2014

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Understanding how organisms adjust breeding dates to exploit resources that affect fitness can provide insights into impacts of climate change on avian demography. For instance, mismatches have been reported in long-distance migrant bird species when environmental cues experienced during spring migration are decoupled from conditions on breeding grounds. Short-distance migrant bird species that store reproductive nutrients prior to breeding may avoid or buffer adverse phenological effects. Furthermore, reduced short-term reproductive success could be offset by higher future recruitment of surviving offspring. We evaluated whether recruitment of locally-hatched female offspring was related to hatching date alone or strength of mismatched breeding date for 405 individually-marked adult female common goldeneyes *Bucephala clangula* (a short-distance migrant) and their ducklings from a site in central Finland where ice-out date has advanced by ~2 weeks over 24 yr. Path analyses revealed that older, early-nesting females with good body condition and larger broods recruited the most female offspring. Offspring recruitment decreased strongly among females that bred late relative to other females in the population each year; the extent of mismatched breeding date, i.e. hatching date scaled to annual ice-out date, was less influential. Overall, most females advanced breeding dates when ice-out occurred earlier in spring, but some females exhibited greater flexibility in response to ice-out conditions than did others. In general, directional selection favoured early breeding over a wide range of ice-out dates. Our results seem most consistent with a hypothesis that some short-distance migrant species like goldeneyes have the capacity to track and respond appropriately to changing environmental conditions prior to onset of breeding.

Responses of organisms to global climate change have been the focus of much ecological research in recent years (Walther et al. 2002, Parmesan and Yohe 2003, Møller et al. 2010). For example, several large-scale analyses indicate that timing of breeding in birds has advanced with warming spring temperatures (reviewed by Dunn and Winkler 2010). Despite potential to advance breeding date in response to changing temperatures (Charmantier et al. 2008), Visser et al. (1998) reported that individual great tits *Parus major* were unable to fully adjust breeding dates to exploit earlier peaks in food resources; they interpreted their findings in the context of a 'match–mismatch' hypothesis proposed to explain recruitment processes in marine fishes (Cushing 1974). This explanation has since been extended to other terrestrial systems to account for population declines in migratory birds that are unable to adjust migration schedules (Both et al. 2006).

Intra and interspecific analyses suggest that short-distance migrants may be better able to adjust timing of breeding due to closer contact with local phenological cues than are long-distance migrants (Both and te Marvelde 2007, Durant et al. 2007, Møller et al. 2008, Both et al. 2010, Jones and Cresswell 2010, Rubolini et al. 2010), although the veracity of this claim has been questioned (Knudsen et al. 2011). Collectively, this body of work has profoundly improved our understanding about the influence of seasonally-interacting factors on breeding times and productivity in terrestrial and marine bird species. Although phenological response of birds to variation in climatic conditions has been studied extensively, especially in terms of the timing of spring migration and breeding (reviewed by Møller et al. 2010, Saino et al. 2011), studies addressing fitness consequences of those responses are more limited (Nussey et al. 2005, Charmantier et al. 2008). To understand and predict effects of climate change on population dynamics we need to know effects of changing phenology on offspring recruitment.

Variation in breeding success of migratory birds may be related to carry-over effects of conditions on spring migration or wintering areas, timing of migration or breeding, food conditions, offspring characteristics, weather-related

events and even chance events (Forslund and Pärt 1995, Verhulst and Nilsson 2008). Within species, annual and lifetime reproductive success may also be related to parental age, quality and experience, as well as longevity and stochastic events (Newton 1989, Grant and Grant 2000, Blums and Clark 2004). The impact of environment changes may also be mediated by parental quality and age. Two or more mechanisms acting in widely-separated areas could influence reproductive success of migratory animals, so it is often difficult to evaluate hypothesized causes of fitness variation. Other than the classic work on sedentary great tits (Visser et al. 1998), and more recent Finnish studies on sedentary precocial black grouse *Tetrao tetrix* (Ludwig et al. 2006) and willow tit *Poecile montanus* (Vatka et al. 2011), we are not aware of studies addressing phenological effects in relatively sedentary or precocial birds, including short-distance migrant species. Furthermore, how individuals adjust their timing of breeding in response to changing phenology is often evaluated in terms of short-term reproductive success rather than offspring recruitment so the net impact of longer-term or interacting population processes could be overlooked (Wilson and Arcese 2003, Ahola et al. 2012). Thus, the generality of climate–breeding time interactions could be clarified by further tests based on long-term studies of species that can store reproductive nutrients (e.g. capital breeders) or short-distance migrant species (see also Visser and Both 2005, Dunn and Winkler 2010).

