

Carry-Over Effects of Winter Location Contribute to Variation in Timing of Nest Initiation and Clutch Size in Black Brant (*Branta bernicla nigricans*)

Authors: Schamber, Jason L., Sedinger, James S., and Ward, David H.

Source: *The Auk*, 129(2) : 205-210

Published By: American Ornithological Society

URL: <https://doi.org/10.1525/auk.2012.11249>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.



RAPID COMMUNICATIONS

CARRY-OVER EFFECTS OF WINTER LOCATION CONTRIBUTE TO VARIATION IN TIMING OF NEST INITIATION AND CLUTCH SIZE IN BLACK BRANT (*BRANTA BERNICLA NIGRICANS*)

JASON L. SCHAMBER,^{1,3} JAMES S. SEDINGER,² AND DAVID H. WARD¹

¹Alaska Science Center, U.S. Geological Survey, 4210 University Drive, Anchorage, Alaska 99508, USA; and

²Department of Natural Resources and Environmental Science, University of Nevada Reno, 1000 Valley Road, Reno, Nevada 89512, USA

ABSTRACT.—We assessed carry-over effects from winter location on timing of nest initiation and clutch size of Black Brant (*Branta bernicla nigricans*) using observations of individually marked brant breeding at the Tutakoke River colony in Alaska, and wintering along a latitudinal gradient at three areas on the Pacific coast of Baja California: northernmost Bahia San Quintin (BSQ), Laguna Ojo de Liebre (LOL), and southernmost Laguna San Ignacio (LSI). Black Brant initiated nests according to a north–south trend in winter location, although year was a stronger predictor of initiation date than was wintering site. Female Black Brant that wintered at BSQ initiated nests 2.2 days earlier than females from LSI. Conversely, Black Brant showed only a weak south–north trend in clutch size; individuals from LSI laid slightly larger clutches than individuals from BSQ, probably because a smaller proportion of only high-quality females from the southernmost wintering area in Baja California were able to attain the nutritional condition necessary to breed. These results indicate that winter location can influence individual reproductive performance and, potentially, limit population growth of southern segments of the wintering Black Brant population. *Received 2 November 2011, accepted 29 February 2012.*

Key words: Alaska, Baja California, Black Brant, *Branta bernicla nigricans*, carry-over effects, clutch size, nest initiation, reproduction, winter.

Efectos de la Localidad de Invernada Contribuyen a la Variación en el Momento en que Inicia la Anidación y en el Tamaño de la Nidada en *Branta bernicla nigricans*

RESUMEN.—Evaluamos los efectos de la localidad de invernada sobre el momento de inicio de la anidación y el tamaño de la nidada en *Branta bernicla nigricans*. Usamos observaciones de individuos marcados que se reproducen en la colonia del río Tutakoke en Alaska y pasan el invierno a lo largo de un gradiente latitudinal en tres áreas de la costa pacífica de Baja California: la bahía San Quintin (BSQ) al norte, la laguna Ojo de Liebre (LOL) y la laguna San Ignacio (LSI) al sur. La anidación de *B. b. nigricans* inició de acuerdo a una tendencia norte-sur según el sitio de invernada, aunque el año fue un predictor más fuerte de la fecha de iniciación que el sitio de invernada. Las hembras que invernaron en la BSQ iniciaron sus nidos 2.2 días antes que las hembras de la LSI. De manera inversa, *B. b. nigricans* presentó una débil tendencia sur-norte en el tamaño de la nidada; los individuos de la LSI tuvieron nidadas un poco más grandes que los individuos de la BSQ, probablemente porque sólo una pequeña proporción de hembras de alta calidad del área más al sur en Baja California pudo alcanzar la condición nutricional necesaria para reproducirse. Estos resultados indican que la localidad de invernada puede influir sobre el desempeño reproductivo individual y, potencialmente, limitar el crecimiento poblacional de los segmentos meridionales de la población invernante de *B. b. nigricans*.

