

# Direct and indirect effects of winter harshness on the survival of Mallards *Anas platyrhynchos* in northwest Europe

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To understand population dynamics it is necessary to understand vital rates, which may be affected by a wide range of factors including environmental variables such as weather. Weather conditions can affect birds' vital rates directly through increased mortality due to impaired conditions, or indirectly via changes in body condition and/or behaviour. Most understanding of direct and indirect effects of weather comes from studies of breeding birds, whereas the situation in non-breeding periods is less clear. Here, we analysed annual survival of non-breeding Mallard *Anas platyrhynchos*, the most hunted waterfowl species in Europe, and assessed whether survival is related directly to winter harshness and/or indirectly via changes in winter recovery distributions. Recovery data on Mallards, initially marked in southeast Sweden, were analysed with an information-theoretic approach using program MARK. Over 10 000 Mallards were marked in two time periods, 1964–1982 and 2002–2008, of which 13.3 and 4.7%, respectively, were later recovered. Mallards had lower annual survival in the early trapping period (0.58–0.63) than in the later period (0.69–0.71), with no clear effects of sex, age or year. Within each study period, winter harshness did not directly correlate with survival. However, milder winters may have contributed indirectly to higher survival in the second period, as winter harshness data were correlated with the distances to recovery positions for females, and also because winter recovery areas have shifted northeast during the past decades, possibly indicating a shortened migratory distance. Migration is costly, and there is therefore a likely linkage between migration behaviour and survival of dabbling ducks, in which direct as well as indirect effects of winter harshness may play a role. Other factors, such as hunting pressure, are also likely to have changed in the past decades, and may also have contributed to improved survival of Mallards in northwest Europe.

**Keywords:** climate change, dabbling ducks, flyway, hunting, weather.

Population dynamics of birds are affected by both intrinsic and extrinsic factors (Newton 1998), of which climate and weather belong to the latter. Numerous recent studies have tried to assess how birds are affected by climate change, usually in terms of phenology and distribution of migratory species, and less frequently to assess how vital rates are affected directly. Many migratory species have

responded with advanced arrival dates or shifts in distribution, although this does not apply to all studied species (Stenseth *et al.* 2002, Walther *et al.* 2002, Parmesan & Yohe 2003, Both *et al.* 2004, Crick 2004, Torti & Dunn 2005, Weatherhead 2005, Jonzén *et al.* 2006). Birds may be negatively affected by altered habitats, and also by a mismatch between the phenologies of the birds and their resources (Visser *et al.* 1998, Drever & Clark 2007).

Productivity and survival may also be affected by a changing climate. Altered weather conditions

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may not necessarily be adverse as they may induce not only negative (see reviews in Crick 2004, Leech & Crick 2007, Hamer 2010) but also positive or neutral responses in birds' vital rates (Crick 2004, Leech & Crick 2007, Robinson *et al.* 2007, Jónsson *et al.* 2009, Wright *et al.* 2009, D'Alba *et al.* 2010, Hamer 2010, Glenn *et al.* 2011), which may be explained in part by different life-history strategies (e.g. Cormont *et al.* 2011, but see Jonzén *et al.* 2007). Thus, climate change is expected to have an impact on populations because of the well-established effects of weather on birds' vital rates.

Weather may affect vital rates directly, for example through disrupted thermoregulation or breeding failure, but weather more frequently affects birds' vital rates indirectly (Newton 1998). Therefore, survival and/or productivity may be affected by weather through alterations in, for example, migration behaviour leading to range shifts (Walther *et al.* 2002, Parmesan & Yohe 2003), habitat, food availability and body condition (Newton 1998).

