Behavioral Ecology
doi:10.1093/beheco/arq208
Advance Access publication 21 January 2011

Original Article

Divergence in timing of parental care and migration in barnacle geese

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In migratory geese, the extended association of parents and offspring is thought to play a crucial role in culturally transmitting the migration strategy to the next generation. Goslings migrate with their parents and associate closely with them almost until the next breeding season. Families do not break up until spring migration, when the parent–offspring conflict intensifies during preparation for the next generation of offspring. Recently, the commencement of spring migration of the Russian population of the barnacle goose has been delayed by about 1 month. Here, we investigated whether the duration of parental care behavior changed with this alteration in migratory behavior. In contrast to our expectation, we found that parental care terminated well before the commencement of spring migration and that parent–offspring associations were nearly absent during spring migration. We argue that the mechanisms for determining the duration of parental care is different from that determining the commencement of spring migration; hence, we conclude that a divergence in timing has developed between both behaviors. A consequence of this divergence could be that the cultural transmission of migratory behavior is disrupted, possibly playing a role in the recent establishment of new populations of Barnacle geese across the Russian flyway. *Key words:* adaptation, *Branta leucopsis*, bird migration, parental care, parent–offspring conflict. *[Behav Ecol 22:326–331 (2011)]*

Migration is an adaptation to maximize fitness in seasonally changing environments by selecting the best habitat throughout the year. Individuals need to base migratory decisions, such as when to start migration or where to stopover, on the temporal and spatial distribution of food and safety (Alerstam and Lindström 1990; Jonzén et al. 2007). Migration is most successful when an individual has information on when to be where. Timing and direction of migration are known to be influenced by the earth's magnetic field, photoperiod, and/or polarized light (Alerstam et al. 2003), and the sensitivity for these cues is suggested to be genetically programmed. For example, studies on blackcaps *Sylvia atricapilla* showed that both the migratory restlessness (Berthold and Querner 1981) and the migratory direction (Helbig 1991) have a genetic basis.

In contrast, there are some species in which all migratory behavior, including the decision on whether to migrate or not, is culturally determined. Consequently, individuals of these species can adapt better to environmental changes than those that have genetically transmitted migration (Sutherland 1998). For example, herring *Clupea harengus* are suggested to develop migratory routines early in life by adopting the same migratory routine as their predecessors, even when the environment changes. Young herring adopt these routines due to their innate tendency to school with other, experienced herring (Corten 2002). A similar cultural transmission of migration is present in geese, and this has been shown in an experiment to "teach" Lesser White-fronted geese *Anser erythropus* a new migration strategy to The Netherlands instead of totheir original wintering grounds in Eastern Europe. To this end, barnacle geese *Branta leucopsis*, wintering in The Netherlands, were used as foster parents in Sweden and this resulted in Lesser White-fronted geese adopting the migratory behavior of these barnacle geese (Von Essen 1991). There are also cases known in which humans acted as foster parents and consequent migration "teachers" for Canada geese *B. canadensis* and Trumpeter swans *Cygnus buccinator* (Sladen et al. 2002).

This cultural transmission of migration is possible because parental care and the accompanying parent–offspring association extents until during migration. It is widely accepted that one of the functions of this long parental care is to guide or teach the offspring the migration routes (Mayr 1942; Hochbaum 1955; Kear 1970; Owen 1977; Baker 1978; Owen 1980). For example, Kear suggests that: "family life lasts longest in the migratory arctic-breeding swans and geese, who tolerate their young and indeed defend them, until the next breeding season. The group migrates together and this is probably extremely important in establishing traditional flight paths and feeding grounds" (Kear 1970, p. 374).

Barnacle geese that winter in the UK and migrate to breeding grounds on Spitsbergen provide parental care for approximately 9–10 months (Black & Owen 1989). The termination of the parent–offspring association coincides with the period of spring migration. Before migration, 20% of the young are not attached to any family, whereas the percentage of unattached young increases to 65% during migratory stopover (Black and Owen 1989). During the migratory stopover in Norway, parents sharply increase attacks toward offspring, suggesting that the extended parental care conflicts with the preparation for the next breeding attempt.

