COLONY SIZE, ADULT SURVIVAL RATES, PRODUCTIVITY AND POPULATION PROJECTIONS OF BLACK-LEGGED KITTIWAKES *RISSA TRIDACTYLA* ON FAIR ISLE

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Rothery P., Harris M.P., Wanless S., & Shaw D.N. 2002. Colony size, adult survival rates, productivity and population projections of Black-legged Kittiwakes *Rissa tridactyla* on Fair Isle. Atlantic Seabirds 4(1): 17-28. *The numbers of Kittiwakes on Fair Isle, Shetland, Scotland declined at a rate of approximately 6% per annum between 1987 and 1999. Breeding success over this period was extremely variable but averaged 0.81 young reared per completed nest. Average annual survival of adults between 1986 and 1996 was 86.0% with no significant annual differences. Survival in 1997 (51.6%) was significantly lower and preliminary estimates for 1998 suggested that survival was again low. Using our empirical data for adult survival and breeding success, we estimated a 20% survival from fledging to recruitment and an age of first breeding of 4-5 years. Incorporating these values into a simple population model indicated that the Fair Isle colony will decline by a further 13-48% over the next three seasons.*

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INTRODUCTION

Black-legged Kittiwakes *Rissa tridactyla* are an important component of the marine avifauna of the North Atlantic and North Pacific. They are small, surface-feeding gulls with high foraging costs and a high risk of predation of unattended eggs and chicks, characteristics that render them particularly sensitive to changes in prey abundance (Monaghan 1996; Furness & Tasker 2000). The Kittiwake has therefore often been used as a bio-indicator to monitor changes in the marine environment. The numbers of Kittiwakes nesting at many colonies in the North Sea have declined substantially over the last 10-15 years. Similar declines have been recorded at colonies in the far north-west of Britain, e.g. Handa and St. Kilda, whereas counts of nests at some colonies on Atlantic and Irish Sea coasts, e.g. Rathlin Island and the Cliffs of Moher, have increased substantially (details in Upton *et al.* 2000). Comparisons of temporal and spatial trends in demographic rates could assist in the diagnosis of the causes of

declines but as yet there are too few published data on the survival of adults to allow this.

Most monitoring studies have concentrated on assessing changes in the size of the breeding population and breeding success (see listings in Upton *et al.* 2000; Byrd *et al.* 2000) but a few have also monitored the survival of adults between breeding seasons (Coulson & Strowger 1999; Danchin & Monnat 1992; Erikstad *et al.* 1998; Poole *et al.* 1998; Harris *et al.* 2000). At colonies where an integrated approach to monitoring has been adopted it is possible to carry out simple population modelling both retrospectively and to provide population projections. In this paper we use this approach for the colony of Kittiwakes on Fair Isle (59°32'N, 1°38'W) at the southern edge of the Shetland Islands where numbers, adult survival and productivity have been monitored annually since 1986 as part of the UK Joint Nature Conservation Committee's Integrated Seabird Monitoring Programme.

METHODS

Breeding population size and breeding success The number of occupied nests in 10 fixed plots dispersed through the colony were counted each year between 1987 and 1999 and the total used as an annual index of population size (JNCC contract reports; Heubeck *et al.* 1999). Complete censuses of all the nests on the island were made in 1988, 1992, 1997 and 2000. In these years, there was a high correlation between the whole-island counts and the plot totals ($r = 0.99$, $P = 0.017$), which suggests that changes in the numbers of nests in these plots were representative of the population as a whole. Data on breeding success (number of young fledged per completed nest) resulted from standardised checks of nests in these study plots throughout each breeding season in 1986 (five of the plots) and between 1987 and 1999 (all 10 plots; details of methodology in Harris 1987). Annual values were the means of the plot means.

