Survival and dispersal in a newly-founded temperate Barnacle Goose *Branta leucopsis* population

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Abstract

Survival rates and dispersal were studied in a newly-founded temperate Barnacle Goose *Branta leucopsis* population in the Netherlands using marked individuals. Birds were ringed at three localities: two in the Delta area in the southwest of the Netherlands and one in Fryslân in the north. Annual survival decreased during 2004–2012 from *c.* 95% to *c.* 75%, probably due to an increase in hunting pressure introduced to reduce the size of the population and its damage to agricultural crops. A decrease in survival should lead to a decline in numbers in the population, but this was not apparent from the summer counts. Natal dispersal was high: 56% of males attempted to breed > 10 km from their natal site, and 38% at > 100 km from their natal area. In females, these figures were 30% and 24%, respectively. A substantial number of male Barnacle Geese most probably emigrate to the large population that breeds along the shores of the Barents Sea, and the Dutch Barnacle Goose population currently is a source, from which restocking of the Barent's Sea population takes place. Breeding dispersal was low. Disturbance of colonies may influence dispersal as birds from one colony disturbed by foxes showed remarkably high natal and breeding dispersal.

Key words: annual survival, Barnacle Geese, breeding dispersal, hunting pressure, natal dispersal.

Survival and dispersal are key processes in animal populations that affect the rate at which populations change numerically and spatially, and the amount of genetic exchange between populations. A good understanding of these processes is of particular relevance in expanding or newly-founded populations of species, such as geese, where human-wildlife conflicts or other management issues might arise. These processes are difficult to study because this requires following many individuals over long periods of time and over a large area. The study of survival is possible within the capture-recapture framework, where the probability of survival can be estimated separately from the probability of re-sighting in series of repeated observations of individuals (Lebreton *et al.* 1992; White & Burnham 1999). However, survival studies are particularly sensitive to biases in re-sighting probabilities. For example, survival estimates from pure re-sighting studies may be substantially negatively biased because of permanent emigration of individuals outside the study area. Using both capture–recapture and mark–recovery data in the same multi-state models allows a more efficient use of all available data and reduces this bias (Duriez *et al.* 2009; le Gouar *et al.* 2011).

Dispersal is often difficult to study because dispersing individuals potentially can settle anywhere outside the study area where suitable habitat exists (van Noordwijk 1995). Most dispersal studies therefore focus on local movements between study plots, and ignore longer distance dispersal. Colonial-breeding birds such as Barnacle Geese *Branta leucopsis* are highly suitable for the study of dispersal, because their colonies are discrete, often conspicuous, and comparatively easy to monitor, so dispersers can be clearly identified (Pradel 1996). Another way of quantifying dispersal in colonial birds is to assume, for individuals known to be alive and at breeding age, yet known not to be in a colony in the study area, that those birds have dispersed (van der Jeugd 2001).

Here we study survival and dispersal in a recently-established temperate Barnacle Goose population, which breeds in the southwest of the Netherlands. Reliable estimates of important population parameters and their variation are needed to predict the future development of this population, to explore the potential effects of various management scenarios, and to evaluate the effects of measures that are taken to mitigate conflicts. The Barnacle Goose has long been considered a high-Arctic breeding species, benefiting from the short but productive Arctic summer at the cost of a long migration and potentially severe environmental conditions encountered particularly at the start and end of the breeding season. However, during the last decades, it has rapidly adapted to a wide range of habitats in the temperate zone, thereby considerably shortening the migration route, or even giving up migration altogether (van der Jeugd *et al.* 2009).

Methods

Ringing, resighting and recovery data

Ringing and ring re-sightings data for 804 Barnacle Geese caught and colour-marked as breeding birds in the Netherlands from 2004–2010 inclusive were used in the analyses. Birds were rounded up during the annual moult in July at Hellegatsplaten (at the east end of Goeree-Overflakkee Island, Delta area; 51°42'N, 4°22'E) in 2004 and 2005, at Krammerse Slikken (in the southeast of Goeree-Overflakkee Island, Delta area; 51°40'N, 4°14'E) in 2007, 2008 and 2010 and at Jan Durkspolder (Alde Feanen, Fryslân; 53°07'N, 5°57'E) in 2009. In total, 804 individuals were colour-ringed (Table 1). Most of the birds were ringed in the northern part of the Dutch delta area, where most of the colonies of Barnacle Geese breeding in the Netherlands are

Table 1. Number of birds of each age and sex category ringed at different sites in the Netherlands each year. Jan Durkspolder is in Fryslân; the other sites are in the Delta area.

