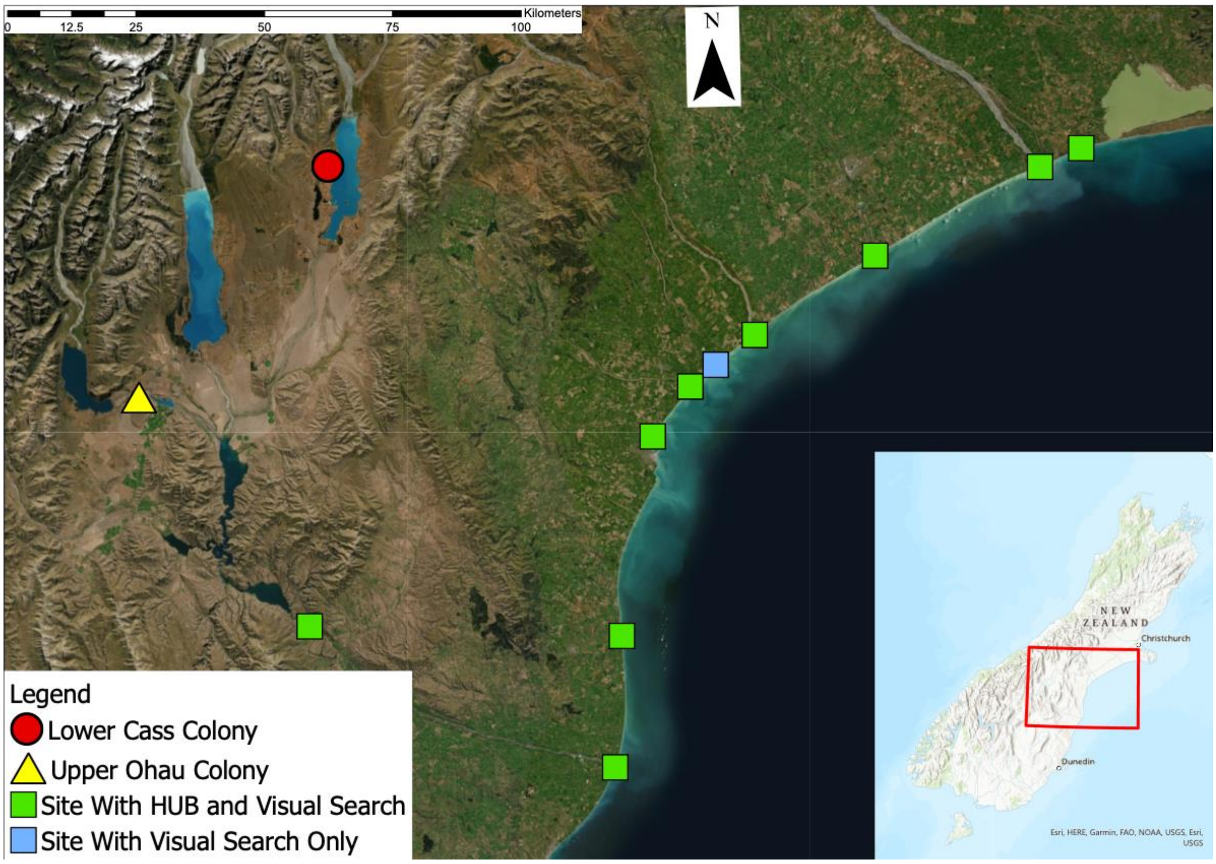

Figure 18: Map of sites visited during winter search for black-fronted terns with GPS trackers, upper Ohau and lower Cass breeding colonies also visible. Created in ArcGIS Pro.

In anticipation of terns with NANO devices returning for the 2021/2022 breeding season, the two HUB devices were returned to the lower Cass and upper Ohau colonies respectively on 15/09/2021. From this point the online Druid data centre was checked weekly to monitor any data transmission from returning birds fitted with NANOs. As data was recorded it was downloaded as CSV files. If the device of a returning bird transmitted any data, that specific device was checked weekly to see if more data had been transmitted or previous transmissions had been updated. In addition to this, two days were spent at each colony visually checking for birds with transmitters. At the Ohau colony seven hours were spent searching on 15/10/2021 and five hours on 27/10/2021. At the Cass colony five hours were spent searching on 16/10/2021 and six hours on 28/10/2021.

3.3 Results

The cellphone boosted by the QUEST device registered the NANO device at a distance of 200 m, while in a car travelling 100 km per hour (Figure 19). The HUB was able to link with the NANO at 152.4 m above ground level (AGL) and at a horizontal distance of 600 m (Figure 19).

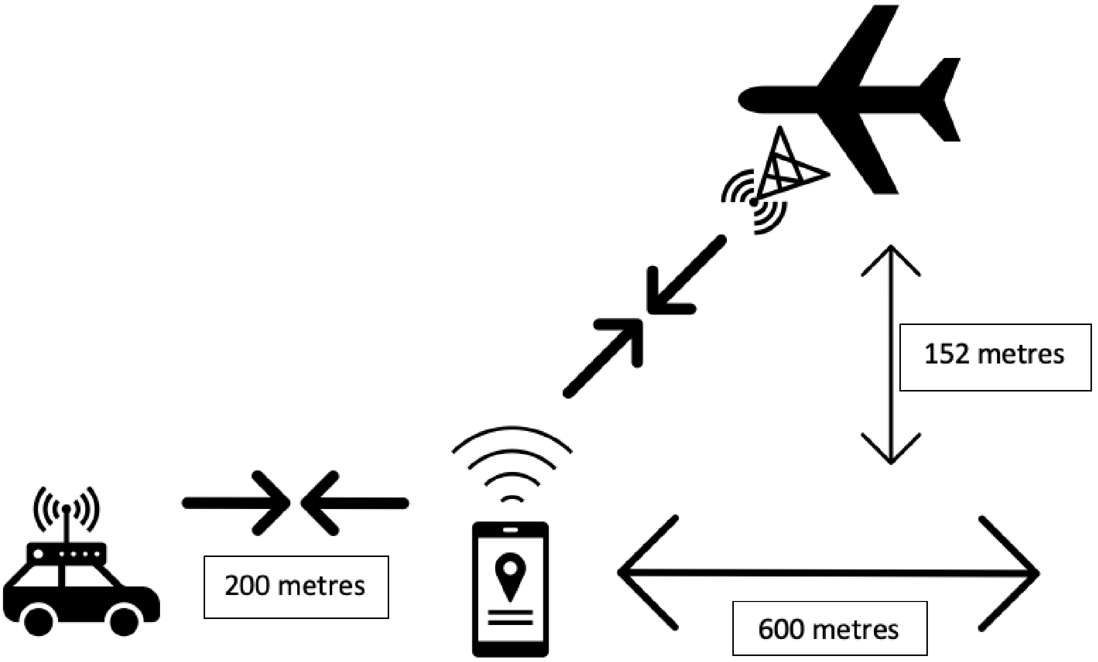

Figure 19: Diagram showing the horizontal distance at which a NANO device can be linked with a QUEST device (car symbol) and the vertical and horizontal distances at which a NANO device can be linked with a HUB device (plane symbol), based on field tests of these devices.

The HUB devices placed along the Canterbury coast did not detect, connect with, or download any data from NANO devices during the search period in winter 2021. The HUB device placed on the shores of Lake Waitaki for more than a month in spring 2021 likewise did not detect any NANO devices. Black-fronted terns were observed at every coastal location where a search was carried out, except for Washdyke Lagoon where none were seen on either day. At Wainono Lagoon, two terns were seen on the first day and none were seen on the second day. At the Waitaki River mouth, one tern was seen on both days. At the Opihi River mouth, three terns were seen on the first day and none were seen on the second day. At both the Orari River mouth and at Rhodes Lagoon (where no Hub was set) only one tern was observed at these sites. At the Rangitata River mouth, five terns were seen on the first day and two on the second day. At the Ashburton River mouth, 29 terns were seen on the first day and 16 on the second day. At the Rakaia River mouth, 40 terns were seen on the first day and 23 on the second day. At Coopers Lagoon, three birds were seen on the first day and one on the second day. All black-fronted terns observed were either roosting in river deltas, feeding just offshore of the river mouths, feeding over lagoons or flying along the coast close to the land-sea divide. Most terns seen were adults in breeding (alternate) plumage, although immatures were seen at the Opihi, Rangitata, Ashburton and Rakaia River mouths. None of the terns observed at these sites appeared to be fitted with NANO devices. No black-fronted terns were seen on either day at the HUB location at Lake Waitaki.

During October 2021 (the beginning of the 2021/2022 black-fronted tern breeding season) a black-fronted tern fitted with a NANO device was seen at the Ohau colony on 15/10/2021. No signal could be detected from the NANO device and the tern was not seen to associate with a nest site within the colony. On the same day at the Ohau colony, a second bird, with what appeared to be a NANO device, almost entirely covered by feathers, was observed. No signal could be detected from the potential NANO device but the presence of a metal band on the right tarsus increases the chances this tern was one of the study birds. This tern was seen excavating a nest in close proximity with another black-fronted tern, presumed to be its partner. On 27/10/2021 a black-fronted tern with a NANO device was briefly seen at the Ohau colony, but again no signal could be detected from the NANO device. The tern was not seen to associate with a nest site within the colony although it did favour the northern end of the colony island. The black-fronted tern seen at the Ohau colony on 15/10/2021, with what appeared to be a NANO covered by feathers, was seen again on 27/10/2021, sitting on a nest. The potential device was still covered by feathers and was not emitting a signal. No birds with NANO devices were seen on 16/10/2021 or 28/10/2021 while searching at the Cass colony. Due to the low number of terns with NANO devices sighted during this search period (the only one associating with a specific nest site may not have had a tracker on at all) no recapture of terns to recover devices was attempted.

3.3.1 Post-breeding Data

During the 2021/2022 black-fronted tern breeding season, 10 of the 34 NANO devices deployed in the previous breeding season (2020/2021) made a connection with a HUB device at the Cass and/or Ohau breeding colonies. Of these 10 devices, eight transmitted data which had been collected after the terns had gone out of range of the HUBs at the end of the previous breeding season (i.e., data collected after the terns had finished breeding and stopped returning to their breeding colony). Two of the 10 NANO devices (Tern31, a Cass male, and Tern27, an Ohau male) were detected by a HUB but failed to transmit any data or had no data to transmit. All 10 terns that connected with HUB devices in the 2021/2022 breeding season were fitted with their devices during the second round of field work in December 2020, none were from the first round of field work in November 2020.