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Received 28 May 2010; revised 17 September 2010; accepted 20 September 2010.

The population of barnacle geese breeding in Russia migrates in spring from wintering grounds in The Netherlands via a stopover in the Baltic to breeding grounds the Russian Arctic. The phenology of the Russian population was comparable with the Spitsbergen population until the 1990s. That is, the timing of migration from the wintering area to the staging area, respectively, Baltic or Norway, occurred in the first half of April (Owen 1980; Madsen et al. 1999), the migration from the staging area to the prebreeding area in Russia or Spitsbergen occurred in second half of May (Owen 1980; Leito 1996; Madsen et al. 1999), the arrival at the breeding area occurred in early June, and breeding was initiated in both populations shortly after arrival at the breeding area (Syroechkovskiy et al. 1991; Madsen et al. 1999). We can also assume that the timing of parental care was similar for these populations (Owen 1980), which is supported from observations of families during spring migration in Estonia (Leito 1996). Hence, we assume that the timing of parental care behavior of the Russian population was comparable with the Spitsbergen population, and thus lasted until spring migration in April in the 1970–1980s.

The Russian population, however, has delayed commencement of spring migration with approximately 1 month over the past 2 decades (Eichhorn et al. 2008; Jonker et al. 2010). We thus asked whether the timing of the termination of parental care changed in parallel to the change in timing of spring migration in Russian breeding Barnacle geese.

Because barnacle geese have shown various changes, such as a reduction in clutch size (Eichhorn et al. 2010) and an advancement of laying date (Van der Jeugd et al. 2009), in response to changes in their migratory behavior, we hypothesize that the termination of parental care has delayed with 1 month and that parental care thus still lasts until during migration. We tested this hypothesis by recording the attachment of offspring to a family in addition to comparing agonistic, vigilance, and foraging behavior of parents and nonparents.

MATERIALS AND METHODS

We observed barnacle geese during autumn migration of 2008, winter of 2008–2009, and spring migration of 2009 over 6 observational periods (Table 1). We selected a migratory stopover area on the island of Saaremaa in Estonia (lat 58°05'N, long 22°06'E), hosting approximately 10 000 barnacle geese in autumn and spring. The site for winter observations in the north of The Netherlands (lat 53°02'N, long 5°25'E) was designated as a goose accommodation area for approximately 40 000 barnacle geese.

Table 1

Overview of the date, place, and number of observations per category

Dates	Place	No. of parents	No. of nonparents
15–30 October 2008	Estonia	135	142
17–28 November 2008	The Netherlands	34	34
15–20 December 2008 and 11–19 February 2009	The Netherlands	39	52
11–19 March 2009	The Netherlands	21	49
6–16 April 2009	The Netherlands	26	55
6–21 May 2009	Estonia	10	348

The average length of our remaining protocols was 8.4 min, and the median length was 10 min for more than 945 protocols.

We observed geese with and without goslings, hereafter called "parents" and "nonparents," respectively, and quantified parental care as the behavioral difference between the 2 groups. Adults and goslings were identified using the description of Svensson et al. (1999). To determine parental status, we observed an adult goose for up to 10 min until we were sure whether there were goslings attached or not. We then continuously observed the focal individual up to 10 min recording behavior with a Psion Workabout MS (RACO Industries, Cincinnati, OH) and Noldus Observer 5.0 (Noldus Information Technology, Wageningen, The Netherlands). We categorized behavior as "foraging," "vigilance," "walking," "preening," "resting," "attacking," and "other." Additionally, whether goslings were attached to a family or not was noted every day from February onwards. A test with 4 observers observing a filmed protocol independently showed that the standard deviation around the estimated mean percentage for both foraging and vigilance was less than 1 percent.

Of the behavioral categories, foraging, vigilance, and attacking are considered most important for parental care in barnacle geese (Black and Owen 1989), and we thus restricted analyses to these behaviors. Nonparents always greatly outnumbered parents, and to balance observations, we first searched for parents. This became more difficult as the season progressed (as indicated by the sample sizes in Table 1). Ringed individuals were few, and we thus used mainly observations of unringed birds.