To understand population dynamics, it is necessary to determine the underlying vital rates and factors that give rise to variation in these rates. For hunted species this is particularly important to assess sustainable harvest levels. Dabbling ducks in the genus *Anas* are important game species in many parts of the world, and in Europe the most hunted waterfowl species is the Mallard *Anas platyrhynchos*, with an annual harvest of about 4.5 million birds (Hirschfeld & Heyd 2005). It is unclear whether hunting translates into population effects (Pöysä *et al.* 2004), partly because the contribution of other factors has not been fully investigated. One candidate variable affecting survival in Mallard is weather. Weather effects on duckling survival are quite well understood in dabbling ducks, including both direct (chilling) and indirect (e.g. food shortage) effects (Solman 1945, Koskimies & Lahti 1964, Talent *et al.* 1983, Cox *et al.* 1998a, Gunnarsson *et al.* 2004), whereas such effects on fledged birds during the non-breeding period have been less studied and the few existing studies on Mallard yield conflicting evidence. Bergan and Smith (1993) found negative effects of cold weather on survival, whereas Doolley *et al.* (2010) did not. However, intricate indirect patterns may prevail, as cold weather may affect survival indirectly through impaired body condition (Bergan & Smith 1993) or increased

vulnerability to hunting (Hepp *et al.* 1986, Dufour *et al.* 1993, Robb 2002). However, a lack of consensus (Jeske *et al.* 1994, Cox *et al.* 1998b, Lee *et al.* 2007) encourages more studies on direct and indirect impact of environmental variables on survival in dabbling ducks, especially for non-breeding periods.

Long-term data with complete encounter histories, i.e. with information about marking and subsequent recaptures and/or recovery, are very useful, not only because they enable accurate estimations of survival and re-encounter probabilities, but because they may also be used to assess effects of temporal changes in crucial factors. One variable that is known to vary over time is climate, and the impact of climate change has been studied in breeding dabbling ducks (Drever & Clark 2007, Oja & Pöysä 2007, Cormont *et al.* 2011). Climate may thereby not only affect the population dynamics of birds directly, for example via survival or hunting vulnerability, but also indirectly by changes in migration patterns. Although Cormont *et al.* (2011) suggest that waterfowl are expected to profit from milder winters, the consequences of recent milder winters in northern Europe (Klein Tank *et al.* 2002) have not yet been fully assessed.

The aims of this study were to assess linkages between winter temperature data and annual survival of Mallards in the northwest European flyway (cf. Guillemain *et al.* 2005), as well as to assess possible indirect links via potential changes in the winter range. Direct effects of hunting pressure on Mallard survival were also evaluated.

## METHODS

### Trapping of ducks

Mallards were captured in a large trap situated close to the southernmost tip of Öland (Ottenby) in the Baltic Sea (56°13'N, 16°27'E). The trap is situated on the shoreline, partly on land, partly in water. A wall inside the trap divides it in two halves (total size: 7 × 34 m), one of which hosts 10 lure ducks (Mallard), the other having narrow openings through which wild ducks can swim into the trap. Once each day, trapped wild ducks are pushed towards a small closable compartment in the end of the trap where they are subsequently captured. All birds are ringed, aged and sexed (body mass and size are also measured, but were not analysed in this study) and thereafter released

in the vicinity of the trap. Grain is added daily inside and outside the trap to attract ducks. We acknowledge a potential bias in using baited traps, i.e. a greater chance of catching birds in poor condition (Weatherhead & Greenwood 1981). The number of captured birds in the trap correlates well with the total number in the staging site (J. Waldenström unpubl. data) and we therefore assume that the composition of the catches was representative of the population in the area. The trap is operated daily during the ice-free period of the year (March/April to December).

The duck trap at Ottenby was built in 1962 and was then in use for about 20 years, until it was partly dismantled in 1983. During this period (the early trapping period) more than 13 000 ducks were captured. A period with no captures followed, but after almost 20 years the trap was rebuilt in 2002 (the late trapping period), with the same trap design. The late trap is still in use and more than 1000 ducks are normally caught each year (e.g. Wallensten *et al.* 2007). The Ottenby duck trap is probably unique as there are, to our knowledge, no similar long-term mark-recapture data in the world on ducks based on standardized catches ranging over almost half a century.

### Marking and recovery data

Although duck captures started in 1962, Mallard data from 1962–1963 were excluded from the analyses due to uncertainties in age determination. Data that were used for the early trapping period were thus collected during 1964–1982. Only markings from 1 July to 31 December were considered because few ducks were trapped in spring, and also due to a lower precision in age determination at that time of the year. There was no such restriction for inclusion of recovered ducks, which were from the whole year. Data were included only if ducks (1) were classified as either juvenile (i.e. first calendar year) or adult (i.e. second calendar year or older), (2) were sexed as either female or male, and (3) did not have any reported warning codes (such as abnormal plumage, morphology or injuries) according to the EURING manual (Speak *et al.* 2001). Moreover, for the re-encountered ducks, criteria to be included in the analyses were that they had a certain recovery status (i.e. dead) and a certain recovery date ( $\pm 1$  day; i.e. the true recovery date could be the reported date, the previous day or the following day).

