Survival and breeding success of wrybills (*Anarhynchus frontalis*) in the Tekapo and Tasman Rivers, South Canterbury, New Zealand

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Abstract: The wrybill (Anarhynchus frontalis) is an endemic plover that breeds only in braided rivers east of the main divide in the South Island of New Zealand. It is threatened by a range of factors, including loss and degradation of habitat, flooding, and predation. We monitored wrybills in 2 sites in the Tekapo River and 2 in the Tasman River in the Mackenzie Basin, South Canterbury, during 3 breeding seasons (1997/98–1999/2000). We aimed to compare survival and productivity between areas with and without trapping (mammalian predator control) to determine whether predator control was associated with higher survival and / or breeding success of wrybills. In the Tekapo River, results were similar between trapped and un-trapped areas, suggesting that control had little effect. In the Tasman River, there were large differences between the two sites and trapping appeared to be beneficial; in the upper river (un-trapped), productivity and survival were very low and in the lower (trapped) site they were high. Over the whole study, 67.3% of nests hatched, and depredation was the largest cause of nest failure. Fledging success (the proportion of chicks hatched that fledged) averaged 35.4%. Losses at the chick stage were higher than at the egg stage, and there was only a weak correlation between nesting success and overall breeding success; we therefore caution against the use of nesting success as a proxy for overall breeding success. Productivity averaged 0.49 chicks fledged per pair over the whole study; when the very low values from the upper Tasman site were excluded, productivity averaged 0.61. Survival of adult male wrybills was lower than survival of females in all four study sites. Measurement of adult survival is important in determining the full effect of predator control (and in determining population trends) but is often overlooked. At the time of our study, wrybill populations in 3 of our 4 study sites appeared not to be self-sustaining and, in the absence of immigration, were in decline. A number of factors, including depredation by mammals, can affect breeding success. Trapping may be beneficial, but temporal and geographic differences in predator densities, as well as variability in other threats (such as flooding and levels of avian predation) mean that predicting when and where mammalian predator control may benefit wrybills is currently difficult.

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INTRODUCTION

The wrybill (*Anarhynchus frontalis*) is a threatened plover endemic to New Zealand. It is classified

Received 24 *May* 2019; *accepted* 8 *July* 2019 *Correspondence: *jdowding@xtra.co.nz* internationally as Vulnerable (BirdLife International 2019) and by the New Zealand threat classification scheme as Threatened (Nationally Vulnerable) (Robertson *et al.* 2017). Wrybills currently breed only in braided rivers east of the main divide in the South Island, from the Waiau River, North

Canterbury (43°40′S) to the Dart River in northern Otago (44°50′S). Within this range, the bulk of the population is found in three large catchments: the Rakaia River, the upper Rangitata River, and the Mackenzie (Upper Waitaki) Basin (Riegen & Dowding 2003). Following breeding, birds migrate to the North Island and most of the population winters in the large harbours around Auckland. In recent years, the population has probably numbered 5,000–5,500 birds (Dowding 2017).

The breeding range of the wrybill has contracted southwards over the past century (Riegen & Dowding 2003), but the reasons for this are not clear. The main threats to the species appear to be loss or degradation of breeding habitat, loss of nests or small chicks to flooding, and predation by introduced mammals and native birds, but the relative importance of these threats is unknown (Dowding & Murphy 2001).

Large numbers of shorebirds of a range of species breed in the braided rivers of the Mackenzie Basin, including at least 15% of the wrybill population (Maloney et al. 1997). Predation is a major cause of breeding failure for some of these species, including black stilts (*Himantopus novaezelandiae*) (Pierce 1986), banded dotterels (*Charadrius bicinctus*) (Rebergen et al. 1998), and black-fronted terns (Chlidonias albostriatus) (Keedwell et al. 2002a). The main predators at nests of these species in three Mackenzie Basin rivers were feral cats (*Felis catus*), ferrets (Mustela furo), and hedgehogs (Erinaceus europaeus) (Sanders & Maloney 2002). In the case of black-fronted terns, Norway rats (Rattus norvegicus) were also implicated in predation of chicks, juveniles, and adults (Keedwell *et al.* 2002a). A study of the diet of stoats (*Mustela erminea*) in the Tasman River (a site not included in the Sanders & Maloney 2002 study), showed that banded dotterels, wrybills, and black-fronted terns were impacted by stoats there (Dowding et al. 2015).