Testing whether individuals express phenotypic plasticity and determining to what extent individuals differ in their plasticity could provide important insights into climate change effects (Charmantier et al. 2008, Love et al. 2010). Mechanisms advanced to explain observed population level responses to climate change include phenotypic plasticity and selection against a particular strategy (i.e. microevolution; Sheldon 2010). Climate-change-driven phenotypic plasticity has been demonstrated (Gienapp et al. 2008, Sheldon 2010), including in studies with individual data on the timing of breeding (Brommer et al. 2008, Reed et al. 2009, Husby et al. 2010, Porlier et al. 2012). Here, we evaluate simultaneously effects of age, quality, reproductive investment and timing of hatching on annual offspring recruitment patterns in a short-distance migrant bird species, the common goldeneye *Bucephala clangula* (hereafter, goldeneye). The goldeneye is a cavity-nesting diving duck with precocial (mobile, self-feeding) offspring and uniparental female care. Recent population estimates indicate that the European population of common goldeneye is stable (Delany and Scott 2006). We exploited a 26-yr mark–recapture data set for adult female goldeneyes and their female offspring breeding in central Finland. We focused on females because, like other waterfowl (Anderson et al. 1992), female offspring and adult females are philopatric to the breeding site (Ruusila et al. 2000, 2001). We tested whether females with late breeding dates relative to local spring phenology would recruit fewer offspring, after controlling for possible mediating effects of parental age and quality, annual timing of breeding and levels of reproductive investment. Alternatively, if females are able to time their breeding dates to correspond closely with local environmental cues, then offspring recruitment may be unrelated to spring phenology. Thus, we also evaluated and described the extent to which goldeneye females exhibit phenotypic plasticity in the timing of breeding in response to varying spring environmental conditions.

Material and methods

Study area

Work was conducted near Maaninka, central Finland (63°09′N, 27°17′E). The study area consists of 23 lakes and ponds and four bays of larger lakes, surrounded by agricultural land and intensively managed mixed and coniferous forests. The size of the study area increased in the first years of the study and reached its current size (ca 280 km^2) in 1989 (Ruusila et al. 2000, 2001).

Lake ice conditions were monitored from late winter through early spring to determine dates when most study area lakes were ice-free. Here, we used ice-out dates from Lake Maaninkajärvi located in the middle of the study area; ice-out date was the date when it was possible to cross the lake in a rowboat. The ice-out dates from Lake Maaninkajärvi were strongly correlated (r = 0.885, p < 0.0001, n = 23 yr) with those from the nearest lake (Lake Kallavesi, ca 40 km apart) used in the national monitoring of lake ice conditions by the Finnish Environment Inst. (Korhonen 2005). In general, the dates of ice break-up are strongly correlated between lakes within a region (Oja and Pöysä 2007, Dessborn et al. 2009 and references therein). Furthermore, there was a positive correlation (r = 0.552, p = 0.003, n = 27 yr) between annual local lake ice-out dates and regional spring snow cover duration estimated using Northern Hemisphere spring snow cover data, derived from multiple satellite sources (Brown and Robinson 2011). Hence, we are confident that the ice-out dates from the Lake Maaninkajärvi properly measure overall ice conditions on the study area.

Goldeneyes breeding in northern Europe winter mainly in the Baltic and North Seas (Scott and Rose 1996). As reported in another area of southeast Finland (Pöysä 1996), paired females in the present study area arrive on breeding lakes prior to ice-off, staying and feeding in an ice-free whitewater (Viannankoski) and two larger open-water sites (Ruokovirta and Mustavirta) that are free of ice considerably earlier than other lakes in the area. Diets of adult females consist mainly of animals, including molluscs, small crustaceans, dytiscid beetles and larvae and dragonfly larvae (Cramp and Simmons 1977). Goldeneye ducklings are mobile, leave the nest soon after hatching and feed themselves, generally on a diet similar to that of adults (Eriksson 1976 and references therein).