Year	Location	Juvenile		Adult		Total
		Female	Male	Female	Male	
2004	Hellegatsplaten	77	77	87	64	305
2005	Hellegatsplaten	24	33	32	20	109
2007	Krammerse Slikken	20	20	19	26	85
2008	Krammerse Slikken	58	48	67	59	232
2009	Jan Durkspolder	8	11	8	6	33
2010	Krammerse Slikken	15	25	0	0	40
Total		202	214	213	175	804

situated (Meininger *et al.* 1994; Ouweneel 2001; Voslamber *et al.* 2007). All birds were fitted with steel leg-rings issued by the Dutch ringing centre (Vogeltrekstation); all adults and those juveniles large enough to be colour-marked were additionally fitted with two colour rings (each inscribed with a unique code), one on each leg. Colour rings can be read at distances of up to 500 m with a telescope. Further information on catching and marking procedures can be found in Pouw *et al.* (2005) and van der Jeugd *et al.* (2006, 2008).

Observations of marked geese, identified by their engraved colour-rings or neck-bands, can be added to a specially designed website (www.geese.org) by goose researchers and also by members of the public. This website is dedicated to tracking individually marked geese and swans and its primary objective is to encourage volunteer observers by providing them with immediate feedback on the birds reported. The website is used by thousands of active observers in many countries world-wide and facilitates the gathering of large numbers of re-sightings from a large geographical area. All sightings in the www.geese.org database of the 804 individuals colour-ringed in the Netherlands were selected for analysis. Most sightings were made in the Netherlands during late winter, spring and summer (January–July), but sightings from other months and outside the Netherlands were also included.

Of the 804 birds selected, 55 were reported as having died by June 2012. Any sightings recorded for dates after the reported date of death were checked. Eleven of the 55 dead birds had, in total, 22 observations after the death date; these were all removed from the dataset. One bird was recorded on 26 occasions after its reported death; these were retained as it was assumed that the recovery details were incorrect.

Annual re-sighting rates of marked geese in the Netherlands are generally very high and typically exceed 90%. Hence, it is rare for birds that are alive to go undetected for long periods of time. All observations made after a bird had not been observed for at least two years were checked. Usually, these concerned single observations after which the bird was never seen again, they were often entered by the same observers, and were made at localities that the birds had never visited before. These observations were removed. When more than three observations were made by *bona fide* observers, or when the frequency of observations was always low in a given bird, the observations were retained. All observations that were made before the ringing date were removed (66 cases). Using these criteria, a total of 168 out of 20,860 observations (0.81%) were classed as incorrect, and 20,692 observations were retained for analysis.

Counts

Summer counts of all species of geese, including both adults and young of the year, were conducted in the Delta area around the 15th of July each year by Sovon, the Dutch Centre for Field Ornithology, in 2006 and 2007 (van der Jeugd & de Boer 2006; de Boer & van der Jeugd 2007) and by Centrum voor Landbouw en Milieu (CLM) in 2007–2011 (Tolkamp & Guldemond 2007; Guldemond & Tolkamp 2008; Tolkamp & Guldemond 2009; Visser, Guldemond & Tolkamp 2010; Den Hollander & Visser 2011). Counts were performed within two days by a team of volunteers and professionals and were carried out to estimate the total numbers of each species present in each year, to provide data for planning and evaluating the management of geese breeding in the Netherlands.

Survival

Survival analyses were performed using Program MARK (White & Burnham 1999). Model selection was based on a modified Akaike Information Criterion (Q-AICc). Birds ringed as juveniles and birds ringed as adults were held separately in two groups. The analyses commenced with a model where the probability of survival during the first year after ringing was held separately from the probability of survival during subsequent years in both groups, hereafter referred to as age classes 1 and 2. For birds ringed as juveniles, survival in age class 1 measures survival during the first year of life, from fledging until the first summer, and survival in age class 2 measures survival during subsequent years. For birds ringed as adults, survival in both age classes measures adult survival in birds that are at least one year of age, although in age class 2, all birds are one year older than in age class 1. In this way, we could test for a possible age-effect on survival for birds ringed as juveniles, and accommodate a possible transient effect in adults (Pradel 1997). Re-sightings were grouped according to calendar year. The median month of the first observation was February in each of the years 2005–2009 and 2011, March in 2010 and January in 2012. In all years of the study, 90% of the first observations of individual geese were made before the end of May. Hence, survival was analysed from late winter/spring until late winter/spring the next year, with the exception of the first year, when the time-span was slightly shorter. This shorter (*c.* 6–9 months) survival duration estimated for first-year birds was unavoidable, since grouping the re-sightings differently (*e.g.* from July–June, instead of from January–December) would lead to the median month of the first observation being in December or January, and an even shorter time-span during the first year. The use of a two-age class structure introduced for both groups accounted for the discrepancy in time span between the first and second age-class.

