

## Rapid adaptive adjustment of parental care coincident with altered migratory behaviour

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**Abstract** The optimal duration of parental care is shaped by the trade-off between investment in current and expected future reproductive success. A change in migratory behaviour is expected to affect the optimal duration of parental care, because migration and non-migration differ in expectations of future reproductive success as a result of differential adult and/or offspring mortality. Here we studied how a recent emergence of non-migratory behaviour has affected the duration of parental care in the previously (until the 1980s) strictly migratory Russian breeding population of the barnacle geese *Branta leucopsis*. As a measure of parental care, we compared the vigilance behaviour of parents and non-parents in both migratory and non-migratory barnacle geese throughout the season. We estimated the duration of parental care at 233 days for migratory and 183 days for non-migratory barnacle geese. This constitutes a shortening of the duration of parental care of 21% in 25 years. Barnacle geese are thus able to rapidly adapt their parental care behaviour to ecological conditions associated with altered migratory behaviour. Our study demonstrates that a termination of migratory behaviour resulted in a drastic reduction in parental care and highlights the importance of studying the ecological and behavioural consequences of changes in migratory behaviour and the consequences of these changes for life-history evolution.

**Keywords** Barnacle geese · Parent-offspring conflict · Migration ·  
Life-history evolution · *Branta leucopsis* · Colonization

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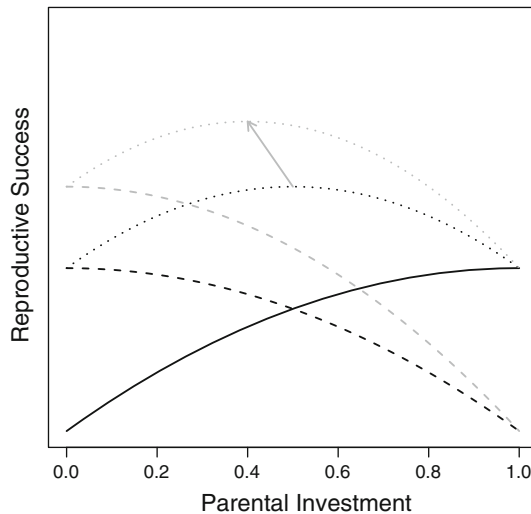
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## Introduction

Parental investment is widely studied because of its consequences for reproductive success. From Trivers' definition of parental investment: 'any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring' (Trivers 1972, p. 67), the trade-off between investment in current reproductive success and in expected future reproductive success is evident (Fig. 1). The trade-off is shaped by the opposing effects of further investment on current and expected future reproductive success. The level of investment maximizing lifetime reproductive success occurs at the point that the marginal benefit of further investment in terms of current reproductive success is offset by marginal cost in terms of expected future reproductive success. Differences in life-style or environment that affect the marginal costs or benefits of investment are expected to cause differences in parental care behaviour (Clutton-Brock 1991).

Migration is behaviour typically associated with high rewards and high risks to future breeding opportunities as compared to non-migration and as such alters the balance between investment costs and benefits. Migration comes with costs, in terms of increased energy expenditure but also in terms of survival: during migration animals face a higher risk of predation, they have a higher risk of starvation because the resource availability during migration is hard to predict and they can lose their way. Several studies show that the period of migration has a much greater mortality than the period of non-migration. For



**Fig. 1** Trade-off between current and future reproductive success. Graphical representation of the trade-off between current and expected future reproductive success. The *solid line* is the current reproductive success with increasing investment in current offspring  $C(i)$ . The *dashed line* is the expected future reproductive success with increasing investment in current offspring  $F(i)$ . The *dotted line* is the sum of both  $C(i)$  and  $F(i)$ , equalling expected lifetime reproductive success  $T(i)$ . The marginal benefit (increase in current reproductive success) declines with investment, while the marginal cost (decrease in future reproductive success) increases with investment. The *grey line* portrays an environmental change, so that the expected future reproductive success resulting from any level of investment is higher. With more future at stake (i.e.  $F(i)$  is everywhere higher), the rate of increasing marginal costs of investment in current offspring has increased (i.e., steeper cost curve) causing a shift to lower levels of investment. The 2nd differential of  $F(i)$  equals  $R_{mc}$ , whereas the 2nd differential of  $C(i)$  equals  $R_{mb}$