Across the eight devices that collected data, 4999 GPS points were collected with a maximum and minimum GPS points per individual of 2048 and 68 points respectively (Table 3). These GPS points were collected between 22/12/2020 (the earliest departure from a breeding colony by a bird that returned the next season) and 15/05/2021 (The last day a GPS point was collected after a tern left its 2020/2021 breeding colony). The interval of GPS fixes for each device became more sporadic until it stopped collecting fixes entirely (presumably due to battery level), meaning there were often large gaps (up to several weeks) between GPS points. The sporadic nature of the GPS points on only eight birds meant no meaningful analysis could be performed on the data. The data collected between 22/12/2020 and 15/05/2021 was transmitted between 15/09/2021 and 07/01/2022 (Table 3). Five of the terns returned to the same breeding colony for the 2021/2022 breeding season as they had used in 2020/2021 (Table 3). The NANO devices on the other five returning birds did not transmit any or enough data in the 2021/2022 breeding season to tell which colony they were using (Table 3).

Table 3: Summary of GPS points collected by black-fronted terns after finishing breeding for the 2020/2021 breeding season.

Tern ID	Sex and Breeding Colony in 2020	Date of Device Attachment	Date of Last 2020/2021 Breeding Season Transmission	Date of First 2021/2022 Breeding Season HUB Connection	Number of Post-breeding GPS Points	Returned to Same Colony?
Tern16	Female, Ohau	07/12/2020	19/01/2021	29/12/2021	177	Unknown
Tern20	Male, Ohau	10/12/2020	16/01/2021	14/10/2021	1073	Yes
Tern21	Male, Ohau	10/12/2020	21/01/2021	07/12/2021	451	Yes
Tern23	Female, Ohau	10/12/2020	09/01/2021	07/01/2022	746	Unknown
Tern27	Male, Cass	10/12/2020	22/12/2020	15/02/2022	0	Unknown
Tern28	Female, Cass	10/12/2020	22/12/2020	15/09/2021	2048	Yes
Tern29	Female, Ohau	11/12/2020	14/03/2021	24/11/2021	68	Yes
Tern31	Male, Ohau	11/12/2020	04/01/2021	08/01/2022	0	Unknown
Tern32	Female, Ohau	11/12/2020	31/01/2021	06/12/2021	171	Yes
Tern33	Female, Ohau	11/12/2020	14/01/2021	15/11/2021	265	Unknown

On 23/12/2020 Tern28 (female) moved from the Cass colony to the upper Rangitata River, travelling east over Two Thumb Range and then north over Tara Haoa Range to reach the Rangitata Riverbed. It stayed in the upper Rangitata, with almost all of its GPS points between the Havelock/Clyde River confluence and where Forest Creek enters the Rangitata. On 07/02/2021 it travelled down the Rangitata to the coast, where it ranged widely inland and up and down the Rangitata River before returning to the upper Rangitata on 14/02/2021. It continued to move between the upper and lower Rangitata before leaving the upper Rangitata for the last time on 04/03/2021. From there Tern28 began ranging NE over farmland before moving overland to the Rakaia River near Methven on 19/03/2021. On 21/03/2021 it returned to the Rangitata River near the State Highway 1 (SH1) bridge and travelled frequently between the two rivers as the data became more sporadic, collecting its last GPS point on 15/05/2021. This data was transmitted on 15/09/2021 (Table 1).

On 06/02/2021, Tern20 (male) left the Ohau colony and based itself at the Tekapo delta, travelling between the Tekapo delta, Lake Ohau and farmland south of Lake Ruataniwha. On 08/02/2021 it travelled overland (over the Grampian and Dalgety Ranges) from the Tekapo delta to the lower Rangitata, where it stayed using river and nearby farmland until it collected its last non-breeding GPS point on 15/04/2021 (6.926 km off the coast from the Rangitata River mouth). This data was transmitted on 14/10/2021 (Table 1).

On 14/01/2021, Tern33 (female) left the Ohau colony and spent 11 days travelling between the Tekapo delta, Lake Ohau and farmland south of Lake Ruataniwha. On 25/01/2021 it moved towards the coast with its GPS points beginning on that day inland east of the Opihi River heading overland to the lower Rangitata. It travelled overland between the lower Rangitata River (occasionally heading further upstream) and the mid Rakaia River before the last non-breeding GPS point was collected on 21/04/2021. This data was transmitted on 15/11/2021 (Table 1).

On 31/01/2021, Tern32 (female) left the Ohau colony and spent 14 days travelling between the Tekapo delta, Lake Ohau and farmland south of Lake Ruataniwha. On 13/02/2021 its last GPS point for the day was at the Tekapo delta and the next day only a single GPS point was recorded, inland near Ashburton. It then moved between here and the mid Rangitata River until its last non-breeding GPS point was collected on 26/04/2021. This data was transmitted on 06/12/2021 (Table 1).

On 14/03/2021, Tern29 (female) left the Ohau colony and moved to the mid/lower Waitaki River where it stayed until returning to the Tekapo delta on 21/03/2021. On 22/03/2021 it was back in the mid Waitaki (opposite the Otekaieke River confluence). On 08/04/2021 it was inland near the Ashburton River before single points inland on the Rakaia River on 9, 12 and 17/04/2021 when it collected its last non-breeding GPS point. This data was transmitted on 24/11/2021 (Table 1).

On 19/01/2021, Tern16 (female) left the Ohau colony and for 33 days had very sparse/sporadic GPS data. On 21/01/2021 it moved to the Ahuriri delta, on to the mid Waitaki River on 23/01/2021 and on to the lower Waitaki on 26/01/2021. On 12/02/2021 it moved back up to the mid Waitaki and stayed there until 15/02/2021 when it appeared in the mid/upper Rangitata River. On 17/02/2021 it appeared in the lower Rangitata, after which it stayed in or near the lower Rangitata (except for two GPS points in the mid/upper river) until its last non-breeding GPS point was collected on 22/02/21. This data was transmitted on 29/12/2021 (Table 1).

On 20/01/2021, Tern21 (male) left the Ohau colony and spent 54 days travelling between the Tekapo delta, Lake Ohau and farmland south of Lake Ruataniwha. On 16/03/2021 it headed overland east and over the Opihi River to farmland around the lower Rangitata River where it stayed until its last non-breeding GPS point was collected on 17/03/2021. This data was transmitted on 07/12/2021 (Table 1).

On 09/01/2021, Tern23 (female) left the Ohau colony and for 72 days travelled between the Tekapo delta, Ahuriri delta and farmland south of Lake Ruataniwha. On 21/02/2021 it stopped returning to the Tekapo delta and was focused around the Ahuriri delta. It returned to the Tekapo delta on 03/03/2021 and moved between the two deltas before moving down the Waitaki River on 22/03/2021. It stayed around the mid Waitaki until its last non-breeding GPS point was collected on 15/04/2021 (1.631 km off the coast from the Waihao River mouth). This data was transmitted on 07/01/2022 (Table 1). The non-breeding GPS points of the terns which transmitted non-breeding data (Tern28, Tern20, Tern33, Tern32, Tern29, Tern16, Tern21 and Tern23) can be seen in relation to each other below in Figure 20.

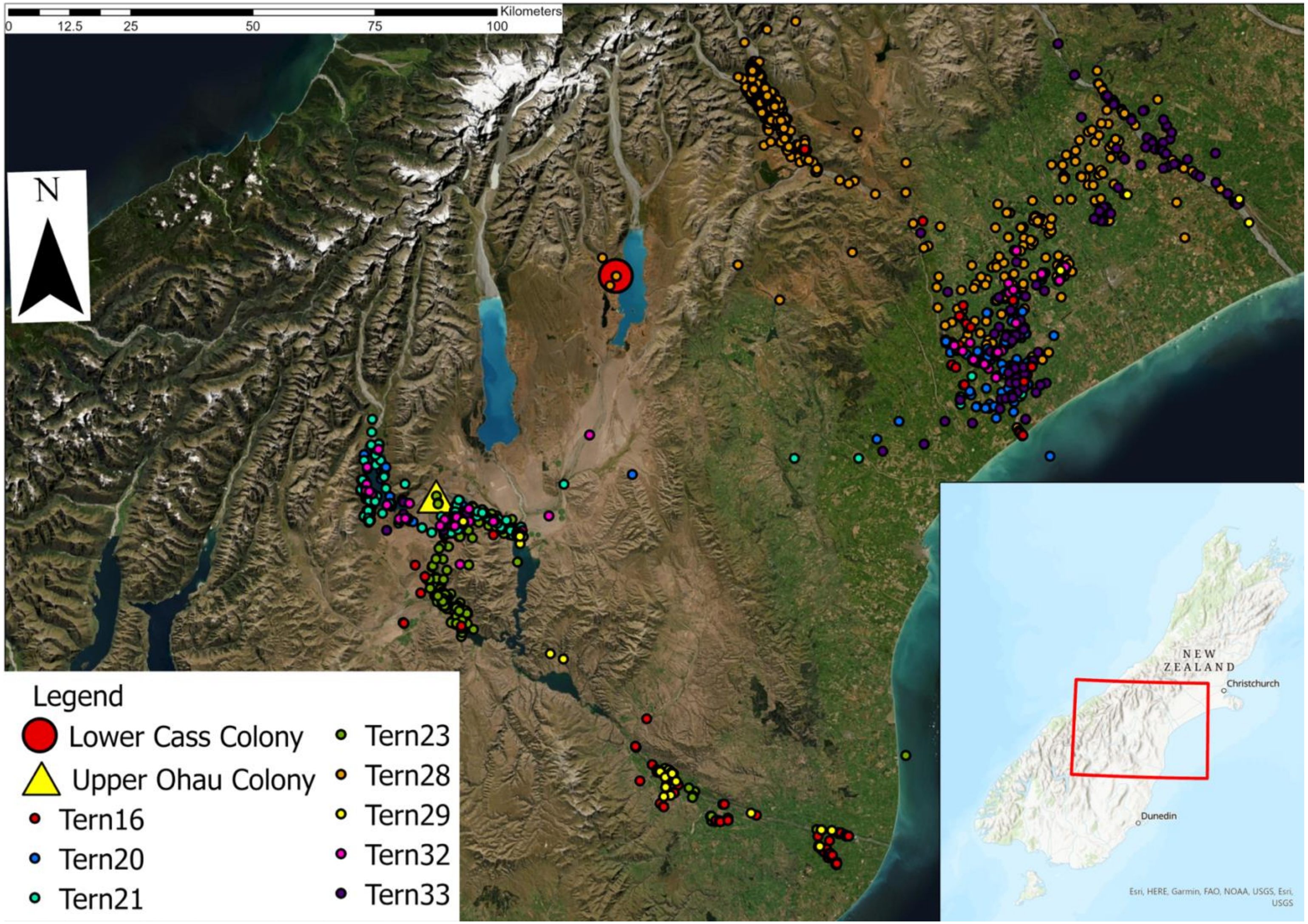

Figure 20: Map showing the location of 10 black-fronted terns post-breeding GPS points in the central South Island of New Zealand, lower Cass and upper Ohau River breeding colonies also shown. Each colour represents a different bird. Created in ArcGIS Pro.