Data from birds ringed at the two localities in the Delta area were analysed separately from data on birds ringed in Fryslân in 2009. Because dead recoveries of (mainly shot) birds were available for geese ringed in the Delta area, in addition to the live observations, the Burnham model was used as this estimates survival using both re-sightings and recovery data simultaneously. Data from Fryslân were analysed with a standard Cormack-Jolly-Seber (CJS) model using re-sightings of live birds only. First, the most parsimonious model was found for the re-sightings data, incorporating *resighting rate* (p) and, in the delta area, the *reporting rate* (r) and the *fidelity parameter* (F), prior to estimating survival rates. Additional models based on the initial model then tested whether survival was time-, group-, or age-dependent, with group reflecting the bird's age on ringing. In order to test whether survival during the first year differed from survival rates thereafter, survival in age class 2 (*i.e.* birds ringed as juveniles) was set as being equal to the survival of birds ringed as adults in both age classes, to make optimal use of all available data. To test for overdispersion, ĉ was calculated to be 1.247 based on 100 simulations in MARK. AIC and Deviance values therefore were subsequently adjusted with this value.

Dispersal

The dispersal distance from the site of ringing to a breeding area in one of subsequent years was calculated using all 20,692 observations. For each observation, the distance between the site of ringing (the place of birth or the breeding / moulting site) and the site of breeding was calculated as the great circle distance between the two sited, using the following formula:

$$Distance = 6372.8 \times \arccos(\sin lat_r \times \sin lat_w + \cos lat_r \times \cos lat_w \times \cos \Delta long)$$

where:

$(lat_r, long_r)$ = latitude and longitude of ringing site in radians ($\pi \times$ lat / 180, $\pi \times$ long / 180)

$(lat_w, long_w)$ = latitude and longitude of breeding site in radians ($\pi \times$ lat / 180, $\pi \times$ long / 180)

$\Delta long$ = difference between longitude of ringing and breeding site, and

6372.8 = radius of the earth in km.

It was assumed that all sightings made of Barnacle Geese in the Netherlands between 1 April–15 August were in (potential) breeding habitat, and that birds ringed as adults or birds ringed as juveniles but at least two years old on the observation date, attempted or at least intended to breed there. The probability of Dutch-breeding birds being identified was assumed to be high, as most Barnacle Goose colonies, brood-rearing areas and moult flocks are screened for the presence of ringed birds by observers. It was further assumed that observations outside the Netherlands but within the flyway between 1 April–15 May were of birds on their way to breeding grounds in northern Russia, and that observations made between 16 May–15 August outside the Netherlands but within the flyway were of birds that had attempted to breed at the observation site. For example, a bird that was observed at the coast of Schleswig-Holstein, northern Germany, on 14 May was assumed to be on its spring migration to Russia, but a second bird seen at the same location on 16 May was assumed to be a local breeding bird. There is a risk that the first bird also is a local breeding bird, but it was classified as migrating because there were no further observations at the same locality. The risk of misclassification is probably small because sightings made from 16 May–15 August overrule those made earlier in the year, as being more likely to reflect the area used by the bird during the breeding season.

For each individual bird, the mean distance between the ringing site and the breeding site was then calculated, using all observations made in potential breeding habitat based on the criteria mentioned above. This resulted in a dispersal distance being determined for 557 of the 804 ringed birds included in the study.

Birds that were never observed within these dates (1 April–15 August), but were regularly seen outside these dates (*i.e.* outside the breeding season), *and* that were at least two years old at the time of these observations (hence capable of breeding) were assumed to have dispersed to somewhere outside the Netherlands, most probably to the Russian (sub-) Arctic (after van der Jeugd 2001). This resulted in a further 71 birds that could be classified as having dispersed. Although it can be assumed that these birds bred outside the Netherlands, a precise dispersal distance could not be calculated because their breeding location was not known, but as most of the birds probably dispersed to the vast breeding areas of northern Russia, a dispersal distance of 3,000 km was substituted for these individuals.

For 176 of the ringed birds it was not possible to infer anything about their dispersal status because there were no observations > 1 year after ringing; these birds most probably had died.

The dispersal rate from the colony at Jan Durkspolder in Fryslân was considered likely to be much higher than in the Delta area, because of the recent disturbances in this colony by foxes (R. Kleefstra, pers. comm.). Dispersal from this colony therefore was analysed separately.

Results

Survival in the Delta area

Survival of birds ringed in the Delta area was calculated from observations made of live birds as well as on reports of dead, mainly shot, birds. The final model, which best fitted the data, indicated that there was no effect of age class, age at ringing (group) or sex on survival (S), but that the survival rate varied with time (Table 2). Re-sightings

Table 2. Model outputs from survival analyses for Barnacle Geese ringed in two breeding areas in the Netherlands. Models are ranked on the basis of their Q-AICc values (see text), with the best (most parsimonious) model at the top. S = survival; p = re-sighting rate; t = time (year); g = group (ringed as juvenile or adult); s = sex; a = age (first year or older, as a continuous variable). Following development of an initial model (see text), the model structure for reporting rate (r) and the fidelity parameter (F) were reduced, and all models in the table share a common structure for these parameters: r(g*s*t),F(.). All other models for r and F provided a poorer fit to the data and were not used in subsequent models. In the best model fit there was no age or group effect on survival; in model 2 this effect was present. AIC and deviance values were adjusted to account for overdispersion, at $\hat{c} = 1.247$.