IN WINTER, MIGRATORY birds are distributed nonrandomly, often on the basis of attributes such as sex and age or social status, across habitats that may differ in type or quality.^{1,2,3} Winter distribution exposes individuals to varying habitat-specific ecological conditions that can have important individual fitness

consequences and potentially influence population dynamics.^{1,4} Winter habitat-specific effects on fitness may not only be immediate (e.g., overwinter survival⁵), but can carry over to influence reproductive traits in the next breeding season.⁶ For example, a few studies of long-distance migrant passerines used stable

³Present address: Alaska Department of Fish and Game, 525 W. 67th Avenue, Anchorage, Alaska 99518, USA. E-mail: jason.schamber@alaska.gov

isotopes to infer winter habitat use and link disparity in winter habitat quality to differences in reproductive traits.^{7,8,9} Individuals that occupied high-quality winter habitats arrived earlier to breeding areas, nested earlier, and produced more offspring than conspecifics that occupied low-quality winter habitats. Such interseasonal effects on fitness are known as “carry-over effects,” whereby nonlethal seasonal events or processes result in individuals transitioning between seasons with different levels of physiological condition, consequently affecting individual performance in a later season.^{8,10} An individual’s physiological condition is largely determined by its ability to gain access to resources, mediated by factors such as habitat quality and social status. Thus, carry-over effects from winter habitats often arise when high-quality habitat is limited and social status influences an individual’s access to high-quality habitat.¹⁰

Carry-over effects from winter habitat are likely common in migrants that use capital or mixed-income breeding strategies because they rely on nutrients stored during the non-breeding period for reproduction. Nutrient stores in large-bodied migrants, like geese, are known to influence timing of egg laying,¹¹ clutch size,^{12,13} and the number of offspring recruited to winter.^{14,15} Nutrient uptake during winter or spring stopover affects their ability to store nutrients, and differential nutrient intake has been associated with either social status^{16,17} or winter location,^{7,18} two factors that are unlikely to be independent. Previous studies have shown that sex and age¹ or social structure¹⁷ influence winter distribution. Thus, nonrandom winter distribution can influence variation in nutrient stores and, therefore, affect individual reproductive performance. Sedinger et al.³ demonstrated that Black Brant (*Branta bernicla nigricans*; hereafter “brant”), which bred successfully and lived as family groups (which are dominant in geese¹⁹), occupied higher-quality winter habitat, which resulted in a higher probability of breeding and returning to the wintering area that produced the highest probability of breeding. Success thus begot success.

Brant are unique among geese in that they winter in Pacific coastal maritime habitats and feed almost exclusively on marine plants that include, primarily, Common Eelgrass (*Zostera marina*; hereafter “eelgrass”) and some species of marine seaweeds.²⁰ The winter distribution of brant is closely related to eelgrass abundance,²¹ and ~50% of the entire Pacific population of brant winters in three estuaries that are situated along a latitudinal gradient in western Baja California: northernmost Bahia San Quintin (BSQ), Laguna Ojo de Liebre (LOL), and southernmost Laguna San Ignacio (LSI). In general, the biomass and intertidal availability of eelgrass decline from north to south latitude²²; therefore, northern areas of Baja California are ostensibly of higher quality than southern locations (see Supplementary Materials). Brant differentially migrate to wintering areas in Baja California such that family groups appear to occupy more northern areas,^{3,23} which suggests that access to higher-quality resources may be determined, at least in part, by social status. Sedinger et al.³ found a relationship between the relative effects of differential migration, breeding probability, and winter distribution. We expand upon the previous study of Sedinger et al.³ and assess the influence of winter location on timing of breeding and clutch size. We hypothesize that the apparent latitudinal variation in winter food abundance will carry over to influence variation in factors related to timing of breeding and fecundity of brant. We used observations

of uniquely marked brant during winter and summer to examine variation in nest initiation date and clutch size of females in relation to winter location. Because nutritional status is a strong determinant of reproductive success in geese, we predicted that individuals using wintering locations with a greater biomass of eelgrass would initiate nests earlier and lay larger clutches than individuals from areas with lower eelgrass biomass.

