

Divorce in Canada Geese (*Branta canadensis*): frequency, causes, and consequences

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Abstract

Most Canada Geese (*Branta canadensis*) form lifelong pair bonds (same-mate geese), but some pairs break apart and the geese mate with new partners while their former mates are still alive (divorcees). Over 25 years, we assessed lifelong reproduction of 160 collared Canada Geese that nested for multiple years in New Haven County, Connecticut. We examined whether same-mate geese and divorcee geese differed from each other prior to or after the divorce. Fifteen percent of females and 18% of males divorced during their lifetimes. Divorces were more frequent in pairs that produced fewer hatchlings during their prior nesting year. Most divorcees that nested again did so on their former nesting territories. Replacement partners of divorcees averaged younger and had fewer years of nesting experience than the divorcees' prior mate. Usually after a divorce, one divorcee of each former pair nested immediately while the other skipped one or more years before nesting again. Under such circumstances, the partner able to nest immediately can increase its direct fitness by finding a new partner and nesting rather than foregoing the opportunity to nest that year. During their first nesting year after the divorce, the reproductive success of divorcees and same-mate geese were similar.

Key words: Canada Geese; lifelong reproduction; mate fidelity; mate selection; monogamy; pair bonds

Introduction

Many bird studies have found a positive relationship between the duration of a pair bond and the pair's reproductive success (Pyle *et al.* 2001; van de Pol *et al.* 2006). Black (2001) and Cooke *et al.* (1981) hypothesized that this was because mates were able to coordinate their behaviour so they are better able to watch for predators, defend their nesting territory from conspecifics, and provide their young with access to better foraging areas. Despite the advantages of a durable pair bond, some individuals pair with a new partner while their former partner is still alive. We refer to this as a divorce and the individuals as divorcees, terms widely used in the ornithological literature (Ens *et al.* 1993; Dhondt and Adriaensen 1994; Choudhury 1995).

Several hypotheses explain divorce in species that normally have lifelong pair bonds. Owen *et al.* (1988) hypothesized that a divorce results when a pair becomes separated during winter or migration, and one mate reached the nesting grounds before the other and pairs with a new bird before its former mate arrives (lost-mate hypothesis). The incompatible-mates hypothesis argues some geese cannot work well together when nesting due to individual incompatibilities, but these same individuals could be good partners for other geese (Coulson 1972; Choudhury 1995; Dhondt 2002). The territorial-improvement hypothesis predicts that divorces occur when one mate has the opportunity to gain

access to a better territory by switching mates (Dhondt and Adriaensen 1994; Garcia-Navas and Sanz 2011) while the mate-improvement hypothesis argues that divorces result when one mate has an opportunity to mate with a better partner (Ens *et al.* 1993; Choudhury 1995).

Geese and swans (Anatidae) are renowned for their lifelong pair bonds; most geese and swans have only one mate during their entire lives (Bellrose 1980; Baldassarre 2014). Yet, some pairs break apart while both mates are alive and in the same area, and the former mates reproduce with others. The frequency of divorce (proportion of pairs that divorce) was <2% in Lesser Snow Geese (*Chen caerulescens caerulescens*; Cooke *et al.* 1981), <2% in Richardson's Cackling Geese (*Branta hutchinsii hutchinsii*; MacInnes and Lief 1968), 7% in Canada Geese (*Branta canadensis*; Raveling 1988), and 8% among Barnacle Geese (*Branta leucopsis*; Black *et al.* 1996). Among swans, divorce rates were 0% in Bewick's Swans (*Cygnus bewickii*), 3.7% in Mute Swans (*Cygnus olor*), and 5.8% in Whooper Swans (*Cygnus cygnus*; Rees *et al.* 1996). Baldarrasse (2014) is the authority for the names of subspecies in this paper.

For 25 years, we studied a marked (collared) population of Canada Geese located in Connecticut to determine the frequency of divorce, why some geese divorce while others remain with their prior mates, and the consequences of divorce. We tested the hypotheses that 1) the new partners of divorcees were older and had more

years of nesting experience than their former mates (Ens *et al.* 1993; Choudhury 1995), 2) divorcees were unable to retain their prior nesting territory because a single bird cannot defend a territory alone (Abraham *et al.* 1981), 3) divorcees are more common in pairs that had experienced reproduction failures (Coulson 1972), and 4) divorcees were less successful reproducing than geese that remained with their prior mates (Catry *et al.* 1997).