Reproductive performance of female goldeneyes

The number of nest boxes increased from 63 to ~470 during 1984–2010, and occupancy was < 100% in every year. Nest boxes were checked for eggs in late April or early May and boxes with no eggs present during the first survey were checked again ~2 weeks later. After that, unoccupied nest boxes were visited at least one more time during the breeding

season. All nesting attempts were recorded and classified as successful (≥ 1 duckling left the nest box) or unsuccessful (no young left the nest box). Unsuccessful nesting attempts were further identified as depredated, deserted during egg laying or deserted during incubation. Adult female goldeneyes were captured in the nest boxes a few days prior to hatch. Females were weighed (with a spring scale to the nearest 1 g), measured (wing length measured with a wing rule to the nearest 1 mm) and marked with standard numbered leg bands. Unmarked females were recorded as 3 yr old (Milonoff et al. 2002). All ducklings were banded at hatch using plasticine-filled leg bands similar to those described in Blums et al. (1999). Subsequent recaptures and recoveries of these birds provided data on recruitment; thus, exact age could be determined for females marked as ducklings. Hatching date and the number of ducklings banded (brood size) were recorded for each brood; hatch date was known exactly for each brood since ducklings leave the nest, and therefore were ringed, within 24 h from hatching.

Nests that failed before females were captured and identified were excluded. One might ask if the exclusion of failed nests could mask putative effects of varying breeding phenology. Most (38%) failed nests (n = 459, 1985–2008) were deserted during egg laying, likely due to conspecific brood parasitism (Paasivaara et al. 2010). About 29% of nests were abandoned during incubation for reasons other than human disturbance or predation. We estimated the start of egg laying for successful nests and for nests deserted during incubation by back-calculating from the visit when a nesting attempt (≥ 1 egg) was first recorded. For all nests we assumed it takes 1.5 d to lay one egg, except if final clutch size was ≥ 9 eggs, in which case we assumed egg laying had taken 14 d (to adjust for parasitic eggs; see also Eadie et al. 1995). For nests found during incubation, we used egg floating to estimate stage of incubation with an accuracy of 1 day (PR unpubl.). We compared the start of egg laying between nest types (i.e. deserted during incubation and successful) with linear mixed models including year as a random factor, ice-out date as a continuous fixed effect, and an interaction between nest type and ice-out date; in other words, to see if possible differences in egg-laying date between the two types of nests vary with ice-out conditions. We found that egg laying date varied with ice-out date ($F_{1,1478} = 61.16$, p < 0.001) but not with nest type ($F_{1,1478} = 0.22$, p = 0.641), and there was no interaction between nest type and ice-out date ($F_{1,1478} = 0.65$, p = 0.420). In a simplified mixed model, egg laying started earlier in successful nests than in deserted nests ($F_{1,1501} = 26.91$, p < 0.001). However, annual difference between the mean date of the start of egg laying in deserted clutches and the mean date of the start of egg laying in successful clutches (i.e. the former minus the latter) was only 5.3 d (range = −8.5 to 17.7 d; note that in some years deserted clutches were started earlier than successful clutches), an inconsequential difference considering overall variation in relative timing of breeding within a year (cf. reproductive success in relation to relative hatch date in Fig. 2). Therefore, we do not believe that excluding abandoned nests masked putative effects of varying breeding phenology.

Females do not start nesting until they are at least 2 yr old, so we included nest records until 2008 because offspring marked at these nests could be recaptured in 2010. We also excluded nests monitored in 1984 because the study was beginning and few known-age females were available in the population. Relative hatch date was calculated each year by subtracting the annual date when 5% of all nests had hatched from a nest's hatch date.

Spring phenology

Local ice phenology affects timing of breeding in ducks, including goldeneyes (Oja and Pöysä 2007). Other studies have demonstrated that the timing of ice break-up may affect lake physical and chemical conditions (Weyhenmeyer 2009), and the phenology and population processes of different species throughout the aquatic food web (Adrian et al. 1999, Weyhenmeyer et al. 2008). Moreover, because the timing of ice break-up is driven by air temperature and regional atmospheric circulation (Weyhenmeyer 2001, 2009, Blenckner et al. 2004), it is a useful integrated measure of critical environmental variables. Therefore, we suggest that the timing of ice break-up provides a biologically sound basis to assess phenological events in goldeneye breeding (Love et al. 2010). To account for annual variation in ice-out date and nesting phenology, we computed an annual index for each female's nesting attempt as, breeding phenology index = (hatch date − ice-out date), with both dates being scaled to 1 January (day 1). Thus, a larger index signified a later hatch date relative to annual ice-off date for the study area.

Statistical analyses

Associations between variables were measured with correlation and linear regression techniques (Zar 2009), whereas path analysis was used to evaluate interrelationships among explanatory variables and reproductive success (Hatcher 1994, Shipley 2000). Path analysis is ideally suited for assessing multiple causal pathways in complex natural systems (Kingsolver and Schemske 1991). All analyses described below were executed in SAS (SAS Inst. 2004).