METHODS SUMMARY

We conducted the study at the Tutakoke River brant colony (TRC) on the Yukon–Kuskokwim Delta (YKD) and at the three primary winter locations in Baja California: BSQ, LOL, and LSI (Fig. 1). We identified individual brant during summer and winter by observing their colored tarsal bands, each engraved with a unique alphanumeric code. Since 1987, about 2,000 brant at the TRC have been captured annually and marked with a colored tarsal band. In the summers of 1992–1993 and 1997–2001, we searched for brant nests at the TRC, and for each nest we recorded the female’s colored-tarsal-band code, clutch size (total number of eggs surviving to incubation), and calculated nest initiation date (either by direct observation during egg laying or by estimation from hatch date). We assigned a winter location to nesting females if their colored tarsal band was resighted at BSQ, LOL, or LSI during the preceding winter; however, no resighting attempts were made in 1991–1992, 1997–1998, and 2000–2001 at LOL. We determined clutch size for 224 females and nest initiation date for 229 females that we associated with a wintering area the previous winter. To examine the quantitative link between winter location and variation in clutch size and nest initiation date, we developed a candidate set of mixed linear models and selected the best approximating model among them using Akaike’s information criterion (AIC_c) corrected for small sample size.²⁴ Please see the online Supplementary Materials for details about field and analytical methods (see Acknowledgments).

RESULTS AND DISCUSSION

The most parsimonious model of nest initiation date included year + winter location and was the only model to receive appreciable support ($w_i = 0.99$) among candidate models (Table 1). Under this model, nest initiation dates among brant wintering in Baja California varied annually and showed a trend from north to south latitude, although standard errors of the means from mid-latitude LOL overlapped those of BSQ and LSI (Fig. 2). Females wintering in southernmost LSI initiated their nests 2.2 days later, on average, than females from the northernmost wintering area of BSQ (Fig. 2). However, the improvement in estimated deviance from the null (random effects only) model was much smaller for the model containing only the effects of winter location than for the model with only year (Table 1), which suggests that year was a better predictor of nest initiation date than winter location.

We included only females ≥ 5 years old in our analysis. Among candidate models of clutch-size variation, the most parameterized model (year + winter location + initiation date) was the best-supported model ($w_i = 0.96$). Lower-ranked models that were less complex were not competitive ($\Delta AIC_c > 7.0$) with the top model. In the top model, clutch size varied annually, showed a pattern of seasonal decline ($\beta = -0.10 \pm 0.02$), and exhibited an increasing



FIG. 1. Locations of the Tutakoke River Black Brant breeding colony in Alaska and three wintering locations in Baja California, Mexico.

TABLE 1. Ranking of mixed linear models of initiation date and clutch size of Black Brant nesting at Tutakoke River on the Yukon–Kuskokwim Delta, Alaska. Individuals were included as random effects in all models. Also reported are the number of model parameters (k), model deviance ($-2\log L$), the difference in Akaike’s information criterion compared to the best model (ΔAIC_c), and the likelihood of each model in a set (Akaike weight, w_i).

Model	k	$-2\log L$	ΔAIC_c	w_i
Initiation date				
Year + winter location	11	1,135.7	0.0	0.99
Year	8	1,149.5	9.5	<0.01
Winter location	5	1,227.0	80.7	<0.01
Null	2	1,249.0	98.6	<0.01
Clutch size				
Year + winter location + initiation date	12	605.6	0.0	0.96
Year + initiation date	9	617.0	7.1	0.02
Winter location + initiation date	6	630.2	13.9	<0.01
Initiation date	3	634.8	14.3	<0.01
Year + winter location	11	623.9	16.2	<0.01
Year	8	628.7	16.6	<0.01
Null	2	643.7	21.2	<0.01
Winter location	5	641.7	23.2	<0.01