Methods

We examined reproduction of Canada Geese (*Branta canadensis*) in New Haven County, Connecticut, USA (centroid: 41.3267°N, 72.89043°W). The terrain is mostly flat near the coast of Long Island Sound but rises to low hills (up to 320 m) in the northern part of the county. The county has numerous ponds, streams, and rivers. Several reservoirs have been created to provide power or store water.

Canada Geese started nesting in New Haven County during the late 1970s (Conover and Chasko 1985). These geese were non-migratory and rarely left the county once they started nesting (Conover 2012). We started banding these geese and studying their movements, survival, and reproductive success in 1984 and continued through 2008.

Most Canada Geese in the county built their nests on islands, abandoned Muskrat (*Ondatra zibethicus*) lodges, and abandoned Mute Swan nests scattered throughout the county but brought their broods to one of three brood-rearing sites, sometimes travelling several kilometres to reach them (Conover 2012). Each brood-rearing site was located on a reservoir complex of two to four lakes. The three complexes were Konold's Pond-Lake Dawson, Whitney Lakes, and Maltby Lakes. Adjacent to these lakes were golf courses, shopping centres, and apartment buildings. The broods usually foraged on the lawns associated with these areas (Conover and Kania 1991). For instance, the broods from Maltby Lake complex spent most of their time on Yale University Golf Course, which offered both rich foraging grounds (lawns) and sanctuaries (water hazards and ponds; Conover 2012).

In Connecticut, Canada Goose eggs hatch in late April and early May, and goslings fledge in early July (Conover and Frank 2018). Adult geese moult their primary feathers and become flightless in late June. During the moult, we rounded up goslings and adults at all brood-rearing areas in New Haven County by herding them into funnel traps (Smith *et al.* 1999). We weighed each bird upon capture, determined its sex through a cloacal examination, and banded it with a U.S. Geological Survey (USGS) aluminum leg band and either a large leg band or neck collar made of plastic by Spinner Plastics (Springfield, Illinois, USA). Each large leg band and neck collar had a unique combination of letters and numbers large enough (letters were 1.3 cm in height on leg bands and 3 cm on collars) so we could

identify individuals from far enough away that our presence did not disturb the geese. Collars were identical to those used extensively throughout the Atlantic Flyway (Hestbeck and Malecki 1989). We replaced worn or lost leg bands or neck collars by identifying individuals by their USGS leg bands. We searched Connecticut for geese wearing large leg bands and neck collars year-round and observed most birds dozens of times each year. We also used sightings of marked geese reported to the U.S. Bird Banding Lab to locate birds. Once Canada Geese started nesting, they exhibited great fidelity to nesting and brood-rearing areas; only one goose we observed nesting in New Haven County was ever observed nesting outside the area (Conover 2012). We considered a female to have reproduced during any year that it was observed incubating a nest or attending a brood and a male to have reproduced during any year that it was observed attending a brood or defending a territory in which a female was incubating a nest.

All geese were banded by us when they were goslings (HY geese) or adults (AHY geese) prior to 2001; those born after 2001 were excluded from the analysis because we were interested in the long-term consequences of divorce. We knew the age of all HY geese, but not for AHY geese. Because most Canada Geese breeding in the area were banded as goslings, most birds first captured as adults were probably relatively young (i.e., one to three years old). Hence, we assumed each AHY goose was two years old when first banded. Including AHY geese in our study introduced some imprecision into the aging of geese. Previously, Conover (2012) assessed whether any bias was created by including AHY geese in the database and found HY and AHY geese were similar in all measures of age-related reproduction.

We visited every known Canada Goose nest in New Haven County to determine clutch size. Goose nests were located by flights over the county by Connecticut Department of Environmental Protection staff and by searching all water bodies appearing on USGS topographical maps from shore or a boat. Most nests were discovered by observing a lone male. We observed each nest from a distance at least weekly to determine if it was still being incubated. We mapped nesting territories each year by noting the location of both mates during the incubation period and where they confronted intruding geese. Usually the territory consisted of a small island or shoreline and the water around it. Sometimes, we recorded the exact location of nesting territories, but not always.

We determined brood sizes at least twice a week for the first month after hatching and then every week or two until the goslings could fly in July. Broods were identified by the parents that were attending them. Individual goslings were not marked at hatching, but broods were individually dyed or marked with ink at hatching when multiple broods were at the same place so we could keep track of goslings. We assumed all gos-

lings in a brood died when the parents were observed without their brood, provided that 1) none of their marked goslings were observed with another brood and 2) no other brood at the same site increased in size when the brood disappeared.