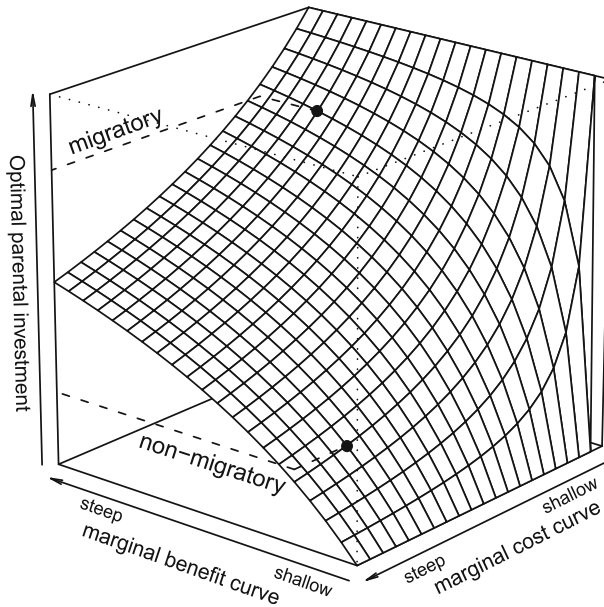
example, black-throated blue warblers *Dendroica caerulescens* experience a 15 times higher mortality rate during the migratory season than during the non-migratory season, and more than 85% of the annual mortality occurs during migration (Sillett and Holmes 2002). These costs are presumed to be offset by benefits to current reproduction such as decreased nest predation risk (e.g. McKinnon et al. 2010) or higher offspring quality. Here we show how the altered costs and benefits affect parental investment decisions in the Barnacle Goose *Branta leucopsis*.

The population of barnacle geese wintering in The Netherlands provides us with the unique situation of distinct migratory and non-migratory (sub-)populations within the same geographical area, allowing a comparison of migration and non-migration. The migratory sub-population breeds in Russia, migrating to and from The Netherlands via staging sites in the Baltic Sea (Ganter et al. 1999). The non-migratory sub-population resides year round in the Netherlands, has only emerged in the 1980s (Ouweneel 2001) and is growing rapidly (Van der Jeugd et al. 2009). Because the non-migratory population only recently emerged, presumably from the migratory population (unpublished data), this allows testing how parental care in natural populations is affected by changing ecological circumstances, which is important for understanding the evolution of parental care (Clutton-Brock 1991).

Geese have extended parental care behaviour which lasts until long after fledging. Geese provide parental care by increasing vigilance to protect offspring against predation and competition of conspecifics. They are among the very few avian species in which parents and offspring stay together for nearly a year (Mayr 1942; Kear 1970), with the termination of parental care taking place during spring migration preceding the breeding season (Black and Owen 1989). Additionally, the extended period of parental care supposedly plays an important role in the social structure of the populations (Van der Jeugd et al. 2002) and in the cultural transmission of migratory behaviour (Owen 1980). As in other (groups of) species such as Meerkats *Suricata suricatta* and corvids, extended duration of parental care functions as a period to socially transmit important skills, such as foraging or vigilance (Clayton and Emery 2005; Thornton and McAuliffe 2006; Graw and Manser 2007). This underlines the potential importance of an effect of migratory change on parental care behaviour in geese.

Here we study whether this recent change in migratory behaviour influences the parental care behaviour of barnacle geese. Based on the effects of non-migratory behaviour on both the costs and benefits of parental investment, we predict shorter parental care in the non-migratory than the in migratory sub-population. First, the lower mortality (and hence greater expected future) of non-migrants, results in a higher rate of increasing marginal costs of investment ( $R_{mc}$ ; see Fig. 1 for schematic overview and Fig. 2 for predictions). Second, the higher offspring survival of non-migrants results in a lower rate of decreasing marginal benefits ( $R_{mb}$ ; Fig. 2). Juvenile survival, based on ring resightings, is 0.55 for the offspring of migratory and 0.97 for offspring of non-migratory individuals (Van der Jeugd et al. 2009). Thus, increased investment by non-migratory geese can hardly increase offspring survival, making the marginal benefit of investment smaller (i.e., lower rate of decreasing marginal benefits and a more shallow benefits curve) for non-migratory than for migratory barnacle geese. The interaction of various cost and benefit scenarios and the consequent optimal level of parental investment are visualized in Fig. 2.