We used recoveries reported during the period 1 December to 28 February to describe the winter recovery distribution. Distance from the ringing site in Ottenby to recovery sites in winter was modelled (generalized linear modelling, GLM) as a function of trapping period (early vs. late), sex, age and winter harshness. Winter harshness was defined following Sauter *et al.* (2010), using the Hellmann index (Ijnsen 1988), which is the absolute value of the sum of all negative mean daily temperatures between December and February. The first principal component from a factor analysis with Hellmann indices based on temperature data from five weather stations around the southern Baltic Sea (Bornholm, Copenhagen, Falsterbo, Visby and Rostock) was used. The extent to which winter harshness data differed between early and late trapping periods was evaluated with an additional GLM analysis. GLM models were compared using Akaike information criterion (AIC<sub>c</sub>) values (see below). Statistical analyses were done in SPSS (18.0) (IBM, Chicago, IL, USA).

### Model analyses with survival and recovery estimations

Program MARK (version 5.1; White & Burnham 1999) and the Seber model option (Seber 1970) were used to analyse the mark-recovery data. The models included separate parameters for survival ( $S_i$ ) and recovery ( $r_i$ ; i.e. the probability that ducks were found dead and reported; see Brownie *et al.* 1985). The input files were constructed with the live-dead (LD) format for encounter histories, with a yearly time interval between occasions. Recovery year did not follow the calendar year. Mallards were marked between 1 July and 31 December (i.e. no spring markings; see above) and recovered between 1 July and 30 June of the following year.

Mark-recovery data from the early trapping period (1964–82) and the late trapping period (2002–08) were treated in separate analyses. Recoveries after the end of each study period (1982 and 2008, respectively) were not considered. Previous studies of Mallards have reported differences in survival estimates due to sex, age and year (Johnson *et al.* 1992, Smith & Reynolds 1992, Lake *et al.* 2006), so these variables were included as factors in the analyses by dividing the annual mark-recovery data into four groups according to the age and sex of the birds:

juvenile females, adult females, juvenile males and adult males. The theoretically most complex model with all possible interactions added to the main effects (sex, age and year) always resulted in parameters not being estimated accurately (i.e. inaccurately estimated parameters were those with abnormally high beta values and standard errors), which may be caused by insufficient data (Cooch & White 2010). Therefore, the model was reduced to find a global model that included as many parameters as possible (only two-way interactions were considered), but with accurately estimated parameters only. For each of the two datasets, goodness-of-fit of the global model was evaluated using a bootstrapping procedure with 500 simulations of the global model, after which the deviances from these simulations were ranked and compared with the observed deviance of the global model. The deviance of the observed model was divided by the deviance from the simulations, and this quotient was used to estimate the variance inflation factor ( $\hat{c}$ ) and to correct for overdispersion in the data.

Once the global model had been defined and the  $\hat{c}$  value estimated, reduced models were run to find more parsimonious models and to evaluate the contributions of the different parameters (Doherty *et al.* 2002). To achieve this, we used model ranking based on the quasi-likelihood Akaike's information criterion adjusted for low sample size (QAIC<sub>c</sub>; Akaike 1973, Burnham & Anderson 2002). Reduced models were considered as potential best models if  $\Delta\text{QAIC}_c < 2$ , unless higher-ranked models were a hierarchical subset of a lower-ranked model. If the latter was the case, the more complex and lower-ranked model was excluded (Burnham & Anderson 2002, Arnold 2010). When the most parsimonious model had been identified, a final set of models was run in which variables were omitted one at a time to assess their individual effect. Alternatively, if an intercept model was ranked highest, main variables were added one at a time to assess their contributions.

To assess the effect of winter temperature on survival and recovery parameters, continuous winter harshness data (based on Hellmann indices) were added as a constraint to the best supported model.