We recorded brood sizes at hatching and fledgling. We defined brood size at hatching as the number of goslings in a brood when first sighted (usually within 48 hours of hatching), and brood size at fledgling as the number of goslings in a brood the day before we captured the parents and brood, which took place immediately before the goslings gained the ability to fly. We recorded whether the parents raised their brood by themselves (two-parent family) or whether they joined with other parents to form a gang brood. A gang brood occurred when two or more families joined together with their offspring, resulting in a cohesive group of young accompanied by four or more parents (Conover 2009). The number of fledglings in a gang brood was divided by the number of adult pairs attending the brood to determine the number of fledglings each pair produced, with the provision that the number of fledglings assigned to a pair could not exceed its brood size at hatching.

We identified nesting adults by their band or collar numbers and determined their age, the age and identity of their mates, clutch size, brood size at hatching, and brood size at fledgling. We noted if the marked geese had nested on the same territory during prior years.

Usually, paired geese nested together year after year, but sometimes, we found a banded goose nesting with a new partner while its former partner was still alive and in the area. We defined this as a divorce. At least one of the prior partners had to nest again because otherwise we would not know a divorce had occurred. We wanted to compare divorcees to other geese that remained paired with their former mates (same-mate geese). There were two criteria for a nesting goose to be a subject for this study (i.e., either a divorcee or same-mate geese). First, both the subject and its mate had to wear either a large leg band or neck collar so that we could individually recognize them. Second, a subject had to nest at least two years during its life so that it had the opportunity to switch mates from one year to the next and its former mate had to be alive and in the area during the second year the subject nested. All geese that met these criteria in New Haven County were included in this study.

We determined the divorce rate, which is the proportion of subjects that became a divorcee anytime during their lives, and the annual divorce rate, which is the proportion of nesting birds that initiated a divorce from one year to the next. The annual divorce rate was calculated as the number of divorcees divided by the total number of nest-years by subjects after their first nesting year. Each subject's first nesting year was excluded from this analysis because a divorce cannot occur during the first nesting year. We compared the frequency of divorce among females and males using a 2×2 contingency test

corrected for continuity (Siegel 1956). Results were considered statistically significant when $P \leq 0.05$. We hypothesized that some divorces result when a goose that has nested during a prior year has an opportunity to move to a better nesting territory by divorcing its former mate and mating with a new partner that had a better territory. To test this hypothesis, we determined the number of divorcees that remained on the same territory they had prior to the divorce.

In Canada Geese, reproductive performance is positively correlated with parental age and nesting experience (Baldassarre 2014), and we hypothesized that divorces result when one mate has the opportunity to nest with an older, more experienced goose than its current mate. We used a paired *t*-test (Siegel 1956) to compare the age and years of nesting experience of a divorcee's replacement mate (i.e., the individual a divorcee nested with after its divorce) during its first nesting year with the divorcee against the age and prior nesting experience of divorcee's prior mate (i.e., the individual a divorcee nested with prior to its divorce) during that same year.

Divorce prediction analyses

Factors predicting the probability of divorce were evaluated with binary generalized linear models (GLM). Same-mate geese were coded as the reference category. Models with all possible combinations of age, sex, mass, and reproductive success prior to divorce were compared using Akaike Information Criterion adjusted for small sample sizes (AICc) and Akaike weights (w_i). Metrics of reproductive success were highly correlated; thus, we selected the best metric for reproductive success by comparing single-variable models with AICc. Only the reproductive success variable with the lowest AICc was used in models with age, sex, and body mass to predict divorce. We used these models to test the hypotheses that divorces were more frequent among pairs that had been less successful during their last nesting attempt or during all nesting attempts in the past or when one of the partners was in poor body condition.