Both the higher marginal costs and lower marginal benefits of non-migration separately predict lower parental investment in non-migratory barnacle geese, and when combined the difference is predicted to be even larger, as we assumed these effects are additive. To test this prediction, we studied how long barnacle geese provide parental care in the migratory and non-migratory population.



**Fig. 2** Predicted level of parental investment. Prediction of optimal level of parental investment with changing rate of increasing marginal costs ( $R_{mc}$ ), and changing rate of decreasing marginal benefits ( $R_{mb}$ ). The surface indicates the level of investment giving maximum expected lifetime reproductive success ( $I^*$ ) and is calculated by taking the maximum of  $T(i)$  of Fig. 1 (being the sum of  $C(i)$  and  $F(i)$ ) (as the maximum life time reproductive success is at the point where the marginal benefits and marginal costs are equal), resulting in the equation:  $I^* = \frac{R_{mb}}{R_{mc} + R_{mb}}$ . Dots indicate hypothetical positions of migratory and no-migratory populations and our prediction for parental investment in these populations

## Methods

To quantify parental care behaviour we observed migratory and non-migratory barnacle geese. We observed migratory geese during migratory stopover (October 2008 and May 2009) on the island of Saaremaa in Estonia ( $58^\circ 05' N$ ,  $22^\circ 06' E$ ), hosting approximately 10,000 barnacle geese in autumn and spring. We observed the migratory population during winter and spring (November 2008–April 2009) in the northern part of The Netherlands ( $53^\circ 02' N$ ,  $5^\circ 25' E$ ). We observed non-migratory geese in the southern part of the Netherlands near the Krammersche Slikken ( $51^\circ 40' N$ ,  $4^\circ 13' E$ ) from November 2008 until April 2009. The distance between the observation locations in the Netherlands is approximately 170 km. We alternated observation periods between the migratory and non-migratory sub-populations, which resulted in six periods (Table 1), named after the months for convenience. We used observations of ringed individuals to validate the migratory or non-migratory status of observed individuals. In the non-migratory observation area, 95.5% (85/89) of the observed ringed individuals had been ringed during the breeding season in the Netherlands. In the migratory observation area in the Netherlands, 97% (35/36) of the ringed individuals had been ringed either on the Russian (Van der Jeugd et al. 2003) or at the Baltic breeding area (Larsson et al. 1988).

We observed geese with and without goslings, hereafter called ‘parents’ and ‘non-parents’ respectively, and quantified parental care based on the behavioural differences between the two groups. Adults and goslings were identified following Svensson et al. (1999). To

**Table 1** Overview of observations

Population	Period	Dates	Total samples	Parents/non-parents
Migratory	October	17/10–29/10	277	135/142
	November	18/11–28/11	68	34/34
	December–February	17/12–19/2	91	39/52
	March	11/3–19/3	70	21/49
	April	6/4–16/4	81	26/55
	May	7/5–19/5	358	10/348
Non-migratory	October	5/11–14/11	42	18/24
	November	2/12–11/12	54	29/25
	December–February	6/1–6/2	44	19/25
	March	25/2–5/3	78	38/40
	April	26/3–2/4	86	43/43
	May	21/4–29/4	77	22/55

determine parental status, we observed an adult goose for up to 10 min, to determine whether there were goslings attached or not. We then observed the focal individual again up to 10 min, recording behaviour with a Psion Workabout MS (RACO Industries, Cincinnati, Ohio, USA) and Noldus Observer 5.0 (Noldus Information Technology, Wageningen, The Netherlands). We categorized behaviour as ‘foraging’, ‘vigilance’, ‘walking’, ‘preening’, ‘resting’, ‘attacking’ or ‘other’ behaviour. We quantify parental care by comparing the vigilance behaviour. Vigilance is an often used measure for parental care in geese (Black and Owen 1989) and swans (Scott 1980). In a previous study on this system, we showed that the percentage of unattached goslings quickly increased after the difference in vigilance between parents and non-parents disappeared (Jonker et al. 2011).

