Survival of breeding Finsch's oystercatchers (*Haematopus finschi*) on farmland in Canterbury, New Zealand

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Abstract We investigated the annual survival of Finsch's oystercatchers (*Haematopus finschi*) breeding on farmland in mid-Canterbury, New Zealand. Annual survival from 1987 to 2000 averaged 0.892, with evidence of a small amount of variation in survival rates through time (estimated SD = 0.034). We found no indication that survival rates differed between males and females. However, recapture probabilities showed that males had stronger fidelity to breeding territories than did females. These results are similar to those reported from populations of *H. ostralegus* in Europe. Because oystercatchers are long-lived, the survival rate of adults is the key component in determining population size. Intensification of agriculture on the breeding grounds and disruption to coastal feeding grounds may reverse the trend for population increase in this species. Consequently, the survival rate presented here provides a basis for predicting future population trends.

INTRODUCTION

The endemic avifauna of New Zealand has undergone major change in the past 2000 years, with 76 of the 245 breeding species present when humans colonised now locally or globally extinct (Holdaway *et al.* 2001). Losses amongst endemic species are even greater, with at least 41% becoming extinct, solely as a result of introduced predators, including humans (Holdaway 1999; Holdaway *et al.* 2001). Of 10 extant species of endemic waders in New Zealand considered by Dowding & Murphy (2001) in a review of the impact of predation, only 3 are still relatively numerous, widespread, or both. The South Island pied oystercatcher (hereafter referred to as Finsch's oystercatcher to distinguish it from other pied forms of oystercatcher found elsewhere) *Haematopus finschi* is the most numerous and widespread of the endemic waders in New Zealand (Sagar *et al.* 1999). Note that we recognise *H. finschi* as being specifically distinct from *H. ostralegus*, thus following the original description by Martens (Oliver 1955) and more recently by Marchant & Higgins (1993) and Holdaway *et al.* (2001), *contra* Turbott (1990).

Numbers of Finsch's oystercatchers declined during the period 1870 to 1940, but this trend was reversed following the prohibition of shooting (Sibson 1966). Although Finsch's oystercatchers traditionally bred inland on gravel riverbeds of the South Island (Oliver 1955), since about 1950 they have begun breeding on agricultural land and grasslands (Turbott 1969; Baker 1974a). Morgan (2001) showed that pairs breeding on farmland had higher breeding success than those breeding on gravel-bed rivers, therefore, this is one species that has benefited from the conversion to agricultural land. With numbers rising from an estimated 49,000 in 1970-71 (Baker 1973) to an estimated

112,000 in the period 1984-1994 (Sagar *et al.* 1999), expansion of the breeding range and higher breeding success are both likely to have contributed to the population increase.

Rate of survival is a necessary component of models that examine the causes of changes in the size of bird populations (Newton 1998). Survival data from Europe (Schnakenwinkel 1970; Safriel *et al.* 1984) show that oystercatchers are long-lived, and so adult survivorship is a key feature influencing the population size of the species (Clutton-Brock 1988; Finch 1990). To develop a population model that assesses the overall effect of human-induced mortality of oystercatcher populations, it is first necessary to determine the survival rate of adults and the nature and extent of its annual variation. However, we know of no other estimate of the survival rate of adult Finsch's oystercatchers.

We studied birds breeding on farmland in mid-Canterbury, New Zealand. The main aims of our study were to: (1) determine adult survival rates from 1987 to 2000; (2) determine whether there was any change in survival over time; (3) compare male and female survival rates; and (4) identify any causes for possible sex- or time-related changes in survival rate.

METHODS

Field observations

We banded and recaptured Finsch's oystercatchers during the period 1 August to 30 November each year from 1987 to 2000 in farmland of the Valetta and Mayfield areas (44°45'S, 171°30'E) of mid-Canterbury. Breeding birds were caught using a drop trap, which the birds activated when they returned to their nests to incubate (Mills & Ryder 1979). Each bird was sexed by bill measurements (Baker 1974b) and was fitted with a unique colour band combination before being released. After the first 2 years at least 95% of the breeding birds in the study area were banded; subsequently, most new birds entering the population were captured and banded. In addition, where loss of colour bands was detected, birds were recaptured and fitted with their original colour band combination. In no instance was a metal band known to have been lost, and so the few individuals that lost colour bands could always be identified when recaptured.