The Department of Conservation has undertaken predator trapping in the Mackenzie Basin since the 1980s, although the number and sizes of the areas trapped, the types of traps used, and the intensity and timing of trapping have varied between years. This trapping was designed primarily to protect the critically endangered black stilt, but other riverbed species are likely to have benefited (Keedwell *et al.* 2002b).

Our study aimed to measure survival and productivity of wrybills in the Tekapo and Tasman Rivers, Mackenzie Basin, South Canterbury, and to compare these parameters between areas with and without trapping to determine whether control of mammalian predators was associated with enhanced breeding success and/or survival. The study was conducted over three breeding seasons (September to January 1997/1998, 1998/1999, and 1999/2000).

STUDY AREAS & METHODS Study areas

Two study sites were located in the Tasman River and two in the Tekapo River (Fig. 1). The locations and sizes of the sites were dictated largely by the distribution and density of wrybills in the two rivers, and by accessibility. There were obvious differences in habitat type between the two rivers, and the use of two sites in each was an attempt to control for this. The bed of the Tekapo River is generally narrower (mainly between 200 and 800 m in width) than that of the Tasman and contains more vegetation. The bed of the Tasman is very wide (2.5–3.5 km) and contains much larger areas of open gravel.



Figure 1. Locations of the four study sites in the Mackenzie Basin, South Canterbury. A = Upper Tasman, B = Lower Tasman, C = Upper Tekapo, and D = Lower Tekapo.

The Upper Tekapo site started at 44°04'S 170°26'E, about 8 km SSW of Lake Tekapo township, and extended downstream about 12 km to 44°10'S 170°24'E. The upstream end of the Lower Tekapo site was at 44°18'S 170°17'E (about 4 km above the confluence of the Tekapo and Pukaki Rivers). The site extended about 7 km downstream to 44°20'S

170°13′E. This site also included a short stretch of the Pukaki River from its confluence with the Tekapo River to 44°18′S 170°13′E, about 1.5 km NW of the confluence. The minimum distance between the upper and lower Tekapo sites was 17.5 km.

Both sites in the Tasman River were located west of the main channel, and close to the true right side of the river. The upstream boundary of the Upper Tasman site was just north of Fred Stream at 43°49'S 170°08'E. The site extended downstream to a point about 1 km north of Bush Stream (43°51'S, 170°08'E). The Lower Tasman site extended from a point 0.5 km north of Dead Horse Stream (43°53'S, 170°07'E) downstream to the shoreline of Lake Pukaki, near Glentanner airstrip (43°55'S, 170°08'E). The minimum distance between the upper and lower Tasman sites was 3.5 km. The minimum separation between the Tekapo River and Tasman River study sites was 30 km and the maximum separation was 58 km.

Predator control was undertaken between September and January to coincide with the birdbreeding season. Details of trap types, trapping procedures, and numbers of trap-nights during the three years of our study are given in Cook & Maloney (1999), Cook *et al.* (2000), and Keedwell & Brown (2001).

Wrybill monitoring

During each of the three breeding seasons, adults and chicks were caught and fitted with individual colour-band combinations consisting of a numbered metal band and 3 or 4 plastic colour bands. Adults were sexed by the presence (males) or absence (females) of a narrow black frontal bar between the forehead and crown (Marchant & Higgins 1993). Most pairs being monitored contained one or two colour-banded birds, which allowed families to be monitored when they sometimes moved away from the nest area after hatching.

Nests were found by watching from a distance as birds returned to them. Pairs were normally monitored every 2-4 days, but intervals were occasionally longer (e.g., when a pair had recently lost a clutch or brood and no activity was expected). Nests were monitored by walking past them (as opposed to up to them and back) in an attempt to avoid leaving scent trails that might be followed by mammalian predators. Nesting success was the proportion of nests that hatched one or more eggs (Miller & Johnson 1978). Nest outcomes were recorded as i) Hatched (at least one chick seen), ii) Flooded (eggs disappeared from the nest before they were due to hatch and following a flood that reached the nest), iii) Abandoned (not seen to be incubated during multiple visits and failed to hatch), iv) Depredated (eggs disappeared and nest bowl contained yolk and shell fragments, or eggs disappeared before they were due to hatch and nest had not been flooded or abandoned), and v) Unknown. In a very few cases, adult behaviour (agitation, vocalisation, and distraction displays) indicated nesting but the nest could not be found, and breeding was not confirmed until small chicks were seen.