Tern16 and Tern33 were both females from the Ohau colony, both also left the colony at similar times (19/01 and 14/01 respectively) in 2021 and recorded a similar number of post-breeding GPS points (177 and 265 respectively). In January 2021 both terns left the Ohau colony, spent time in the southwest Mackenzie Basin and travelled to the lower reaches of braided rivers. In February 2021 both terns moved northward, with Tern16 moving from the Waitaki River to the Rangitata River and Tern33 moving from the Rangitata River to the Rakaia River. A monthly comparison of GPS points from Tern16 and Tern33 for January and February can be seen in Figure 21 and Figure 22 below.

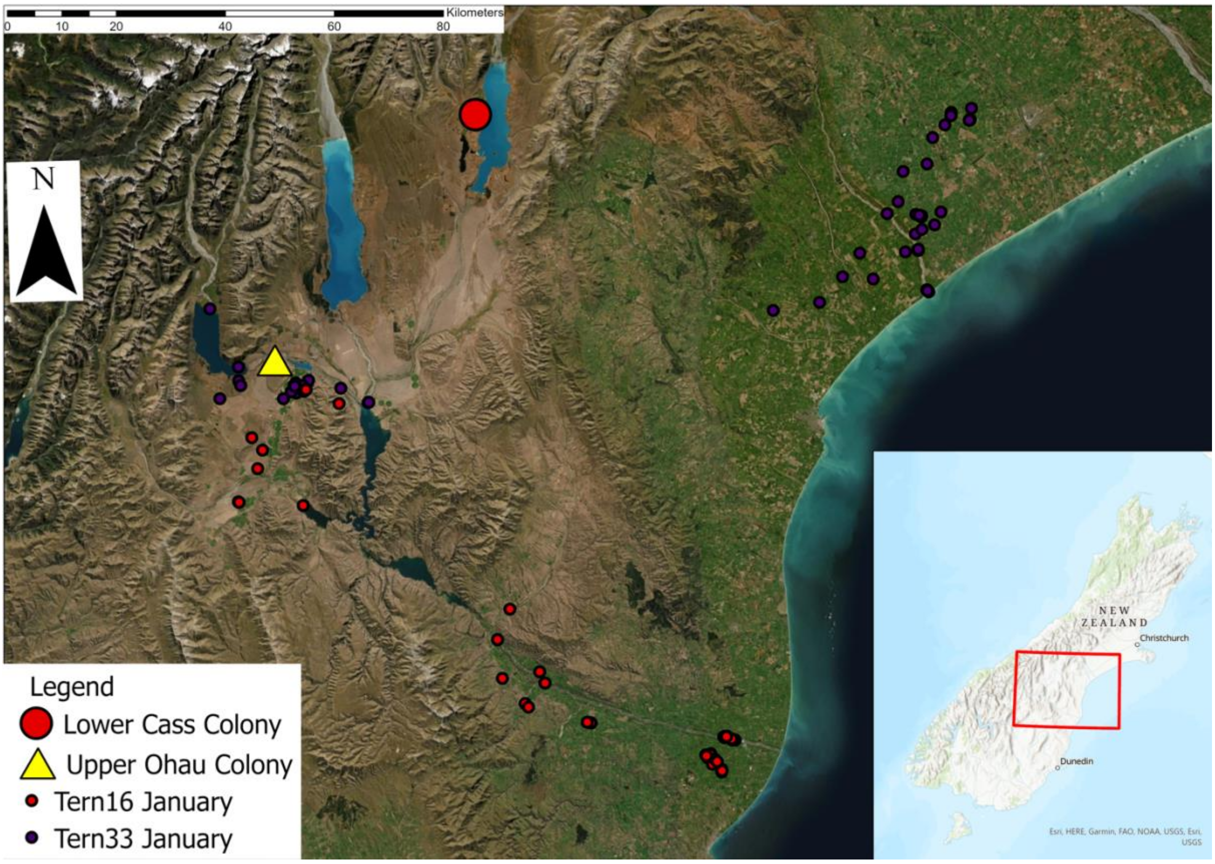

Figure 21: Map of GPS points for Tern16 and Tern33 from January 2021. Upper Ohau and lower Cass breeding colonies also visible. Created in ArcGIS Pro.

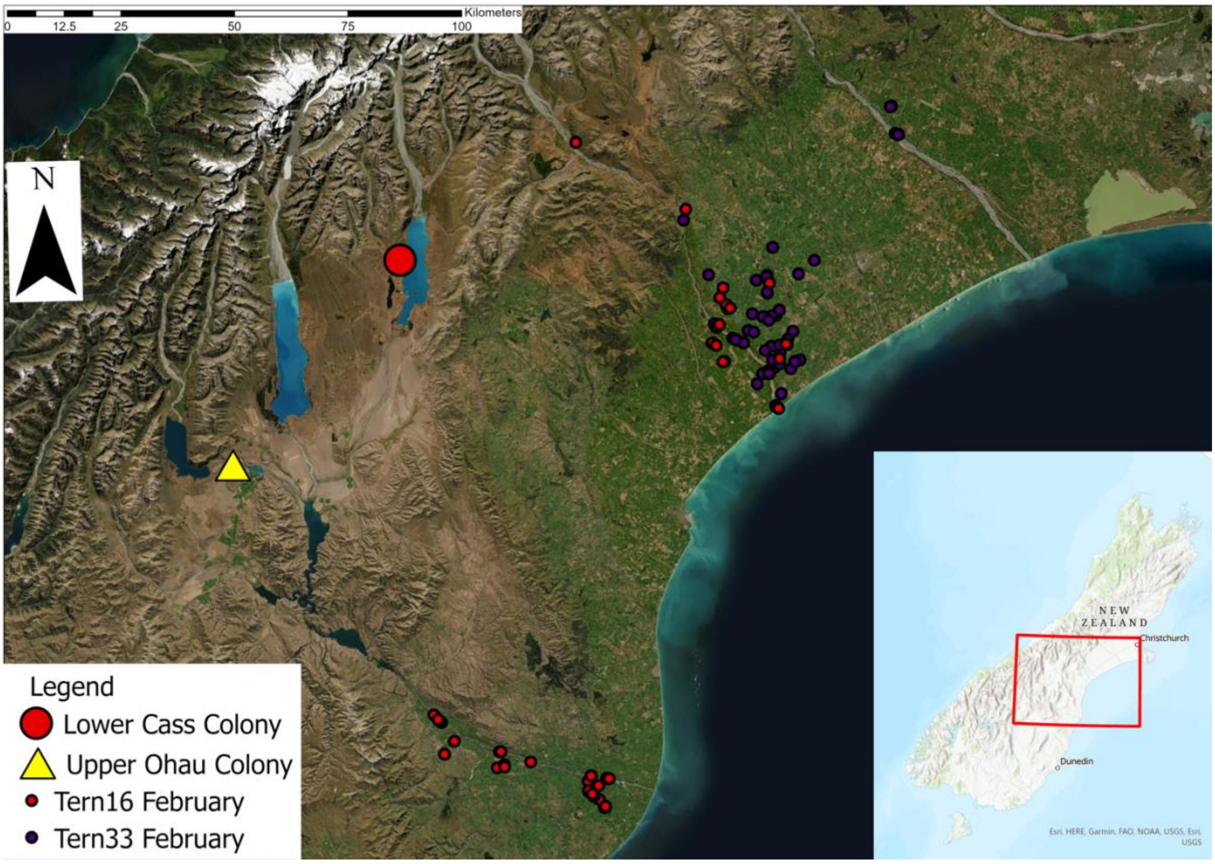

Figure 22: Map of GPS points for Tern16 and Tern33 from February 2021. Upper Ohau and lower Cass breeding colonies also visible. Created in ArcGIS Pro.

Across the eight terns that transmitted non-breeding GPS points there were several areas with concentrations of GPS points from multiple terns. Tern20, Tern21, Tern32 and Tern33 had clusters of GPS points at the Tekapo River delta, in a patch of farmland in the Glenbrook area south of Lake Ruataniwha and around the shores of Lake Ohau (including a patch of several lagoons immediately south of the lake). These four terns used these areas after leaving the Ohau breeding colony for the season, but before moving towards the coast. During this period these four terns used the Hopkins River delta at the north end of Lake Ohau as a roosting area after. Of these four terns, only Tern32 had used this area during the breeding season (one GPS point recorded here), in addition to five other terns that did not transmit any non-breeding data.

When moving out of the Mackenzie Basin and towards the coast, there were two separate routes the terns took. The first was directly overland from the vicinity of the Tekapo delta towards the lower Rangitata River/Rangitata River mouth and the second started in a similar area before travelling down the Waitaki River. Four terns (Tern20, Tern21, Tern32 and Tern33) took the overland route and three the Waitaki (Tern16, Tern23 and Tern29). Tern28 travelled directly down the Rangitata River after it had spent 48 days in the upper Rakaia after leaving the Cass colony. Once in the Waitaki River, specific sections of farmland around the river and parts of the river itself were used by Tern16, Tern23 and Tern29 in their non-breeding period. All but one (Tern23) of the terns with non-breeding data used the Rangitata and Rakaia Rivers and the area between the two rivers on the Canterbury Plains. Tern28 and Tern33 travelled between these two rivers multiple times (approximately 57 km between the respective areas in each river with the most GPS points), while Tern20, Tern28, Tern 32 and Tern33 all used a roost site in the Rangitata River less than a km south of the SH1 bridge.

3.4 Discussion

Despite the patchy and sporadic nature of the post-breeding data, this research did produce some information on post-breeding movements and several natural history observations worthy of discussion. Six of the black-fronted terns from the Ohau colony (all except Tern29) that transmitted post-breeding GPS data did not move towards the coast immediately after leaving the Ohau colony for the last time. Before moving towards the coast these terns stayed in the southwest Mackenzie Basin for varying amounts of time (between two and 72 days), frequently visiting the Tekapo, Hopkins and Ahuriri River deltas, as well as the shores of Lake Ohau and farmland in the Glenbrook area. It is possible that these areas, particularly the river deltas, were being used as staging areas for the terns prior to migration. Staging is when birds prepare for an energetic challenge (Warnock, 2010), in this case the move from the Mackenzie Basin to more coastal areas. The fact that the six Ohau terns with post-breeding data used the Hopkins delta far more during post-breeding than during the breeding season supports the idea that it could be used as a staging area.

The idea of staging before migration is further supported by previous observations that some black-fronted terns do not immediately move to the coast following breeding (Lalas, 1979). Other tern species, such as common and Caspian terns, show post-breeding staging behaviour (Nisbet et al., 2011; Taber, 2015), however it is often difficult to define when an individual is staging before a migration and when it is actually migrating (Limiñana et al., 2008; Taber, 2015). Other than building up energy reserves for a journey, reasons for staging behaviour can include shifting diets and areas to track shifts in resource availability and visiting potential colonies or breeding areas to aid decision making for the next breeding season (Graham & McWilliams, 2022; Limiñana et al., 2008; Warnock, 2010). The latter reason seems plausible when considering the low site fidelity exhibited by black-fronted terns (Hamblin, 2017), although the dynamic nature of braided rivers means nesting habitat can be destroyed or become newly available well before the terns return to the area.