	Model	**Q-AICc**	***Δ* Q-AICc**	**AICc weight**	**Likelihood**	***N* par**	**Deviance**
Delta							
1	S(t),p(g*t),r(g*s*t),F(.)	3544.848	0.000	0.9120	1.0000	46	570.3262
2	S(a2(a2:juv = ad)*t),p(g*t),r(g*s*t),F(.)	3549.527	4.680	0.0878	0.0963	52	562.6819
3	S(t),p(t)r(g*s*t),F(.)	3564.333	19.485	0.0001	0.0001	40	602.0956
4	S(g*a2(a2:juv = ad)*t(a2)),p(g*t)r(g*s*t),F(.)	3565.005	20.158	0.0000	0.0000	54	574.0428
5	S(g*a2(a2:juv = ad)*s*t),p(g*t),r(g*s*t),F(.)	3566.693	21.845	0.0000	0.0000	64	555.0789
6	S(g*s*t),p(g*t)r(g*s*t),F()}	3568.411	23.563	0.0000	0.0000	68	548.5046
7	S(g*s*t),p(g*s*t)r(g*s*t),F(.)	3581.701	36.853	0.0000	0.0000	81	534.7196
8	S(g*a2*s*t),p(g*t)r(g*s*t),F(.)	3582.628	37.780	0.0000	0.0000	80	537.7367
Fryslân							
1	{S(t),p(.)}	129.8771	0.000	0.2853	1.0000	4	121.322
2	{S(.),p(.)}	130.1789	0.302	0.2454	0.8600	2	126.017
3	{S(t),p(t)}	130.3939	0.517	0.2203	0.7721	7	119.549

rates (p) were also time-dependent and differed between the two groups. The reporting rate (r) for birds found dead differed between groups, sexes and years, whereas the fidelity parameter (F) could be reduced to a single parameter (constant). The AICc weight for the final model was 0.912 compared with an AICc weight of 0.088 for the next best model, in which survival differed between years (as in the best model), but additionally survival in the first year of life differed from survival later in life, as an adult (Table 2). The effect of time (year) on survival is very significant; all models without a time effect on S performed poorly, with Δ AIC values of at least 79.42 (Table 2).

Survival of Barnacle Geese in the Delta area was initially very high, with 98% surviving during the first year of the study. Thereafter, annual survival rates gradually declined, until they were < 80% in the year to the mid-winter/spring of 2011 (Fig. 1, Table 3). Buckland (1982) demonstrated that in long-lived species you can expect a trail-off in apparent survival, due to the number of individuals not seen but still alive during the latter stages of the study. The high re-sightings rate for Barnacle Geese in the Netherlands (92.3% *per annum*) meant that most live birds were re-sighted and that the drop in survival was likely to be real in this case.

Survival in Fryslân

The survival analysis for birds ringed in the breeding colony at Jan Durkspolder, Fryslân, was based on re-sightings of live birds only. There are, as yet, no reports of shot birds from this group. In the best

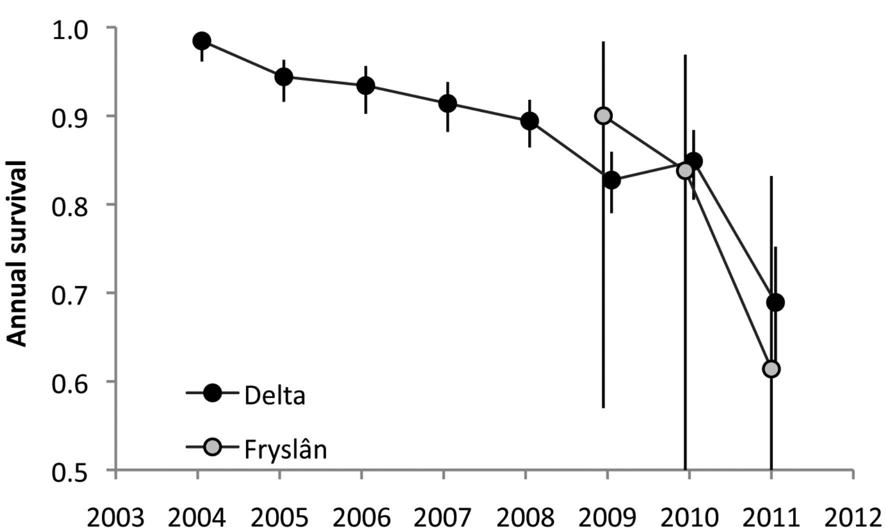

Figure 1. Annual survival of Barnacle Geese breeding in the Netherlands, for birds ringed in the Delta area and in Fryslân. Vertical lines represent 95% confidence intervals. Values shown are from the best models for both areas in Table 2.