Chicks were often hard to find by day, but the presence of one or more could be inferred from parental distraction behaviour (Hay 1984). The number of chicks present could be determined either by torchlight searches at night (when chicks were very active), or by waiting until fledging, when they ceased hiding and were obvious. Fledging success was the proportion of chicks hatched that fledged. Minimum productivity was the mean number of chicks definitely known to have fledged per breeding pair.

During the study, 181 breeding adults (91 females and 90 males) were individually colourbanded; other breeding birds could often be identified from a combination of location and metal bands applied in another study. Annual adult survival was determined (as Minimum Number Alive from one year to the next) by recording the presence or absence of colour-banded individuals in Auckland-area post-breeding flocks in February or March each year. Some individuals were not seen at these flocks (which together hold about 85%) of the wintering population; Riegen & Dowding 2003); status of these individuals was noted when they returned (or did not return) to breeding sites in August or September. Wrybills display very high fidelity to both breeding site and wintering site (Hay 1984). Adult life-expectancy in years was calculated from annual mortality (m) using the formula (2-m)/2m (Lack 1954).

The intrinsic capacity for increase (*r*) of the wrybill population at each study site was calculated using the Lotka equation (Krebs 1994). Values for adult survival and productivity were from this study. The few data available suggest that first-year survival of wrybills is about 0.50 (Riegen & Dowding 2003). The oldest known wrybills are about 25 years old (A. Riegen, *pers. comm.*), and this was set as the maximum age for breeding. The finite rate of increase/decrease (a measure of potential annual change in the population size) $\lambda = e^r$ (Krebs 1994).

In the first year of the study, visits to the upper Tasman and upper Tekapo sites were infrequent (about once per fortnight), and data were only obtained from the lower Tasman and lower Tekapo. In years 2 and 3, all study areas were larger, more birds were banded, more pairs were monitored, and the frequency of monitoring (once every 2-4 days) was similar across all sites.

Site	Hatched	Flooded	Abandoned	Depredated	Unknown	Totals
Upper Tekapo	25 (65.8%)	4 (10.5%)	1 (2.6%)	8 (21.1%)	0 (0.0%)	38
Lower Tekapo	31 (70.5%)	3 (6.8%)	2 (4.5%)	8 (18.2%)	0 (0.0%)	44
Upper Tasman	22 (47.8%)	2 (4.3%)	4 (8.7%)	16 (34.8%)	2 (4.3%)	46
Lower Tasman	70 (76.1%)	4 (4.3%)	7 (7.6%)	8 (8.7%)	3 (3.3%)	92
All sites	148 (67.3%)	13 (5.9%)	14 (6.4%)	40 (18.2%)	5 (2.3%)	220

Table 1. Hatching success and causes of loss of wrybill nests in the four Mackenzie Basin study sites, 1997–2000.

Nomenclature of birds follows Checklist Committee (2010), and that of mammals follows King (2005).

RESULTS

Breeding success

Over the 3 years of the study, the proportion of nests that hatched varied from 47.8% to 76.1% between sites (Table 1) and was lowest in the upper Tasman. Combining all sites, 13 nests were lost to flooding; 7 of these were lost in a single event in the Tekapo River in Nov 1998, when a high flow of water was deliberately discharged down the river from Lake Tekapo over a period of 5 weeks. In the Tasman River (where flows were not controlled), floods accounted for the loss of only 6 (4.3%) of 138 nests. In all, 14 nests were abandoned, and in 6 of those cases abandonment was accompanied by the permanent disappearance of a colour-banded adult from the pair. Depredation was the largest cause of nest failure, accounting for at least 40 (56%) of the 72 nests that did not hatch. Loss of nests to depredation was highest by far in the upper Tasman (Table 1).

Overall fledging success was similar between years (range 30.4–42.4%) but there were differences between sites. Success was similar in the two Tekapo sites and the lower Tasman but, as for nesting success, was markedly lower in the upper Tasman (Table 2).