Based on the limited post-breeding GPS data from this study, black-fronted terns from the Ohau breeding colony appeared to show two distinct migration routes away from the Mackenzie Basin. Of the seven terns with post-breeding data, four travelled east overland to the lower Rangitata River and three travelled southeast to the lower Waitaki River. Both these routes have patchy GPS points but the data that is available is relatively clustered in similar areas. The terns travelling overland to the Rangitata appear to fly directly over the north end of the Grampian Mountains and the Dalgety

Range, travelling in the shortest straight-line distance to the lower Rangitata rather than following rivers and lower elevation areas. This is difficult to confirm as the GPS points from these terns are closer to the Rangitata end of the trip (between the Fairlie and Opihi River area and the lower Rangitata), although the few points available do suggest this. The terns using the Waitaki route possibly travelled down the Waitaki River itself, although there are no GPS points to confirm or deny this. Once in the lower Waitaki, the three terns that travelled this route used the same patches of river and surrounding farmland, with all three having overlapping clusters of GPS points. This overlap suggests it is likely these three terns travelled similar routes to reach this area.

The Rangitata River appears to be an important post-breeding area for black-fronted terns from the Ohau colony. Five of the Ohau terns had GPS points in the Rangitata River and the surrounding farmland, as well as Tern28 from the Cass colony. The two Ohau terns with no GPS points near the Rangitata could possibly have been in the area without recording data due to very sporadic GPS fixes that were occurring for these birds (Tern23 and Tern29). When looking at all the post-breeding GPS points, the biggest cluster away from the Mackenzie Basin containing multiple birds was in and around the lower Rangitata. There were also several locations in the lower Rangitata where up to five terns had tight clusters of overlapping points, indicating a roost or productive feeding site. These sites were likely post-breeding roosts as black-fronted terns were observed roosting at two such points on multiple occasions, one less than a km south of the SH1 bridge (high count 30 birds) (personal observation, see (Gurney, 2022a)), the other near the end of Badham Road (high count 128 birds) (personal observation, see (Gurney, 2022b)). Both of these locations have supported black-fronted tern breeding colonies in the past (Schlesselmann et al., 2017). Areas like this with high overlap between individual terns are good candidates for placing HUB devices for future research.

Tern28 made use of both the upper and lower Rangitata River, although its extensive use of a specific stretch of the upper Rangitata near a known colony location (Schlesselmann et al., 2017) means there is a possibility it attempted to breed here after leaving the Cass colony on 22/12/2020 (only 12 days after device attachment, indicating that its Cass nest failed). Terns usually move very small distances when renesting within a breeding season(González-Solís et al., 1999), although the black-fronted tern's close relative, the black tern, has been recorded renesting approximately one mile away from its original nest site (Eichhorst & Reed, 1985). These small movements mean it is unlikely Tern28 renested in a different river system to its first attempt and it was likely dispersing to a non-coastal area, as black-fronted terns are known to do (possibly to stage) (Lalas, 1979), before moving to the coast. In March 2021 Tern28 moved to the lower Rangitata where it overlapped with several other birds from this study. Both Tern28 and Tern33 moved back and forth between the Rangitata and Rakaia Rivers for more than a month, demonstrating how mobile the terns can be when not tethered to a breeding site. The extensive use of the Rangitata by post-breeding black-fronted terns indicates its importance to the species. This is supported by the Rangitata supporting a major breeding population (O'Donnell & Hoare, 2011) and the river being an Important Bird Area (IBA), with black-fronted terns listed as a trigger species for this designation (Forest & Bird, 2016).

Once the post-breeding black-fronted terns reached coastal area, there was a general trend of northward movement. The three terns that had moved to the lower Rakaia moved north; the last GPS points for these birds were the Rangitata River, the Rakaia River and offshore of the Waihao River mouth. Three of the five terns that travelled to lower Rangitata also showed northwards movement, with final GPS points for these birds in farmland near Ashburton and in the Rakaia River. The movement northwards took place over several weeks; there was no evidence of rapid movement up the coast. This movement north fits with previous observations of migrating black-fronted terns (Hamblin, 2017; Latham, 1981), as does its gradual nature that has previously been described as taking place at a “leisurely” pace (Higgins & Davies, 1996).

Five of the 10 black-fronted terns that connected with HUB devices in the 2021/2022 breeding season returned to the same breeding colony as the previous season. It was unknown which colony the other five returned to as they recorded no data that season or failed to register which HUB they connected with. This is too little data to draw any conclusions from, even though the five birds that had their 2021/2022 breeding season location confirmed all returned to the same colony. Four of these five birds were from the Ohau colony at Tern Island, which supports the idea that colonies in stable locations (such as Tern Island) have higher return rates than those in less stable locations (Hamblin, 2017). The timing of the connections with HUBs from NANO devices on returning birds (one tern in September 2021, one in October 2021, two in November 2021, three in December 2021, two in January 2022 and one in February 2022) is slightly later than the August to October peak numbers in other studies focused on black-fronted tern movements in the Mackenzie Basin (Lalas, 1979; Pierce, 1983). This apparent lag is potentially caused by the low battery levels in the NANO devices approximately one year after they were deployed, rather than the terns actually arriving later at the colonies. As spring and summer progress, more sunlight is available to charge the devices to the required level via their solar panels, meaning data may be transmitted weeks or months after the terns arrive within range of the HUB devices. Migration timing can also be affected by other factors, such as weather, meaning the date of return may vary between years (Pakanen, 2018).

There were several major limitations in this section of the study. First and foremost, the dataset for the black-fronted tern non-breeding season was much smaller than that for the breeding season. Only 4999 GPS points were recorded in the non-breeding season, compared with 112852 points during the breeding season. The number of individual terns with recorded GPS points was also much lower than during the breeding season, eight as opposed to 33. With the eight terns that did collect data, there were large differences between the number of GPS points individuals collected, with the lowest being 68 points and the highest 2048 points. Only one of the eight terns with non-breeding data was from the Cass colony, creating a heavy bias towards terns from the Ohau colony. All eight terns with non-breeding data were from the second round of attachment, biassing the data towards later breeding terns and completely excluding earlier breeding birds. The GPS points that were collected were all within approximately three months of the end of the breeding season, meaning only a partial picture of one leg of black-fronted tern migration was captured. Because of this it would be more accurate to call the data “post-breeding” rather than “migration”. The GPS fixes became increasingly sporadic as the non-breeding season progressed, creating temporally patchy data which provided very limited information on tern movements. These limitations precluded any statistical analysis on the GPS points and severely limited this section of the study’s ability to answer its research questions.

The limitations themselves were likely caused by low battery levels in the NANO devices. When deployed, the devices sat close to the back feathers of the terns, making it highly likely solar panels were at some point at least partially covered and prevented from recharging the device’s batteries. To support this, one tern was observed at the Ohau colony a year after the devices were deployed with what looked like a device completely covered by feathers (this device gave off no signal). On the Druid online data centre many of the NANOs were displayed as having low battery throughout the 2020/2021 breeding season, indicating the devices were not charging as they should. The sporadic nature of GPS fixes after the 2020/2021 breeding season ended, with none collected after May 2021, also supports the idea of failing batteries. This should be addressed in any future study by ensuring the solar panels are at no point covered by feathers, potentially by raising the devices further above the backs of the terns. The batteries also have less opportunity to charge during the post-breeding phase as daylight hours decrease and the sun moves away from the meridian.

Aside from battery levels, it is possible that some terns bred at different colonies in the 2021/2022 breeding season, meaning they may not have come within range of a HUB device to transmit post-breeding data. Of 14 black-fronted terns banded in the Marlborough region, only four were recaught at the same location (Wildlife Management International & Department of Conservation, 2022). The other 10 were recaught/resighted at different locations, with three breeding at a different colony 45.5 km away (Wildlife Management International & Department of Conservation, 2022). This rate of return is similar to the one observed in this study, with both indicating a site fidelity rate of approximately 25-30%. Some of the black-fronted terns may have perished before returning to breed in the 2021/2022 season. Death of birds in this study may have been natural, although there is a chance they may have been affected by the GPS devices and the harness they are attached with - as happened in another tern study using GPS trackers with a harness attachment (Paton et al., 2021).

However, there was no evidence of adverse effects of the devices in this study. After device deployment, several terns were observed behaving normally during follow-up trips to the two colonies. None of the GPS data itself indicated a tern behaving abnormally or being hindered by its device.

Based on the limited data in this study, the southwest Mackenzie basin appears to be an important area for black-fronted terns from the Ohau colony before migrating to more coastal areas. Specifically, the Tekapo, Hopkins and Ahuriri River deltas, as well as the shores of Lake Ohau and farmland in the Glenbrook area, were hotspots for post-breeding terns. When migrating to the coast, terns from the Ohau colony took one of two routes: overland east to the lower Rangitata and southeast (either overland or down the Waitaki River) to the lower Waitaki. The apparent lack of variation in migration routes is common among terns, which are known for using specific routes and flyways (Kralj et al., 2020). The lower Rangitata appeared to be an important area for post-breeding black-fronted terns, with a concentration of GPS points in the river and surrounding farmland. When returning to their breeding colonies, the five terns whose colony could be determined all returned to the same colony as the previous season. Despite the limited post-breeding data returned by this study, several important observations were able to be made and the information gathered serves as an important starting point for future study of black-fronted tern migration and wintering patterns.

Chapter 4

General Discussion

A black-fronted tern nest in the Cass River (Fraser Gurney).

Black-fronted terns are endemic to New Zealand and are currently listed as nationally endangered species due to their small and declining population (Robertson et al., 2017). Black-fronted terns breed almost exclusively in braided rivers in the eastern half of the South Island, where they are vulnerable to several threats, particularly introduced mammalian predators (Bell, 2017). The terns rely on conservation practices for their ongoing survival (Robertson et al., 2017), with a focus on controlling mammalian predators around their breeding colonies (Schlesselmann et al., 2018). However, conservation efforts are hampered by large knowledge gaps around black-fronted tern breeding foraging movements, migration pathways, and important wintering areas. This study aimed to fill these knowledge gaps using GPS trackers, the first time this technology has been applied to black-fronted terns.

4.1 Main Findings

GPS trackers were deployed on black-fronted terns from breeding colonies in the lower Cass and upper Ohau rivers in the Mackenzie Basin. Using this technology on black-fronted terns was successful, with a large dataset of 112,852 GPS points collected over the 2020/2021 breeding season. This is the first time that black-fronted terns have been studied in this way, making all the information gathered highly relevant to better understanding the species.