Nests were found each breeding season and the identity of the parents recorded. In addition, territorial pairs with no nest were also recorded each year, as were colour-banded birds that joined a flock of non-breeders within the study area. After breeding, all oystercatchers dispersed from the study area to coastal sites to which individuals showed extreme fidelity year after year (Sagar & Geddes 1999). During the period December 1987 to December 2000, we received 373 reports of 56 individuals at coastal sites; these data are included in the following analysis. In addition, all 25 banded birds found dead, either in the study area or elsewhere, were included in the analysis.

In any study of survival where observations of colour-banded birds are used, there will be problems when colours of bands are confused, combinations on left and right legs are reversed, and birds lose bands. The error rate introduced by such reports is difficult to determine. However, many Finsch's oystercatchers returned to the same coastal sites year after year and remained at those sites for several months (Sagar & Geddes 1999), and so within and between years most were reported by more than 1 observer which allowed for cross-checking of potential reporting errors. We examined the reports of birds from coastal areas and excluded 1 bird from the dataset when the colour combination reported corresponded to a bird that was known to be dead.

Analysis

A joint analysis of recapture, resighting and dead recovery data was carried out using the model of Barker (1997) and using the computer program MARK (White & Burnham 1999). Sightings of colour-banded oystercatchers during the breeding season (1 August to 30 November) each year were treated as recaptures and reports of birds seen outside the breeding season were considered resightings. Dead recoveries from the entire year were considered together.

The notation used and parameters investigated in this analysis were as follows:

S_i = Probability a bird alive at i is alive at $i+1$;

p_i = Probability a bird at risk of capture at i is captured at i;

r_i = Probability a bird that dies between i and $i+1$ is found dead and the band reported;

R_i = Probability that a bird that survives from i to $i+1$ is resighted (alive) sometime between i and $i+1$;

R'_i = Probability a bird that dies between i and $i+1$ without being found dead is resighted alive sometime between i and $i+1$ before it died.

F_i = Probability a bird at risk of capture at i is at risk of capture at $i+1$;

F'_i = Probability a bird not at risk of capture at i is at risk of capture at $i+1$.

Model selection

Models were selected using a small-sample version of Akaikie's Information Criterion (AIC$_c$) (Burnham & Anderson 1998), in which the best approximating model has the lowest AIC$_c$. Because AIC$_c$ is measured on a relative scale we report ΔAIC$_c$, the difference between AIC$_c$ for each model

and that for the model with the smallest observed AIC_c from the set of models considered. Burnham & Anderson (1998) suggested as an approximate guide that models with $\Delta AIC_c \leq 2$ are considered to have substantial support, provided that there is no evidence of lack-of-fit of the global model in the set considered, and should be used for making inferences. Models having ΔAIC_c of about 4 to 7 have considerably less support, and models with $\Delta AIC_c > 10$ are taken to have no support. In addition, we calculated the $QAIC_c$ weight (w_i) for each model according to the Burnham & Anderson (1998) procedure, which provides an indication of the weight of evidence in favour of a given model. The weights for all models sum to 1, and so provide relative weights for each model considered.

The analysis began with a fully sex- and time-dependent model, and then the models selected from a set of models constructed by introducing various constraints on the parameters in this most general model. We expected resighting effort to have varied through time as it depends on the number of observers active each year, but did not expect resighting probabilities to depend on the sex of the bird. The latter expectation was based on the fact that although the sexes were differentiated on beak size, which may indicate that they fed in or frequented different habitats within estuaries, most sightings of colour-banded birds were made at high-tide roosts. Therefore, we screened for sex- and time-effects on the survival probabilities and movement probabilities by considering a set of 16 models that all had time- but no sex-variation in resighting probabilities. The 16 models were generated by considering all combinations of constant, sex-dependent, time-dependent, or sex- and time-dependent survival with constant, sex-dependent, time-dependent, or sex- and time-dependent movement probabilities.