Weighted averages of the estimated effect sizes ( $\beta$ ; Burnham & Anderson 2002) with estimated

unconditional standard errors (Buckland *et al.* 1997) were evaluated for each of the variables, and model averaged real estimates for survival and recovery (i.e. annual estimates) were scrutinized accordingly.

## RESULTS

### Survival in the early trapping period

Among the Mallards captured in 1964–82, 2690 were juvenile males, 1197 adult males, 2063 juvenile females and 459 adult females (Supporting Information Table S1). In total, 853 (13.3%) Mallards were recovered, mostly through hunting (98.7%). Goodness-of-fit testing revealed that there was lack of fit for the global model (model 10 in Table 1). Overdispersion was controlled for by estimating  $\hat{c}$  to 1.40 (i.e. 467.78/335.00).

The highest ranked model for survival included sex. However, this effect was not strong ( $\beta = 0.15$ , SE = 0.11), as also suggested by the small  $\Delta\text{QAIC}_c$  (0.22) when models 1 and 2 were compared (Table 1). Including age in the model (model 3 in Table 1) gave a similar fit to the top model, but was considered unimportant because of high variation relative to the effect size ( $\beta = 0.03$ ,

**Table 1.** Model output from program MARK including survival (S) and recovery (r) parameters for Mallards marked at Ottenby 1964–82 ( $n = 6409$ ). Age is either juvenile or adult, and winter is an index of winter harshness. The global model is no. 9 and was used to estimate the variance inflation factor ( $\hat{c}$ ).

Model	$\Delta\text{QAIC}_c^a$	$w_i^b$	$K^c$
1. $S_{(\text{sex})} r_{(\text{sex}+\text{age}+\text{year})}$	0.00	0.30	23
2. $S_{(.)} r_{(\text{sex}+\text{age}+\text{year})}$	0.22	0.26	22
3. $S_{(\text{sex}+\text{age})} r_{(\text{sex}+\text{age}+\text{year})}$	1.01	0.18	24
4. $S_{(\text{sex}+\text{winter})} r_{(\text{sex}+\text{age}+\text{year})}$	1.56	0.14	24
5. $S_{(\text{sex})} r_{(\text{sex}+\text{age}+\text{year}+\text{winter})}$	2.02	0.11	24
6. $S_{(\text{sex})} r_{(\text{sex}+\text{age})}$	6.21	0.01	5
7. $S_{(.)} r_{(.)}$	9.15	0.00	2
8. $S_{(\text{year})} r_{(.)}$	13.97	0.00	20
9. $S_{(\text{sex}*\text{age})} r_{(\text{sex}*\text{age}+\text{sex}*\text{year}+\text{age}*\text{year})}$	53.71	0.00	62
10. $S_{(\text{sex})} r_{(\text{sex}+\text{year})}^{\S}$	89.61	0.00	22
11. $S_{(\text{sex})} r_{(\text{age}+\text{year})}^{\S}$	94.71	0.00	22

<sup>a</sup>Difference between QAIC<sub>c</sub> of the current model and the minimum QAIC<sub>c</sub> value.

<sup>b</sup>Normalized Akaike weight.

<sup>c</sup>Number of parameters.

<sup>\S</sup>One parameter estimated imprecisely; number of parameters adjusted accordingly.



se = 0.03). This was confirmed by the annual survival estimates with only small differences between sex and age groups; juvenile females: 0.58 (se = 0.03–0.04 for the different years); adult females: 0.58–0.59 (se = 0.03–0.04); juvenile males: 0.61–0.62 (se = 0.02–0.03); adult males: 0.62–0.63 (se = 0.02–0.03). Adding the winter harshness index did not improve model fit and was therefore considered an unimportant predictor of survival ( $\beta = -0.01$ , se = 0.02).

For recovery probability, sex, age and year all initially seemed important based on high  $\Delta\text{QAIC}_c$  values (compare models 1, 6, 10 and 11 in Table 1). However, excluding sex and age from the highest ranked model led to inestimable parameters in models 10 and 11. Evaluation of the effect sizes from the top model confirmed that sex was an important factor ( $\beta = 0.22$ , se = 0.10), whereas age was not ( $\beta = 0.09$ , se = 0.10). Also, the annual recovery estimates verified effects of sex and year, but not of age (Fig. 1). The winter harshness index did not affect recovery probability ( $\beta = 0.02$ , se = 6.43).