### Statistical analysis

We calculated for each focal sample the proportion of time spent vigilant. Vigilance and foraging together add up to approximately 90% of the time budget of geese (Black and Owen 1989), and are strongly and inversely related. We therefore use the percentage of time vigilant as our measure of the time budget. The behaviour of both parents and non-parents changed during the season, and so we defined parental care as the extra vigilance carried out by a parent relative to that of non-parents of the same sub-population (Jonker et al. 2011), hereafter called residual vigilance  $\text{Res}_V$ , calculated as:

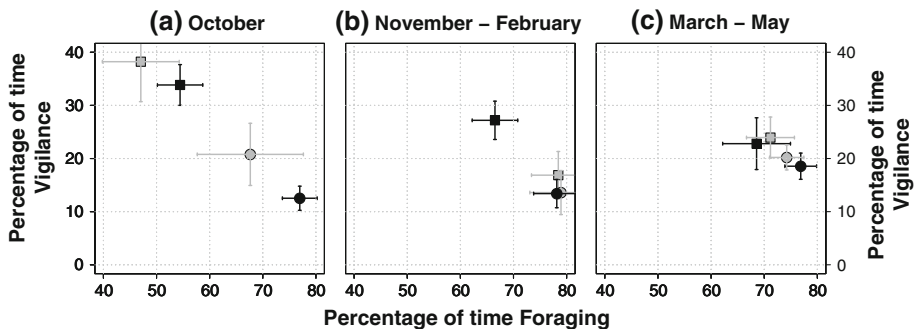
$$\text{Res}_V = V_p^{\text{parent}} - \bar{V}_p^{\text{non-parent}}, \quad (1)$$

where  $p$  is observation period,  $V_p^{\text{parent}}$  is the percentage of time vigilance of an observation of a parent in period  $p$ , and  $\bar{V}_p^{\text{non-parent}}$  is the mean vigilance of all non-parents for that period. By using the difference between parents and non-parents we could control for potential site-specific differences in vigilance behaviour. The  $\text{Res}_V$  allows statistical comparison between the two populations. For graphical representation we use the raw data of vigilance and foraging. We used a linear model to test for the effect of parental status, migratory status, group size, period of the year (and all possible interactions between these variables) on the  $\text{Res}_V$  and selected models by stepwise AIC comparison (function `step` in *R*). Subsequently we tested for differences in  $\text{Res}_V$  between parents and non-parents in every period for both

the migratory and non-migratory sub-populations, using an independent samples  $t$  test for unequal variances, and used a Bonferroni correction for multiple comparisons. To estimate the termination of parental care, we used the date half way between the end of the last observation period with significant parental care and the beginning of the first period without parental care.

## Results

As stated previously, vigilance and foraging are strongly and negatively correlated, and together constitute about 90% of the time budget. Consequently, any decrease in time spent vigilance corresponded with an equal increase in foraging time (Fig. 3). There was significant parental care in the migratory sub-population until February, but in the non-migratory sub-population only until November, indicated by a significant interaction between period of the year, parental status and migratory status on the difference in vigilance between parents and non-parents ( $Res_V$ ) in the linear model (see Table 2 for model results). This is illustrated in Fig. 3 as follows: in the migratory sub-population, the percentage of time vigilant is twice that for parents (33.84%) as for non-parents (12.52%) in October. In this period, the non-migratory population parents (38.22%) were also more vigilant than non-parents (20.78%) (Fig. 3a; Table 3). From November until February parents (27.18%) were more vigilant than non-parents (16.86%) only in the migratory population, whereas vigilance levels were equal in the non-migratory population (13.59% vs. 13.40%) (Fig. 3b; Table 3). From March onwards there was no difference in vigilance between parents and non-parents in either sub-population (migratory: 22.79% vs. 18.55%; non-migratory: 23.94% vs. 20.20%) (Fig. 3c; Table 3). No interactions including group size significantly influenced the  $Res_V$ . The use of a linear model was justified because the residuals approximated a normal distribution.