Statistical analysis

We calculated for each observation the proportion of time foraging, the proportion time being vigilant, the mean foraging bout length, mean vigilance bout length, and the number of attacks. We excluded as unreliable all (22) observations shorter than 2 min.

Because we defined parental care as the difference in behavior between parents and nonparents and because not only the behavior of the parents changed during the season but also that of the nonparents, we also used a measure of difference between parents and nonparents for each observation, hereafter called residual vigilance or residual foraging. For this residual foraging or vigilance, the behavior of the nonparents was used as a baseline. For example, the residual vigilance (R_V, with subscript V for vigilance and subscript F for foraging) is calculated as

$$R_V = V_p^{\text{parent}} - \bar{V}_p^{\text{nonparent}}, \tag{1}$$

where p is observation period, V_p^{parent} is the vigilance of an observation of a parent in period p, and $\bar{V}_p^{\text{nonparent}}$ is the mean vigilance of all nonparents for that period. So each observation now had, in addition to a percentage foraging or vigilant, a measure for the difference between parents and nonparents, relative to the nonparents, where the mean R_V per period for the nonparents was obviously zero. For each period, we tested for differences in vigilance and R_V, between parents and nonparents with an independent sample t-test for unequal variances (see Table 2) and a Bonferroni correction.

To compare the number of attacks, we used a linear model with number of attacks per minute as response variable and parental status, period, and the interaction term as predictor variables. Additionally, we tested post hoc for each period whether there was a difference in number of attacks per minute between parents and nonparents with a Welch t-test for unequal variances.

We analyzed the attachment of offspring to a family with a generalized linear model for binomial distribution and logit-link function, with attachment as binomial response variable

Table 2

Test results for vigilance and R_V in each period between parents and nonparents

	Vigilance			PCI_V		
Period	t	df	P	t	df	P
October	−9.382	218.901	<0.001	−9.382	218.901	<0.001
November	−5.0217	65.752	<0.001	−5.0217	65.752	<0.001
December–February	−3.6048	67.514	<0.001	−3.6048	67.514	<0.001
March	−0.4653	43.266	0.6441	−0.4653	43.266	0.644
April	−1.095	40.14	0.28	−1.095	40.14	0.28
May	−0.7547	9.168	0.4694	−0.7595	9.168	0.467

Test results are from Welch *t*-test from package “stats” in *R*. df, degrees of freedom.

and period as predictor variable. Additionally, we did a post hoc analysis with a Bonferroni correction, using a binomial test. We used a lognormal regression to test the effect of time and parental status on foraging and vigilance bout lengths. Furthermore, we used an independent sample *t*-test for unequal variances to test whether the length of a foraging bout or vigilance bout were different for parents and nonparents in each “period.” Statistical tests were performed with *R* (R Development Core Team 2009).

RESULTS

Vigilance was significantly influenced by the interaction between time of year (period) and parental status (linear model: R^2 adjusted: 0.16, $F_{3,940}$: 58.71, $P < 0.0001$; interaction “period–parental status”: estimate: −3.38, standard error [SE] of estimate 0.72, t: −4.67, $P < 0.0001$). Parents were vigilant for 34% of the time in October, whereas nonparents were only vigilant for 13% of the time. In November, parents were still more vigilant than nonparents, with 31% versus 16%. During winter (December–February), parents were less vigilant than before, but still more vigilant than nonparents (23% vs. 12%). From March onwards, there was no difference in vigilance between parents and nonparents (March: 20% vs. 18%, April: 26% vs. 21%, and May: 21% vs. 15%) (see Figure 1a and Table 2 for summary). Because foraging and vigilance were dependent on each other, an increase in vigilance resulted in an approximately similar decrease in foraging time for parents.

