Short communication

Between-winter emigration rates are linked to reproductive output in Greenland White-fronted Geese *Anser albifrons flavirostris*

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Keywords: capture–mark–recapture, density-dependent dispersal, multi-state models, source/sink.

Many animals, from insects to vertebrates, appear to show density-dependence in relation to reproduction and mortality, but also dispersal (e.g. Stiling 1988, Watkinson & Sutherland 1995, Matthysen 2005). Density-dependent processes may be manifested through competition or predation pressure (Sinclair & Pech 1996), yet factors causing dispersal amongst normally site-faithful animals have rarely been explored. Here, we examine two competing hypotheses to explain differences in between-winter emigration rates of individually marked Greenland White-fronted Geese *Anser albifrons flavirostris* to show that winter dispersal rates were not density-dependent, and that emigration of known-age birds was dependent on age and the numbers of young in the previous winter.

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Wexford Slobs (southeast Ireland, 52°22′N, 6°25′W) has held 25–40% of the world wintering population of Greenland White-fronted Geese since the 1950s (Ruttledge & Ogilvie 1979, Fox *et al.* 2006). Some 85% of the Geese that are seen in successive years return to the same wintering site (Wilson *et al.* 1991, Warren *et al.* 1992a). Since 1999, numbers of Greenland White-fronted Geese wintering at Wexford have declined, reflecting the overall trend in total population size (Fox *et al.* 2006). Wintering White-Fronted Geese feed in a restricted number of fields at Wexford (Wilson *et al.* 1991) and show consistent intra-specific aggression, with large family parties dominating access to the best food patches (Boyd 1953). Therefore, it would be expected that, if food quality in the fields remained the same, the population would approach the potential carrying capacity of the site as numbers increase. As this limit is approached, the food intake and therefore condition of (particularly low-ranking) individuals would be affected, potentially affecting their decision to remain at the site or winter elsewhere. This argument suggests that more individuals would emigrate from Wexford with increasing population density at this wintering site.

However, there is no evidence that such a theoretical carrying capacity has been reached – indeed, despite increasing numbers at Wexford up until 1999, Greenland White-fronted Geese accumulated fat stores earlier each winter (monitored in the field through the use of abdominal profile scores, Fox *et al.* 2003, and unpubl. data). Geese are known to shift winter site most frequently when they pair (normally at 2–3 years; Warren *et al.* 1992b), as pairing takes place away from the wintering grounds and therefore involves individuals that may winter at different sites (Warren *et al.* 1992a). In recent years, the proportion of young Geese wintering at Wexford has fallen, perhaps linked to weather conditions on the breeding grounds (Boyd & Fox 2008), so emigration rates potentially simply reflect the relative numbers of young Geese pairing and changing to the wintering site of their partner rather than any density-dependent effect.

The aim of this study was to assess support for two competing hypotheses: that either (1) winter dispersal rate amongst the Wexford population is density-dependent or (2) winter dispersal rate reflects the recruitment of young (i.e. the density of first-winter birds) in the population. In the case of (1), we predicted that annual winter dispersal rate would be positively correlated with density (i.e. Goose abundance given constant feeding area) at Wexford. As the Wexford population has suffered low productivity in recent years and older individuals are more likely to return to the same wintering site (Warren *et al.* 1992a), in the case of (2) we predicted that the emigration rate from Wexford would be positively correlated with the annual numbers of young at this site. We used multi-state mark–recapture methods (e.g. Hestbeck *et al.* 1991) to model the

probability of Wexford-marked individuals shifting sites in successive winters, based on resighting data from throughout the wintering range.

METHODS

Geese were cannon-netted annually over bait at Wexford Slobs, and marked with neck collars and leg rings readable in the field using telescopes; all were aged and sexed at capture (Warren 1990). From 1983 to 2008, 1666 birds were caught and marked during 82 catches, but here the analysis is confined to the 1562 individuals (adults: 359 females, 389 males; first-winters: 408 females, 406 males) with resighting histories sufficiently long to allow their wintering site fidelity to be assessed. A.J.W. carried out regular (at least weekly) observations of marked Geese at Wexford from late September to April and undertook an annual sample of the ratio of adults to juveniles. Counting and searches for collars were also carried out each winter at the other wintering sites by a network of counters and observers, which resulted in much lower resighting probabilities than at Wexford. Up to the end of March 2008, the scheme had generated 55 326 resightings from these marked birds.