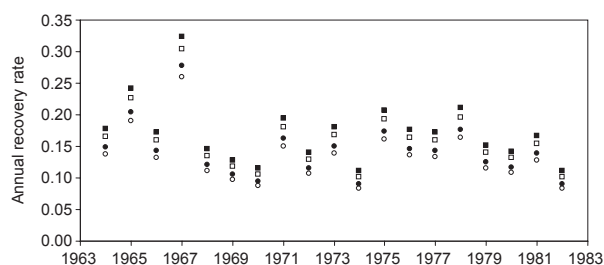
### Survival in the late trapping period

For the years 2002–08, 1759 juvenile males, 707 adult males, 1217 juvenile females and 398 adult females were marked (Supporting Information Table S2). There were fewer recoveries ( $n = 193$ ; 4.7%) compared with the early trapping period, although hunting was still the most common cause of recovery (92.7%).

Goodness-of-fit was tested for model 10 in Table 2, i.e. the most complex model with estimable parameters only. Lack of fit was detected, and  $\hat{c}$

was estimated to 1.59 (99.56/62.64) accordingly. The most parsimonious model (model 1 in Table 2) had no main effects on survival, although models including sex, age and winter harshness (models 2, 4 and 5 in Table 2) had some model weight ( $\Delta\text{QAIC}_c < 2.00$ ; Table 2). However, effect sizes revealed imprecise estimations of these factors (sex:  $\beta = 0.05$ , se = 0.07; age:  $\beta = 0.03$ , se = 0.05; winter:  $\beta = 0.01$ , se = 0.03) and were therefore considered to have minor importance to survival. Annual survival estimates were similar among groups and thus corroborated the absence of age and sex effects: 0.69 (se = 0.05–0.06) for juvenile females, 0.69–0.70 (se = 0.06) for adult females, 0.70 (se = 0.05) for juvenile males and 0.71 (se = 0.05–0.06) for adult males.

Year was not an important factor for recovery as its inclusion resulted in higher  $\text{QAIC}_c$  ( $\Delta\text{QAIC}_c = 7.14$ ; model 8 in Table 2). Sex, age and winter harshness all had some model weight for recovery (models 3, 6 and 7 in Table 2), but based on the effects sizes they were considered to be of minor importance (sex:  $\beta = 0.003$ , se = 0.02; age:  $\beta = -0.02$ , se = 0.03; winter:  $\beta = -0.003$ , se = 0.02). Annual recovery estimates were hence similar among the groups: 0.07 (se = 0.01) in juvenile females and males, and 0.06–0.07 (se = 0.01) in adult females and adult males.



**Figure 1.** Annual recovery rates of Mallard marked at Ottenby, 1964–82. Symbols represent juvenile females (open circles), adult females (filled circles), juvenile males (open squares) and adult males (filled squares). Standard errors range from 0.02 to 0.07.

**Table 2.** Model output from program MARK including survival ( $S$ ) and recovery ( $r$ ) parameters for Mallards marked at Ottenby 2002–08 ( $n = 4081$ ). Age is either juvenile or adult, and winter is an index of winter harshness. The global model is no. 10 and was used to estimate the variance inflation factor ( $\hat{c}$ ).

Model	$\Delta\text{QAIC}_c^a$	$w_i^b$	$K^c$
1. $S_{(.)} r_{(.)}$	0.00	0.27	2
2. $S_{(\text{sex})} r_{(.)}$	1.10	0.16	3
3. $S_{(.)} r_{(\text{age})}$	1.60	0.12	3
4. $S_{(\text{age})} r_{(.)}$	1.69	0.12	3
5. $S_{(\text{winter})} r_{(.)}$	1.90	0.11	3
6. $S_{(.)} r_{(\text{winter})}$	1.98	0.10	3
7. $S_{(.)} r_{(\text{sex})}$	1.98	0.10	3
8. $S_{(.)} r_{(\text{year})}$	7.14	0.01	8
9. $S_{(\text{year})} r_{(.)}$	7.21	0.01	8
10. $S_{(\text{sex} \times \text{age} + \text{sex} \times \text{year} + \text{age} \times \text{year})} r_{(\text{sex} \times \text{age})}$	34.17	0.00	26

<sup>a</sup>Difference between  $\text{QAIC}_c$  of the current model and the minimum  $\text{QAIC}_c$  value.