During the breeding season the terns foraged mainly in six habitat types, spending >92% of their time in depleted grassland, gravel or rock, high producing exotic grassland, lake or pond, low producing grassland and river. Of these habitats, high producing exotic grassland was the most important for foraging, mainly due to the exploitation of irrigated fields. High producing exotic grassland was the most used habitat by both sexes and terns from each colony. Black-fronted terns also selected high-producing exotic grassland more than chance around each breeding colony. Conversely, the terns avoided areas of low producing and depleted grassland, using them less than they were proportionately available as habitats. These habitat preferences were likely due to low producing and depleted grassland being poorer quality habitat than high producing exotic grassland (Landcare Research New Zealand, 2020), implying that there is potentially more prey for black-fronted terns in areas of high producing exotic grassland.

The proportion of time black-fronted terns spend in different habitats depends on their sex, with this study finding a significant ($P<0.001$) interaction between habitat, sex and colony location. The biggest difference between the colonies was with terns from the Cass colony that used gravel and rock far more than terns from the Ohau colony, while terns from the Ohau colony used river far more than terns from the Cass colony. This may be a false difference as it was likely caused by the way the Land Cover Database (Landcare Research New Zealand, 2020) classified the habitats at each breeding colony. The area of the Cass colony was classified as mostly gravel and rock, despite have many river braids, while the area of the Ohau colony was classified as entirely river, despite having gravel and rock between the channels. Many GPS points were recorded at the breeding colonies themselves, leading to this relationship between the two habitats and the two colony locations. For this species, it may be better to group gravel and rock with river as one habitat.

Black-fronted terns spent >99% of their time within 25 km of their breeding colonies and 87.37% of their time within 10 km of their breeding colonies. Terns (both sexes) from the Ohau colony travelled further from their breeding colony on average than terns from the Cass colony. The distance terns travel from their breeding colonies is often dictated by the location of preferred foraging areas (Fasola & Bogliani, 1990). There were extensive areas of high producing exotic grassland within 3.5 km of the Cass colony and within 10 km of the Ohau colony, implying that terns from the Ohau colony have to travel further to reach these areas. This study also provided the first evidence of breeding black-fronted terns roosting away from their colonies at night. Terns from the Ohau colony often roosted overnight at the Tekapo River delta, approximately 19 km from the Ohau colony. Terns from the Cass colony were also recorded roosting away from their colony overnight, approximately two km away at the Cass River delta. The larger distance Ohau terns had to travel to reach this night roost also likely contributed to Ohau terns travelling further on average than Cass terns.

Following the breeding season, the terns left their breeding colonies. The GPS devices had battery issues at this point with only eight tern transmitting post-breeding data when they returned to their breeding colonies the following season. Most of the terns that did collect data for this period spent time in the southwest Mackenzie Basin before moving to the lower reaches of braided rivers on the east coast. The terns left the Mackenzie Basin using discrete routes, overland to the lower Rangitata River and down the Waitaki River to its lower reaches. The terns then moved north gradually, with most birds spending time in the lower Rangitata, which appears to be an important post-breeding area for black-fronted terns. While the terns were in the lower Rangitata, the majority of GPS points were recorded in the riverbed and in the surrounding farmland, with relatively few at or near the river mouth.

4.2 Future Conservation and Study

Future black-fronted tern conservation efforts can draw on several pieces of useful information from this study. Habitat preferences of the terns can now be considered when making decisions about potential land-use change near black-fronted tern colonies. Promoting areas of high producing exotic grassland near breeding colonies would provide more favoured foraging habitat and potentially increase the energy intake, and subsequently the breeding success, of terns from those colony. However, high producing grassland is also beneficial to predators of black-fronted terns such as black-backed gulls (Schlesselmann et al., 2018), so promoting this habitat may overall be detrimental to the terns and other aspects of the surrounding environment. The scale around a colony at which black-fronted tern habitat preferences are important can also now be considered. Terns spent most of their time within 10 km of their colonies and rarely ventured beyond 25 km, meaning conservation actions should be carried out within this distance. As such, having areas of high producing exotic grassland within 10 km of Mackenzie Basin breeding colonies could possibly be beneficial and should be considered when making land use decisions or when attempting to influence where the terns nest.

The discovery of nocturnal black-fronted tern roosts associated with specific breeding colonies is also useful for conservation. As black-fronted terns are particularly vulnerable to predation by introduced mammals at night (Keedwell, 2002), predator control around these nocturnal roosts would likely benefit the colony that the roost is associated with. Identifying these roosts attached to other colonies, and protecting them from mammalian predators, weed encroachment and human disturbance, would be an important step to protect black-fronted terns and a novel conservation technique away from the breeding colony itself.

Data collected by GPS tracking devices attached to birds can be used to answer a wide range of questions relating to foraging trip distance and duration and habitat use (Maynard & Ronconi, 2018). The dataset collected by this study is sufficiently large that there are research questions outside the scope of this thesis that can be addressed with the same data. For instance, in this study two breeding pairs of black-fronted terns were fitted with devices (one from each colony) which could be used to determine any similarities or differences in foraging habits within breeding pairs of black-fronted terns. A cursory look at the data from these pairs revealed large areas of overlap in the habitat use and foraging ranges within each pair, although each of the four terns had distinctly separate areas that they visited and that their partner did not. A more thorough investigation could be especially useful for determining how pairs of terns use the night roosts for either colony. Examining this could reveal further information about the roles of the different sexes in black-fronted tern parental care. The dataset from this study could also be re-examined to determine the temporal length of black-fronted tern foraging trips, in addition to the spatial aspects. Future analysis of the data could also exclude GPS from the breeding colonies themselves, potentially revealing more about the habitat selection of the terns by removing many GPS points that may not be foraging points or associated with foraging movement.

There are several levels of study that can be built on top of the current research to enhance its value. Extending device attachment to multiple, consecutive years would increase the robustness of any findings and reveal any season-to-season variation in black-fronted tern foraging habits. In a multiple year study like this, the HUB devices could be more mobile when waiting for terns to transmit their non-breeding data, moving them between multiple breeding colonies in case any terns have returned to breed at a different colony to the one where their device was attached. Different types of GPS tracker, attachment methods and solar panel attachments and enhancements could also be tried to see if they improve the longevity of the device batteries. Winter searching for black-fronted terns with devices should be based on the results from this study, with areas that terns were recorded from being regarded as key search areas (such as the lower Rangitata).

Another layer of research that would enhance the habitat use findings would be to investigate why the terns are selecting for or against particular habitats. For instance, comparing the number and abundance of prey species in high producing exotic grassland with other habitats would confirm if this were the main reason they favour the grassland. The quality and energy value of the food available in the different habitats could also be assessed to determine if areas of high producing exotic grassland are “healthy” for black-fronted terns Furthermore, closely monitoring the nests of terns with GPS devices would enable the data to be split between incubation and chick-rearing to see whether there are differences in movements between these two breeding stages.

Perhaps the most important next step for research is to complete the picture of black-fronted tern movements year-round. The GPS trackers used in this study collected no data between May and November due to low battery levels. The lack of battery charge was likely caused by the solar panels on the trackers being partially or completely covered by feathers and the lower levels of sunlight at that time of year. This lack of data means no information could be gained on black-fronted tern movements in winter or for their return to Mackenzie Basin to breed. To fill this data gap, terns would likely have to be caught in winter (or a different attachment method identified to increase solar panel efficiency through the non-breeding season), given the ability of the GPS devices to collect detailed data in the short term. This brings a new set of challenges as at this time of year the terns would not have nests to be caught on, meaning alternate capture techniques, such as cannon netting, would have to be used. Gaining an understanding of black-fronted tern movements through an entire year is key to creating a complete, year-round protection network for the species. Another important step would be to do some comparative research, particularly at black-fronted tern colonies surrounded by a landscape less human-modified than at the Cass and Ohau colonies. Comparisons with more coastal colonies would also be useful for determining nation-wide movement trends, rather than just in the Mackenzie Basin.

The outcomes of this study potentially have broader applications to other species of birds. Black-billed gulls are another species of endemic braided river breeding bird that also have large knowledge gaps around their foraging and migration movements (McClellan & Habraken, 2013). Black-billed gulls could have similar movement patterns to black-fronted terns (Morris, 1987) as they have similar breeding strategies, often with colonies in close proximity to each other (Popenhagen, 2019). White-fronted terns are a closely related species to black-fronted terns but with a more coastal distribution (Mills, 2020). Like-black-billed gulls, their movements are relatively poorly known with some migrating south-east for the winter (Mills, 2020). Both the black-billed gull and the white-fronted tern are classified as “at risk – declining” and more knowledge is needed to inform the relevant conservation efforts (Robertson et al., 2021). The fact that this study successfully used GPS devices on black-fronted terns is promising for these species as they have relatively similar body types to black-fronted terns and would experience similar environmental conditions. Therefore, conducting a GPS study similar to this one would likely successfully fill the relevant knowledge gaps for black-billed gulls and white-fronted terns.

4.3 Conclusion

Black-fronted terns currently rely on conservation efforts for their survival. This conservation is focused around black-fronted tern breeding colonies and consists mainly of mammalian predator control. Despite individual colonies or stretches of river being successfully protected, conservation efforts have had limited success as the decline of the overall population is predicted to continue. To try and fill knowledge gaps hindering conservation efforts, black-fronted terns are the latest species to be studied using the increasingly common method of GPS tracking. The use of GPS technology was extremely successful in studying this species, with a large and rich dataset gathered. Key information about black-fronted tern habitat use and foraging range was gathered, and a good start was made to understanding the species migration and wintering behaviours. In light of this study’s findings, it would be beneficial for black-fronted tern conservation to also focus away from their breeding colonies, particularly at sites where they roost overnight. The next step for black-fronted tern research is to complete the picture this study began to paint about their non-breeding movements. This would provide a complete understanding of black-fronted tern distribution and movements year-round. This complete knowledge coupled with the findings from this study could potentially have a significant positive impact on black-fronted tern conservation.

References

Ackerman, J. T., Bluso-Demers, J. D., & Takekawa, J. Y. (2009). Postfledging Forster's Tern movements, habitat selection, and colony attendance in San Francisco Bay. *The Condor, 111*(1), 100-110.

Aebischer, N. J., Robertson, P. A., & Kenward, R. E. (1993). Compositional analysis of habitat use from animal radio-tracking data. *Ecology, 74*(5), 1313-1325.

Aidala, Z., & Hauber, M. E. (2011). Checklist of the Birds of New Zealand, Norfolk and Macquarie Islands, and the Ross Dependency, Antarctica. *Wilson Journal of Ornithology, 123*(2), 425.

Aikman, H. (1997). *Department of Conservation response plan for use in the event of an outbreak of rabbit calicivirus disease (RCD)*. Wellington, N.Z. : Dept. of Conservation.

Allen, W., & Gurney, F. (2021). *eBird Checklist: https://ebird.org/atlasnz/checklist/S101157753*. eBird: An online database of bird distribution and abundance [web application]. eBird, Ithaca, New York. Available: http://www.ebird.org. Retrieved 21/04/2022 from https://ebird.org/atlasnz/checklist/S101157753

Ardia, D. R., & Bildstein, K. L. (1997). Sex-related differences in habitat selection in wintering American kestrels, *Falco sparverius*. *Animal Behaviour, 53*(6), 1305-1311.