**Fig. 3** Temporal development of foraging and vigilance behaviour. The percentage of time being vigilant against the percentage of time foraging of parents (*squares*) and non-parents (*circles*) for three periods. In the first graph (October, period 1) there is significant parental care in both the migratory (*black*) and non-migratory (*grey*) population, in the second graph (November–February, period 2 + 3) there is parental care only in the migratory population, in the third graph (March–May, period 4 – 6) there is no parental care in either sub-population. Because of unevenness of number of observations of non-parents between period 4 and 5 and period 6, we used a random sample of the data from period 6, approximately equal to the sample sizes in period 4 and 5, for the graphical representation. **a**  $N_{pm}$ : 135,  $N_{npm}$ : 142,  $N_{pnm}$ : 18,  $N_{nppm}$ : 24. **b**  $N_{pm}$ : 73,  $N_{npm}$ : 86,  $N_{pnm}$ : 48,  $N_{nppm}$ : 50. **c**  $N_{pm}$ : 57,  $N_{npm}$ : 157,  $N_{pnm}$ : 103,  $N_{nppm}$ : 138. Error bars show 95% CI

**Table 2** Results stepwise linear model RES<sub>V</sub>

Dependent variable: RES <sub>V</sub>	Estimate	SE	<i>t</i> value	Pr(>  <i>t</i>  )
(Intercept)	3.15E - 01	1.09E + 00	0.289	0.77287
Period	7.58E - 02	2.26E - 01	0.335	0.73769
Population	6.41E - 01	2.34E + 00	0.274	0.78417
Parental status	1.82E + 01	1.74E + 00	10.498	<2e - 16***
Group size	-7.46E - 04	3.10E - 04	-2.403	0.01639*
Population* parental status	-1.03E + 01	3.54E + 00	-2.904	0.00375**
Period* population	-2.39E - 01	5.30E - 01	-0.45	0.65297
Period* parental status	-3.11E + 00	5.26E - 01	-5.913	4.32e - 09***
Period*population*parental status	2.14E + 00	9.06E - 01	2.362	0.01834*

The model that was selected from a stepwise selection method based on AIC using the `step` function in *R*. The full model include the factors: period (period of the year), population (migratory or non-migratory), parental status (parent or non-parent) and group size, including all interactions between these factors

Residual SE: 11.58 on 1272 *df*

Multiple *R*-squared: 0.1482, Adjusted *R*-squared: 0.1429

*F*-statistic: 27.67 on 8 and 1272 *df*, *P* value: <2.2e - 16

**Table 3** Statistical summary post-hoc *t* tests between parents and non-parents

Population	Period	<i>t</i>	<i>df</i>	<i>P</i>
Migratory	October	-10.83	270.4	<0.001
	November	-5.82	57.8	<0.001
	December-February	-4.19	80.5	<0.001
	March	-0.61	38.6	0.55
	April	-1.26	50.4	0.21
	May	-0.42	9.2	0.68
Non-migratory	October	-3.67	37.3	<0.001
	November	-0.55	51.6	0.58
	December-February	-1.33	41.7	0.19
	March	-1.70	70.6	0.09
	April	-0.70	81.2	0.48
	May	-1.44	31.8	0.16

The termination of parental care was estimated for the migratory sub-population at February 28, against November 23 for the non-migratory sub-population. After correction for the difference in mean hatch date, which is July 11 for the migratory and May 25 for the non-migratory sub-population (Van der Jeugd et al. 2009), parental care lasts approximately 183 days for non-migratory against 233 days for migratory barnacle geese.

## Discussion

The non-migratory sub-population of barnacle geese emerged only approximately 25 years ago from the migratory population (Meininger and Van Swelm 1994) and our results show

that parental care in these non-migrants is much shorter than in the migratory sub-population (183 vs. 233 days). Even though we still found parents after the termination of parental care, the effort needed to find these individuals greatly increased after this termination (see also Jonker et al. 2011). The difference constitutes 21% of the current duration of parental care of the migratory sub-population. An earlier study on the parental care duration of this migratory population of barnacle geese suggests that the duration of parental care has shortened as compared to 30 years ago (Jonker et al. 2011). In our study we assume that the Dutch non-migratory population originates from the Russian migratory population and recent genetic analysis confirms this assumption (unpublished data). Assuming that, before the emergence of the non-migratory sub-population, parental care in the migratory sub-population lasted at least until the commencement of spring migration (Kear 1970; Black and Owen 1989), which was approximately mid-April in the 1970s (Jonker et al. 2010), the difference between the current duration of parental care in the non-migratory sub-population (183 days) and the assumed duration of parental care in the 1970s (279 days) is even larger, viz. 96 days, which amounts to a reduction of 34% of the 'original' duration.