The residual vigilance (R_V) was significantly influenced by the interaction between time of year (period) and parental status (linear model: R^2 adjusted: 0.18, $F_{3,940}$: 70.66, $P < 0.0001$; interaction period–parental status: estimate: −4.29, SE of estimate 0.72, t: −5.97, $P < 0.0001$). The R_V was 21 during autumn migration in October, indicating that the difference in time vigilant between parents and nonparents was 21% of the total time budget. In November, R_V had decreased to 15 and during winter (December–February) R_V decreased to 11, which was still significantly different from zero. From March onwards, R_V was no longer statistically different from zero (see Figure 1b and Table 2 for summary). An indication for the presence of parental care is the effort it took to find actual parents. One can see (Table 1) that the number of observations of parents started to decrease from February onward. From March onward, it took great effort to find the few parents we observed, and during spring migration in May, there were hardly any parents, leading to the unbalance between parents and nonparents in our data in those periods. The search effort to balance the data resulted in a bias toward parents, which is for our question a conservative bias, indicating that parental care certainly did not last longer than we now observed.

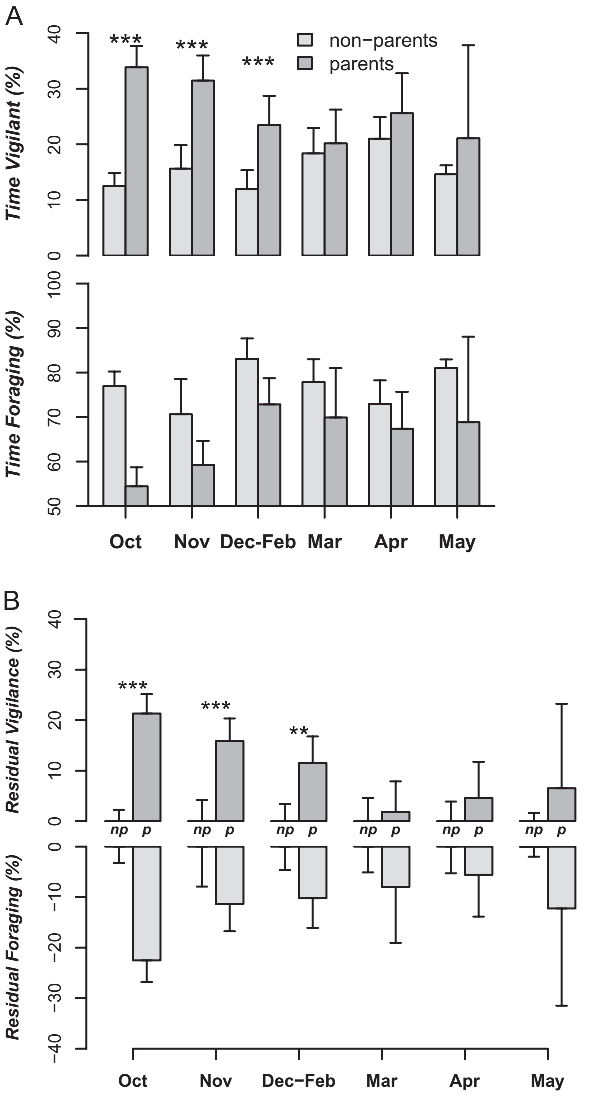

Figure 1

(a) The percentage of time spent on foraging and vigilance per period for parents and nonparents. The error bars show 95% confidence intervals. Significance levels indicate the P values from the t-test between parents and nonparents within each period: $^{***}P < 0.001$, $^{**}P < 0.01$, and $^{*}P < 0.05$. (b) Mean residual vigilance and foraging per period for parents (p) and nonparents (np). The error bars show 95% confidence intervals. Significance levels indicate the P values from the t-test between parents and nonparents within each period: $^{***}P < 0.001$, $^{**}P < 0.01$, and $^{*}P < 0.05$.

The mean number of attacks per minute was significantly influenced (at the 0.10 level) by the interaction between the parent status and period of observation (linear model: R^2 adjusted: 0.014, $F_{3,940}$: 5.49, $P < 0.001$; interaction: estimate: −0.012, SE of estimate: 0.006, $P = 0.07$). The low R^2 is caused by the large number of zeros in the data. In October, parents had an attack rate of 0.07 times per minute, against 0.02 for nonparents. In November, parents attacked 0.05 times per minute, against 0.01 for nonparents. During winter, from December until February, parents attacked with 0.13 attacks per minute significantly more than nonparents with 0.01 attacks per record. From March onward, the number of attacks per minute did not differ between parents and nonparents (Figure 2, see Table 3 for statistical details).