Analyses were performed using multi-state models in the software program MARK (White & Burnham 1999), with goodness-of-fit testing in program U-CARE (Choquet & Pradel 2002). The possible states of our model were 'observed at Wexford' and 'observed at other wintering site'. For simplicity, all the models had (1) time-dependent survival probability equal for the two states, (2) time- and site-dependent resighting probabilities and (3) transition (emigration) probabilities. Because we expected emigration to be age-dependent, known-age (marked during their first winter) birds and adults were analysed separately. For each dataset, a set of models was constructed as follows, only differing with respect to how emigration probability from Wexford varied over time:

(1) Full year-to-year variation, used as the basic comparison model.
(2) Constant emigration probability.
(3) Emigration from Wexford as a function of total population size at Wexford.
(4) Emigration from Wexford as a function of juvenile population size at Wexford.

For the known-age dataset, models including age effects were also fitted. In addition, for both datasets we assessed whether emigration was male-biased by adding an additive sex effect to the highest-ranked model.

The biological hypotheses that guided specification of the structure of models were assessed using AIC_c (Akaike's Information Criterion adjusted for small sample bias; Burnham & Anderson 1998) and Analysis of Deviance (ANODEV; Skalski *et al.* 1993). Models with the lowest values of AIC_c were retained as good candidate models (Anderson *et al.* 1998), while ANODEV was used to quantify the proportion of between-year variation in emigration from Wexford explained by the models.

RESULTS

Goodness of fit was acceptable for known-age birds ($\chi^2 = 305.1$, df = 290, $P = 0.26$), and almost acceptable for adults ($\chi^2 = 289.0$, df = 245, $P = 0.027$). We did not employ an overdispersion factor for either dataset; doing so would not have changed any of the findings reported here. For known-age birds, there was strong evidence that emigration varied with age (Table 1a, model 3 vs. model 6). We used four age classes; exploratory analyses showed that using a different number of classes had little effect. Emigration was substantially higher during the first 2 years after marking than during subsequent years (Fig. 1a). There was substantial year-to-year variation in emigration probability (Table 1a, model 4 vs. model 6), and the number of juveniles explained a substantial part of this variation (model 5: 38% of between-year variation explained, $P = 0.0013$; Fig. 1b). In contrast, there was no relationship between total population size at Wexford and emigration probability (model 7: 0.7% of between-year variation explained, $P = 0.69$). The relationship between juvenile population size and emigration remained when controlling for age-related variation (model 1: 35% of between-year variation explained, $P = 0.0024$). For birds marked as adults, year-to-year variation in emigration probability was less pronounced (Table 1b, model 1 vs. model 2), and neither juvenile nor total population size explained much of this

Table 1. Model selection results from MARK accounting for between-year emigration rates of Greenland White-fronted Geese ringed at Wexford, Ireland. Model deviance, number of estimable parameters, and the difference in Akaike's Information Criterion corrected for sample size (ΔAIC_c) between each model and the highest-ranked model are shown for known-age birds and adults.