We related the number of recruits produced per brood to hatch date, breeding phenology index or relative hatch date while considering effects of other explanatory variables in a common analytical framework (PROC Calis). We presumed that the number of recruited offspring could be positively related to female age or body condition, as reported for some avian species including other duck species in the Baltic region (Blums et al. 2002). Older females are typically heavier and may produce larger broods than younger, light-weight individuals (controlling body size as indexed by wing length); finally, we expected that number of recruited offspring could be positively related to brood size, and negatively related to breeding phenology index, hatch date or relative hatching date. Larger females or those with good body condition might initiate clutches earlier than smaller, light-weight individuals, but we could not adequately test these ideas because females were captured in late incubation. In all analyses described below, we obtained similar results when we used the total number of young that

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were either recruited (females) or shot (both sexes) as > 1 yr old; this last finding for older birds of both sexes implies that natal dispersal had limited impact on our conclusions (see also Blums et al. 2002). We only report results for female recruitment because few banded juveniles of either sex were shot later in life, and we did not have to make unverifiable assumptions about lack of annual variation in hunting effort or success (e.g. the number of juveniles reported shot by hunters each year decreased during the study; $r = -0.779$, $p < 0.001$, $n = 24$ yr).

To improve multivariate normality, body mass was square-root transformed, and extreme values of some variables were truncated by pooling with less extreme values. Female age was recoded to a maximum of 7 yr. In all path analyses, models were simplified on the basis of modification indices provided by SAS; although path analysis with large sample size is robust to non-normal data (Shipley 2000: 188), fit of alternative models was evaluated using χ^2 values (low values [large p values] signify better fit), goodness of fit index (GFI, where 1 is best fit) and inspection of multivariate residuals (Hatcher 1994: 197). Generalized linear modeling procedures also confirmed that path analysis results were robust (Supplementary material Appendix 2, Tables A2.1, A2.2); however, path analysis is explicitly designed for evaluating inter-relationships of correlated variables.

Path analysis also allows for exploration of alternative models in which covariance is estimated between correlated explanatory variables like female age and phenology measurements (Hatcher 1994: 157, 179). Obviously, breeding phenology index, hatch date and relative hatch date were positively correlated, and none has logical primacy over another, so we used two path analysis models that linked female age and 'date' effects via covariance estimates, while also enabling us to compute direct and indirect effects of all explanatory variables on offspring recruitment via path coefficients. The first of these models linked three measurements of phenology (i.e. hatch date, breeding phenology index and relative hatch date) whereas the second model allowed hatch date and breeding phenology index to compete for data. Then, we conducted a third path analysis to explore directly the inter-relationships among ice-out date, hatch date and other explanatory variables; here, hatch date was assumed to respond to variation in ice-out date (i.e. a direct casual path linked ice-out date to hatch date). Finally, we conducted a path analysis that included the best-supported date-specific explanatory variable determined from the initial sets of path analyses described above.

We used randomization procedures to evaluate the fit of final path models (Manly 1997). For this assessment, path analysis was performed with data sets composed of one randomly-selected annual record for each female ($n = 405$), a process that was repeated 1000 times. We retained and reported medians (and in some cases 2.5 and 97.5% values, i.e. 95% confidence interval [CI]) taken from the distributions of 1000 values of standardized path coefficients, GFI and χ^2 (and associated p) values.

Phenotypic flexibility in timing of breeding (indexed by hatch date, 1985–2010) was estimated with mixed models (fixed and random effects; PROC Mixed), following Charmantier et al. (2008); models were compared using

likelihood ratio tests. Clutch initiation (first egg) and hatch dates were strongly correlated ($r = 0.944$, $p < 0.001$, $n = 499$), so we used hatch dates to increase sample sizes. Mixed model analysis was performed for females with ≥ 3 breeding attempts to balance both sample size and breeding experience, but we also evaluated the robustness of these results by repeating the analysis for females with 2, 4 and 5 breeding attempts (Charmantier et al. 2008). Finally, strength of selection on (relative) timing of breeding was estimated with generalized linear models (Poisson regression; PROC Genmod) by relating the number (i.e. 0, 1, ≥ 2) of females recruited per brood to their relative hatch dates (Janzen and Stern 1998). We also categorized data into early and late years according to ice-out date, and reran analyses. Approximate selection gradient ($\beta_{avggrad}$) was estimated using methods described by Janzen and Stern (1998: 1567).