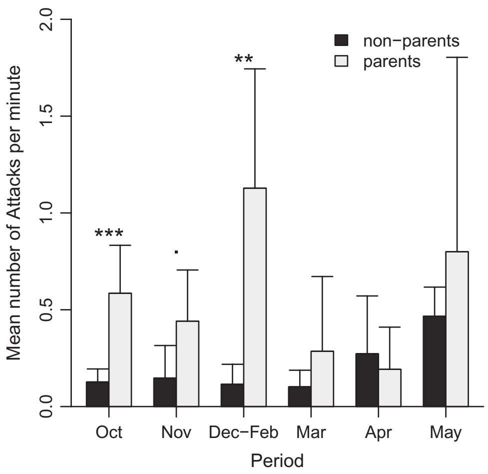

Figure 2
The mean number of attacks per observation for parents and nonparents per period. Error bars show 95% confidence intervals. Significance levels indicate P values from the t-test between parents and nonparents within each period: ***$P < 0.001$, **$P < 0.01$, and *$P < 0.05$.

Log-linear model analysis showed that the length of foraging bouts and the length of vigilance bouts was significantly influenced by the interaction between period and parental status (foraging: R^2 adjusted: 0.15, $F_{3,934}$: 56.77, $P < 0.0001$; interaction period–parental status: estimate: 0.11, SE of estimate 0.03, t: 4.0, $P < 0.0001$; vigilance: R^2 adjusted: 0.08, $F_{3,\ 940}$: 30.83, $P < 0.0001$; interaction period–parental status: estimate: −0.09, SE of estimate 0.04, t: −2.6, $P < 0.01$). The mean vigilance bout length was significantly longer for parents with 9.9 s than for nonparents with only 5.2 s in October. Also foraging bout lengths were different, with 12.3 and 24.4 s for parents and nonparents, respectively. During November, both vigilance (5.9 vs. 4) and foraging (12.8 vs. 21.9) bout lengths were different, as well as from December until February (vigilance: 5.3 vs. 3.2 and foraging: 16.9 vs. 26.8). From March onward, the length of both vigilance (March: 5.3 vs. 5.7, April: 6.1 vs. 5.5, and May: 10.9 vs. 5.6) and foraging (March: 21.6 vs. 24.5, April: 16.7 vs. 19.7, and May: 43.9 vs. 30.8) bouts was statistically the same for parents and nonparents (Figure 3, see Table 4 for statistical details). Note that in contrast to mean percentage of time spent on foraging or vigilance, the length of both foraging and vigilance bouts can increase because they are not dependent on each other.

Table 3
Test results for number of attacks per minute between parents and nonparents within each period

	Attacks per minute		
Period	t	df	P
October	−3.3684	185.135	<0.001
November	−1.9032	55.39	0.062
December–February	−3.1402	41.078	0.003
March	−0.9106	21.995	0.372
April	0.3063	77.15	0.760
May	−0.4654	9.698	0.652

Test results are from Welch t-test from package "stats" in R. df, degrees of freedom.

The percentages of unattached and attached offspring were equal in February, although this equality was influenced by our search bias toward attached offspring. Afterward, the percentage of unattached offspring rapidly increases (Figure 4).