Productivity of wrybills was generally consistent between years at each site, but also varied considerably between sites (Table 3). Over all sites and years, productivity averaged 0.49 chicks fledged per pair. However, productivity was particularly low in the upper Tasman site in both years it was measured, and if that site is excluded, productivity in the other three sites averaged 0.61. Combining vears, there were differences between sites in the two rivers in the number of pairs successfully fledging one or more chicks. In the Tekapo, 17 (61%)of 28 pairs were successful in the un-trapped area and 21 (54%) of 39 were successful in the trapped area; this difference was not significant (Fisher's Exact test, P=0.624). In the Tasman, only 5 (11%) of 46 pairs fledged chicks in the un-trapped area and 32 (40%) of 80 pairs fledged chicks in the trapped area; this difference was highly significant (Fisher's Exact test, P=0.0005).

Our data suggest there were more losses at the chick stage than at the egg stage. We tested for a relationship between nesting success and overall breeding success (productivity), using data from the lower Tasman and lower Tekapo in 1997/98 and from all four sites in the 1998/99 and 1999/00 seasons (Fig. 2). There was only a weak correlation (r^2 =0.313, t=1.907, df=8, P=0.093).

Table 2. Wrybill fledging success (number of chicks fledged / number of chicks hatched) in the four Mackenzie Basin study sites, 1997–2000. ND = not determined.

C'1	Fledging success (chicks fledged / chicks hatched)					
Site	1997/98	1998/99	1999/00	Years combined		
Upper Tekapo	ND	8/24 (33.3%)	12/27 (44.4%)	20/51 (39.2%)		
Lower Tekapo	5/10 (50.0%)	9/20 (45.0%)	10/27 (37.0%)	24/57 (42.1%)		
Upper Tasman	ND	3/20 (15.0%)	3/19 (15.8%)	6/39 (15.4%)		
Lower Tasman	9/23 (39.1%)	15/51 (29.4%)	21/47 (44.7%)	45/121 (37.2%)		
All sites	14/33 (42.4%)	35/115 (30.4%)	46/120 (38.3%)	95/268 (35.4%)		

Site				
Site	1997/98	1998/99	1999/00	Years combined
Upper Tekapo (un-trapped)	ND	0.82 (11)	0.71 (17)	0.75 (28)
Lower Tekapo (trapped)	0.63 (8)	0.64 (14)	0.59 (17)	0.62 (39)
Upper Tasman (un-trapped)	ND	0.15 (20)	0.08 (26)	0.11 (46)
Lower Tasman (trapped)	0.60 (15)	0.47 (30)	0.60 (35)	0.55 (80)

Table 3. Productivity (mean number of chicks fledged per pair) of wrybills at the four Mackenzie Basin study sites, 1997–2000. Numbers of pairs monitored at each site in each year are shown in brackets. ND = not determined.



Figure 2. Correlation between productivity (mean number of chicks fledged per breeding pair) and nesting success of wrybills (proportion of nests hatching 1 chick or more) in the upper Tasman (open squares), lower Tasman (filled circles), upper Tekapo (open diamonds), and lower Tekapo (filled triangles), 1997–2000.

Adult survival

Average annual survival rates and estimates of lifeexpectancy of banded adult wrybills in the four study areas over the 3-year period are shown in Table 4. Survival of both males and females was lower in the upper Tasman than in any of the other 3 sites. When banded adults disappeared, the cause of death was normally unknown. However, direct evidence of adult predation came from a subsequent study in the Tasman River in which the remains of 7 colour-banded wrybills from the present study were found in stoat dens (Dowding *et al.* 2015).

Combining seasons, annual survival of females was higher than survival of males at all four sites (Table 4). Overall, annual survival of females (0.818) indicated average life-expectancy of 5.0 years, and annual survival of males (0.710) indicated lifeexpectancy of 3.0 years.

Population trends

At the time of our study, the intrinsic capacity for increase in the two Tekapo sites was similar and suggested a potential decline in that river's local population of about 5% per year. In the upper Tasman, r was strongly negative and in the absence of immigration, suggested an annual decline of about 27.5%. The trapped lower Tasman site was the only population in which r was positive, with a potential annual increase of 3.5% (Table 5).

Table 4. Average annual survival of adult wrybills based on Minimum Number Alive estimates in the four Mackenzie Basin study sites. Figures in brackets are calculated life-expectancy in years. Data from the three seasons (1997/98 – 1999/2000) are combined.