To put this rate of change in perspective we calculated the rate of phenotypic change in darwins (Haldane 1949). This method allows to compare rates of relative phenotypic change over a given time period, corrected for the measurement interval. For example, when one bone length has increased by 10% and another by 20% in a million year (the example given by Haldane), one can use the darwin to compare these rates. Here the phenotypic change is from 233 to 183 over 25 years, resulting in 9662 days. When this rate of phenotypic changes is corrected for the time scale of the change (Gingerich 1983), it results in 9.17 days (with  $\ln(\text{time of change})$  being  $-10.6$ ), which fits the pattern of rates of phenotypic change in colonization events (category II in Fig. 1; Table 1 in Gingerich 1983).

A well-known example of behavioural adaptation to a new environment that differs in mortality is that of guppies introduced to an environment with different predators adapted their parental investment to producing fewer and larger offspring (Reznick and Endler 1982; Reznick et al. 1990). Using the results on the change of reproductive allotment of the introduction experiment of Reznick and Endler gives a rate of change of 118900 days (time scale corrected: 11.7d with  $\ln(\text{time of change})$  being  $-12.9$ ). Another more recent example of phenotypic change in response to a changed environment is that several species of songbirds have responded to afforestation by adapting their wing morphology (Desrochers 2010). The rate of change expressed in darwins for this study equals 968 days (time scale corrected: 6.9 days with  $\ln(\text{time of change})$  being  $-9.2$ ). So, we cannot exclude that the rate of change in duration of parental care demonstrated in our study is caused by evolution.

When we look at the patterns of parental care in the Anatidae, a striking feature is that geese and swans provide long parental care. Most of the other Anatidae groups provide short parental care and the long (bi)parental care is considered to be the ancestral form of parental care in this family (Kear 1970). The pattern of adaptive radiation of parental care seems to match with the phylogeny of the Anatidae (Gonzalez et al. 2009). Apparently the pattern of long parental care was always very stable in this group. We now observe this rapid change in parental care duration in barnacle geese coincident with altered migratory behaviour. This raises questions whether similar changes are possible too in other species within the family and whether this assumed apparent stability of parental care duration is valid at all.



In ducks it has been shown that post hatching parental care is regulated by high levels of prolactin (Boos et al. 2007), which in turn seems to have a genetic basis in geese (Jiang et al. 2009). Future common garden experiments could elucidate whether this change in parental care is caused by phenotypic plasticity or evolution. Based on our study, we cannot discriminate between these two mechanisms.

To understand the implications of this change, we need to address the functional aspects of extended parental care in geese. In other animals, such as Corvids, long periods of parental care allow offspring to copy foraging skills from parents, and hence increase parents' fitness via increased survival chances of the offspring (Clayton and Emery 2005). It is known from geese that in the first weeks after hatching parents assist their offspring with finding the best plants to eat by allowing them to forage from the same tussock of grass or even the same plant ('food sharing' according to Black and Owen 1989). However, whether this is a kind of provisioning or teaching is unclear, but this behaviour does not last long enough to explain the duration of parental care in geese. An obvious benefit for caring for offspring as long as geese do is that it provides protection for offspring against potential predators and competition by the increased vigilance level of the parents. In Bewick swans *Cygnus bewickii*, parental care during winter protects offspring from competition with conspecifics, which can have far stretching consequences as the conditions experienced in the first year are crucial for future breeding and survival changes of the offspring, especially as the time available for foraging becomes limiting as a result of the short days in winter (Scott 1980). Additionally, the parents also benefit directly from the presence of offspring during migration because they are suggested to assist their parents in claiming the most profitable foraging patches Loonen et al. 1999.

The benefits of extended care are much less present in the non-migratory sub-population. The non-migratory sub-population does not experience the predation danger that the migratory sub-population does, making parental vigilance less beneficial. In the period prior and during migration, migratory geese have to store enough reserves to both successfully complete a 3,000 km migration and a costly period of breeding. On the contrary, non-migratory geese only have to prepare for breeding, whereas the competition for food is probably comparable because of the worse food conditions (Van der Jeugd et al. 2009).