<sup>b</sup>Normalized Akaike weight.

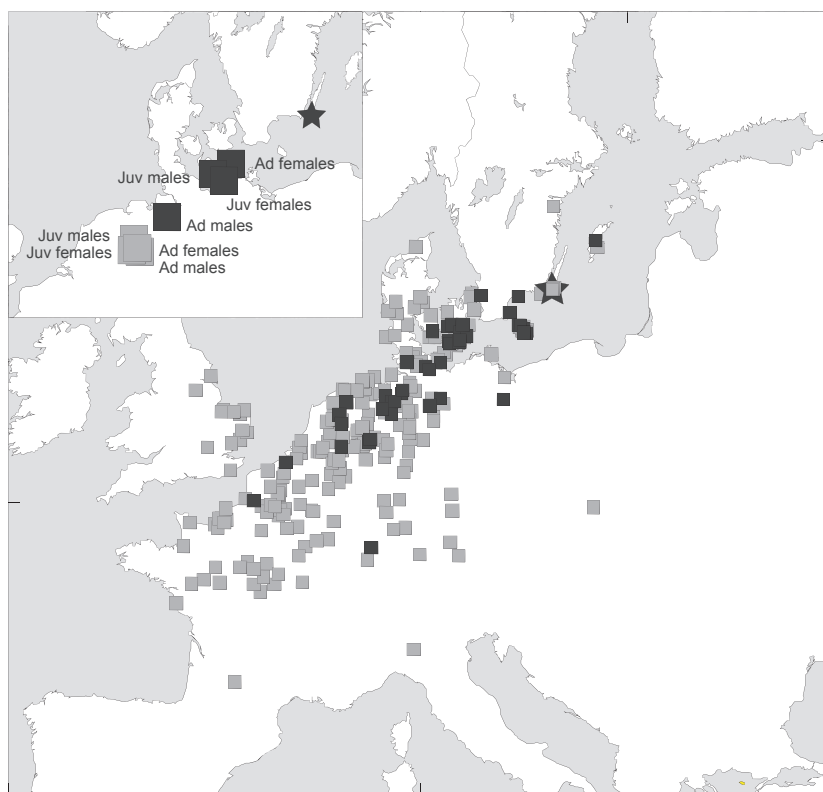
<sup>c</sup>Number of parameters.

### Contrasting early and late trapping periods

Mallards marked in the early trapping period and recovered in winter (December–February) were distributed in western Europe including parts of France and Great Britain, with a mean distance between marking and recovery sites of 752 km ( $se = 25$ ), and only small differences between birds of different age and sex (Fig. 2). Mallards in the late trapping period were recovered much closer to the trapping site (mean = 465 km,  $se = 39$ ) than Mallards in the early trapping period, with no recoveries in Great Britain and only two in northern France (Fig. 2). GLM analyses (dependent variable: distance from marking to recovery; factors: age, and trapping period; covariate: winter harshness index; separate analyses for males and females due to lower precision in fit with data when interaction between sex and winter harshness was excluded) confirmed an effect of

trapping period: males –  $\Delta AIC_c = 5.88$ , the highest ranked model including a period effect only compared with the intercept model; and females –  $\Delta AIC_c = 9.61$ , the highest ranked model including effects of period and winter harshness contrasted with a model including winter harshness only). Age emerged as important for neither males nor females as including the factor resulted in an increase of  $AIC_c$  compared with the model excluding the factor. Winter harshness correlated positively with distance between ringing and recovery sites for females ( $\Delta AIC_c = 2.00$ , highest ranked model including effects of both period and winter harshness contrasted with the model including a period effect only), but not for males (adding winter harshness data resulted in an increase of  $AIC_c$  by 1.96).

Winters in the late period were milder than in the early period (GLM:  $\Delta AIC_c = 25.86$ , contrasting the model including a period effect with the intercept model).