Battley, P. F., Warnock, N., Tibbitts, T. L., Gill Jr, R. E., Piersma, T., Hassell, C. J., Douglas, D. C., Mulcahy, D. M., Gartrell, B. D., Schuckard, R., Melville, D. S., & Riegen, A. C. (2012). Contrasting extreme long-distance migration patterns in bar-tailed godwits *Limosa lapponica*. *Journal of Avian Biology, 43*(1), 21-32. https://doi.org/10.1111/j.1600-048X.2011.05473.x

Bauer, S., & Klaassen, M. R. J. (2013). Mechanistic models of animal migration behaviour – their diversity, structure and use. *Journal of Animal Ecology, 82*(3), 498-508. https://doi.org/10.1111/1365-2656.12054

Beal, M., Byholm, P., Lötberg, U., Evans, T. J., Shiomi, K., & Åkesson, S. (2021). Habitat selection and foraging site fidelity in Caspian Terns (*Hydroprogne caspia*) breeding in the Baltic Sea. *Ornis Fennica, 98*(4), 182-141.

Bell, M. (2013). *Black-fronted Tern*. In Miskelly, C.M. (ed.) New Zealand Birds Online. Retrieved 10/09/2021 from www.nzbirdsonline.org.nz

Bell, M. (2017). Population size, breeding success and predators of black-fronted tern (*Chlidonias albostriatus*) in the Upper Clarence River catchment, New Zealand. *Notornis, 64*(3), 154-161.

Birdlife International. (2021). *Species factsheet: Chlidonias albostriatus*. Retrieved 09/09/2021 from http://www.birdlife.org

Bowie, M. H., Black, L., Boyer, S., Dickinson, N. M., & Hodge, S. (2016). Persistence of biodiversity in a dryland remnant within an intensified dairy farm landscape. *New Zealand Journal of Ecology, 40*(1), 121-130.

Bridge, E. S., Jones, A. W., & Baker, A. J. (2005). A phylogenetic framework for the terns (Sternini) inferred from mtDNA sequences: implications for taxonomy and plumage evolution.

Molecular Phylogenetics and Evolution, 35(2), 459-469. https://doi.org/10.1016/j.ympev.2004.12.010

Britto, V. O., Gil–Delgado, J., Gosálvez, R. U., López–Iborra, G. M., & Velasco, A. (2018). Foraging habitat selection by gull–billed tern (*Gelochelidon nilotica*) in Central Spain (Castilla–La Mancha). *Animal Biodiversity and Conservation, 41*(2), 301-310.

Burger, J. (1984). Colony Stability in Least Terns. *The Condor, 86*(1), 61-67. https://doi.org/10.2307/1367347

Caruso, B., Newton, S., King, R., & Zammit, C. (2017). Modelling climate change impacts on hydropower lake inflows and braided rivers in a mountain basin. *Hydrological Sciences Journal, 62*(6), 928-946.

Caruso, B. S. (2006). Project River Recovery: Restoration of braided gravel-bed river habitat in New Zealand's high country. *Environmental Management, 37*(6), 840-861. https://doi.org/10.1007/s00267-005-3103-9

Chan, K. (2001). Partial migration in Australian landbirds: a review. *Emu, 101*(4), 281-292. https://doi.org/10.1071/MU00034

Christensen-Dalsgaard, S., Mattisson, J., Bekkby, T., Gundersen, H., May, R., Rinde, E., & Lorentsen, S.-H. (2017). Habitat selection of foraging chick-rearing European shags in contrasting marine environments. *Marine Biology, 164*(10), 1-12. https://doi.org/10.1007/s00227-017-3227-5

Cody, M. L. (1985). *Habitat selection in birds*. Academic press.

Connor, H. E., & Vucetich, C. (1964). Tussock grassland communities in the Mackenzie country, South Canterbury, New Zealand. *New Zealand Journal of Botany, 2*(4), 325-351.

Cruz, J., Pech, R. P., Seddon, P. J., Cleland, S., Nelson, D., Sanders, M. D., & Maloney, R. F. (2013). Species-specific responses by ground-nesting Charadriiformes to invasive predators and river flows in the braided Tasman River of New Zealand. *Biological Conservation, 167*, 363-370.

Dowding, J., Elliott, M., & Murphy, E. (2015). Scats and den contents as indicators of the diet of stoats (*Mustela erminea*) in the Tasman Valley, South Canterbury, New Zealand. *New Zealand Journal of Zoology, 42*(4), 270-282.

Dowding, J. E. (2017). *Wrybill*. In Miskelly, C.M. (ed.) New Zealand Birds Online. Retrieved 10/12/2021 from www.nzbirdsonline.org.nz

Dowding, J. E., & Murphy, E. C. (2001). The impact of predation by introduced mammals on endemic shorebirds in New Zealand: a conservation perspective. *Biological Conservation, 99*(1), 47-64.

Duncan, M., Hughey, K. F. D., Cochrane, C., & Bind, J. (2008). *River modelling to better manage mammalian predator access to islands in braided rivers*. B. H. Society.

Duncan, R. P., & Blackburn, T. M. (2004). Extinction and endemism in the New Zealand avifauna. *Global Ecology and Biogeography, 13*(6), 509-517. https://doi.org/10.1111/j.1466-822X.2004.00132.x

Dunlop, J. (1997). Foraging range, marine habitat and diet of Bridled Terns breeding in Western Australia. *Corella, 21*, 77-82.

Egevang, C., Stenhouse, I. J., Phillips, R. A., Petersen, A., Fox, J. W., & Silk, J. R. (2010). Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration. *Proceedings of the National Academy of Sciences, 107*(5), 2078-2081.

Eichhorst, B. A., & Reed, J. R. (1985). Renesting of a Black Tern. *Condor, 74*, 46-53.

Fasola, M., & Bogliani, G. (1990). Foraging ranges of an assemblage of Mediterranean seabirds. *Colonial Waterbirds*, 72-74.

Fijn, R. C., de Jong, J., Courtens, W., Verstraete, H., Stienen, E. W. M., & Poot, M. J. M. (2017). GPS-tracking and colony observations reveal variation in offshore habitat use and foraging ecology of breeding Sandwich Terns. *Journal of Sea Research, 127*, 203-211. https://doi.org/10.1016/j.seares.2016.11.005

Fijn, R. C., & Gyimesi, A. (2018). Behaviour related flight speeds of Sandwich Terns and their implications for wind farm collision rate modelling and impact assessment. *Environmental Impact Assessment Review, 71*, 12-16. https://doi.org/10.1016/j.eiar.2018.03.007

Forest & Bird. (2016). *New Zealand Seabirds: Sites on land, rivers, estuaries, coastal lagoons & harbours*. N. Z. The Royal Forest & Bird Protection Society of New Zealand, Wellington, New Zealand.

Fuller, R. A. (2016). Animal migration: Dispersion explains declines. *Nature, 531*(7595), 451-452. https://doi.org/10.1038/531451a

Goławski, A., Kasprzykowski, Z., Mróz, E., Rzępała, M., & Chmielewski, S. (2015). The differences in habitat selection in two sympatric species of eastern Poland: the White-winged Tern (*Chlidonias leucopterus*) and the Black Tern (*Chlidonias niger*). *The Wilson Journal of Ornithology, 127*(1), 52-58.

González-Solís, J., Wendeln, H., & Becker, P. H. (1999). Within and between season nest-site and mate fidelity in Common Terns (*Sterna hirundo*). *Journal für Ornithologie, 140*(4), 491-498.

Goodenough, K. S., & Patton, R. T. (2019). Satellite telemetry reveals strong fidelity to migration routes and wintering grounds for the Gull-billed tern (*Gelochelidon nilotica*). *Waterbirds, 42*(4), 400-410.

Graham, C. L., & McWilliams, S. R. (2022). Body composition of American Woodcock during fall staging: a validation of the non-invasive deuterium dilution method. *Journal of Ornithology, 163*(1), 213-222.

Gray, D., & Harding, J. S. (2007). *Braided river ecology: a literature review of physical habitats and aquatic invertebrate communities*. Wellington, N.Z. : Science & Technical Pub., Dept. of Conservation.

Gray, J. E., Hooker, J. D., Gray, G. R., White, A., & Doubleday, E. (1845). *Zoology of the Voyage of HMS Erebus and Terror, Under the Command of Sir James C. Ross, 1839-43: During the Years 1839 to 1843: by Authority of the Lords Commissioners of the Admiralty*. Longman, Brown, Green, and Longmans.

Green, R. E., Cornell, S. J., Scharlemann, J. P., & Balmford, A. (2005). Farming and the fate of wild nature. *Science, 307*(5709), 550-555.

Guillemette, M., & Brousseau, P. (2001). Does culling predatory gulls enhance the productivity of breeding common terns? *Journal of Applied Ecology, 38*(1), 1-8.

Gurney, F. (2022a). *eBird Checklist: https://ebird.org/atlasnz/checklist/S100637174*. eBird: An online database of bird distribution and abundance [web application]. eBird, Ithaca, New York. Available: http://www.ebird.org. Retrieved 14/06/2022 from https://ebird.org/atlasnz/checklist/S100637174

Gurney, F. (2022b). *eBird Checklist: https://ebird.org/atlasnz/checklist/S101064731*. eBird: An online database of bird distribution and abundance [web application]. eBird, Ithaca, New York. Available: http://www.ebird.org. Retrieved 14/06/2022 from https://ebird.org/atlasnz/checklist/S101064731

Hamblin, C. (2017). *Colony dynamics and social attraction in black-fronted terns, Chlidonias albostriatus* [Lincoln University].

Hamblin, C. H. (2019). Black-fronted tern (*Chlidonias albostriatus*) colony dynamics in New Zealand braided rivers. *Notornis, 66*(4), 192-199.

Hart, J., Milsom, T., Fisher, G., Wilkins, V., Moreby, S., Murray, A., & Robertson, P. (2006). The relationship between yellowhammer breeding performance, arthropod abundance and insecticide applications on arable farmland. *Journal of Applied Ecology*, 81-91.

Hedenström, A., & Åkesson, S. *Data from: Ecology of tern flight in relation to wind, topography and aerodynamic theory* Dryad. https://doi.org/10.5061/dryad.hj13q

Hennicke, J. C., James, D. J., & Weimerskirch, H. (2015). Sex-specific habitat utilization and differential breeding investments in Christmas Island frigatebirds throughout the breeding cycle. *PLoS One, 10*(6), e0129437-e0129437. https://doi.org/10.1371/journal.pone.0129437

Higgins, P. J., & Davies, S. J. J. F. (1996). Handbook of Australian, New Zealand & Antarctic Birds. In (Vol. 3, Snipe to pigeons, pp. 384-385, 573-576, 699-708). Melbourne, Oxford University Press.