Divorce consequence analyses

We used binary GLMs to compare divorcees to same-mate geese to determine the reproductive benefits or costs of a divorce. Same-mate geese were coded as the reference category. For this analysis, we compared reproductive success of divorcees to same-mate geese after divorce. We also used variables describing the change in these reproductive success variables from before divorce to after divorce; these variables describing change were calculated as reproductive success after divorce minus reproductive success prior to divorce (e.g., brood size during the year after the divorce minus brood size the year prior to divorce). Models with all possible combinations of age, sex, reproductive success after divorce, and change in reproductive success were compared with AICc and w_i . To avoid auto-correlation of reproductive success metrics, we selected the best metric for reproductive success after a divorce (brood size at hatching,

or brood size at fledging the year after a divorce or the number of fledglings produced during all nesting years following a divorce) by comparing single variable models with AICc. The same procedure was conducted to select the best predictor of change in reproductive success. We used the best post-divorce reproductive variable and the best change in reproductive success variable based on AICc to compare the reproductive consequences of divorce.

All GLMs were evaluated using statistical program R (R Core Development Team 2015). For divorce prediction and divorce consequence analyses, we report on variables that were informative (85% CI of parameter estimates that did not overlap 0) and variables that were highly precise (95% CI of parameter estimates that did not overlap 0). For the divorce consequence analysis, we compared the nesting year following a divorce for divorcees with the nesting year following the randomly selected year for same-mate geese. Likewise, we compared for divorcees all nesting years following a divorce with all nesting years following the selected nesting year for same-mate geese.

Results

We banded 858 females of which 207 nested at least once, and 883 males of which 152 nested at least once. We observed 84 females and 76 males that nested for multiple years; these were the subjects of this study. Among them, 13 females (15%) and 14 males (18%) divorced; the divorce frequency did not differ between sexes ($\chi_1^2 = 0.25, P = 0.62$). The annual divorce rate was 7.6% for females based on 172 nest-years and 7.3% for males based on 190 nest-years (first nesting years were not included because birds cannot divorce during their first nesting year). Annual divorce rates were similar among female and male subjects ($\chi_1^2 = 0.01, P = 0.95$). No divorcee ever returned to its original partner following a divorce.

Prior mates of female divorcees were older ($t_{10} = 2.21, P = 0.05$) and had more years of nesting experience ($t_{10} = 4.66, P = 0.001$) than the replacement mates of female divorcees; prior mates were 7.8 ± 3.9 (mean \pm SD) years old and had 3.3 ± 3.6 years of experience while the replacement mates were 5.0 ± 3.2 years old and had 1.1 ± 1.0 years of experience. Male divorcees' prior mates also were older ($t_{11} = 2.76, P = 0.02$) and had more years of nesting experience ($t_{11} = 2.86, P = 0.02$) than the replacements; prior mates were 7.8 ± 3.9 years old and had 3.3 ± 3.6 years of experience while replacement mates were 5.0 years old and had 1.1 ± 1.0 years of nesting experience.

We often did not record the exact location of nesting territories, but for four male and four female divorcees we noted the nesting territories before and after their divorce. All of the males retained their former nesting territories after their divorces, as did three females. For the one female exception, its former partner retained its former nesting territory, and the female divorcee moved

to a new nesting territory on an island in an adjacent lake.

Divorce prediction analyses

Our GLMs indicated body mass prior to divorce was a poor predictor of the probability of divorcing. Thus, body mass was excluded from AIC modeling. We used the brood size at hatching in our GLM modelling because it was the best reproductive metric for predicting divorce.

Our best GLM for predicting divorce had $w_i = 0.28$ and indicated pairs with small broods at hatching were more likely to divorce in the subsequent year (Table 1). Future divorcees produced fewer hatchlings prior to divorce than same-mate pairs (parameter estimate = -0.18 [95% CI = $-0.38-0.00$]). However, the best GLM model was only 1.67 AICc lower than the intercept-only model indicating while the effect of brood size at hatching was a precise predictor (based on 95% CI) of the probability of divorce, the model did not account for much of the variance in the data. Although two models that included age prior to divorce ($\Delta\text{AICc} = 0.92, w_i = 0.18$ and $\Delta\text{AICc} = 1.5, w_i = 0.13$) had w_i similar to our top AICc model, age had parameter estimates with 85% CI that widely overlapped zero in both models. No model with sex was better than the intercept-only model (Table 1). This indicated age prior to divorce and sex was not different among same-mate geese and geese that divorced.