Results

Environmental conditions and nesting

Annual mean ice-off date advanced by ~13 d during the study (linear regression: $\beta = -0.535 \pm 0.190$ SE, $p = 0.010$, $n = 24$ yr [1985–2008]), from mid-May in the mid-1980s to end of April by the mid-2000s (Fig. 1; Supplementary material Appendix 1, Table A1); annual mean hatch date also gradually advanced over time ($\beta = -0.342 \pm 0.125$, $p = 0.012$, $n = 24$ yr; Fig. 1). Mean hatch date was positively related to annual ice-out date ($\beta = 0.589 \pm 0.060$, $p < 0.001$, $n = 24$ yr), implying that in general female goldeneyes were able to adjust their nesting dates in response to changing spring conditions, but mean breeding phenology index tended to increase over time ($\beta = 0.192 \pm 0.103$, $p = 0.074$, $n = 24$ yr). Measurement of adjusted relative recruitment rate did not change over this time period ($\beta = 0.0005 \pm 0.0005$, $p = 0.31$), nor did annual mean brood size ($\beta = -0.008 \pm 0.014$, $p = 0.59$; Supplementary material Appendix 1, Table A1).
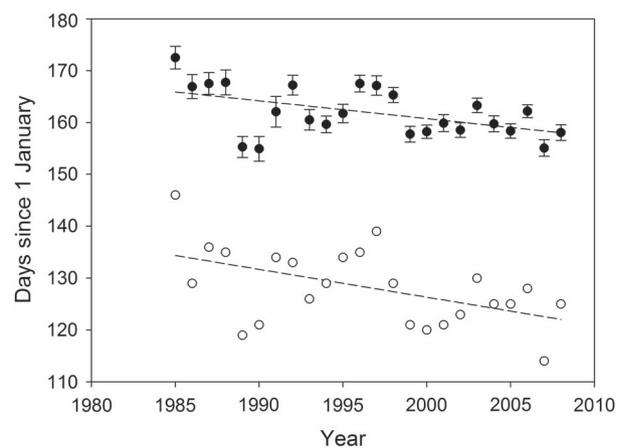

Figure 1. Annual estimates of ice-out (open circles) and mean hatch ($\pm$ SE; closed circles) dates, central Finland, 1985–2008. Day 150 is 30 May (151 in leap years). Annual median number of broods was 56, and ranged from 21 (1985) to 89 (2005). Dashed lines were estimated by linear regression (see text for details).

General patterns of reproductive success

From 1985–2008, 405 adult females were individually marked at nests that hatched successfully; 129 (32%) of these birds produced one brood during their lifetime, 197 (49%) produced 2–5 broods, and 79 (19%) females produced 6–14 broods. Median brood size was 8 ducklings (5–95% values = 5–12 ducklings; n = 1374). From 1374 broods that hatched during this period, 454 individuals were shot as juveniles in their first year of life, 38 were reported shot by hunters at least one year later and 128 adult females that had been banded as ducklings were recaptured on nests. The annual number of recruited females averaged 5.3 (range = 1–18); after adjusting for number of banded ducklings, 50:50 sex ratio (Blums and Mednis 1996) and removal of juvenile females shot by hunters, annual recruitment rate averaged 2.5% (range = 0.3–5.5%). Most adult females (79%) produced no detected female recruits over their lifetime, with the remainder producing 1–5 females.

Overall, reproductive success tended to decrease seasonally, especially in terms of female recruitment to the breeding population (Fig. 2). The earliest broods produced relatively high numbers of recruited females, whereas late broods produced few. The number of male and female juvenile (< 1 yr old) goldeneyes shot by hunters revealed a weaker seasonal pattern of offspring survival.