DISCUSSION

Our results on vigilance, foraging, residual vigilance, attacks, and bouts all show that parental care lasted until February. Our use of a measure for the difference between parents and nonparents helps to see what parents do, in case of vigilance, or do not, in case of foraging, compared with nonparents. Aided by the absolute time spent on vigilance and foraging, it gives good insight in the efforts parents make for their offspring. The added value of using an R_V is that it allows for, for example, comparison of different populations because the behavior of nonparents is used as a baseline. These results are supported by our observation that the number of offspring unattached to a family greatly increased after February. In contrast to earlier studies that showed that parental care in barnacle geese lasted until during migration (Black and Owen 1989), we show that parental care, and thus parent–offspring association, in Russian breeding barnacle geese currently does not last until during migration. Actually, where the commencement of spring migration has delayed from April to May, termination of parental care has advanced from April to February, resulting in a 2-month gap between the end of parental care and the beginning of spring migration. That both timing of termination of parental care and commencement of spring migration are diverging from a formerly overlapping situation, and thus no longer overlap or phenologically match, suggests that the timing of these behaviors is regulated by different mechanisms. From other Anatidae, such as ducks, it is known that extended parental care is regulated by hormones such as prolactin (Boos et al. 2007), and other aspects of breeding in geese are also regulated by prolactin (Jonsson et al. 2006). It thus likely that an innate mechanism, not connected to the mechanism determining commencement of migration, is regulating extended parental care. But because offspring is expected to disagree with the parents over termination of parental care (Trivers 1974), the behavior of the offspring is suggested to also influence this termination (Black and Owen 1989). Experimental studies could provide insights in how the moment of family breakup can change.

There are some other examples of studies suggesting that changes in migration phenology have population consequences. Pied flycatchers *Ficedula hypoleuca*, for example, are constrained in their laying date by their arrival date in The Netherlands. This arrival date is constrained by their departure from wintering grounds in Africa, which are triggered by local climate variables. The changing conditions in The Netherlands require an advancement of laying date, but because the locale climate in Africa is not changing at the same rate as in The Netherlands, the arrival date cannot advance sufficiently (Both et al. 2006). Another example is that cuckoos *Cuculus canorus* are advancing their first arrival date, in response to climate changes, less than some of their host species. Because the arrival dates are a good predictor for laying dates and because cuckoos synchronize breeding with their hosts, cuckoos may miss breeding opportunities (Saino et al. 2009). Both studies suggest that this results in decreased reproductive success and ultimately a population decline. However, in our study system, this is clearly not the case.

Despite this divergence, Russian Barnacle geese are very successful, which suggests that the assumed mechanism of teaching migration behavior to offspring was either never present or not so important for successful migration as previously thought or has became less important, for this species. The

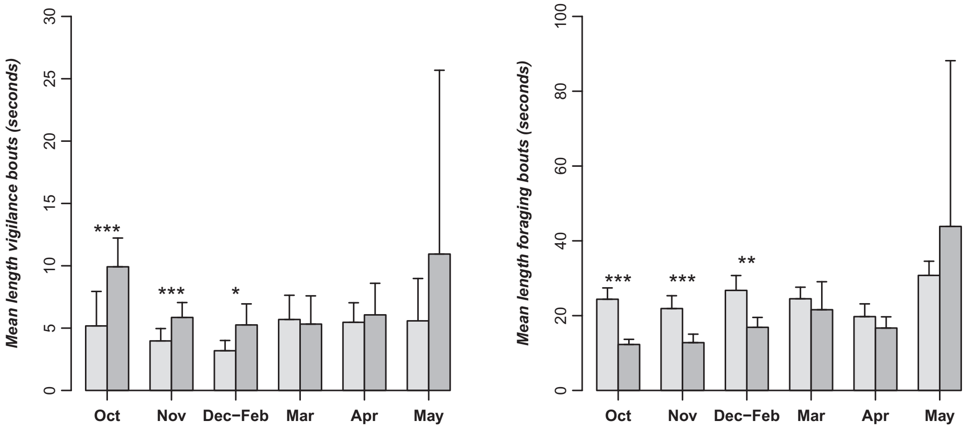

Figure 3
The mean bout length for vigilance (left) and foraging (right) for parents (dark gray) and nonparents (light gray) per period. Error bars show 95% confidence intervals. Significance levels indicate P values from the t-test between parents and nonparents within each period: $^{***}P < 0.001$, $^{**}P < 0.01$, and $^{*}P < 0.05$.

data to support the long parental care or family duration of geese are very scarce (Prevett and MacInnes 1980; Black and Owen 1989) and yet it is often (Mayr 1942; Hochbaum 1955; Kear 1970; Owen 1977, 1980; Baker 1978; Newton 2008)presented as an established fact. Our study suggests that this might not be as general as previously assumed, and studies on other species within the Anserinae, and on populations within these species with respect to parental care could clarify this issue.