Standard procedures were used to estimate confidence intervals, except a parameter estimate on the boundary of the parameter space and for which a profile likelihood confidence interval (McCullagh & Nelder 1989) was constructed.

RESULTS
Survival rates and resighting probabilites
From 1987 to 1999, we banded 217 different breeding Finsch's oystercatchers (97 ♂♂, 120 ♀♀) in the study area. The numbers of birds banded and recaptured each year are summarised in Table 1.

Model fitting results (Table 2) indicated strong support for the model $S\,p_t r_t R_t\,R'_t F_{sex} F'_{sex}$, indicating that there was little difference in the survival rates of males and females, but that their movements differed. There also appeared to be some support for the model $S_{sex} p_t r_t R_t R'_t F_{sex} F'_{sex}$ which indicated little

evidence of differences in the survival rates of males and females, but this model has almost the same deviance as the previous model without a sex-effect on survival. Further testing using a likelihood ratio (χ^2) indicated that there was no evidence for a sex-effect on survival ($\chi_1^2 = 0.348$, $P = 0.55$). These top 2 models had very high AIC_c weights, with a combined weight of 0.988 indicating strong support for a model with a sex effect on the movement parameters and little time (year to year) variation in survival probabilities. However, the likelihood test comparing $S\,p_t r_t R_t R'_t F_{sex} F'_{sex}$ with $S_t p_t r_t R_t R'_t F_{sex} F'_{sex}$ ($\chi_{12}^2 = 16.289$, $P = 0.18$) suggested that a model with time-varying survival probabilities was worth considering. We suggest that the discrepancy between model selection using AIC_c and likelihood ratio tests indicated that time-variation may have been present, but that 12 additional parameters were too many to express this variation.

An intermediate model of potential value was a random-effects model where the true year-specific survival probabilities are a random sample from some distribution with a few (<13) parameters. The model we considered was $S_i = \Psi + \mathcal{E}_i$ where Ψ is the average survival rate during the study and $\mathcal{E}_i$ represents random error. Recomputing Akaike weights for this model and the models $S.p_t r_t R_t R'_t F_{sex} F'_{sex}$ and $S_t p_t r_t R_t R'_t F_{sex} F'_{sex}$, this model received some support ($w_i = 0.361$) and model $S.p_t r_t R_t R'_t F_{sex} F'_{sex}$ and the random effects model had a combined Akaike weight of 0.999. Therefore, model selection indicates that there is probably some annual variation in survival probabilities, but that this variation is small. From the random effects model we obtained an estimate of average annual survival of $\hat{\Psi} = 0.898$ (SE = 0.014) with an estimate of the standard deviation of e_i of 0.034 (95% CI = 0.000 to 0.074). In comparison, for the model assuming constant survival we obtained the estimate $S = 0.886$ (Table 3). In the constant survival model the probability of recapture (p) was consistently high for all years (Table 3). However, the probability that a banded bird was found dead and the band recovered (r) was low and varied considerably between years. Generally, the estimated proportion of birds known to be alive and reported at coastal sites (R) was low, ranging from 1.3% to 28.3% of the birds known to be alive, but varied little from year to year (Table 3). The probability that a bird died between years and was seen at a coastal site in the year that it is assumed to have died (R') varied widely (0.000-0.443).

Estimates of the movement parameters (F, F') indicated that males returned to the same breeding area year after year. However, this behaviour was less pronounced in females. Under the model $S.p_t r_t R_t R'_t F_{sex} F'_{sex}$, the estimated probability that a male oystercatcher that was at risk of capture at time i was also at risk of capture at time $i+1$ was

Table 1 Capture-recapture data for breeding Finsch's oystercatchers (Haematopus finschi) , 1987 to 2000.