Divorce consequences analyses

We compared the reproductive success of 23 divorcees (13 females and 10 males) to 110 same-mate geese (58 females and 52 males) during their first nesting year after the divorce. We used brood size at hatching during the year following divorce, the difference in number of fledglings in the final nesting year before divorce, and number of fledglings in the next nesting year after divorce in AIC modelling to compare geese that divorced to geese that nested a second year with their former mate. Although multiple models that also included age post-divorce, sex, and/or change in fledglings per nesting years were within $\Delta\text{AICc} = 4$ and cumulative $w_i = 0.95$ (Table 2), all of these variables had parameter estimates with 85% CI that overlapped zero in both models. Thus, we decided to only discuss the top model as the most parsimonious description of the consequences of divorce. Our best GLM for assessing the consequences of divorce had $w_i = 0.22$ and indicated divorcees had smaller brood sizes at hatching and more years of nesting hiatus compared to same-mate geese (Figure 1). The poor fit of any change in reproductive success variable indicated neither divorcees nor same-mate geese had increased reproductive success with successive nesting years.

Discussion

Canada Geese are long-lived. In New Haven County, Connecticut, 15% of nesting geese that were recruited

TABLE 1. Results of generalized linear models comparing Canada Geese (*Branta canadensis*) that will divorce their mates during their next nesting year (13 females and 14 males) to geese that will remain paired with their prior mate during their next nesting year (58 females and 52 males). Models were used to determine why some geese divorce but not others. Models were compared with Akaike Information Criterion adjusted for small sample sizes (AICc) and Akaike weights (w_i). Data were from the divorcees' last year with their prior mate compared to the same-mates' first of two years nesting with the same mate. Dependent variables included the subjects' age, sex, and brood size at hatching. Data were collected in New Haven County, Connecticut (1984–2008).

Models	<i>K</i>	Δ AICc	w_i	Deviance
Brood size at hatch*	2	0.00	0.28	132.26
Brood size at hatch + age	3	0.92	0.18	131.10
Age	2	1.50	0.13	133.76
Intercept only	1	1.67	0.12	135.99
Brood size at hatch + sex	3	1.96	0.11	132.13
Brood size at hatch + age + sex	4	2.81	0.07	130.86
Age + sex	3	3.22	0.06	133.39
Sex	2	3.55	0.05	135.81

*AICc = 136.40.

Table 2. Top 10 generalized linear models comparing divorced Canada Geese (*Branta canadensis*; 13 females and 14 males) to geese that will remained paired with their same mate (58 females and 52 males). These models were used to determine if divorce reduces the ability of geese to reproduce. Models were compared with Akaike Information Criterion adjusted for small sample sizes (AICc) and Akaike weights (w_i). Data were from the first nesting year or all years after divorce for divorcees compared to the same-mates' second year nesting or all subsequent years with the same mate. Dependent variables included the subjects' age, sex, brood size at hatching, and change in fledglings produced per year (Δ FPY). Data were collected in New Haven County, Connecticut (1984–2008).

Models	<i>K</i>	Δ AICc	w_i	Deviance
Brood size at hatch + nesting hiatus*	3	0.00	0.22	120.92
Brood size at hatch + nesting hiatus + age	4	0.75	0.15	119.55
Brood size at hatch + Δ FPY + nesting hiatus	4	1.59	0.10	120.39
Brood size at hatch + nesting hiatus + sex	4	1.83	0.09	120.63
Brood size at hatch + Δ FPY + nesting hiatus + age	5	2.40	0.07	119.04
Brood size at hatch + nesting hiatus + age + sex	5	2.45	0.06	119.09
Nesting hiatus + age	3	3.18	0.04	124.10
Nesting hiatus	2	3.32	0.04	126.33
Brood size at hatch + Δ FPY + nesting hiatus + sex	5	3.50	0.04	120.14
Δ FPY + nesting hiatus	3	4.04	0.03	124.96

*AICc = 127.10.

Intercept only AICc = 138.00.

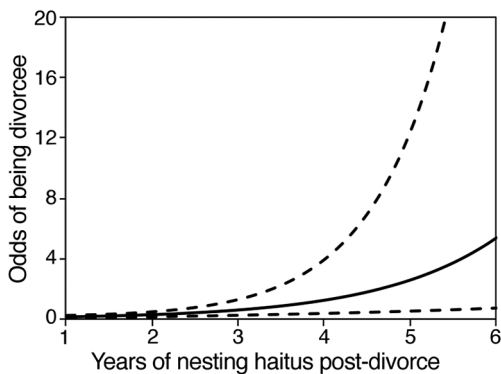


FIGURE 1. Predicted odds of Canada Geese (*Branta canadensis*) being a divorcee (solid lines) compared to a same-mate pair with 95% CI (broken lines) from generalized linear models comparing post-divorce or second year reproductive measures (divorcees to same-mate pairs, respectively).

into the breeding population lived more than 15 years, and 3% lived more than 20 years (Conover 2013). Despite their longevity, most Canada Geese nest with only one mate during their lives; 15% of females and 18% of males divorced during their lives. Raveling (1988) reported a 7% divorce rate among Canada Geese nesting in Manitoba, Canada.