Table 3. Annual survival rates for Barnacle Geese breeding in two distinct breeding areas (the Delta area and Fryslân) in the Netherlands, from mid-winter/spring 2004 onwards. Parameter estimates are from the best models for both study areas. Re-sighting rate = the overall re-sighting rate for colour-marked geese; reporting rate = the probability that a colour-mark is found and reported, given that the bird has died.

Survival interval (years)	Delta area				Jan Durkspolder, Fryslân			
	Estimate	**s.e.**	**Lower C.I.**	**Upper C.I.**	**Estimate**	**s.e.**	**Lower C.I.**	**Upper C.I.**
2004–2005	0.985	0.007	0.961	0.994	–			
2005–2006	0.944	0.012	0.916	0.963	–			
2006–2007	0.934	0.013	0.902	0.956	–			
2007–2008	0.914	0.014	0.882	0.938	–			
2008–2009	0.894	0.014	0.864	0.918	–			
2009–2010	0.827	0.018	0.790	0.859	0.900	0.088	0.570	0.984
2010–2011	0.849	0.020	0.805	0.884	0.838	0.124	0.464	0.969
2011–2012	0.689	0.034	0.618	0.752	0.614	0.137	0.339	0.832
Re-sighting rate	0.923				0.794	0.069	0.627	0.899
Reporting rate	0.174				–			

model there was no difference in survival between birds ringed as juvenile compared with birds ringed as adult, and survival did not differ between the sexes, but survival did vary between years (Table 2). Although only three years of re-sightings data are available to date, survival does seem to be in the same order of magnitude as for geese from the Delta area (Fig. 1, Table 3), and decreased from 90% in 2009 to < 70% in 2011.

Effects of hunting

In the Delta area, survival rates have declined since the first year of ringing in 2004, and in Fryslân survival similarly decreased between 2009 and 2012. This decrease may be associated with increasing hunting pressure on Barnacle Geese during the summer months, to prevent damage to agricultural crops. Prior to 2006, Barnacle Geese were legally protected from hunting in the Netherlands throughout the year. Summer hunting of Barnacle Geese has been permitted in the province of Zuid-Holland since 2006, however, and annual bag numbers have risen from 679 in 2006 to 5,852 in 2011 in the Delta area (Faunabeheereenhed (FBE) Zuid-Holland, unpubl. data; Table 4). In Fryslân, Barnacle Geese have been shot legally during summer since 2010, but bag numbers are still modest (Table 4). The number of ringed birds reported as shot has also increased over the past six years, but is low compared with the total bag numbers (Table 4); it is difficult to relate bag numbers to survival because the accuracy of the numbers reported has not been determined. Estimates of the numbers of geese breeding in the two areas are based on a single annual count in July, and the July count is in the middle of the hunting period so includes an unknown part of the annual hunting bag. Nevertheless, these figures do give some hint about the potential impact of hunting on the number of geese breeding in the Netherlands. When the annual bag numbers are simply divided by the annual July count, this yields a figure that should at least be indicative of the proportion of the breeding geese removed by hunting in recent years. It is also possible to estimate hunting mortality from the number of ringed birds reported shot, with the number reported shot, divided by the reporting rate (derived from the survival analyses) and divided again by the number of birds 'at risk' (calculated as the expected number of colour-marked birds alive during each summer using the annual survival figures) yielding an estimated value for hunting mortality. However, this is far from precise as the reporting rate does not differentiate between shot birds and birds that died from other causes, and the reporting rate is also unreliable because of the relatively low numbers of ring recoveries. Results of both calculations are given in Table 4. The calculated annual figures for hunting mortality were then considered in relation to the annual survival estimates from the survival analyses (Fig. 2).

Dispersal

Natal dispersal of Barnacle Geese hatched in the Netherlands was considerable. Of those males for which a breeding location was known or could be inferred from the data, 56% bred within 10–100 km from their original site of ringing and 38% bred > 100 km from their site of ringing (Fig. 3).

Table 4. Summer counts of Barnacle Geese in the two study areas in the Netherlands (the Delta area and Fryslân), and the proportion of geese removed by hunting based on: (1) annual hunting bag data, and (2) reports of shot ringed birds, with an average reporting rate of 17.4% *per annum* (see text for details of the calculations).

Year	Bag number	Numbers counted*	Hunting mortality (1)	Number reported	Hunting mortality (2)
Delta					
2004	0		0.000	0	0.000
2005	0		0.000	1	0.019
2006	679	13,172	0.052	3	0.045
2007	1,718	14,995	0.115	5	0.080
2008	2,531	11,683	0.217	8	0.113
2009	3,801	15,672	0.243	2	0.020
2010	5,255	16,107	0.326	12	0.146
2011	5,852	25,414	0.230	15	0.198
2012	–	23,975	–	20	0.383
Fryslân					
2009	0	*1,000***	0.000	0	–
2010	31	*1,000***	0.031	0	–
2011	108	*1,000***	0.108	0	–

*Based on annual summer counts of Barnacle Geese in the northern part of the Delta area, where the majority of the Dutch Barnacle Goose population breeds, on the island of Goeree-Overflakke, and in the regions Voorne, Putten and Hoekse Waard, conducted by Sovon and CLM (see text).
**Only a rough estimate is available for the numbers in Fryslân in July.