Year	No. banded	Year of recapture													Not recaptured
		1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	
Adult males															
1987	15	12	12	8	9	7	6	6	6	5	4	3	3	3	2
1988	19	-	16	14	14	14	14	11	10	8	7	5	5	4	1
1989	6	-	-	4	4	4	4	3	4	3	2	2	0	0	2
1990	6	-	-	-	6	4	4	3	3	2	0	1	1	0	0
1991	4	-	-	-	-	4	3	3	2	2	2	2	2	1	0
1992	6	-	-	-	-	-	4	4	4	4	2	2	1	2	1
1993	7	-	-	-	-	-	-	6	4	4	4	4	4	3	3	1
1994	7	-	-	-	-	-	-	-	7	5	5	3	3	2	0
1995	4	-	-	-	-	-	-	-	-	3	3	3	3	2	1
1996	5	-	-	-	-	-	-	-	-	-	4	3	2	2	0
1997	5	-	-	-	-	-	-	-	-	-	-	2	2	2	3
1998	4	-	-	-	-	-	-	-	-	-	-	-	3	0	1
1999	9	-	-	-	-	-	-	-	-	-	-	-	-	6	3
Adult females															
1987	18	13	11	10	9	8	8	7	7	6	5	5	5	4	4
1988	20	-	16	13	11	10	7	7	7	5	5	3	2	2	3
1989	9	-	-	9	7	7	6	5	5	4	3	4	4	2	0
1990	9	-	-	-	8	5	6	6	5	3	2	2	0	0	0
1991	7	-	-	-	-	4	4	5	4	3	2	2	1	0	1
1992	7	-	-	-	-⟩	-	7	5	3	2	3	1	1	1	0
1993	7	-	-	-	-	-	-	6	5	6	4	3	4	2	0
1994	8	-	-	-	-	-	-	-	5	4	4	4	2	3	2
1995	6	-	-	-	-	-	-	-	-	4	4	3	3	3	0
1996	10	-	-	-	-	-	-	-	-	-	6	6	2	3	3
1997	10	-	-	-	-	-	-	-	-	-	-	5	6	4	4
1998	4	-	-	-	-	-	-	-	-	-	-	-	3	0	1
1999	5	-	-	-	-	-	-	-	-	-	-	-	-	3	2

Table 2 Summary of the best 5 models fitted to resighting data from Finsch's oystercatchers (*Haematopus finschi*) banded in mid Canterbury, New Zealand, between 1987 and 1999. These models represent various restrictions on the a fully sex- and time-dependent model for jointly analysing live recapture, live resighting and dead recovery data. w_i, the weight of evidence in favour of a given model, calculated according to Burnham & Anderson's (1998) procedure. S, annual survival; p, probability of recapture; r, probability that a bird dies and the band is reported; R, probability that a bird is resighted; R', probability that a bird dies without being found dead and is resighted before it dies; F, probability that a bird at risk of capture is at risk of capture in the following year; F', probability that a bird not a risk of capture in a year is at risk of capture the following year.

Model	AIC_c	ΔAIC_c	w_i	No. parameters	Deviance
$S.p_tr_tR_tR'_tF_{sex}F'_{sex}$	2503.100	0.000	0.709	59	2376.817
$S_{sex}p_tr_tR_tR'_tF_{sex}F'_{sex}$	2504.967	1.867	0.279	60	2376.469
$S_tp_tr_tR_tR'_tF_{sex}F'_{sex}$	2511.388	8.287	0.011	71	2360.528
$S_{sex}p_tr_tR_tR'_tF.F'$	2518.790	15.690	0.000	59	2394.718
$S.p_tr_tR_tR'_tF.F'$.	2521.754	18.653	0.000	58	2399.889

Table 3 Parameter estimates of Finsch's oystercatchers (*Haematopus finschi*) under the model $S.p_tr_tR_tR'_tF_{sex}F'_{sex}$. S, average annual survival; p, probability of recapture; r, probability that a bird dies and the band is reported; R, probability that a bird is resighted; R', probability that a bird dies without being found dead and is resighted before it dies; F, probability that a bird at risk of capture is at risk of capture in the following year; F', probability that a bird not a risk of capture one year is at risk of capture the following year. Note that where the estimate is 0.000, the point estimate is valid, but not the SE.