Several hypotheses have been proposed to explain why divorces occur (Table 3). Owen *et al.* (1988) reported most divorces in Barnacle Geese resulted from pairs that became separated during migration or on the wintering grounds and were unable to find each other (the lost-mate hypothesis). This hypothesis, also called the asynchronous-arrival hypothesis for species where mates remain apart during the winter and reunite on the breeding grounds, does not explain divorce among our subjects. In New Haven County, Canada Geese are year-round residents; any pairs that became separated could easily relocate each other. During fall and winter, geese roost in large groups on large waterbodies (e.g.,

TABLE 3. Hypotheses to explain divorce in monogamous birds.

Hypothesis	Reference	Explanation	Supported by our study?
Lost mate	Owen <i>et al.</i> 1988; Ludwig and Becker 2006	Divorce occurs when mates become separated.	No. Our geese were non-migratory and mates could find each other if separated. Nevertheless, divorces still occurred.
Incompatible mates	Coulson 1972	Some birds cannot work together as pairs due to personal differences.	No. Divorces occurred after years of successful nesting. Nest success did not increase after divorce.
Territorial improvement	Dhondt and Adriaenssen 1994	One mate divorces to obtain a better territory.	No. Few divorcees changed territories.
Mate improvement	Ens <i>et al.</i> 1993; Choudhury 1995	One mate divorces to obtain a higher-quality mate.	No. Quality of new mates were similar to former mates. Nesting success did not increase after a divorce.
Unwilling partner	Our study	Divorces occur during a year when one goose is willing to nest but its partner is not.	Yes. One former mate in each pair failed to nest the year after a divorce.

New Haven Harbor, Konolds Pond, and Whitney Lake in our study area). Usually, individual geese use the same roost every night unless disturbed (M.C. pers. obs.). Hence, any goose pair that became separated during the day could reestablish contact that same night.

The incompatible-mates hypothesis argues some birds cannot work well together when nesting due to individual incompatibilities, but these same individuals could be good partners for other birds (Coulson 1972; Choudhury 1995; Dhondt 2002). If this hypothesis is correct, then divorces should be more frequent among young birds than old birds, and divorces should occur soon after a pair starts nesting. This hypothesis also predicts both partners should re-nest quickly following a divorce, and the reproductive success of both partners should increase after divorce. Our results do not support this hypothesis because nesting success of divorcees was similar before and after the divorce. Divorcees were not younger than same-mate geese, and divorce often occurred after pairs had nested together for several years. In contrast to our findings, Raveling (1988) reported that the four divorces he observed in Canada Geese all occurred after only one or two nesting seasons with their former partners.

The territorial-improvement hypothesis predicted that divorces occur when one mate (the initiator) switched to a new mate to gain access to a better territory (Dhondt and Adriaenssen 1994; García-Navas and Sanz 2011). In Eurasian Magpies (*Pica pica*) and European Nuthatches (*Sitta europaea*), divorce resulted when a neighbouring bird with a higher-quality territory disappeared. In this situation, a male with a lower-quality territory abandoned its partner to pair with the widow and take over the higher-quality territory (Baeyens 1981; Matthysen 1990). Also supporting this hypothesis were the findings of Heg *et al.* (2003) that European Oystercatchers (*Haematopus ostralegus*) with low-quality nesting territories were more likely to divorce than birds with high-quality territories. We located the nesting territo-

ry for eight divorcees both before and after the divorce; all but one occupied the same territories both before and after the divorce. Hence, our results do not indicate Canada Geese divorce to obtain a better territory.

The mate-improvement hypothesis predicted divorcees resulted when one mate tries to increase its reproductive success by switching to a higher-quality mate (Table 3). However, we found that the previous mates of divorcees were both older and had more years of nesting experience than did their replacements. Furthermore, this hypothesis predicted the reproductive success of divorcees should increase after a divorce (Ens *et al.* 1993). However, we found divorces did not improve reproductive success. In Barnacle Geese, divorcees produced fewer young with their new mates than they had during their last year with their former spouse, but this was only true for their first year of nesting with their new mate (Owen *et al.* 1988; Forslund and Larsson 1991).