trend from northern to southern wintering locations. Brant that wintered at BSQ had mean clutch sizes that were ~ 0.7 eggs smaller than those of brant from LSI (Fig. 3). However, the 95% confidence intervals of the means from winter location overlapped (Fig. 3), indicating that this parameter was a weak predictor of clutch size. We note that the deviance value estimated by the top model was only modestly smaller than that of the null model (Table 1), which suggests that factors other than those that we considered were likely more important determinants of clutch size in brant. The fifth-ranked model (excluding initiation date as a continuous variable) produced a similar relationship between wintering location and clutch size as the top model (Fig. 3).

Our results suggested that timing of nest initiation in brant was strongly influenced by the effect of year but also depended on wintering site during the previous winter. Other studies have demonstrated that variation in environmental conditions during spring (e.g., timing of snowmelt) is a strong determinant of the annual patterns in timing of nesting of brant²⁵ and many other long-distance migrants^{11,26,27}; however, carry-over effects from habitat conditions on nonbreeding areas also may influence nesting phenology.^{8,28} In the present study, brant exhibited a north–south trend in initiation dates that was similar to the annual patterns in quality and quantity of eelgrass found among wintering areas in Baja California. BSQ supported a greater biomass of intertidal eelgrass than the more southern areas of LOL and LSI, where eelgrass grows primarily in subtidal areas^{22,29}; eelgrass occurred at ~ 1 m lower elevation at the middle and southernmost areas than at BSQ.²² The subtidal nature of eelgrass in locations

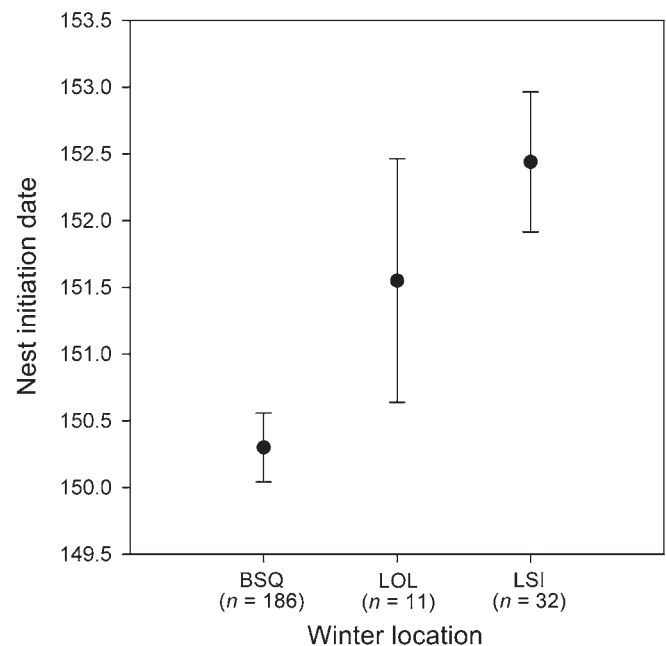


FIG. 2. Estimated least-squares mean nest-initiation dates (Julian days \pm SE) for Black Brant nesting in the Tutakoke River colony and wintering at Bahia San Quintin (BSQ), Laguna Ojo de Liebre (LOL), or Laguna San Ignacio (LSI). Shown are estimates from the best-performing mixed linear model, which included individuals as random effects, and year and winter location as fixed-effects variables.