Year/sex	Parameter	Estimate	SE	95%CI Lower	95%CI Upper
1987-2000	1:S	0.886	0.011	0.862	0.905
1987-88	2:p	0.946	0.050	0.718	0.992
1988-89	3:p	0.950	0.031	0.840	0.986
1989-90	4:p	0.968	0.027	0.844	0.994
1990-91	5:p	1.000	0.000	1.000	1.000
1991-92	6:p	1.000	0.000	1.000	1.000
1992-93	7:p	0.976	0.021	0.875	0.996
1993-94	8:p	0.984	0.016	0.897	0.998
1994-95	9:p	1.000	0.000	1.000	1.000
1995-96	10:p	0.970	0.026	0.853	0.994
1996-97	11:p	0.935	0.035	0.824	0.978
1997-98	12:p	0.929	0.038	0.810	0.976
1998-99	13:p	0.944	0.041	0.788	0.987
1999-2000	14:p	0.766	0.066	0.614	0.871
1987	15:r	0.446	0.244	0.104	0.848
1988	16:r	0.589	0.215	0.200	0.891
1989	17:r	0.084	0.081	0.011	0.418
1990	18:r	0.210	0.195	0.026	0.726
1991	19:r	0.000	0.000	0.000	0.000
1992	20:r	0.333	0.202	0.078	0.748
1993	21:r	0.383	0.129	0.176	0.644
1994	22:r	0.000	0.000	0.000	0.000
1995	23:r	0.000	0.000	0.000	0.000
1996	24:r	0.356	0.154	0.129	0.675
1997	25:r	0.251	0.115	0.092	0.527
1998	26:r	0.000	0.000	0.000	0.000
1999	27:r	0.097	0.097	0.012	0.482
2000	28:r	0.000	0.000	0.000	0.000
1987	29:R	0.000	0.000	0.000	0.000
1988	30:R	0.036	0.025	0.009	0.134
1989	31:R	0.144	0.044	0.077	0.254
1990	32:R	0.129	0.040	0.069	0.230
1991	33:R	0.256	0.049	0.171	0.364
1992	34:R	0.073	0.029	0.033	0.153
1993	35:R	0.232	0.047	0.153	0.335
1994	36:R	0.283	0.048	0.198	0.386
1995	37:R	0.191	0.043	0.120	0.290
1996	38:R	0.221	0.045	0.145	0.322
1997	39:R	0.183	0.043	0.113	0.283
1998	40:R	0.119	0.036	0.065	0.208
1999	41:R	0.088	0.037	0.038	0.191
2000	42:R	0.013	3.010	0.000	1.000
1987	43:R'	0.000	0.000	0.000	0.000
1988	44:R'	0.280	0.320	0.017	0.897
1989	45:R'	0.165	0.119	0.035	0.517
1990	46:R'	0.116	0.247	0.001	0.936
1991	47:R'	0.000	0.000	0.000	0.000
1992	48:R'	0.443	0.282	0.078	0.882
1993	49:R'	0.379	0.171	0.128	0.717
1994	50:R'	0.000	0.000	0.000	0.000
1995	51:R'	0.206	0.126	0.054	0.541
1996	52:R'	0.291	0.219	0.049	0.767
1997	53:R'	0.226	0.155	0.049	0.623
1998	54:R'	0.000	0.000	0.000	0.000
1999	55:R'	0.241	0.244	0.023	0.812
2000	56:R'	0.960	23.287	0.000	1.000
Male 1987-2000	57:F	0.982	0.009	0.950	0.994
Female 1987-2000	58:F	0.905	0.017	0.866	0.934
Male 1987-2000	59:F'	0.000	0.000	0.000	0.000
Female 1987-2000	60:F'	0.222	0.063	0.122	0.370