Because the commencement of migration has delayed and the arrival on the breeding grounds not (Eichhorn et al. 2006), the duration of migration has become shorter and more energetically costly (Hedenström 1992). Possibly, this has made time more valuable during migration and has changed the balance between the cost and benefits of extending parental care. Hence, making it no longer beneficial to extend parental care into migration. A possible consequence of this divergence can be that the migratory traditions are broken, as suggested by Owen: “Most wildfowl are highly traditional, … , but how are these traditions maintained? Geese and swans are highly gregarious family birds and the adults and parents lead their inexperienced young during the first year of their life. The old geese may remember particular feeding fields or parts of fields. Once this tradition has been broken (…) young will not find their way automatically to suitable breeding grounds” (Owen 1977, p. 39). Although there are many other individuals in goose flocks to learn or copy migratory behavior from, the chance that offspring will develop other migratory behavior than their parents increases with an increasing time gap as a result of the divergence in timing of parental care and migration. We currently see many new migratory strategies emerging for Barnacle geese, and the emergence of these strategies coincides with the delay in commencement of migration. In the 1980s, a population was established on a former stopover site (Larsson et al. 1988), thereby shortening migration distance with almost 2000 km. Ten years later, a population was established in the former wintering site, The Netherlands (Ouweneel 2001), thereby stopping migration at all. Clear mechanistic explanations for these emergences have not been given yet, and the population genetics structure could help answering this question, as well as on how the 3 different flyways (Greenland, Spitsbergen, Russia) of barnacle geese have emerged historically. We argue that the

Table 4
Test results for foraging and vigilance bout lengths between parents and nonparents within each period

Period	t	df	P
Vigilance bouts			
October	−2.58	267.3	<0.05
November	−2.38	63.8	<0.05
December–February	−2.16	55.8	<0.05
March	0.24	49.2	0.81
April	−0.39	44.8	0.70
May	−0.69	10.0	0.50
Foraging bouts			
October	7.14	193.9	<0.0001
November	4.34	55.7	<0.0001
December–February	4.05	84.1	<0.001
March	0.71	27.1	0.48
April	1.32	74.1	0.19
May	−0.58	9.1	0.58

Test results are from Welch t-test from package “stats” in R. df, degrees of freedom.

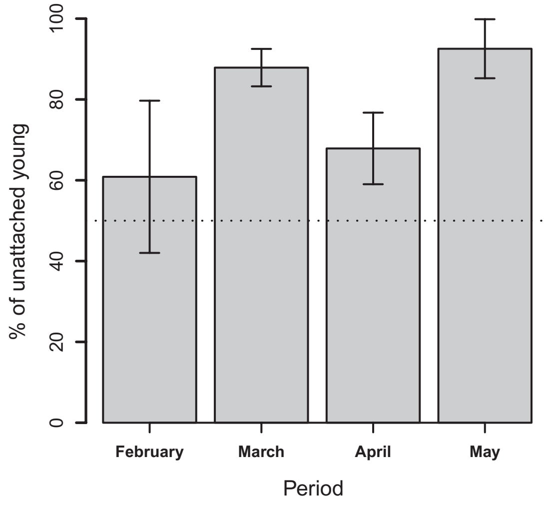

Figure 4
The percentage of unattached young. The dotted line indicates the 50% line, which was our aim throughout the observations.

potential disruption of transmission of migration strategy, as a result from a divergence between the commencement of spring migration and the end of parental care, can explain the emergence of new migration strategies in barnacle geese.

FUNDING

Dutch Faunafonds; the Royal Netherlands Hunters Association (KNJV); and the Schure-Beijerinck-Popping Fund of the Royal Netherlands Academy of Arts and Sciences (KNAW).

We thank Michiel Faber, Alexander van de Bilt, and Ralf Kurvers for their assistance with field observations. Kate Lessells provided valuable comments to an earlier version of the manuscript. We thank Hans Hofmann and 2 anonymous reviewers for their constructive comments. We thank Veljo Völke and Aivar Leito for their advice and help with the fieldwork in Estonia and the Tamme family for providing a field station during our stay in Estonia.

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