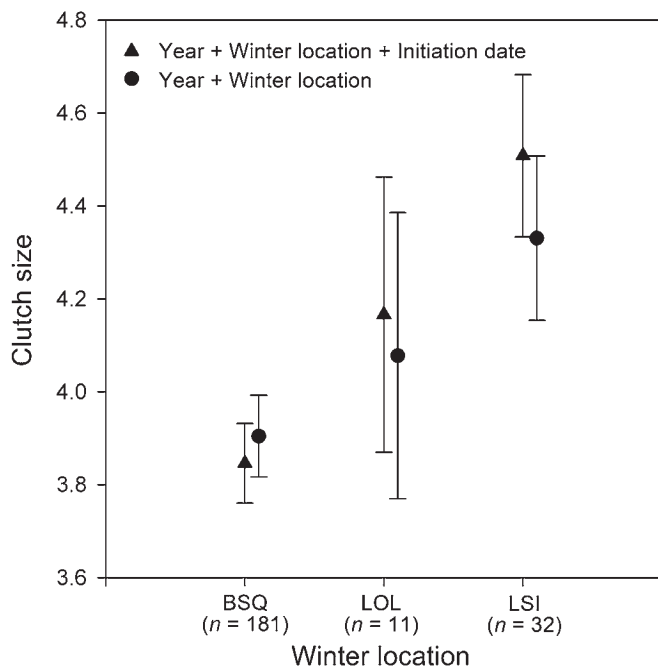


FIG. 3. Estimated least-squares mean clutch sizes (\pm SE) for Black Brant nesting in the Tutakoke River colony and wintering at Bahia San Quintin (BSQ), Laguna Ojo de Liebre (LOL), or Laguna San Ignacio (LSI). Estimates are from two mixed linear models, one of which excluded nest initiation date. These models included individuals as random effects, and year, winter location, or year, winter location, and nest initiation date as fixed-effects variables.

south of BSQ resulted in more frequent tidal inundation, which reduced the availability of eelgrass to foraging brant at the southern sites compared with BSQ.³⁰ Also, the quality of foraging for brant on wintering areas was likely influenced by the nutrient content of eelgrass, which declined with decreasing latitude³¹; thus, food availability and quality appeared to be higher at northern areas of Baja California. Consequently, female brant that wintered at BSQ nested earlier than females from LSI and, possibly, LOL, which is consistent with a hypothesis that carry-over effects from spatial variation in winter habitat quality influenced reproductive traits of brant. This pattern may reflect a combination of lower winter habitat quality and nutritional status of females from southern areas, which delayed breeding,^{11,15} combined with a longer migration to the breeding area.¹⁸ Length of migration likely explained only a small amount of the variation in timing of nesting, however, because BSQ and LSI were separated by only 500 km, which brant can fly in about 6–8.5 h.³² Thus, additional required flight time accounted for only about 16% (8.5 h/2.2 days) of the difference in timing of nesting by brant that wintered at LSI versus those that wintered at BSQ. Furthermore, a small sample of radiotagged brant (D. H. Ward, U.S. Geological Survey, unpubl. data) indicated that differences in timing of northward movement were present when these birds departed from BSQ on their northward migration. Brant that wintered at LOL and staged at BSQ departed 5 days later than brant that wintered at BSQ, despite the fact that only ~6 h were required to fly between the two

locations. In addition, radiotagged females from LOL and LSI that did not stage at BSQ initiated northward migration earlier than females from BSQ and arrived earlier at a major spring staging area in Alaska, which suggests that a modestly longer migration distance from a more southern location, by itself, was unlikely to delay nest initiation.

Female brant that wintered in BSQ nested 2.2 days earlier than females from LSI. A 2.2-day delay represents 30% of the range of dates during which 70% of nests are initiated at the TRC.³³ Delayed nesting has a strong negative effect on the nutrition³⁴ and growth rates of goslings,^{35,36,37} and gosling size has a strong effect on first-year survival^{38,39}; smaller goslings are less likely to survive their first year.³⁹ The delays in nesting experienced by brant wintering at LSI likely reduced first-year survival of the goslings they produced by about 10%³⁹ compared with that of goslings produced by females wintering at BSQ.