Almost 30% of all surviving males probably emigrated to a breeding colony in the large population along the shores of the Barents Sea in northern Russia, although there are only two male birds for which breeding in this population was proven by observations made during the breeding season at both Kolokolkova Bay and on Kolguev Island, the only two sites where regular work on Barnacle Geese has been carried out in recent years. Among females, corresponding figures are 30% and 24%, respectively. Breeding dispersal was low; 9% of both males and females bred during subsequent years at sites > 10 km from their ringing site, and 3% of males and 4% of females

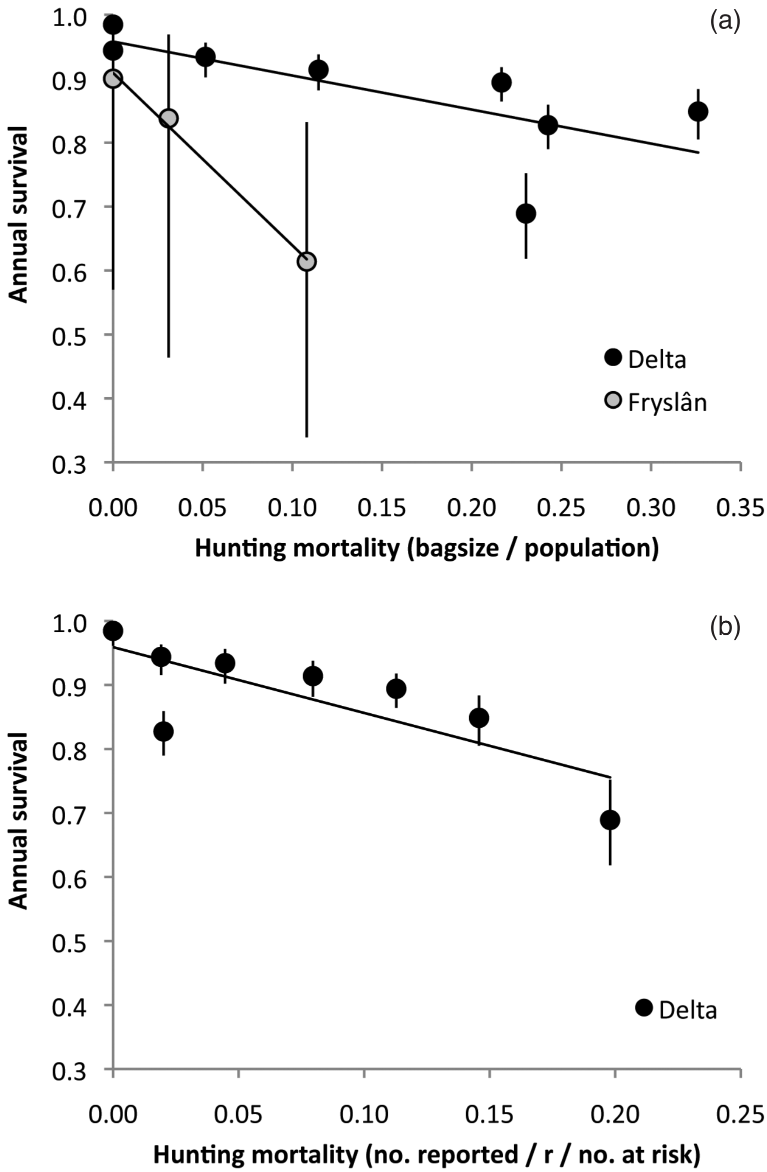

Figure 2. Annual survival rates for Barnacle Geese breeding in the Netherlands (in the Delta area and in Fryslân), in relation to two mortality estimates attributable to hunting (Table 4). Values shown are from the best models for both areas, described in Table 2. (a) = hunting mortality calculated as the bag number divided by the total population size, (b) = hunting mortality calculated as the number of marked birds reported shot divided by the reporting rate (r) divided by the number of birds at risk (see text). Vertical lines represent 95% confidence intervals.