Out of 23 divorced pairs, we found one member of each divorced pair failed to nest during the year of the divorce with only one exception. This suggests at least some divorces occur when one mate is willing and able to nest, but its partner is not. We propose this as a new hypothesis to explain divorce in Canada Geese: the unwilling-mate hypothesis. That is, divorces occur during a year when one mate wants to reproduce, and its partner does not. Under such circumstances, the willing partner can increase its direct fitness by finding another mate and reproducing rather than foregoing the opportunity to nest that year. Unfortunately, other studies did not report if both members of a divorced pair nested during the first year following the divorce.

We found divorcees were more likely to take a nesting hiatus than same-mate geese. During the first nesting year following divorce, divorcees were older than same-mate geese and produced smaller broods at hatching. In Lesser Snow Geese, divorcees and same-mate individuals were similar in their reproductive success (Cooke *et al.* 1981); the same was true in Barnacle Geese after

their first year following the divorce (Black *et al.* 1996). In contrast, Great Skua (*Stercorarius skua*) divorcees fared worse than same-mate birds in annual reproduction (Catry *et al.* 1997).

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Literature Cited

- Abraham, K.F., P. Mineau, and F. Cooke. 1981. Re-mating of a Lesser Snow Goose. *Wilson Bulletin* 93: 557–559.
- Baeyens, G. 1981. Functional aspects of serial monogamy: the magpie pair-bond in relation to its territorial system. *Ardea* 69: 145–166.
- Baldassarre, G.A. 2014. Ducks, Geese and Swans of North America. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Bellrose, F.C. 1980. Ducks, Geese, and Swans of North America. Stackpole Books, Harrisburg, Pennsylvania, USA.
- Black, J.M. 2001. Fitness consequences of long-term pair bonds in Barnacle Geese: monogamy in the extreme. *Behavioral Ecology* 12: 610–645. <https://doi.org/10.1093/beheco/12.5.640>
- Black, J.M., S. Choudhury, and M. Owen. 1996. Do Barnacle Geese benefit from lifelong monogamy? Pages 91–117 in *Partnerships in Birds*. Edited by J.M. Black. Oxford University Press, Oxford, England.
- Catry, P., N. Ratcliffe, and R.W. Furness. 1997. Partnerships and mechanisms of divorce in the Great Skua. *Animal Behaviour* 54: 1475–1482. <https://doi.org/10.1006/anbe.1997.0552>
- Choudhury, S. 1995. Divorce in birds: a review of the hypotheses. *Animal Behaviour* 50: 413–420. <https://doi.org/10.1006/anbe.1995.0256>
- Conover, M.R. 1998. Reproductive biology of an urban population of Canada Geese. Pages 67–70 in *Biology and Management of Canada Geese*, Proceedings of the International Canada Goose Symposium. Edited by D.H. Rusch, M.D. Samuel, D.D. Humburg, and B.D. Sullivan. Milwaukee, Wisconsin, USA.
- Conover, M.R. 2009. Gang brooding in Canada Geese: role of parental condition and experience. *Condor* 111: 276–282. <https://doi.org/10.1525/cond.2009.080073>
- Conover, M.R. 2012. Population growth and movements of Canada Geese in New Haven County, Connecticut. *Waterbirds* 34: 412–421. <https://doi.org/10.1675/063.034.0403>
- Conover, M.R. 2013. Effects of increasing age on fecundity of old-aged Canada Geese (*Branta canadensis*). *Waterbirds* 36: 378–384. <https://doi.org/10.1675/063.036.0317>
- Conover, M.R., and G.G. Chasko. 1985. Nuisance goose problems in the eastern United States. *Wildlife Society Bulletin* 13: 228–233.
- Conover, M.R., and M.G. Frank. 2018. Determinants of growth rates and mass of temperate Canada Geese goslings. *Journal of Wildlife Management* 82: 1161–1168. <https://doi.org/10.1002/jwmg.21465>
- Conover, M.R., and G.S. Kania. 1991. Characteristics of feeding sites used by urban-suburban flocks of Canada geese in Connecticut. *Wildlife Society Bulletin* 19: 36–38.