Correlates of offspring recruitment

Path analyses were based on 1374 broods produced by 405 adult females (2 yr or older) with complete information for all explanatory variables. For initial analyses, we estimated
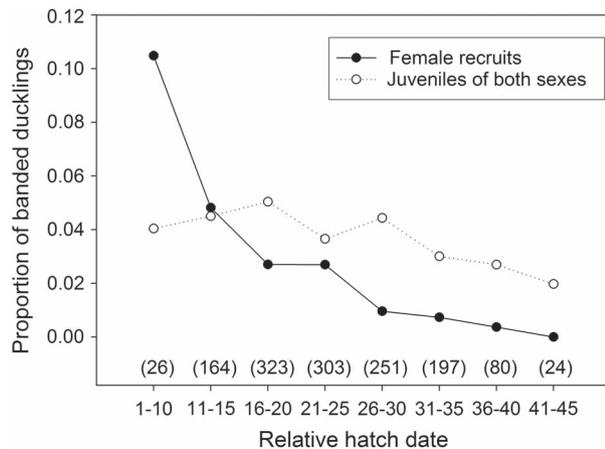
Figure 2. Proportions of banded ducklings either recaptured as breeding females (female recruits; closed circles) or reported shot by hunters as juveniles (< 1 yr old; open circles) in relation to relative hatch date periods (in days), central Finland, 1985–2010. Number of broods is shown in parentheses. The proportion of females shot (and recruited) was adjusted to account for an assumed 50:50 sex ratio; the number of recruited females was further corrected for the number of females shot by hunters each year as estimated by: (known-sex females + [juveniles of unknown sex × C]), where C was calculated as: (1 − [juvenile females shot (n = 32)/total known-sex juveniles shot (n = 86) = 0.372]), using the ratio of known-sex juveniles reported in all years.
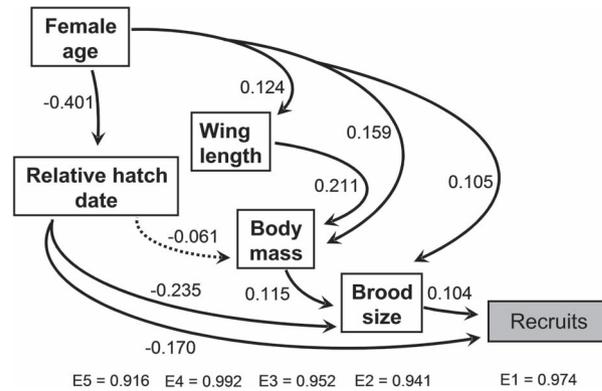
Figure 3. Relationships among explanatory variables and offspring recruitment for adult female common goldeneyes from Finland, 1985–2010. Shown are median values of standardized path coefficients for each of the variables obtained via randomization (see text for details), and median residual errors (E1 [recruits] – E5 [relative hatch date]), corresponding to each exogenous variable (right to left) in the path analysis. The relationship (dotted line) between relative hatching date and female late incubation body mass is equivocal. Summaries for the direct and indirect effects of each variable on offspring recruitment are given in Table 1.

covariances among female age, breeding phenology index, hatch date and relative hatch date, and linked these and remaining explanatory variables to offspring recruitment with putative causal pathways. Relative hatch date consistently out-performed hatch date or breeding phenology index as a predictor of offspring recruitment (Supplementary material Appendix 3, Tables A3.1, A3.2); likewise, we detected only weak evidence of generally higher recruitment of female offspring from years with earlier ice-out dates (Supplementary material Appendix 3, Table A3.2). Therefore, we focused on effects of relative hatch date in the next analysis.

The best-supported model containing relative hatch date had ten path coefficients, standardized residuals < |1.80| and fit the data well (GFI = 0.998; χ^2 = 9.49, DF = 5, p = 0.09; Fig. 3). The randomization procedure indicated very good model fit, with median GFI = 0.995 (95% CI = 0.988–0.999), and χ^2 and p-values of 6.24 (95% CI = 1.47–15.19) and 0.310 (95% CI = 0.009–0.911), respectively. The strongest correlate of offspring recruitment was relative hatch date and, with brood size, was the only variable with a direct effect on recruitment (Table 1).

Table 1. Direct, indirect and combined effects of explanatory variables on offspring recruitment for female common goldeneyes, Finland, 1985–2010, as estimated by path analysis. Indirect effects were computed by summing the products of all indirect median path coefficients from each explanatory variable to the number of offspring recruited from each brood (Fig. 3). The combined effect is the sum of direct and indirect median path coefficients.

Explanatory variable	Direct paths	Indirect paths	Combined effect
Female age	0	+0.091	+0.091
Relative hatching date	−0.170	−0.025	−0.195
Wing length	0	+0.003	+0.003
Body mass	0	+0.012	+0.012
Brood size	+0.104	0	+0.104

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Higher offspring recruitment was related most directly to earlier nesting by older females, but recruitment was not directly related to female age.

Phenotypic plasticity and selection in relation to hatch date

Timing of breeding varied among females, and some females exhibited a more flexible response to spring ice-out conditions than did other females as judged by the female $\times$ ice-out date interaction (Table 2), consistent with evidence of individual by environment interaction (i.e. I $\times$ E; Nussey et al. 2007). Similar results were obtained when analyses were repeated using females with two, four, or five lifetime breeding attempts.