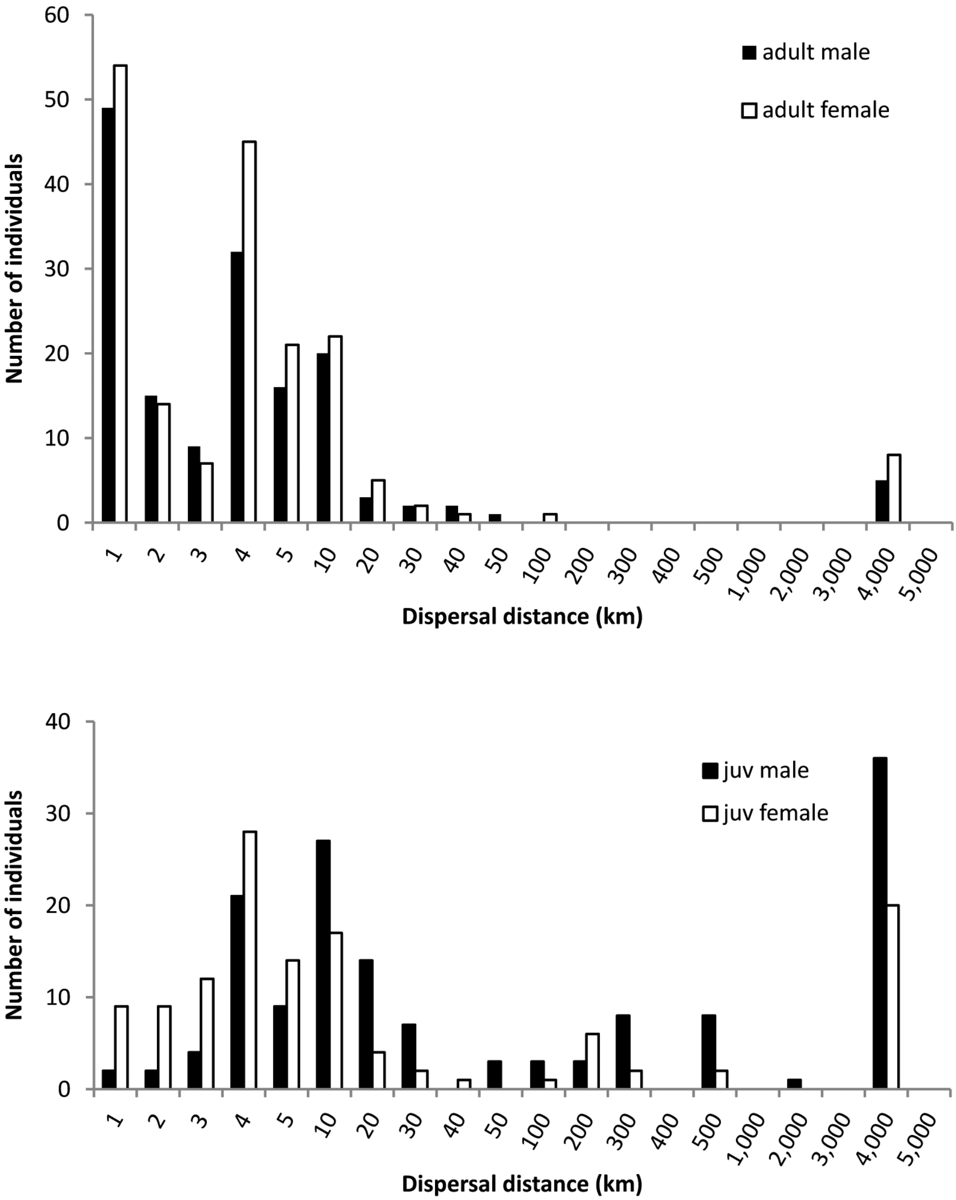

Figure 3. Natal dispersal (upper) and breeding dispersal (lower) of Barnacle Geese hatched or breeding in the Netherlands. Dispersal distances are given in distance classes on the x-axis where the number given represents the upper limit (in km) of each class. Birds that were classified as "having left" were arbitrarily assigned a dispersal distance of 3,000 km, the approximate distance to the breeding grounds of the Barents Sea population (see text).

may have emigrated to the Barents Sea population.

Discussion

Annual survival of Barnacle Geese breeding in the Netherlands was initially very high, with> 98% of geese surviving in the year from mid-winter/spring 2004, and > 94% in the year from 2005, the first two years of the study. This is higher than has been reported for most other non-hunted goose populations (*e.g.* 94.2–96.6% for adult Barnacle Geese in Gotland, Sweden, Larsson *et al.* 1998; and 92.7% for the Svalbard Barnacle Goose population, Owen & Black 1989), and is substantially higher than reported for hunted species (78–88% for Lesser Snow Geese *Anser c. caerulescens* in 1970–1987, Francis *et al.* 1992; 89–94% for Lesser Snow Geese in 1990–1994, Cooke *et al.* 2000; 72.3% for adult Icelandic Greylag Geese *Anser anser*, Frederiksen *et al.* 2004; and 81.4% for adult Icelandic Pink-footed Geese *Anser brachyrhynchus*, Frederiksen *et al.* 2004). This high survival may be attributable to a combination of the absence of migration and a longer breeding season (van der Jeugd *et al.* 2009). However, survival gradually declined and reached especially low numbers during the last three years of the study. The observed decrease in survival can most probably be explained by the introduction of a Barnacle Goose hunt during the summer. Bag numbers in the Delta area steadily increased from < 700 birds in 2006 (the first year of the summer hunt) to > 5,000 in 2010 and 2011, representing 25–30% of the total population in the northern part of the Delta recorded during summer (July) counts. Relating the estimated mortality attributable to hunting to annual survival rates reveals a 'baseline' survival of approximately 95% that gradually drops to around 75% as hunting mortality increases to 20%. In Fryslân the drop in survival seems too large in relation to the bag numbers, but this may be due to a combination of a crude estimate of the summer population size and the small number of ringed birds reported dead.