$F = 0.982$ and for females it was $F = 0.905$ (Table 3). For a male that was not at risk of capture in year i, the probability that it was at risk of capture at time $i+1$ was estimated to be $F' < 0.000$; for females the corresponding estimate was $F' < 0.222$ (Table 3). Thus, males are more likely to be recaptured in the breeding area year after year and if they are not recaptured in any year then it is unlikely that they will be recaptured subsequently. Our data contained little information on return probabilities of males except that they appear to be $< c.30\%$. For females there was evidence of more movement away from the breeding territories and a moderately high probability (95% CI = 0.122, 0.370) that a bird not at risk of capture in year i is at risk of capture the following year.

Causes of death

Of the 217 breeding birds banded during this study, 163 were not recaptured during 2000 (Table 1). Of these 163 birds, 25 had been subsequently recovered dead — 24 (14.7%, 12 ♂♂, 12 ♀♀) within the breeding area and 1♀ at a coastal site. Given New Zealand's extensive coastline and its relatively small human population it is not surprising that so few birds were reported dead outside the breeding season. Within the breeding area, 10 of the recovered birds were killed on the road by vehicles, 3 died as a result of injuries sustained probably by flying into fence wires, 2 were killed by predators, 1 was probably shot, and 8 died from unknown causes. All of the road-kills were during the chick-rearing stage, when family groups walked between suitable damp areas to feed, and often crossed roads or fed on roadside verges. Of the birds that probably died as a result of flying into fence wires, one was found dead caught in barbed wire, another had 2 broken legs, and another had a broken wing. We observed territorial disputes between oystercatchers, when the birds flew low and fast, often just avoiding fence wires. We assume that the 3 birds reported here hit the fence wires, and sustained fatal injuries.

DISCUSSION

In this study we have shown constantly high survival of Finsch's oystercatchers over a 13-year period, with no discernible difference in survival between males and females, among Finsch's oystercatchers breeding on farmland in mid-Canterbury. This study of oystercatcher survival took into account variable probability that a bird would be resighted, and so was able to incorporate instances where particular birds were not recorded in any year. Our analyses strongly supported the random effects and constant survival models, and so we preferred to average the estimates of annual survival from these models. Our estimated annual survival rate averaged 0.892 a not unusual level in

waders, where annual survival is typically high (Evans 1991). With an annual adult survival rate of 0.892, a breeding bird would have, on average, a reproductive life-span of 8.75 years (expectation of further life was calculated from $-1/\ln(S)$; Seber 1982), with the oldest birds surviving over 25 years.

Comparison of survival rate with other studies

Results from our study were similar to those reported for European populations of H. ostralegus, including the 0.902 resulting from an analysis of banded oystercatchers breeding on Skokholm, Wales, over a 14-year period (Safriel et al. 1984) and 0.891 for colour-banded oystercatchers overwintering at the Exe Estuary, England, over an 11-year period (Durell et al. 2000). However, it was lower than the 0.919 annual survival over 14 years for oystercatchers breeding on the Isle of May (Harris & Wanless 1997), the 0.937 annual survival for oystercatchers on the Friesian Islands, Germany, over 14 winters (Schnakenwinkel 1970), and the 0.950 annual survival over 10 years of oystercatchers breeding on the island of Schiermonnikoog, the Netherlands (Hulscher 1989).

The reason or reasons for the difference in survival rates between British and New Zealand and European populations of oystercatchers has not been identified. All populations migrate to the coast after breeding, where it is easier for them to be counted. Trends in the total population size of oystercatchers show that in Britain winter numbers increased during the periods of the Skokholm and Exe studies (Goss-Custard et al. 1996), as did numbers in New Zealand (Sagar et al. 1999). However, on continental Europe numbers have fluctuated more widely, with no obvious trend (Goss-Custard et al. 1996). During severe winter weather, oystercatchers of all adges on continental Europe suffered an additional mortality of 0.07-0.15 (Hulscher 1989), something not recorded in British and New Zealand populations (Goss-Custard et al. 1996; this study). Consequently, the apparent higher annual survival rates of oystercatchers in Germany and the Netherlands are probably offset by additional high mortality during severe winters.