**Figure 2.** Recovery locations of Mallards during December–February marked in the early trapping period (1964–82, dark grey,  $n = 237$ ) were more distant to the ringing site in Ottenby (star) compared with locations in the late trapping period (2002–08, black,  $n = 47$ ). Mean positions, calculated according to formula 3 of Perdeck (1977), for different age and sex classes for the early (dark grey) and late trapping period (black) are shown in the inset figure.

## DISCUSSION

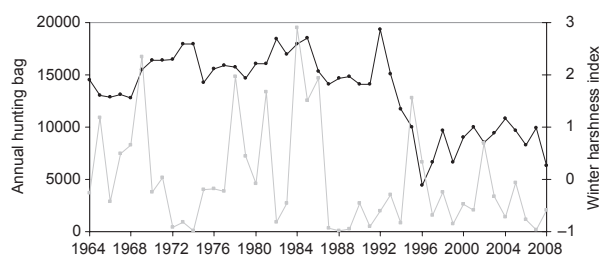
The annual survival of Mallard has increased in northwest Europe over the last five decades from 0.58–0.62 to 0.69–0.71. Most of the earlier studies of birds and climate change have focused on behavioural effects, e.g. timing of breeding, and the distribution of populations (see Introduction for references). Demographic impact has been less studied and mainly concentrated to the breeding season (Crick 2004). The few studies addressing climate change impacts on bird survival during the non-breeding period are mostly from Antarctic regions (e.g. Barbraud & Weimerskirch 2001, Jenouvrier *et al.* 2005, Barbraud *et al.* 2011). A few Atlantic seabirds have been studied in the northern hemisphere, generally with a negative relationship between North Atlantic Oscillation and adult survival (Grosbois & Thompson 2005, Sandvik *et al.* 2005). However, including winter harshness as a covariate in the survival analyses in our study did not directly explain the variation in survival within each time period.

However, winters have become milder in recent decades, and for several reasons we cannot rule out the possibility that higher survival in the late trapping period may in part be explained by indirect impact from weather/climate. First, there has been a simultaneous shift in the mean positions of the recovered Mallards in recent years, perhaps the result of a shorter distance travelled to the winter grounds. Migration is costly (Alerstam 1990) and if less energy is spent on migration, more resources can instead be allocated to body condition, which may enhance survival (Bergan & Smith 1993). A shorter migration distance could explain the finding of Gunnarsson *et al.* (2011) that body mass of Mallard along the northwest European flyway has increased in recent years. Also, the shift in winter distribution, as suggested by our results, could explain why the number of wintering Mallards has increased in Sweden over the past 40 years (Nilsson 2008). Similar trends for within-winter movements have previously been reported for Mallard in different parts of Europe, with suggestions that such trends could be due to warmer winters in recent decades or possibly to changes in the reporting of recovered birds (Sauter *et al.* 2010, see also Robinson *et al.* 2009). Sauter *et al.* (2010) rejected the 'reporting probability' hypothesis, and instead found support that movements were positively related to winter harshness. We also find a winter

harshness effect, but only for females, which may be due to males being less sensitive than females to lower temperatures due to their greater body mass (Saylor & Afton 1981). Nevertheless, an impact of winter harshness on the movements of Mallards has significant bearing in a climate change context, as winters have become milder (Klein Tank *et al.* 2002). Although there was no direct effect of winter temperature on Mallard survival, indirect effects could therefore not be ruled out, as a shorter migration, possibly due to milder winters in recent years, may have enhanced their survival.

Although speculative, an alternative explanation for higher Mallard survival in recent years is related to a direct effect of changes in duck hunting activity. First, the hunting pressure hypothesis is not mutually exclusive from the migration cost hypothesis described above, as hunting efforts may be higher in more southern areas than in northern (although there are no accurate hunting bag data available to help distinguish between causes). Alternatively, it is possible that hunting pressure has decreased. Annual recovery rates in the early trapping period were generally higher than in the late trapping period, and although causal relationships cannot be described by simply correlating survival rates with hunting bag statistics, it is possible that duck hunting in northern Europe has become less popular in recent years. Although estimates are generally imprecise, hunting bag data exist for ducks in Europe, but for Mallard there arises the problem of introductions of large numbers of hand-reared birds, which are likely to be over-represented in the hunting bag record. In contrast, such birds are probably under-represented in the duck trap at Ottenby, which mainly captures migratory and wild ducks. It is therefore inappropriate to use the Mallard as a representative of hunting trends of wild dabbling ducks. The second most common waterfowl game species in Europe is the Eurasian Teal *Anas crecca* (Hirschfeld & Heyd 2005), which is not subjected to massive introductions and so perhaps a surrogate for hunting intensity of wild Mallard. In Denmark (Fig. 63 in Bregnballe *et al.* 2003) and Sweden (Fig. 3 in this paper, Table 26 in Ottvall *et al.* 2008) fewer Eurasian Teal have been harvested in recent years than in earlier decades. If this trend holds for wild Mallard, lower hunting pressure may have affected survival rates directly.