- Cooke, F., M.A. Bousfield, and A. Sodura. 1981. Mate change and reproductive success in the Lesser Snow Goose. *Condor* 83: 322–327. <https://doi.org/10.2307/1367500>
- Coulson, J.C. 1972. The significance of the pair-bond in the Kittiwake. *Proceedings of the International Ornithological Congress* 15: 424–433.
- Dhondt, A.A. 2002. Changing mates. *Trends in Ecological Evolution* 17: 55–56.
- Dhondt, A.A., and F. Adriaensen. 1994. Causes and effects of divorce in the Blue Tit *Parus caeruleus*. *Journal of Animal Ecology* 63: 979–987. <https://doi.org/10.2307/5274>
- Ens, B.J., U.N. Safriel, and M.P. Harris. 1993. Divorce in the long-lived and monogamous oystercatcher, *Haematopus ostralegus*: incompatibility or choosing the better option? *Animal Behaviour* 45: 1199–1217. <https://doi.org/10.1006/anbe.1993.1142>
- Forslund, P., and K. Larsson. 1991. The effect of mate change and new partner's age on reproductive success in the Barnacle Goose, *Branta leucopsis*. *Behavioral Ecology* 2: 116–122. <https://doi.org/10.1093/beheco/2.2.116>
- García-Navas, V., and J.J. Sanz. 2011. Females call the shots: breeding dispersal and divorce in Blue Tits. *Behavioral Ecology* 22: 932–939. <https://doi.org/10.1093/beheco/arr067>
- Heg, D., L.W. Bruinzeel, and B.J. Ens. 2003. Fitness consequences of divorce in the oystercatcher, *Haematopus ostralegus*. *Animal Behaviour* 66: 175–184. <https://doi.org/10.1006/anbe.2003.2188>
- Hestbeck, J.B., and R.A. Malecki. 1989. Estimated survival rates of Canada Geese within the Atlantic Flyway. *Journal of Wildlife Management* 53: 91–96. <https://doi.org/10.2307/3801312>
- Ludwig, S.C., and P.H. Becker. 2006. Waiting for the mate? Spatial behaviour of Common Terns, *Sterna hirundo*, during courtship. *Animal Behaviour* 72: 1093–1102. <https://doi.org/10.1016/j.anbehav.2006.03.013>
- MacInnes, C.D., and B.C. Lieff. 1968. Individual behavior and composition of a local population of Canada Geese. Pages 93–101 in *Canada Goose Management*. Edited by R. L. Hine and C. Schoendeld. Dembar Educational Research Services, Madison, Wisconsin, USA.
- Matthysen, E. 1990. Behavioral and ecological correlates of territory quality in the Eurasian Nuthatch (*Sitta europaea*). *Auk* 107: 86–95.
- Owen, M.F., J.M. Black, and H. Libor. 1988. Pair bond duration and timing of its formation in Barnacle Geese (*Branta leucopsis*). Pages 23–38 in *Waterfowl in Winter*. Edited by M.W. Weller. University of Minnesota, Minneapolis, Minnesota, USA.
- Pyle, P., W.J. Sydeman, and M. Hester. 2001. Effects of age, breeding experience, mate fidelity and site fidelity on breeding performance in a declining population of Cassin's Auklets. *Journal of Animal Ecology* 70: 1088–1097. <https://doi.org/10.1046/j.0021-8790.2001.00567.x>

- R Core Development Team.** 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Raveling, D.G.** 1988. Mate retention in giant Canada Geese. *Canadian Journal of Zoology* 66: 2766–2768. <https://doi.org/10.1139/z88-403>
- Rees, E.C.P., P. Lievesley, R.A. Pettifor, and C. Perrins.** 1996. Mate fidelity in swans: an interspecific comparison. Pages 118–137 in *Partnerships in Birds*. Edited by J.M. Black. Oxford University Press, Oxford, England.
- Siegel, S.** 1956. *Nonparametric Statistics: for the Behavioral Sciences*. McGraw-Hill, New York, New York, USA.
- Smith, A.E., S.R. Craven, and P.D. Curtis.** 1999. Managing Canada Geese in urban environments. Jack Berryman Institute Publication 16, and Cornell University Cooperative Extension, Ithaca, New York, USA.
- van de Pol, M., D. Heg, L.W. Bruinzeel, B. Kuijper, and S. Verhulst.** 2006. Experimental evidence for a causal effect of pair-bond duration on reproductive performance in Oystercatchers (*Haematopus ostralegus*). *Behavioral Ecology* 17: 982–991. <https://doi.org/10.1093/beheco/arl036>

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