In common with other species of waders breeding in temperate latitudes (Evans 1991), mortality of H. ostralegus on the breeding grounds is low, and has been estimated at 0.01 (Safriel et al. 1984; Ens 1992). Our analysis did not partition survival rates of pied oystercatchers breeding in mid-Canterbury between seasons. However, despite intensive searching of the study area, we could account for only about 15% of annual mortality during the breeding season, and so also presume that most birds die outside of the breeding season. In Britain, both Goss-Custard & Durell (1984) and Durell et al. (2000) estimated

winter mortality of the intensively studied population of oystercatchers at the Exe Estuary at 0.032, and so with annual mortality estimated at 0.109 predicted that mortality in spring would be higher than that in winter. The oystercatcher population overwintering in Britain has increased over the past few decades (Goss-Custard *et al.* 1996). Consequently, Durell *et al.* (2000) further hypothesised that increased intraspecific competition on the wintering grounds results in more birds being less fit when they migrate in early spring, and so are more likely to die if they encounter adverse conditions on migration or on arrival on the breeding grounds. This hypothesis was supported by the observations of Lambeck & Wessel (1991, cited in Goss-Custard *et al.* 1995) who found that many dead adult oystercatchers were found in late winter and early spring, during territory establishment and pair formation.

As in our study, Zwarts *et al.* (1996) found that in the Netherlands collisions with traffic and wire fences were the main causes of death of oystercatchers during the breeding season.

Survival rate of male and female oystercatchers
Safriel *et al.* (1984) found no differences between the survival rates of male and female pied oyster-catchers, a result similar to that found in our study. However, we also found that males not seen on the breeding grounds in one season were unlikely to be recorded subsequently. In contrast, females not recorded in a season had a 30% chance of being recorded in later years. We presume that such movements away from a breeding territory occur following the death or divorce of a mate, and so indicate a stronger fidelity to breeding territory by males than females. This was demonstrated by Ens *et al.* (1993) who determined that among European oystercatchers, the probability of changing territory following the death or divorce of a mate was far greater for females than for males. Consequently, it is important to consider such sex-related differences in fidelity to breeding territory when estimating survival rates. For example, during this study we banded more females than males (120/97) and this could have been construed as indicating a greater mortality rate of females than males. However, by including an analysis of movements in our calculations we showed that, in fact, the survival rate of males and females was similar and that the difference in banding totals could be explained by the greater proportion of females moving territory.

Conclusions
In New Zealand, although human influences on pied oystercatchers have probably allowed the population to increase since the 1940s, more recent developments may reverse this trend. Of particular

concern are the effects of changes in land use affecting breeding oystercatchers and increased disturbance and disruption to birds in coastal areas between breeding seasons. For example, in Canterbury, the conversion of sheep to dairy farming reduces the breeding success of Finsch's oystercatchers because cattle trample a greater proportion of nests than do sheep (P.M. Sagar & D. Geddes, unpubl. data). Likewise, for temperate areas of Europe, Evans (1991) identified agricultural changes that lowered the water table, changes in the timing of the use by cattle, and earlier cutting of grass as further threats to the survival of wading birds breeding in wet meadows. Also, in recent years the intertidal area disturbed by the mechanical harvesting of cockles (*Austrovenus stutchburyi*) has increased in Golden and Tasman Bays (Schmechel 2001), which are favoured wintering sites of Finsch's oystercatchers (Sagar *et al.* 1999; Sagar & Geddes 1999). In Europe, this method of harvesting cockles has been shown to decrease the numbers of invertebrate prey available to oystercatchers (Ferns *et al.* 2000), and so potentially reduce the survival rate of the affected birds. Consequently, our calculation of the survival rate of breeding Finsch's oystercatchers during the period 1987-2000 may be used in models that examine the causes of any future changes in the size of the Finsch's oystercatcher population.

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