Adult survival Starting in 1986, breeding Kittiwakes at South Gunnawark were caught and marked with unique combinations of three colour-rings. A total of 177 individuals were marked, and the average number of colour-ringed birds present in the colony at the end of each season between 1986 and 1990 was 109 (range 72-119). Searches were made for these birds each subsequent year up to 1994 and the data used to calculate annual survival rates between 1986 and 1991. In 1991, the study site was moved to Goorn where access was easier, thereby allowing more frequent checks to be made. A total of 91 birds was marked and the annual average number of colour-ringed birds present at the end of each season was 39 (range 24-48). Thorough searches were made for these

birds each year up to 1999 and these observations were used to calculate survival rates from 1991 to 1997.

Annual survival and resighting probabilities were estimated using the program SURGE 4.2 (Pradel & Lebreton 1993). The analysis cannot separate mortality and permanent emigration. However, Kittiwakes normally exhibit high colony fidelity once they have bred (Aebischer & Coulson 1990; Fairweather & Coulson 1995; Golet *et al.* 1998; but see Danchin & Monnat 1992) and we had no reason to believe that permanent emigration was important in our study.

We followed Lebreton *et al.* (1992) in determining survival rates by fitting models of increasing complexity and using the Akaike Information Criterion for model selection. The goodness-of-fit of the Cormack-Jolly-Seber model with time-dependent survival and resighting probability was examined using TESTS 2 & 3 of the program RELEASE (Burnham *et al.* 1987). However, as the resighting probability was high most of the birds were resighted in the first year after release. In this case the component 3.Sm of TEST 3 and TEST 2 are not informative, and most of the information relating to goodness-of-fit resides in TEST 3.SR (Lebreton *et al.* 1992). The values are as follows: 1986-1992: $\chi^2_3 = 5.39$, $P = 0.15$; 1991-1999: $\chi^2_3 = 5.35$, $P = 0.15$; combined periods: $\chi^2_6 = 10.64$, $P = 0.10$. Thus, there was only weak evidence to suggest that subsequent survival depended on whether the bird had been previously resighted. Furthermore, the high resighting probability suggests that the survival estimates should be robust to heterogeneity in resighting.

During 1986-1991 the most parsimonious model had time-dependent survival of both resighting rates and survival, whereas in 1991-1998, there was again time-dependent resighting rate but a constant survival rate. Likelihood ratio tests were used to calculate the statistical significance of differences between years in survival and resighting probabilities. For convenience, survival between two years is referred to by the former year, i.e. 1995 survival refers to the survival between the 1995 and 1996 breeding seasons.

Population model We used a simple matrix model in which the size of the breeding population in a given year was expressed as the sum of the breeding pairs surviving from the previous year plus the number of recruits. For example, if birds breed for the first time as 4- or 5-year olds (the usual age of first breeding; Porter & Coulson 1987), the model is:

$$N_t = s_{At} N_{t-1} + s_{4t} Y_{t-4} + s_{5t} Y_{t-5}$$

where N_t denotes the number of breeding pairs in year t, Y_t denotes the number of young females fledged, s_{At} is adult survival, and s_{4t} and s_{5t} are the survival

rates from fledge to recruitment into the breeding population as 4- and 5-year olds respectively. The model assumes a 50:50 sex ratio in young and a closed population in which adults breed annually. Average recruitment rates (s_4 and s_5) were estimated by a two-variable linear regression of $N_t - s_A N_{t-1}$ against Y_{t-4} and Y_{t-5}, with no intercept, using the estimated pattern of adult survival and breeding success.

The fit of the model was examined using stepwise and free-running predictions. In the former, population size in a given year is predicted from the observed population size in the previous year. This effectively highlights particular years in which predictions are poor. In the free-running method, population size in a given year is predicted by repeatedly applying the model to the population size at the beginning of the series. This method was used to obtain long-term population projections.

RESULTS

Breeding population size and breeding success The total number of nests in the plots declined by almost 50% from 1 446 in 1987 to 751 in 1999. This represented a significant annual decrease averaging 6% (log-transformed counts, $r = 0.98$, $n = 13$ years, $P < 0.001$) (Fig. 1). Breeding success over the study period averaged 0.81 young per completed nest. However, productivity was extremely variable, ranging from total failure in 1990 to 1.33 in 1999. There was no obvious time trend in this parameter (Fig. 2).