However, patterns including hunting effects may be more complex, as responses and causes may also include other factors, directly as well as



**Figure 3.** The estimated number of Eurasian Teal in the Swedish harvest (in black) and a winter harshness index (in grey) from 1964 to 2008. Low values of the winter harshness index indicate mild winters. Hunting bag data were compiled by The Association for Hunting and Wildlife Management, Wildlife Monitoring (Sweden), and the winter harshness data are based on the first principal component of the Hellmann indices with weather data sampled at five weather stations around the Southern Baltic Sea.

indirectly, such as weather. Harsh weather may affect the body condition, which in turn not only affects survival directly (Bergan & Smith 1993) but also the propensity to be hunted (Hepp *et al.* 1986, Dufour *et al.* 1993, Robb 2002). Hunting data on Eurasian Teal do not necessarily reflect hunting pressure on Mallards, but the positive population trend of Teal in northwest Europe (Delany & Scott 2006) may result from lowered hunting pressure of the species (Fig. 3), and changes in hunting pressure could similarly affect Mallard. Nevertheless, there does not seem to be any direct or 1-year-delayed connections between winter harshness in the southern Baltic Sea region and the annual hunting bag (Fig. 3). There is, however, a general negative trend over past decades for both parameters (Fig. 3), which coincides with higher survival of Mallard in recent years. Still, the data do not enable us to disentangle hunting and winter harshness effects, nor their reciprocal connection.

Annual survival was relatively stable among age and sex groups. Some of the best supported models included sex and age factors, but from the effect sizes and their variation, these effects were minor. Although Gunnarsson *et al.* (2008) match our findings, others have detected sex effects in Mallard survival. In those studies, annual survival is most often higher for males (Table 14.1 in Johnson *et al.* 1992, Lake *et al.* 2006), suggesting that females have higher mortality rates due to predation while nesting, or due to energetic constraints imposed by incubation

and brood-rearing (Johnson & Sargeant 1977, Johnson *et al.* 1992). Higher female mortality during breeding may skew the sex ratio, which could result in more recovered males than females during the hunting season (Johnson & Sargeant 1977). Such a pattern was found for Mallard in the early trapping period, both in the number of recovered birds and in the estimated recovery probabilities (Fig. 1). Similar figures have also been reported for Mallards marked in Finland (Gunnarsson *et al.* 2008). In contrast to our results, age effects are regularly reported, with lower survival for juveniles than for adult ducks (e.g. Table 14.1 in Johnson *et al.* 1992), older birds perhaps being more experienced in avoiding threats. However, there seems to be no general pattern, as other studies report similar survival estimates for different age classes (Gunnarsson *et al.* 2008), and discrepancies between studies are possibly due to site-specific impacts from, for example, hunting pressure, predation and environmental factors. Inconsistencies have implications in management actions, underlining the importance of accounting for variation in biotic as well as abiotic variables (cf. adaptive harvest management of North American waterfowl, reviewed by Nichols *et al.* 2007).

Possible direct and indirect impacts of winter temperature on the survival of dabbling ducks in non-breeding periods have not been studied in northern Europe before. We encourage further research on the impact of environmental variables and hunting on the vital rates in dabbling ducks, emphasizing that effects may not only be direct but also indirect through changes in behaviour patterns such as migration.

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## SUPPORTING INFORMATION

Additional Supporting information may be found in the online version of this article:

**Table S1.** Number of Mallard (juvenile and adult females and males) marked and recovered (in parentheses) 1964–82.

**Table S2.** Number of Mallard (juvenile and adult females and males) marked and recovered (in parentheses) 2002–08.

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