Site	Males	Females	Sexes combined
Upper Tekapo (un-trapped)	0.63 (2.2)	0.80 (4.5)	0.74 (3.3)
Lower Tekapo (trapped)	0.77 (3.9)	0.81 (4.7)	0.79 (4.2)
Upper Tasman (un-trapped)	0.57 (1.8)	0.73 (3.2)	0.65 (2.4)
Lower Tasman (trapped)	0.87 (7.2)	0.92 (12.3)	0.90 (9.1)
All sites combined	0.71	0.82	0.77

Table 5. Capacity for increase (r) and finite rates of increase/decrease (λ) of the wrybill populations in the four Mackenzie Basin study sites, 1997–2000.

Site	r	λ
Upper Tekapo (un-trapped)	-0.0462	0.9549
Lower Tekapo (trapped)	-0.0621	0.9398
Upper Tasman (un-trapped)	-0.3221	0.7246
Lower Tasman (trapped)	0.0343	1.0349

DISCUSSION

Breeding success

Nesting success

The upper Tasman site stands out as having the lowest nesting success (48%) and the highest percent loss to depredation. Nesting success was higher and similar (66–76%) across the other 3 sites. A continuous catchment-wide predator-control programme was initiated in 2004/05 in the Tasman Valley. Nesting success of wrybills was high early in the programme, but subsequently fell and between 2004/05 and 2009/10 varied between 0.50 and 1.00 (Cruz et al. 2013). In the upper Rakaia River in the period 2011/12-2013/14, nesting success varied widely between 26% (when 42% of nests were lost to floods and snow) and 64% (Leseberg 2014). Similarly, in the upper Rangitata River, nesting success was highly variable (26% to 73%) in the period 2013/14–2016/17 (Edwards & Ure 2017).

Fledging success

Fledging success was very similar in the two Tekapo sites and the lower Tasman, but markedly lower in the upper Tasman (Table 2). Between 2004/05 and 2016/17, fledging success of wrybills in the Tasman varied between 14% and 69% (Cleland et al. 2017); all our values also fell within that range (Table 2). In 4 seasons in the upper Rangitata River between 2010/11 and 2016/17, fledging success varied from 19% to 47% (Edwards & Ure 2017). In the case of precocial shorebird species, reasons for chick loss are particularly difficult to determine (e.g. Evans & Pienkowski 1984). In addition to mammalian predators, native avian predators (notably southern black-backed gull Larus dominicanus and swamp harrier *Circus approximans*) are known to pose a threat to chicks of a range of shorebirds in New Zealand (e.g. Dowding & Murphy 2001; McClellan 2008). Both species are numerous in the Mackenzie Basin, and could have been responsible for some wrybill egg or chick losses.

Productivity

There is thus high variability between sites and years in both nesting and fledging success. As a consequence, productivity of wrybills can be very variable. Hay (1984) recorded average productivity of 0.79 (range 0.61-0.95) over 3 seasons in the upper Rakaia River; in the same study area in 1999/2000, productivity was 0.60 (JED, unpubl. data). Hughey (1985) measured productivity in the lower Rakaia River in 1982 and 1983; results were very different between years, with values of 0.09 in 1982 (due to flooding) and 0.57 in 1983. More recently, productivity in the upper Rakaia River over 3 consecutive years was also highly variable, with values of 0.64, 0.18, and 0.04 in 2011, 2012, and 2013 respectively; the very low value in 2013 was a result of repeated floods (Leseberg 2014). In the Tasman River, minimum productivity ranged from 0.21-1.11 between 2004/05 and 2016/17 (Cleland *et al.* 2017). Similarly, in the upper Rangitata River between 2010/11 and 2016/17, productivity varied from 0.21-0.79 (Edwards & Ure 2017).

Differential susceptibility of eggs and chicks

Our study suggests that for wrybills, losses at the chick stage were higher than at the egg stage, and that the correlation between nesting success and productivity was weak. In California, Neuman et al. (2004) noted that management of mammalian predators improved hatching success of snowy plovers (*Charadrius alexandrinus*) but not fledging success. The lack of a strong correlation is not surprising, as different life stages can be affected by different factors. We therefore suggest that nesting success (which is much easier to measure than productivity) should not be used as a proxy for overall breeding success. There are obvious reasons why chicks and eggs may show different levels of susceptibility to various threats. First, they may be vulnerable to different predators; for example, hedgehogs prey on many shorebird nests in the Mackenzie Basin (Sanders & Maloney 2002) but are too slow to catch most shorebird chicks, which are precocial and highly mobile. Because they are mobile, chicks may be more susceptible to avian predators, which hunt largely by sight. In the case of snowy plovers, it was suggested that when mammalian predators were managed, subsequent decreased fledging success was probably caused by avian predators (Neuman et al. 2004). Being mobile and able to swim well, wrybill chicks often survive floods that destroy nests. Like most shorebird chicks, wrybills are not fed by their parents, so even short periods of low food availability could adversely affect chick survival, while having little impact on egg survival.