Adult survival The average (± SE) annual survival during the study was 83.2 ± 3.4% (Table 1). There was no statistically significant trend over the period 1986-1996 ($r = 0.40$, $P = 0.26$) but the 1997 survival of 51.6 ± 17.4% was significantly lower than the mean for 1986-1996 (86.0 ± 2.0%; $z = 1.97$, $P = 0.05$). However, the 1997 survival rate was based on only 43 birds and should therefore be treated with caution. The program does not allow the calculation of a survival rate for 1998 but only 13 (54%) of the 24 birds present in 1998 had been resighted by the end of 2000, which suggests that survival had again been low. There was no evidence that overwinter survival was related to breeding success the previous season ($r = 0.09$, $n = 12$ years, ns) but there was a suggestion of a relationship between breeding success and survival over the previous winter such that poor survival was followed by low success ($r = 0.87$, $n = 12$ years, $P = 0.09$).

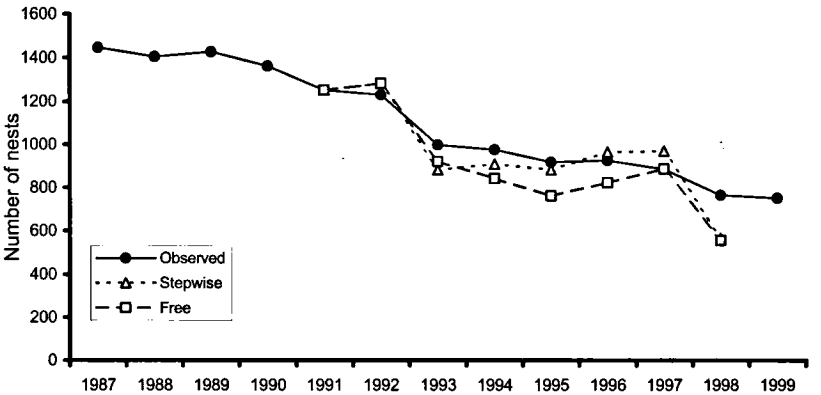

Figure 1. A comparison of the observed numbers of Black-legged Kittiwake nests in study plots on Fair Isle between 1987-1999 (filled circles, solid line) and those predicted using the stepwise method (triangles) and the free-running prediction (squares). Details of the models are given in the text.

Figuur 1. Een vergelijking tussen het waargenomen aantal nesten van Drieteenmeeuwen in studiegebieden op Fair Isle, 1987-1999 (stippen, doorgetrokken lijn) en de voorspelde aantallen volgens de getrapte methode (driehoeken) en de vrije voorspelling (vierkanten). Een beschrijving van de voorspellende modellen wordt in de tekst gegeven.

Population model Average (± SE) recruitment rates were estimated as follows: $s_4 = 0.11 \pm 0.12$, $t_5 = 1.11$, $P = 0.32$, $s_5 = 0.13 \pm 0.11$, $t_5 = 1.11$, $P = 0.32$. Assuming all birds breed for the first time at age 5 years resulted in $s_5 = 0.20 \pm 0.08$, $t_6 = 2.53$, $P = 0.045$. For age 4 years, the corresponding value was $s_4 = 0.18 \pm 0.07$, $t_5 = 2.41$, $P = 0.047$. The overall estimated recruitment rate was about 20% in each case, but the relative proportions of birds breeding for the first time at age 4 and 5 years are estimated rather imprecisely. In a stable population

$$1 - \textit{adult survival} = \textit{breeding success} \times \textit{survival to recruitment} / 2$$

Using our most realistic survival estimate of 0.86 (below) and an average breeding success of 0.81 chicks per pair, survival to recruitment would need to be 0.35 to maintain numbers. The predicted population trend for Fair Isle Kittiwakes using the stepwise method and values of age of first breeding at 5 years and survival from fledging to recruitment at 20%, accorded well with the observed changes in the monitoring plots (Fig. 1). The prediction was poorest in