An alternative hypothesis to explain the observed difference in parental care between the two sub-populations could lie in age structure. The non-migratory sub-population has a very high juvenile survival, and is growing almost exponentially. The migratory sub-population, on the contrary, has a much lower juvenile survival and is growing much more slowly (Van der Jeugd et al. 2009). As a result, the non-migratory sub-population probably consists of relatively more young individuals compared to the migratory sub-population. It may be that the parents observed in the migratory sub-populations are older than those in the non-migratory sub-population. For these older parents the expected future reproductive success will be lower than for the younger parents, resulting in longer parental care for the older parents. However, the difference in age structure should also cause differences in the vigilance behaviour of the non-parents, and our results do not show this.

Concluding, we show that differences in duration of parental care between migratory and non-migratory barnacle geese confirm to the predictions of life-history theory with a drastic shorter parental care in the non-migratory population. To our knowledge, this is the first study that shows how being migratory or not affects the duration of parental care within the same species. These results are in line with our predictions and of predictions of many other studies. For example Klug and Bonsall (2010) show that parental care evolves under conditions where (among others) adult survival is relatively low and where the juvenile survival in the absence of care is low. Both conditions apply to the differences

between migration and non-migration in our system. In African Buffalo *Syncerus caffer*, the population of Manyara continue to produce milk for offspring for 18 months, while those in the Serengeti stop producing milk after 10 months. Similar as in our study the population with the longest period of care experienced the highest levels of predation danger (Prins 1996). However, good comparisons of parental investment between populations are scarce (and absent with respect to differences in migratory behaviour), despite the many theoretical predictions. Because we have compared two populations who only recently diverged, this provides great potential for understanding adaptive life-history evolution, as suggested by Keller and Taylor (2008).

Many migratory species are currently threatened by habitat fragmentation or global change (Wilcove and Wikelski 2008) and this is accompanied with species becoming less migratory or migrating over shorter distances (Visser et al. 2009; Pulido and Berthold 2010). From a theoretical point of view these changes are very interesting, as they may provide insights in the costs and benefits of migration. Our study provides an example of how such a change in migration can affect other behaviour, and illustrates that the migratory behaviour of individuals cannot be taken for granted when studying life-history trade-offs.

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## References

- Black JM, Owen M (1989) Parent offspring relationships in wintering Barnacle Geese. *Anim Behav* 37:187–198
- Boos M, Zimmer C, Carriere A, Robin JP, Petit O (2007) Post-hatching parental care behaviour and hormonal status in a precocial bird. *Behav Process* 76:206–214
- Clayton N, Emery N (2005) Corvid cognition. *Curr Biol* 15:R80–R81
- Clutton-Brock TH (1991) The evolution of parental care: monographs in behaviour and ecology. Princeton University Press, Princeton, New Jersey
- Desrochers A (2010) Morphological response of songbirds to 100 years of landscape change in North America. *Ecology* 91:1577–1582
- Ganter B, Larsson K, Syroechkovsky EV, Litvin KE, Leito A, Madsen J (1999) Barnacle Goose *Branta Leucopsis*: Russia/Baltic. In: Madsen J, Cracknell G, Fox T (eds) Goose population of the Western Palaearctic: a review of status and distribution. National Environmental Research Institute, Rønde, pp 270–283
- Gingerich PD (1983) Rates of evolution—effects of time and temporal scaling. *Science* 222:159–161
- Gonzalez J, Düttmann H, Wink M (2009) Phylogenetic relationships based on two mitochondrial genes and hybridization patterns in Anatidae. *J Zool* 279:310–318
- Graw B, Manser MB (2007) The function of mobbing in cooperative meerkats. *Anim Behav* 74:507–517
- Haldane JBS (1949) Suggestions as to quantitative measurement of rates of evolution. *Evolution* 3:51–56
- Jiang RS, Zhang LL, Geng ZY, Yang T, Zhang SS (2009) Single nucleotide polymorphisms in the 5'-flanking region of the prolactin gene and the association with reproduction traits in geese. *S Afr J Anim Sci* 39:83–87
- Jonker RM, Eichhorn G, van Langevelde F, Bauer S (2010) Predation danger can explain changes in timing of migration: the case of the barnacle goose. *PLoS ONE* 5:e11369
- Jonker RM, Kuiper MW, Snijders L, Van Wieren SE, Ydenberg RC, Prins HHT (2011) Divergence in timing of parental care and migration in Barnacle geese. *Behav Ecol* 22:326–331
- Kear J (1970) The adaptive radiation of parental care in waterfowl. In: Crook JH (ed) Social behavior in birds and mammals. Academic Press, London