Adult survival

Our estimates of adult survival could have been under-estimates if some birds dispersed to breed in other rivers between years during the study. However, wrybills normally show very high site fidelity (Hay 1984; this study), and we are not aware of any subsequent sightings (at breeding or wintering sites) of any of the colour-banded birds that disappeared during the course of our study. The only other study we are aware of that has reported annual survival of wrybills was that of Hay (1984), who estimated mean adult survival at 0.832 over 3 seasons in the upper Rakaia River. In our study, survival of adult male wrybills was lower than survival of adult females (Table 4). This is similar to the situation with southern New Zealand dotterels (Charadrius o. obscurus), where males had lower survival, probably because they (like male wrybills) undertake most of the incubation and brood-rearing duties at night, when many of the mammalian predators are most active (Dowding & Murphy 2001).

We note that even apparently modest differences in adult survival may result in substantial differences in adult life-expectancy. At the time of our study for example, life-expectancy of females in the upper Tasman site was 3.2 years, compared to 12.3 years in the lower Tasman (Table 4). Such differences can clearly have a large impact on lifetime reproductive output.

Effectiveness of mammalian predator control

Overall, values of hatching success, fledging success, productivity, and adult survival in the two study sites in the Tekapo River were similar, suggesting that mammalian predator control had little effect there. In the Tasman River, however, there were significant differences in those measures between the two sites and predator control appeared to be highly beneficial for wrybills.

The study areas in the Tasman and Tekapo Rivers were originally chosen as replicates, but trapping data subsequently suggested there were differences in the abundance of some predators between the rivers. Trap-catch results from the 3 years (data from Cook & Maloney 1999, Cook et al. 2000, and Keedwell & Brown 2001) are summarised in Table 6. It is not possible to compare results between years (there were considerable annual differences in trap types and numbers), but comparisons between the 2 rivers within years are valid (trapping regimes were the same in both rivers in each year). Stoat captures were higher in the Tasman than in the Tekapo in all years. Cat captures were broadly similar between the rivers in years 1 and 2 but were higher in the Tasman in year 3. There were no consistent differences between the rivers in catch rates of ferrets, hedgehogs, or rats.

Predation pressure from stoats (in all years) and cats (in year 3) may therefore have been higher in the Tasman, and this may be one reason why there was such poor survival and productivity of wrybills in the un-trapped upper Tasman site. The suggestion that stoats may have been having an impact on wrybills in the Tasman is supported by a study of stoat diet there undertaken immediately following this study (Dowding et al. 2015). Over a two-year period, 17 (7.8%) of 219 stoat dens excavated contained wrybill remains. The 24 adult wrybills found in those dens accounted for about 20% of the adult wrybill population in the river at that time, and because not all stoat dens would have been found, the figures will be underestimates. Dowding et al. (2015) concluded that stoats were likely to be having a significant impact on local populations of wrybills (and banded dotterels) at that time.

There has been discussion about the effectiveness of the Mackenzie Basin trapping programme, with suggestions that the benefits to black stilts were not clear (Keedwell *et al.* 2002b), and that an effect on nesting success of banded

Table 6. Captures per 100 trap-nights of 5 predator species in the Tasman (TAS) and Tekapo (TEK) Rivers, summarised from Cook & Maloney (1999), Cook *et al.* (2000), and Keedwell & Brown (2001). The trapping regime varied between years but was the same in both rivers within each year.