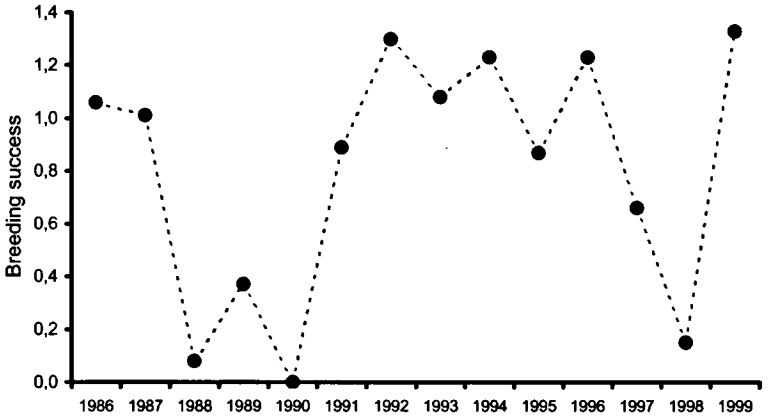

Figure 2. Breeding success (chicks fledged per completed nest) of Black-legged Kittiwakes on Fair Isle, 1986-1999.

Figuur 2. Broedsucces (aantal uitgevlogen jongen per nest) van Drieteenmeeuwen op Fair Isle, 1986-1999.

1998 with the observed population size being markedly higher than that predicted. Very similar results were obtained using the free-running model.

Population projections Fitting the models to the Kittiwake data produced sufficiently realistic estimates of the observed population changes to attempt to use the free-running model to predict population trends over the subsequent five seasons (2000-2004). We ran the model using a range of values for adult survival and recruitment rate (Table 2). With an adult survival rate of 86% (mean during the period 1986-1996, i.e. taking a realistic approach and omitting the low and imprecise estimate for 1997), a 20% survival from fledging to recruitment and age of first breeding of 5 years, the model predicted a population decline of 17% between 1999 and 2004 (Table 2). Substituting an age of first breeding of 4 years and keeping the same adult survival and recruitment rate, a 15% decline between 1999 and 2003 was predicted. We also took a more pessimistic approach and assumed that the recorded decrease in survival at the end of the study was a real effect, and ran the model assuming that survival was 75% (the geometric mean of the last three survival estimates). The corresponding projected declines for a 20% survival from fledging to recruitment and age of first breeding of 5 years and 4 years were 48% and 43% respectively.

Table 1. Estimates of annual survival and resighting probabilities for adult Black-legged Kittiwakes on Fair Isle, 1986-1998. Data were collected at different study sites, 1986-1991, and 1991-1998.

Tabel 1. Schattingen van de jaarlijkse overleving en van de kans op terugmelding voor volwassen Drieteenmeeuwen op Fair Isle, 1986-1998. De gegevens werden in verschillende studiegebieden verzameld: 1986-1991 en 1991-1998.

Period	Year	Survival % (SE)	Resighting % (SE)
1986-1992	1986	93.8 (2.5)	-
	1987	81.9 (3.6)	100 (0.0)
	1988	83.8 (3.7)	96.2 (2.1)
	1989	81.0 (3.6)	89.0 (3.5)
	1990	87.3 (3.3)	96.7 (1.9)
	1991	-	100 (0.0)
1991-1999	1991	90.8 (6.1)	-
	1992	70.8 (9.3)	94.4 (5.4)
	1993	85.9 (5.3)	100 (0)
	1994	90.5 (5.2)	91.7 (4.6)
	1995	93.0 (3.9)	82.1 (6.6)
	1996	87.5 (4.8)	91.3 (4.2)
	1997	51.6 (17.4)	100 (0)
	1998	-	42.2 (16.3)
	mean 1987-1997	83.2 (3.4)	90.3 (4.7)
	mean 1986-1996	86.0 (2.0)	94.7 (1.7)

We were able to make an initial check of the population projections from the model by comparing the plot total recorded in 2000 with the predicted values. A total of 716 nests (4.7% lower than the 1999 count) was recorded for the plots, 5.8% less than the number predicted using an adult survival rate of 0.86 and first breeding at four years (760 nests) and 11.4% more than the predicted value (643) using an adult survival of 0.75 and first breeding at 5 years (Table 2).