Overall, directional selection favoured early breeding ($\beta_{avggrad} = -0.471 \pm 0.064$ SE), as anticipated on the basis of path analysis results. We did not detect stabilizing selection on nesting date (p = 0.15), consistent with the general female recruitment pattern illustrated in Fig. 2, nor was there an interaction between relative hatch and ice-out dates (p = 0.11). Stronger selection for early breeding was not evident when ice-out was delayed (early years, $\beta_{avggrad} = -0.484 \pm 0.083$ SE, n = 836 broods; late years, $\beta_{avggrad} = -0.451 \pm 0.102$ SE, n = 538 broods), implying that early breeding is generally advantageous regardless of ice-out date.

Discussion

Reproductive success in common goldeneyes was directly related to timing of breeding, with early-hatched nests recruiting relatively more female offspring than late nests; this relationship was driven largely by earlier nesting among older females. Many females in this population were able to shift breeding time to coincide with changes in local spring phenology which spanned wide variation in the timing of spring thaw (range = 32 d). In general, selection favoured early breeding regardless of the timing of ice-out from lakes. Furthermore, while individual females responded strongly to

Table 2. Phenotypic plasticity in hatch dates of female common goldeneyes in response to changing spring phenology (as indexed by ice-out dates of local lakes), central Finland, 1985–2010. Random and fixed effects were estimated using the restricted maximum likelihood method in mixed effects models for 1212 breeding attempts made by 225 females (i.e. three or more attempts per female) over 26 yr. Ice-out date was mean-centered; nonlinear effects of ice-out date were not detected. Likelihood ratio tests are shown for nested models of increasing complexity (top to bottom). NA is not applicable and DF is degrees of freedom.

Random effects	Log (likelihood)	Likelihood ratio test	
		ΔDF	Likelihood ratio
NA (intercept-only model)	−4313.1		
NA (fixed effects only)[a]	−4079.3	3	467.5***
Year	−4065.2	1	28.2***
Year, female	−3904.2	1	322.0***
Year, female, female × iceout date	−3900.3	1	7.9**

[a] fixed effects are ice-out date, female age, female age^2.
*** signifies p < 0.001; ** p < 0.01.

changing ice-out conditions, some females seemed more flexible than others in terms of adjusting to these varying spring conditions (Table 2). Early breeding could be counter-balanced by costs of lower duckling survival when ice remains on lakes at the time of hatching, but we did not observe this phenomenon nor did we detect evidence of stabilizing selection on hatch date.

The importance of early breeding has also been demonstrated earlier in goldeneyes (Milonoff et al. 1998), as well as in other waterfowl and numerous taxa (Clutton-Brock 1988). For example, Blums et al. (2002) reported that early-breeding adult females produced relatively more recruited offspring in three duck species nesting in Latvia; Blums et al. were also able to estimate correlates of duckling survival (using locally shot juveniles as a surrogate for survival), but we were unable to do this with certainty because fall hunting effort varied annually and gradually decreased over the study period in Finland (PR unpubl.). Despite this possible bias, duckling survival tended to decrease in late-hatched broods (Fig. 2). Furthermore, a study of radio-marked goldeneye females in southern Finland revealed that hatch date and weather conditions did not affect duckling survival during their first week of life, whereas female body condition did (Paasivaara and Pöysä 2007); only about 47% of the ducklings survived their first week in that study. Regardless, if duckling survival was related more strongly to the breeding phenology index than to relative hatch date in the present study, population processes occurring between fledging and first breeding were sufficient to offset any deleterious effects of delayed nesting that were additive to effects of hatching date. A plausible mechanism for some species would involve density dependence, for instance, with higher survival rates in older pre-breeding cohorts following high mortality of pre-fledged offspring.

Lower recruitment of late-hatched ducklings could possibly be interpreted as a form of 'mismatch'. Females that were capable of advancing their nesting dates produced virtually all recruited offspring, suggesting that their ability to respond to spring phenology (i.e. ice-out) was critical; thus, in a sense, late-nesting females may be strongly mismatched with prevailing environmental conditions. This pattern could potentially arise due to differences in phenotypic quality and flexibility, effects that we could not fully ascribe to those of age, body mass and brood size. After accounting for effects of these last three factors with path analysis, the direct effect of relative hatching date was −0.195, implying that environmental and individual qualities had similar effects on processes affecting offspring recruitment (Table 1). We were unable to weigh females prior to egg-laying but recognise that the importance of body mass may be stronger if heavier females start nesting earlier than light-weight individuals.