	1997/98		199	1998/99		1999/00	
	TAS	TEK	TAS	TEK	TAS	TEK	
Cat	0.207	0.188	0.190	0.100	0.245	0.063	
Ferret	0.414	0.241	0.150	0.270	0.135	0.268	
Hedgehog	1.036	0.786	1.343	0.577	0.955	0.952	
Stoat	0.414	0.004	0.110	0.013	0.037	0.007	
Rat	0.245	0.092	0.020	0.113	0.049	0.042	

dotterels was equivocal (Norbury & Heyward 2008). Wrybills in the upper Tasman site had by far the lowest productivity and adult survival of the four sites in both years they were monitored. The large differences in demographics between the upper and lower Tasman sites (which were only 3.5 km apart at the closest point) suggest that predator control was beneficial for wrybills in that river, and supports the suggestion that predation was at least partly responsible for the low productivity and survival in the upper Tasman. However, the main effect of control may have been to increase adult survival; survival of both males and females was highest in the trapped lower Tasman site (Table 4), yet productivity there did not exceed 0.60 in any year, which was lower than in either of the Tekapo River sites in any year (Table 3). Following our study, productivity was measured in the Tasman River (lower and upper sites combined) in 2002/03, when 0.88 chicks fledged per pair in the absence of predator control (JED & MJE, unpubl. data), but after stoat density in the valley had fallen markedly (Dowding 2004).

The year-round, catchment-wide trapping programme in the Tasman Valley that began in 2004/05 appears to have had little positive impact on wrybill breeding success. Hatching success improved early in the programme (but then declined), and fledging success was similar to that in our study (Cruz *et al.* 2013). Adult survival was not reported by Cruz *et al.* (2013), and the overall impact of the programme on the wrybill population in the river at that time is therefore not clear.

Our observations in the Tasman River may have resulted from a localised effect caused by a temporary rise in stoat density. This suggestion is supported by the finding that when stoat density in the valley fell substantially in 2002 (Dowding 2004), productivity rose to a higher level than at any time in our study. However, it is also possible that predator densities in the Mackenzie Basin have been changing periodically in response to changes in prey availability for many years. Rabbits (Oryctolagus cuniculus) are a staple in the diet of cats, ferrets, and stoats in the Basin, and it has been suggested that large changes in rabbit densities (brought about by trapping, poisoning, and rabbit haemorrhagic disease), have resulted in periodic shifts in predator diet, leading to more birds being eaten (Pierce 1987; Parkes et al. 2002; Murphy et al. 2004).

Outlook for the wrybill population

There can be very large differences in demographic parameters (notably productivity) of wrybills between sites and years. Studies undertaken at one location only, or at several locations in one season only, are therefore almost certain to be inadequate for accurate prediction of overall trends in the whole population. We also note that while productivity commonly measured during management programmes, adult survival is measured less often. Our finding that trapping increased survival but not productivity of wrybills in the lower Tasman site suggests that measuring productivity alone may provide only a partial indication of the effectiveness of management. Like other New Zealand plovers, wrybills are long-lived (Davies 1997). In longlived species, values of *r* are particularly sensitive to changes in adult survival, and measuring adult survival as well as productivity is therefore important (a) to gain a more complete measure of whether predator control is beneficial and (b) to assess population trends.

Our data suggest that at the time of our study, the capacity for increase was negative in three of the four wrybill populations we monitored. In the absence of immigration, they would therefore have been in decline, at least in the short term. Based on our results and the diet study of Dowding et al. (2015), we suggest that in the Tasman River, predators (and probably stoats in particular), were having substantial local impacts on breeding wrybills during our study. Whether this situation is widespread or occurs regularly in some rivers remains to be seen. Nationally, wrybill numbers are thought to be declining slowly (Riegen & Dowding 2003) and it seems likely that if the very low survival and productivity values we recorded in the upper Tasman during this study were repeated elsewhere in the species' range on a regular basis, the entire population would be in more obvious and rapid decline.

Many factors can potentially affect wrybill breeding success, including floods and low flows in rivers, adverse weather, changes in food availability, disturbance, predation by mammals, and predation by avian predators. Low breeding success may not always be a result of mammalian predation (flooding alone can result in almost total breeding failure for a season in a river, for example), and predator control may therefore not always be beneficial. Trapping was beneficial during our study, but only in one of the two rivers. Our understanding of the factors governing the distribution of mammalian predators in braided river systems, and of the reasons behind temporal changes in predator density that may occur in those systems, is limited. In addition, the response of different bird species to mammalian predator control may differ (e.g. Cruz et al. 2013), and the relative importance of avian and mammalian predation may vary between sites and years. Further research is required to refine management protocols for braided river bird species and to decide where, when, and on what scale management should be undertaken to halt or reverse declines in range and numbers.

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