Hoitink, A., Wang, Z. B., Vermeulen, B., Huismans, Y., & Kästner, K. (2017). Tidal controls on river delta morphology. *Nature Geoscience, 10*(9), 637-645.

Hughey, K. F. D. (1985). *Hydrological factors influencing the ecology of riverbed breeding birds on the plains' reaches of Canterbury's braided rivers: a thesis submitted in fulfilment of the requirements for the degree of Doctor of Philosophy in the University of Canterbury* Lincoln College, University of Canterbury].

Hughey, K. F. D. (1986). *Birds of the lower Clutha River: their distribution and habitat use*. Wellington, N.Z. : New Zealand Wildlife Service, Dept. of Internal Affairs.

Hutto, R. L. (1985). Habitat selection by nonbreeding, migratory land birds. *Habitat Selection in Birds, 455*.

Jones, H. P., & Kress, S. W. (2012). A review of the world's active seabird restoration projects. *The Journal of Wildlife Management, 76*(1), 2-9.

Kasinsky, T., Yorio, P., Dell'Arciprete, P., Marinao, C., & Suárez, N. (2021). Geographical differences in sex-specific foraging behaviour and diet during the breeding season in the opportunistic Kelp Gull (*Larus dominicanus*). *Marine Biology, 168*(1), 1-15.

Kearns, M. (2021). *eBird Checklist: https://ebird.org/checklist/S90561561*. eBird: An online database of bird distribution and abundance [web application]. eBird, Ithaca, New York. Available: http://www.ebird.org. Retrieved 08/10/2021 from https://ebird.org/checklist/S90561561

Keedwell, R. J. (2002). *Black-fronted terns and banded dotterels: causes of mortality and comparisons of survival* Massey University]. A thesis presented in partial fulfilment of the requirements for the degree of Doctor of Philosophy in Ecology at Massey University, Palmerston North, New Zealand.

Keedwell, R. J. (2005). Breeding biology of Black-fronted Terns (*Sterna albostriata*) and the effects of predation. *Emu, 105*(1), 39-47. https://doi.org/10.1071/MU04010

Keye, C. (2008). *A study of home ranges, movement and activity patterns of Great Spotted Kiwi (Ateryx haastii) in the Hurunui Region, South Island, New Zealand.* [Lincoln University].

Kolts, J. R., & McRae, S. B. (2017). Seasonal home range dynamics and sex differences in habitat use in a threatened, coastal marsh bird. *Ecology and Evolution, 7*(4), 1101-1111.

Kralj, J., Martinović, M., Jurinović, L., Szinai, P., Sütő, S., & Preiszner, B. (2020). Geolocator study reveals east African migration route of Central European Common Terns. *Avian Research, 11*(1), 1-11.

Krausman, P. R. (1999). Some basic principles of habitat use. *Grazing Behavior of Livestock and Wildlife, 70*, 85-90.

Lalas, C. (1977). *Food and feeding behaviour of the Black-fronted tern, Chlidonias hybrida albostriatus* [Doctoral Dissertation, University of Otago].

Lalas, C. (1979). Seasonal movements of black-fronted terns. *Notornis, 26*, 69-72.

Landcare Research New Zealand. (2020). *LCDB v5.0 - Land Cover Database version 5.0, Mainland, New Zealand*. Retrieved 25/04/2022 from https://lris.scinfo.org.nz/layer/104400-lcdb-v50-land-cover-database-version-50-mainland-new-zealand/

Latham, P. (1981). Black-fronted terns wintering in the Bay of Plenty. *Notornis, 28*, 221-239.

Li, X., Zhang, J., & Yin, M. (2013). Animal migration optimization: an optimization algorithm inspired by animal migration behavior. *Neural Computing and Applications, 24*(7-8), 1867-1877. https://doi.org/10.1007/s00521-013-1433-8

Limiñana, R., Soutullo, A., López-López, P., & Urios, V. (2008). Pre-migratory movements of adult Montagu's Harriers Circus pygargus. *Ardea, 96*(1), 81-90.

Lintott, P. R., Bunnefeld, N., Fuentes-Montemayor, E., Minderman, J., Mayhew, R. J., Olley, L., & Park, K. J. (2014). City life makes females fussy: sex differences in habitat use of temperate bats in urban areas. *Royal Society Open Science, 1*(3), 140200.

Lyons, D. E., Patterson, A. G., Tennyson, J., Lawes, T. J., & Roby, D. D. (2018). The Salton Sea: critical migratory stopover habitat for Caspian terns (*Hydroprogne caspia*) in the North American Pacific Flyway. *Waterbirds, 41*(2), 154-165.

Maloney, R., Keedwell, R., Wells, N., Rebergen, A., & Nilsson, R. (1999). Effect of willow removal on habitat use by five birds of braided rivers, Mackenzie Basin, New Zealand. *New Zealand Journal of Ecology*, 53-60.

Martin, A. E., & Fahrig, L. (2018). Habitat specialist birds disperse farther and are more migratory than habitat generalist birds. *Ecology, 99*(9), 2058-2066.

Maynard, L. D., & Ronconi, R. A. (2018). Foraging behaviour of Great Black-blacked Gulls *Larus marinus* near an urban centre in Atlantic Canada: evidence of individual specialization from GPS tracking. *Marine Ornithology, 46*, 27-32.

McAllan, I. (2000). A possible record of black-fronted tern *Sterna albostriata* from Norfolk Island. *Notornis, 47*(1), 63-64.

McClellan, R. K., & Habraken, A. (2013). *Black-billed gull | tarāpuka*. In Miskelly, C.M. (ed.) New Zealand Birds Online. Retrieved 23/06/2022 from www.nzbirdsonline.org.nz

McGlone, M., & Moar, N. (1998). Dryland Holocene vegetation history, Central Otago and the Mackenzie Basin, South Island, New Zealand. *New Zealand Journal of Botany, 36*(1), 91-111.

McLeay, L., Page, B., Goldsworthy, S., Paton, D., Teixeira, C., Burch, P., & Ward, T. (2010). Foraging behaviour and habitat use of a short-ranging seabird, the crested tern. *Marine Ecology Progress Series, 411*, 271-283.

Medeiros, R., Ramos, J. A., Paiva, V. H., Almeida, A., Pedro, P., & Antunes, S. (2007). Signage reduces the impact of human disturbance on little tern nesting success in Portugal. *Biological Conservation, 135*(1), 99-106. https://doi.org/10.1016/j.biocon.2006.10.001

Mills, J. A. (2020). *White-fronted Tern*. In Miskelly, C.M. (ed.) New Zealand Birds Online. Retrieved 20/10/2021 from www.nzbirdsonline.org.nz

Ministry for the Environment. (2017). *Average annual rainfall, 1972–2016*. Retrieved 25/04/2022 from https://data.mfe.govt.nz/layer/89421-average-annual-rainfall-19722016/

Ministry for the Environment. (2021). *Land*. Retrieved 22/06/2022 from https://environment.govt.nz/publications/environment-new-zealand-2007-summary/section-three-state-of-the-environment/land/

Morris, D. W. (1987). Ecological scale and habitat use. *Ecology, 68*(2), 362-369.

Murphy, E. C., Russell, J. C., Broome, K. G., Ryan, G. J., & Dowding, J. E. (2019). Conserving New Zealand's native fauna: a review of tools being developed for the Predator Free 2050 programme. *Journal of Ornithology, 160*(3), 883-892.

Naugle, D. E., Higgin, K. F., Estey, M. E., Johnson, R. R., & Nusser, S. M. (2000). Local and landscape-evel factors influencing Black Tern habitat suitability. *The Journal of Wildlife Management, 64*(1), 253-260. https://doi.org/10.2307/3802997

Neumann, J., Larose, C. S., Brodin, G., & Feare, C. J. (2018). Foraging ranges of incubating Sooty Terns *Onychoprion fuscatus* on Bird Island, Seychelles, during a transition from food plenty to scarcity, as revealed by GPS loggers. *Marine Ornithology, 46*(1), 11-18.

Newton, I., & Brockie, K. (2007). *The Migration Ecology of Birds*. San Diego: Elsevier Science & Technology.

Nisbet, I. C., Mostello, C. S., Veit, R. R., Fox, J. W., & Afanasyev, V. (2011). Migrations and winter quarters of five Common Terns tracked using geolocators. *Waterbirds, 34*(1), 32-39.

Norbury, G., & Heyward, R. (2008). Predictors of clutch predation of a globally significant avifauna in New Zealand's braided river ecosystems. *Animal Conservation, 11*(1), 17-25. https://doi.org/10.1111/j.1469-1795.2007.00142.x

O'Donnell, C. F., & Hoare, J. M. (2011). Meta-analysis of status and trends in breeding populations of black-fronted terns (*Chlidonias albostriatus*) 1962–2008. *New Zealand Journal of Ecology*, 30-43.

O'Donnell, C. F., Sanders, M. D., Woolmore, C. B., & Maloney, R. (2016). *Management and research priorities for conserving biodiversity on New Zealand's braided rivers*. Department of Conservation Wellington, NZ.

O'Donnell, C. F. J., & Moore, S. G. M. (1983). *The wildlife and conservation of braided river systems in Canterbury*. Wellington : New Zealand Wildlife Service, Dept. of Internal Affairs.

O'Donnell, C. F., & Monks, J. M. (2020). Distribution, long term population trends and conservation status of banded dotterels (*Charadrius bicinctus bicinctus*) on braided rivers in New Zealand. *Notornis, 67*, 733-753.

O'Donnell, C. F., Sedgeley, J. A., & Van Hal, J. (2010). Variation in house cat (*Felis catus*) predation sign at a black-fronted tern (*Sterna albostriata*) colony. *Notornis, 57*, 43-47.

Oliver, W. R. B. (1955). *New Zealand birds* (2nd ed., rev. and enl.. ed.). Wellington, N.Z. : Reed.

Paiva, V. H., Ramos, J. A., Martins, J., Almeida, A., & Carvalho, A. (2008). Foraging habitat selection by Little Terns *Sternula albifrons* in an estuarine lagoon system of southern Portugal. *Ibis, 150*(1), 18-31.

Pakanen, V.-M. (2018). Large scale climate affects the timing of spring arrival but local weather determines the start of breeding in a northern Little Tern (*Sternula albifrons*) population. *Ornis Fennica, 95*(4), 178-184.

Palestis, B. G. (2014). The role of behavior in tern conservation. *Current Zoology, 60*(4), 500-514.

Pasinelli, G., Grendelmeier, A., Gerber, M., & Arlettaz, R. (2016). Rodent-avoidance, topography and forest structure shape territory selection of a forest bird. *BMC Ecology, 16*(1), 1-18.

Paton, P. W., Loring, P. H., Cormons, G. D., Meyer, K. D., Williams, S., & Welch, L. J. (2021). Fate of Common (*Sterna hirundo*) and Roseate Terns (*S. dougallii*) with satellite transmitters attached with backpack harnesses. *Waterbirds, 43*(3-4), 342-347.