Brant that wintered at LSI nested later but laid slightly larger clutches, on average, than brant from BSQ, a trend that contrasts with the observed pattern of seasonal clutch-size decline. We have observed an analogous change in clutch size in late springs,²⁵ when depletion of nutrient reserves would be hypothesized to cause female brant to lay smaller clutches.⁴⁰ By contrast, we observed larger mean clutch size in such years, which we interpreted as indicating that only individuals of higher “quality” (e.g., better competitors with larger nutrient stores¹⁵) were capable of reaching a minimum nutrient threshold^{9,25} that capital or mixed-income breeders must achieve before they attempt to breed.^{11,41} We hypothesize that an analogous restriction on which individuals breed may explain the weak trend in clutch size that we observed, such that stronger selection occurring at LSI, where habitat quality was poorer than at BSQ, restricted breeders from this area to a smaller proportion of relatively “higher-quality” individuals that were capable of attaining the nutrient threshold.

Brant have undergone a northward shift in distribution within Baja California in the past two decades, where they occur at higher population densities (B. Conant and J. F. Voelzer, U.S. Fish and Wildlife Service, unpubl. data). Such changes in distribution may occur because of shifting balances between survival and fecundity⁴² among birds from different locations, or as a behavioral response to changing food abundance.^{43,44,45} Sedinger et al.³ suggested that this northward shift may be explained both by (1) poorer reproduction and lower reproductive effort by brant wintering in southern Baja California and (2) disproportionate migration to northern areas by successful breeders. Our results are consistent with this hypothesis and suggest that variation in nutrient acquisition, coupled with winter distribution of individuals, could substantially influence individual reproductive performance. Geographic variation in reproductive performance, in turn, influences population dynamics and distribution—through population-growth limitations in southern segments of the wintering population, shifts in winter distribution, or both.

ACKNOWLEDGMENTS

Online supplementary materials are available at [dx.doi.org/10.1525/auk.2012.11249](https://doi.org/10.1525/auk.2012.11249). Research was supported by the Alaska Science Center, U.S. Geological Survey; Migratory Bird Management, Region 7, U.S. Fish and Wildlife Service; University of Alaska Foundation;

Ducks Unlimited, Inc.; Ducks Unlimited de Mexico; National Science Foundation (OPP 9214970, DEB 9815383, OPP 9985931, OPP 0196406, DEB 0743152); Morro Bay Brant Group; Phil Jebbia; and the Nevada Agricultural Experiment Station. Logistic support was provided by Yukon Delta and San Diego National Wildlife Refuges, D. and R. Wheeler, La Compania de Exportadora de Sal. S. A., Kuyima Inc., and Ducks Unlimited de Mexico. We thank the dozens of individuals that assisted with field work. C. Nicolai and two anonymous reviewers provided especially helpful comments on the manuscript. Any use of trade names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