A simple population model incorporating constant fledgling production (0.6 young per breeding pair, as observed in the Delta area during 2004–2007; van der Jeugd 2012) and the annual survival values from the present study, indicated that the population in the Delta area should be declining from 2009 onwards. This is not apparent from the summer counts, however, which showed a continuing substantial increase in numbers after 2009 (Table 4). This discrepancy illustrates the importance of continuing demographic monitoring in harvested populations, of validating monitoring using counts, bag numbers and ring re-sighting data, and the performance of analyses using these data. Frederiksen *et al.* (2004) performed such an analysis for two harvested populations of geese in Scotland and concluded that different data sources yielded contrasting results, possibly leading to an over-exploitation of one of the populations concerned.

Natal dispersal was high, with 56% of males attempting to breed > 10 km from their natal site, and almost 38% > 100 km from their natal site. In females, these figures are 30% and 24% respectively. The large amount of natal dispersal, over large distances, from colonies in the Dutch populations is surprising. Van der Jeugd (1999, 2001) concluded that *c.* 25% of all birds hatched in the oldest and largest Barnacle Goose colony in the Baltic on Gotland, Sweden dispersed during a 10-year study, although natal dispersal was much more frequent in males than females. Van der Jeugd & Litvin (2006) estimated that 6.6% of all juvenile Barnacle Geese from the same colony dispersed over long-distances, most probably to the Russian Arctic, a much lower figure than is found here. Between 2002 and 2008, *c.* 2000 fledgling and adult Barnacle Geese were colour-ringed in colonies at Kolokolokova Bay and on the Kolguev Island in the Barents Sea region. Despite this, observations of Barnacle Geese hatched in the Barents Sea population are still lacking from the Dutch breeding grounds. It is therefore concluded that dispersal is probably not balanced by immigration, and that the Dutch Barnacle Goose population currently is a source, from which restocking of the Barents Sea population takes place. Although this may seem counterintuitive, the probability of a Dutch-hatched Barnacle Goose moving from its natal area during its first winter and on finding a flock of Russian-hatched congeners, subsequently joining them on migration to Russia, must be much larger than the probability of a Russian-hatched Barnacle Goose meeting a member of the much smaller Dutch population.

Apart from dispersal to Russia, dispersal to northern Germany was frequent, with both young as well as adult birds dispersing to sites *c.* 400 km away. This was especially apparent from the colony in Fryslân, that was recently disturbed by foxes (Kleefstra 2010; R. Kleefstra, pers. comm.), that may have prompted birds to start a new life elsewhere.

Dispersal over distances < 10 km is partly an artifact of the fact that the location of ringing does not necessarily reflect the exact location of breeding. It is therefore likely that these birds are in fact philopatric. There is only a very minor risk that birds that were ringed during moulting at one of the three localities were in fact breeding or had been born at localities that were further away. The two localities at Goeree-Overflakkee are *c.* 10 km apart from each other and serve as brood-rearing areas for Barnacle Geese breeding in the same area (Hellegatsplaten) or at small islets 1–2 km away from the site (Krammerse Slikken), with little exchange. All marked birds were either fledglings or adult breeding birds leading young and therefore must have hatched or bred relatively close by. We cannot exclude completely the possibility that some adult birds that exhibit long-distance breeding dispersal may in fact be birds breeding in Russia and moulting regularly in the Netherlands, but given the large difference in timing between the populations (van der Jeugd *et al.* 2009) this seems highly implausible. After all, when Dutch birds start moulting by the end of June, most Russian birds have just started incubation. For birds born in the Netherlands and alive at breeding age that are subsequently observed along the flyway during spring migration, and were never sighted in the Netherlands during the breeding season, dispersal seems the only explanation possible.

The study presented here undoubtedly has its shortcomings, and is still of limited duration. However, the sharp drop in survival with time, most probably caused by the rapidly increasing summer hunt, as well as the relatively large proportion of long-distance dispersers, backed-up by the observations of Dutch-hatched birds observed breeding both at Kolokolkova Bay and on Kolguev Island, are clear results that are important to our understanding of this newly-founded population and the impact of management measures. During the coming years, monitoring, including ringing of new birds at old and new localities, will be continued to document the dynamics of this population in further detail.

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