Perrins, C. M. (1996). Eggs, egg formation and the timing of breeding. *Ibis, 138*(1), 2-15.

Pickerell, G. (2015). *Braided-river islands as refuges from introduced mammalian predators: characteristics influencing predator presence, and consequences of reduced flow* University of Otago].

Pierce, R. (1983). The charadriiforms of a high country river valley. *Notornis, 30*(3), 169-185.

Popenhagen, C. (2019). *Waimakariri River Regional Park Braided River Bird Management*. Environment Canterbury.

Rappole, J. H., & Tipton, A. R. (1991). New harness design for attachment of radio transmitters to small passerines (Nuevo Diseño de Arnés para Atar Transmisores a Passeriformes Pequeños). *Journal of Field Ornithology*, 335-337.

Rebergen, A., & Woolmore, C. (2016). Project River Recovery Annual Report.

Robertson, C. J. R. (1983). *Habitat requirements of wetland birds in the Ahuriri River catchment, New Zealand*. New Zealand Wildlife Service, Department of Internal Affairs.

Robertson, H., Baird, K., Dowding, J., Elliott, G., Hitchmough, R., Miskelly, C., McArthur, N., O'Donnell, C., Sagar, P., Scofield, R., & Taylor, G. (2017). *Conservation status of New Zealand birds, 2016*.

Robertson, H. A., Baird, K. A., Elliott, G. P., Hitchmough, R. A., McArthur, N. J., Makan, T. D., Miskelly, C. M., O'Donnell, C. F., Sagar, P. M., & Scofield, R. P. (2021). Conservation status of birds in Aotearoa New Zealand, 2021. *New Zealand Threat Classification Series. Department of Conservation, Wellington*, 43.

Robertson, H. A., Dowding, J. E., Elliott, G., Hitchmough, R., Miskelly, C., O'Donnell, C. F., Powlesland, R., Sagar, P. M., Scofield, R. P., & Taylor, G. A. (2013). *Conservation status of New Zealand birds, 2012*. Publishing Team, Department of Conservation.

Ronald, G. B., & Saskia, J.-B. (1983). Sexual differences in the behavior of adult great black-backed gulls (*Larus marinus*) during the pre- and post-hatch periods. *The Auk, 100*(1), 63-75. https://doi.org/10.1093/auk/100.1.63

Rosselli, L. (1994). The annual cycle of the White-ruffed Manakin *Corapipo leucorrhoa*, a tropical frugivorous altitudinal migrant, and its food plants. *Bird Conservation International, 4*(2-3), 143-160. https://doi.org/10.1017/S0959270900002732

Rueda-Uribe, C., Lötberg, U., Ericsson, M., Tesson, S. V. M., & Åkesson, S. (2021). First tracking of declining Caspian terns *Hydroprogne caspia* breeding in the Baltic Sea reveals high migratory dispersion and disjunct annual ranges as obstacles to effective conservation. *Journal of Avian Biology, 52*(9), n/a. https://doi.org/10.1111/jav.02743

Sagar, P., M. (2013). *South Island Pied Oystercatcher*. In Miskelly, C.M. (ed.) New Zealand Birds Online. Retrieved 10/09/2021 from www.nzbirdsonline.org.nz

Sanders, M. D., & Maloney, R. F. (2002). Causes of mortality at nests of ground-nesting birds in the Upper Waitaki Basin, South Island, New Zealand: a 5-year video study. *Biological Conservation, 106*(2), 225-236. https://doi.org/10.1016/S0006-3207(01)00248-8

Scarpignato, A. L., Stein, K. A., Cohen, E. B., Marra, P. P., Kearns, L. J., Hallager, S., & Tonra, C. M. (2021). Full annual cycle tracking of Black-crowned Night-Herons suggests wintering areas do not explain differences in colony population trends. *Journal of Field Ornithology, 92*(2), 143-155. https://doi.org/10.1111/jofo.12369

Schlesselmann, A.-K. V. (2018). *Linking science and management for effective long-term conservation: A case study of black-fronted terns/tarapirohe (Chlidonias albostriatus)* University of Otago].

Schlesselmann, A.-K. V., Cooper, J., & Maloney, R. F. (2017). Single season colony records of black-fronted terns (*Chlidonias albostriatus*) spanning their entire breeding range. *Notornis, 64*, 38-43.

Schlesselmann, A.-K. V., O'Donnell, C. F., Monks, J. M., & Robertson, B. C. (2018). Clearing islands as refugia for black-fronted tern (*Chlidonias albostriatus*) breeding colonies in braided rivers. *New Zealand Journal of Ecology, 42*(2), 137-148.

Schlesselmann, A.-K. V., & Robertson, B. C. (2017). Isolation and characterization of 18 polymorphic microsatellite loci for the endangered New Zealand Black-Fronted Tern (*Chlidonias albostriatus*). *Waterbirds, 40*(3), 297-301. https://doi.org/10.1675/063.040.0311

Schon, N., Mackay, A., & Minor, M. (2012). Vulnerability of soil invertebrate communities to the influences of livestock in three grasslands. *Applied Soil Ecology, 53*, 98-107.

Seward, A., Taylor, R. C., Perrow, M. R., Berridge, R. J., Bowgen, K. M., Dodd, S., Johnstone, I., & Bolton, M. (2021). Effect of GPS tagging on behaviour and marine distribution of breeding Arctic Terns *Sterna paradisaea*. *Ibis, 163*(1), 197-212. https://doi.org/10.1111/ibi.12849

Shealer, D. A. (1996). Foraging habitat use and profitability in tropical Roseate Terns and Sandwich Terns. *The Auk, 113*(1), 209-217.

Simpfendorfer, C. A., & Heupel, M. R. (2004). Assessing habitat use and movement. *Biology of Sharks and Their Relatives. CRC Press, Boca Raton*, 553-572.

Smith, D., McClellan, R., Lapointe, M., & Shaw, W. (2020). *Braided river bird management plan for the Waimakariri River Regional Park*. Wildland Consultants (Contract Report No. 5255).

Soanes, L. M., Bright, J. A., Brodin, G., Mukhida, F., & Green, J. A. (2015). Tracking a small seabird: first records of foraging movements in the sooty tern *Onychoprion fuscatus*. *Marine Ornithology, 43*(2), 235-239.

Somveille, M., Rodrigues, A. S. L., & Manica, A. (2015). Why do birds migrate? A macroecological perspective. *Global Ecology and Biogeography, 24*(6), 664-674. https://doi.org/10.1111/geb.12298

Southey, I. (2013). *Whiskered Tern*. In Miskelly, C.M. (ed.) New Zealand Birds Online. Retrieved 08/10/2021 from https://www.nzbirdsonline.org.nz/species/whiskered-tern

Spicer-Bell, J. (2021). *eBird Checklist: https://ebird.org/checklist/S90468458*. eBird: An online database of bird distribution and abundance [web application]. eBird, Ithaca, New York. Available: http://www.ebird.org. Retrieved 08/10/2021 from https://ebird.org/checklist/S90468458

Spurr, E. B., & Ledgard, N. J. (2016). Population trends of braided river birds on the Ashley River (Rakahuri), Canterbury, New Zealand, 1963-2015. *Notornis, 63*(2), 73-86.

Stanton, R., Morrissey, C., & Clark, R. (2018). Analysis of trends and agricultural drivers of farmland bird declines in North America: A review. *Agriculture, Ecosystems & Environment, 254*, 244-254.

Steen, V. A., & Powell, A. N. (2012). Wetland selection by breeding and foraging Black Terns in the Prairie Pothole Region of the United States. *The Condor, 114*(1), 155-165.

Steffens, K. E., Sanders, M. D., Gleenson, D. M., Pullen, K. M., & Stowe, C. J. (2012). Identification of predators at black-fronted tern *Chlidonias albostriatus* nests, using mtDNA analysis and digital video recorders. *New Zealand Journal of Ecology*, 48-55.

Stein, A. (2010). *Identification of predators at black-fronted tern nests on the Wairau River using video footage and predator DNA: A follow up study* (Publication Number 234) University of Otago]. Wildlife Management.

Surman, C. A., Nicholson, L. W., & Phillips, R. A. (2018). Distribution and patterns of migration of a tropical seabird community in the Eastern Indian Ocean. *Journal of Ornithology, 159*(3), 867-877.

Taber, B. (2015). Caspian Terns staging on the lower James River. *The Raven, 86*(2), 9-10.

Taylor, G. (2000). *Action Plan for Seabird Conservation in New Zealand. Part A: Threatened Seabirds*. Department of Conservation.

Te Manahuna Aoraki. (2020). Te Manahuna Aoraki Project Annual Report 2020.

Tockner, K., Paetzold, A., Karaus, U., Claret, C., & Zettel, J. (2006). Ecology of braided rivers. *Special Publication-International Association of Sedimentologists, 36*, 339.

van der Winden, J., Fijn, R. C., van Horssen, P. W., Gerritsen-Davidse, D., & Piersma, T. (2014). Idiosyncratic migrations of Black Terns (*Chlidonias niger*): Diversity in routes and stopovers. *Waterbirds (De Leon Springs, Fla.), 37*(2), 162-174. https://doi.org/10.1675/063.037.0205

van der Winden, J., & Nesterenko, M. (2003). A postnuptial staging site for the Black Tern (*Chlidonias niger*) and White-winged Tern (*C. leucopterus*) in the Sivash, Ukraine. *Journal für Ornithologie, 144*(3), 330-344.

Vandenabeele, S. P., Shepard, E. L., Grogan, A., & Wilson, R. P. (2012). When three per cent may not be three per cent; device-equipped seabirds experience variable flight constraints. *Marine Biology, 159*(1), 1-14. https://doi.org/10.1007/s00227-011-1784-6

Vickery, J., Tallowin, J., Feber, R., Asteraki, E., Atkinson, P., Fuller, R., & Brown, V. (2001). The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. *Journal of Applied Ecology, 38*(3), 647-664.

Warnock, N. (2010). Stopping vs. staging: the difference between a hop and a jump. *Journal of Avian Biology, 41*(6), 621-626.

Watola, G. (2021). *eBird Checklist: https://ebird.org/checklist/S38940602*. eBird: An online database of bird distribution and abundance [web application]. eBird, Ithaca, New York. Available: http://www.ebird.org. Retrieved 12/10/2021 from https://ebird.org/checklist/S38940602

Wildlife Management International, & Department of Conservation. (2022). *Data from "Black-fronted Tern Study".* DOC FALCON Database.

Williams, A., Norton, D. A., & Ridgway, H. J. (2012). Different arbuscular mycorrhizal inoculants affect the growth and survival of *Podocarpus cunninghamii* restoration plantings in the Mackenzie Basin, New Zealand. *New Zealand Journal of Botany, 50*(4), 473-479.