Older females nested earlier, were bigger (as indexed by wing length), heavier when captured just prior to hatch, produced larger broods and, thus, were more productive than were younger females (Fig. 3). That only ~21% of females produced virtually all recruits is consistent with patterns reported for other vertebrates (Clutton-Brock 1988, Newton 1989) including several duck species (Blums and Clark 2004). Previous analyses of factors affecting recruitment processes in this goldeneye population had much smaller sample size of recruits (n = 31) and used statistical

techniques (pair-wise comparisons in terms of brood size, timing of nesting and female age; for details see Milonoff et al. 1998) that could not distinguish direct and indirect effects of explanatory variables. Therefore, even though hatching date and female age both affected recruitment rate, it was not possible to assess the relative contribution of age per se to reproductive success (Milonoff et al. 1998). The path analysis results presented here were based on four times more data and revealed that female age did not directly affect offspring recruitment; rather, an age effect is mediated via indirect effects on timing of breeding, body condition and brood size. Age-related experience does not seem to be a major driver of recruitment production in goldeneyes, contrary to the often proposed explanation for improved reproductive performance with age in birds (Forslund and Pärt 1995). In short, the path analysis revealed the dual importance of age in reproductive performance of female goldeneyes: age has a direct effect on reproductive investment (brood size) and timing of breeding and has an indirect effect on reproductive success (recruitment) via these two traits.

Correct interpretation of our results rests on several assumptions that we could not rigorously evaluate. Our conclusions did not change when we included male recruits (i.e. males shot at > 1 yr post-fledging) in several analyses but cannot rule out the possibility that patterns might differ if we had obtained reliable data for males. However, because female offspring are natal philopatric whereas males are not (Pöysä et al. 1997), studying factors affecting female offspring recruitment is most important in terms of goldeneye population dynamics. Annual changes in ice-out conditions presumably reflect local temperatures that in turn could affect invertebrate availability for adult females and ducklings (also see references in Material and methods, Spring phenology). Although we had no information about temporal variation in timing of food resource peaks, a recent study addressed the hypothesis that dabbling ducks (*Anas* spp.) time breeding to coincide with annual peaks in emerging chironomids which are important prey for newly-hatched ducklings; however, no evidence for synchrony between the two was found (Dessborn et al. 2009). Adult female goldeneyes or their ducklings may be emancipated from resource bottlenecks if they are able to exploit efficiently different kinds of foods; because goldeneye diets vary considerably with habitat and availability (Eriksson 1976, Cramp and Simmons 1977 and references therein) this may indeed be the case. Although we had no direct observations of female goldeneye arrival times on the study area, pairs were present prior to ice-out in early spring (PR unpubl.) and, in general, goldeneyes have been wintering progressively farther north over the last three decades (Lehikoinen et al. 2013). Thus, females seem to be able track environmental conditions closely and sequester sufficient nutrients to optimize timing of egg production and hence offspring recruitment. Fewer females may attempt (persistent) nesting during early springs when ice clears lakes early, but we have no estimates of annual breeding or renesting probabilities. Finally, we could not evaluate rigorously whether nesting success rates were negatively related to changing spring phenology, but population-level nesting success was not correlated with ice-out date in this goldeneye population (Spearman rank correlation, $r_s = 0.19$, $p = 0.39$, $n = 23$ yr). In North America, patterns of nesting success aligned with predictions of the mismatch hypothesis in only one of five dabbling duck species (Drever and Clark 2007). Indeed, a recent review suggests there is no clear evidence of mismatch effects in ducks (Guillemain et al. 2013).

Our results are most consistent with a hypothesis that short-distance migrant species with flexible nesting dates, such as common goldeneyes, are able to adjust onset of breeding in response to varying spring conditions. Our study, based on extensive long-term individual data, thus provides an example of a fitness-related mechanism potentially explaining why populations of short-distance migrants may be less vulnerable than populations of long-distance migrants to climate change effects, as hypothesized in recent analyses (Both and te Marvelde 2007, Møller et al. 2008, Both et al. 2010, Jones and Cresswell 2010). Our findings also have relevance to the concern about how continuous advancement of the timing of spring thaw might affect duck populations in general (Guillemain et al. 2013); population-level recruitment of female goldeneye offspring from years with earlier ice-out dates was just as high as from late years. Furthermore, species that store reproductive nutrients on wintering areas or during spring migration may be particularly resilient to shifts in spring resource availability and nest when reproductive success may be optimized. If this is so, we might expect no relationship between adult female survival and timing of breeding relative to spring phenology. On the other hand, species with fixed nesting dates may be less responsive to changing spring phenology and hence more vulnerable to resource mismatches (Hobson et al. 2009, Drever et al. 2011). Further work is needed to evaluate these hypotheses, and to determine whether and why the continuum between flexible and fixed nesting phenology affects timing–productivity relationships in migratory species.

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