DISCUSSION

The average annual survival of Fair Isle Kittiwakes between 1986 and 1996 (86.0%) fell within the range of values reported elsewhere in the east Atlantic, e.g. 80% in north-east England (40 years of data; Coulson & Strowger 1999) and in northern Norway (6 years; Erikstad *et al.* 1998), 81% in Brittany (5 years; Danchin & Monnat 1992), 87% in south Wales (18 years; Poole *et al.* 1998) and 88% in south-east Scotland (11 years; Harris *et al.* 2000). Similarly

Table 2. Black-legged Kittiwake population projections for the monitoring plots on Fair Isle for 2000-2004 using a range of model scenarios. The number of recruits entering the population is based on the numbers of pairs in the plots and their nesting success 4 or 5 years earlier and a 20% survival from fledging to recruitment. The figure in brackets after the total is the geometric rate of change from the previous year.

Tabel 2. Voorspellingen van de populatie Drieteenmeeuwen in de studiegebieden voor de jaren 2000-2004 op basis van verschillende scenario's. Het aantal rekruten in de populatie is gebaseerd op het aantal broedparen in de studiegebieden en hun broedresultaten 4 of 5 jaar eerder, uitgaande van een 20% overlevingskans tussen uitvliegen en terugkeer in de kolonie. Het getal tussen haakjes is de geometrische verandering vergeleken met het voorafgaande jaar.

Adult survival rate	Year	Age of first breeding					
		4 years			5 years		
		Adults	Recruits	Total	Adults	Recruits	Total
86%	1999	-	-	751	-	-	751
	2000	646	114	760 (1.01)	646	80	726 (0.97)
	2001	654	58	712 (0.94)	624	114	738 (1.02)
	2002	612	11	623 (0.88)	635	58	692 (0.94)
	2003	536	99	635 (1.02)	596	11	607 (0.88)
	2004	-	-	-	522	99	621 (1.02)
75%	1999	-	-	751	-	-	751
	2000	563	114	677 (0.90)	563	80	643 (0.86)
	2001	508	58	566 (0.84)	482	114	596 (0.93)
	2002	425	11	436 (0.77)	447	58	505 (0.85)
	2003	327	99	426 (0.98)	379	11	390 (0.77)
	2004	-	-	-	293	99	392 (1.01)

the mean breeding success on Fair Isle (0.81 young per nest) was close to or slightly above that for most British colonies (Walsh *et al.* 1994; Upton *et al.* 2000; Heubeck *et al.* 1999). There was, however, considerable year-to-year variation in the estimates of both adult survival and breeding success on Fair Isle. Our study included the period at the end of the 1980s when breeding success of many Shetland seabirds was severely depressed (Heubeck 1989) and the run of poor breeding years is apparent in the Fair Isle data-set (Fig. 2).

These widespread breeding failures were attributed to poor recruitment of the lesser sandeel *Ammodytes marinus,* the only small shoaling fish available to Kittiwakes and other seabird species breeding in the area (Wright 1996). In accordance with this, there was a positive association between the breeding success of Kittiwakes on Fair Isle and the numbers of sandeels found in fishery

Nesting Black-legged Kittiwakes Nestelende Drieteenmeeuwen (S.C.V. Geelhoed)

tows around Shetland in June in nine years (data for 9 years from ICES 1997, 1998: numbers log-transformed, $r = 0.66$, $P = 0.052$).