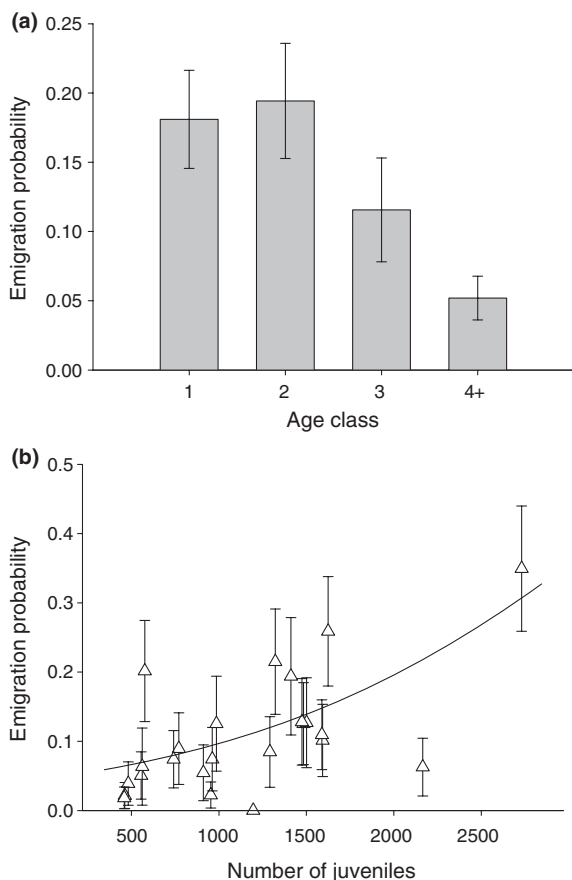|		Deviance	No. of parameters	ΔAIC_c
(a) Model for emigration of known-age birds				
1	Age(4) + Juvdens	2719.18	101	0
2	Age(4) + Time	2674.94	123	3.47
3	Age(4)	2742.85	100	21.51
4	Time	2704.25	119	24.04
5	Juvdens	2761.31	97	33.53
6	Constant	2796.49	96	66.57
7	Totdens	2795.83	97	68.05
(b) Model for emigration of adult birds				
1	Time	2100.24	119	0
2	Constant	2152.46	96	2.46
3	Totdens	2150.87	97	3.02
4	Juvdens	2151.02	97	3.17

Figure 1. Estimates of emigration rates in Greenland White-fronted Geese from Wexford, Ireland. (a) Model-estimated mean (± 95% confidence limits) between-winter emigration probabilities of known-age Geese according to model 3 (Table 1a) with only age effects. Patterns from the highest-ranked model (model 1) were very similar. (b) Model-estimated mean between-winter emigration probabilities of Geese from year *t* to *t* + 1 (solid line) in relation to numbers of juveniles present in year *t*, from a model with only this effect (model 5, Table 1a). Annual emigration estimates (with 95% confidence intervals) from a model with full-time variation (model 4, triangles) are also plotted against the observed number of juveniles. The relationship was similar, although slightly less strong, in model 1 including age variation.

variation (models 3 and 4: < 3% of between-year variation explained, $P > 0.4$). There was some evidence of male-biased emigration in adults ($\Delta AIC_c = -0.08$), but none for known-age birds ($\Delta AIC_c = 1.90$).

DISCUSSION

There was no support for the hypothesis of a constant winter emigration rate from Wexford throughout the time series, or for the hypothesis that the rate of emigration of marked Geese from Wexford was related to local winter numbers and therefore a density-dependent process. Rather, the model selection results supported the hypothesis that emigration rate of Geese marked in their first winter was correlated with the number of juveniles.

The life-history traits of this subspecies offer an explanation for these results. Most permanent changes in wintering site amongst Greenland White-fronted Geese corresponded with pairing amongst young birds (Warren *et al.* 1992a). As adults show high levels of winter site-fidelity and pairing generally occurs away from the winter quarters, when a young bird leaves its family group to pair-up (which happens mostly during the second and third years of life; Warren *et al.* 1992b), it is likely that this frequently will result in a shift to the wintering site of the new mate (Warren *et al.* 1992a,b). The age-related emigration rate found in these results therefore fits well with expectations, as adults generally show low levels of shifts between wintering sites. Furthermore, the reductions in emigration rates recorded in very recent years can apparently be explained by the concurrent dramatic fall in the production of young (Fox *et al.* 2006).

It has been suggested that the two numerically most important sites for this Goose population (Islay in southwest Scotland and Wexford Slobs) have provided a source of recruits dispersing to other winter quarters (Warren *et al.* 1992a). These two sites tend to host Geese with higher reproductive success than do sites elsewhere, and wintering sites with the lowest proportion of young were those showing the greatest rates of decline (see figure 6 in Fox *et al.* 2005). Hence, at least in the 1980s, when emigration rates were much higher than now, Wexford (and perhaps Islay as well) may have functioned as 'sources' for other 'sink' wintering flocks. Unfortunately, we lack marked birds from other winter flocks to confirm exchange rates, but if this is the case, clearly the reduced emigration rates from Wexford in recent years is yet another population consequence of current low reproductive output in the Greenland White-fronted Goose and may contribute to declines at other wintering sites.

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