- Keller SR, Taylor DR (2008) History, chance and adaptation during biological invasion: separating stochastic phenotypic evolution from response to selection. *Ecol Lett* 11:852–866
- Klug H, Bonsall MB (2010) Life history and the evolution of parental care. *Evolution* 64:823–835
- Larsson K, Forslund P, Gustafsson L, Ebbinge BS (1988) From the high arctic to the baltic—the successful establishment of a barnacle goose *Branta leucopsis* population on Gotland, Sweden. *Ornis Scandinavica* 19:182–189
- Loonen MJJE, Bruinzeel LW, Black JM, Drent RH (1999) The benefit of large broods in barnacle geese: a study using natural and experimental manipulations. *J Anim Ecol* 68:753–768
- Mayr E (1942) Systematics and the origin of species, from the viewpoint of a zoologist. Columbia University Press, New York
- McKinnon L, Smith PA, Nol E, Martin JL, Doyle FI, Abraham KF, Gilchrist HG et al (2010) Lower predation risk for migratory birds at high latitudes. *Science* 327:326–327
- Meininger PL, Van Swelm ND (1994) Brandganzen *Branta leucopsis* als broedvogel in het Deltagebied. *Limosa* 67:1–5
- Ouweneel GL (2001) Snelle groei van de broedpopulatie Brandganzen *Branta leucopsis* in het Deltagebied. *Limosa* 74:137–146
- Owen M (1980) Wild geese of the world—their life history and ecology. B T Batsford Ltd, London
- Prins HHT (1996) Ecology and behaviour of the african buffalo: wildlife ecology and behaviour series. Chapman & Hall, London
- Pulido F, Berthold P (2010) Current selection for lower migratory activity will drive the evolution of residency in a migratory bird population. *Proc Natl Acad Sci USA* 107:7341–7346
- Reznick D, Endler JA (1982) The impact of predation on life-history evolution in Trinidadian Guppies (*Poecilia reticulata*). *Evolution* 36:160–177
- Reznick DA, Bryga H, Endler JA (1990) Experimentally induced life-history evolution in a natural population. *Nature* 346:357–359
- Scott DK (1980) Functional-aspects of prolonged parental care in Bewicks Swans. *Anim Behav* 28:938–952
- Sillett TS, Holmes RT (2002) Variation in survivorship of a migratory songbird throughout its annual cycle. *J Anim Ecol* 71:296
- Svensson L, Mullarney K, Zetterstrom D, Grant PJ (1999) Collins bird guide. HarperCollins, London
- Thornton A, McAuliffe K (2006) Teaching in wild meerkats. *Science* 313:227–229
- Trivers RL (1972) Parental investment and sexual selection In: BG Campbell (ed), Sexual selection and the descent of man
- Van der Jeugd HP, van der Veen IT, Larsson K (2002) Kin clustering in barnacle geese: familiarity or phenotype matching? *Behav Ecol* 13:786–790
- Van der Jeugd HP, Gurtovaya E, Eichhorn G, Litvin KY, Mineev OY, van Eerden M (2003) Breeding barnacle geese in Kolokolkova Bay, Russia: number of breeding pairs, reproductive success and morphology. *Polar Biol* 26:700–706
- Van der Jeugd HP, Eichhorn G, Litvin KE, Stahl J, Larsson K, van der Graaf AJ, Drent RH (2009) Keeping up with early springs: rapid range expansion in an avian herbivore incurs a mismatch between reproductive timing and food supply. *Glob Change Biol* 15:1057–1071
- Visser ME, Perdeck AC, Van Balen JH, Both C (2009) Climate change leads to decreasing bird migration distances. *Glob Change Biol* 15:1859–1865
- Wilcove DS, Wikelski M (2008) Going, going, gone: is animal migration disappearing. *PLoS Biol* 6:e188