Inspection of estimates of adult survival suggested that the largest changes occurred at the end of the study period. Indeed, the value for 1997 was one of the lowest recorded for the species. The available evidence suggests that this was not simply a one-off event since the preliminary estimate for 1998 was also low. Great Skuas *Stercorarius [Catharacta] skua* kill substantial numbers of adult Kittiwakes in Shetland, and in the late 1990s such predation was thought to be having a serious effect on the survival of Kittiwakes (Furness 1997, quoted by Heubeck 2000; Heubeck 2000). Predation of eggs and young and the associated disturbance of colonies could also have contributed to the desertion of some colonies (Hamer *et al* 1991; Heubeck *et al.* 1997).

We have no quantitative information on the effects of skuas on Fair Isle Kittiwakes during the period of our study; although some adults and young were killed on the island, the colonies where adult survival was being monitored were not particularly disturbed. Clearly the continued monitoring of adult survival at this colony is of high conservation priority. In contrast to breeding success, adult survival was not correlated with sandeel numbers during the summer. The only correlation that approached statistical significance (at the 10% level) was

the tendency for poor over-winter survival to be followed by poor breeding success.

Average breeding success at the colony was not unusually low, which suggests that pre-breeding survival rates may have been low and/or chicks from Fair Isle were emigrating to other colonies. At present, there are insufficient data to investigate these two possibilities; many breeding populations in Shetland and Orkney are currently also declining so it is difficult to see where these missing recruits might have gone (Heubeck 2000; Thompson & Walsh 2000). Using the empirical data on adult survival and breeding success, the recruitment rate of Kittiwakes on Fair Isle was estimated to be about 20%. In an earlier study, Porter and Coulson (1987) calculated that about 40% of the chicks produced at a colony in north-east England, over a period when pairs normally fledged at least one chick each season, needed to return to nest to maintain a stable population. Currently a survival to recruitment of about 35% should enable the Kittiwake population on Fair Isle to remain stable; however, it appears to be well below this level. Our predicted population trends accorded well with observed changes in the monitoring plots and hence presumably in the colony. Predictions were markedly poorer in 1998 when the observed population size was substantially higher than predicted. The cause of this divergence appeared to stem from the very low (and imprecise) survival rate estimated for 1997. This further emphasises the need to clarify the later survival estimates.

Monitoring counts on Fair Isle indicate that the colony has been declining by about 6% *per annum* since 1987. Our results suggest that this decline will continue with the projected decrease over the next 3 years varying between 13 and 48% *per annum*. In general, adult survival rates and breeding success have not been particularly low, thus suggesting that poor recruitment was responsible for the decline. Monitoring programmes at many other colonies bordering the west coast of the North Sea have also shown that numbers have declined substantially over the last 10-15 years (Heubeck *et al.* 1999; Upton *et al.* 2000). A full analysis of the available data is now needed to see if these declines also might have been due to poor recruitment.

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KOLONIE-GROOTTE, OVERLEVING, VAN VOLWASSEN VOGELS, PRODUCTIE EN POPULATIEVOORSPELLINGEN VAN DRIETEENMEEUWEN OP FAIR ISLE

Het aantal broedparen van Drieteenmeeuwen op Fair Isle (Shetland Eilanden, Schotland) nam van 1987 tot 1999 af met 6% per jaar. Het broedsucces in deze periode was buitengewoon variabel maar bedroeg gemiddeld 0.81 jongen per afgebouwd nest. De overleving van volwassen vogels in de jaren 1986-1996 bedroeg 86% per jaar, zonder dat er significante verschillen tussen de jaren konden worden gevonden. De overleving in 1997 (51.6%) was echter significant lager en ook de voorlopige schattingen voor 1998 suggereren dat de overleving relatief laag was. Op grond van de in dit artikel gepresenteerde gegevens werd de overleving van jongen (tussen uitvliegen en recrutering in de broedpopulatie op een leeftijd van 4-5 jaar) geschat op 20%. Gebruik makend van een eenvoudig populatiemodel voorspellen de auteurs dat de kolonie op Fair Isle gedurende de komende drie seizoenen met nog eens 13-48% zal afnemen.

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