LITERATURE CITED

- KETTERSON, E. D., AND V. NOLAN, JR. 1983. The evolution of differential bird migration. Pages 357–402 in *Current Ornithology*, vol. 1 (R. F. Johnston, Ed.). Plenum Press, New York.
- LOPEZ ORNAT, A., AND R. GREENBERG. 1990. Sexual segregation by habitat in migratory warblers in Quintana Roo, Mexico. *Auk* 107:539–543.
- SEDINGER, J. S., J. L. SCHAMBER, D. H. WARD, C. A. NICOLAI, AND B. CONANT. 2011. Carryover effects associated with winter location affect fitness, social status, and population dynamics in a long-distance migrant. *American Naturalist* 178:E110–E123.
- CRISTOL, D. A., M. B. BAKER, AND C. CARBONE. 1999. Differential migration revisited: Latitudinal segregation by age and sex class. Pages 33–88 in *Current Ornithology*, vol. 15 (V. Nolan, Jr., E. D. Ketterson, and C. F. Thompson, Eds.). Plenum Press, New York.
- KÉRY, M., J. MADSEN, AND J.-D. LEBRETON. 2006. Survival of Svalbard Pink-footed Geese *Anser brachyrhynchus* in relation to winter climate, density and land-use. *Journal of Animal Ecology* 75:1172–1181.
- NORRIS, D. R., AND P. P. MARRA. 2007. Seasonal interactions, habitat quality, and population dynamics in migratory birds. *Condor* 109:535–547.
- MARRA, P. P., K. A. HOBSON, AND R. T. HOLMES. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science* 282:1884–1886.
- NORRIS, D. R., P. P. MARRA, T. K. KYSER, T. W. SHERRY, AND L. M. RATCLIFFE. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings of the Royal Society of London, Series B* 271:59–64.
- LAAKSONEN, T., M. AHOLA, T. EEVA, R. A. VÄISÄNEN, AND E. LEHIKONEN. 2006. Climate change, migratory connectivity and changes in laying date and clutch size of the Pied Flycatcher. *Oikos* 114:277–290.
- HARRISON, X. A., J. D. BLOUNT, R. INGER, D. R. NORRIS, AND S. BEARHOP. 2011. Carry-over effects as drivers of fitness differences in animals. *Journal of Animal Ecology* 80:4–18.
- BÊTY, J., G. GAUTHIER, AND J.-F. GIROUX. 2003. Body condition, migration, and timing of reproduction in Snow Geese: A test of the condition-dependent model of optimal clutch size. *American Naturalist* 162:110–121.
- ANKNEY, C. D., AND C. D. MACINNES. 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. *Auk* 95:459–471.
- ANKNEY, C. D. 1984. Nutrient reserve dynamics of breeding and molting Brant. *Auk* 101:361–370.
- EBBINGE, B. S., AND B. SPAANS. 1995. The importance of body reserves accumulated in spring staging areas in the temperate zone for breeding in dark-bellied brent geese *Branta b. bernicla* in the high Arctic. *Journal of Avian Biology* 26:105–113.
- PROP, J., J. M. BLACK, AND P. SHIMMINGS. 2003. Travel schedules to the high Arctic: Barnacle Geese trade-off the timing of migration with accumulation of fat deposits. *Oikos* 103:403–414.
- STAHL, J., P. H. TOLSMA, J. J. E. LOONEN, AND R. H. DRENT. 2001. Subordinates explore but dominants profit: Resource competition in high Arctic Barnacle Goose flocks. *Animal Behaviour* 61:257–264.
- GUNNARSSON, T. G., J. A. GILL, J. NEWTON, P. M. POTTS, AND W. J. SUTHERLAND. 2005. Seasonal matching of habitat quality and fitness in a migratory bird. *Proceedings of the Royal Society of London, Series B* 272:2319–2323.
- BEARHOP, S., G. M. HILTON, S. C. VOTIER, AND S. WALDRON. 2004. Stable isotope ratios indicate that body condition in migrating passerines is influenced by winter habitat. *Proceedings of the Royal Society of London, Series B* 271:S215–S218.
- LOONEN, M. J. J. E., L. W. BRUINZEEL, J. M. BLACK, AND R. H. DRENT. 1999. The benefit of large broods in Barnacle Geese: A study using natural and experimental manipulations. *Journal of Animal Ecology* 68:753–768.
- EINARSEN, A. S. 1965. *Black Brant: Sea Goose of the Pacific Coast*. University of Washington Press, Seattle.
- MOORE, J. E., M. A. COLWELL, R. L. MATHIS, AND J. M. BLACK. 2004. Staging of Pacific Flyway Brant in relation to eelgrass abundance and site isolation, with special consideration of Humboldt Bay, California. *Biological Conservation* 115:475–486.
- CABELLO-PASINI, A., R. MUÑIZ-SALAZAR, AND D. H. WARD. 2003. Annual variations of biomass and photosynthesis in *Zostera marina* at its southern end of distribution in the North Pacific. *Aquatic Botany* 76:31–47.
- SCHAMBER, J. L., J. S. SEDINGER, D. H. WARD, AND K. R. HAGMEIER. 2007. Latitudinal variation in population structure of wintering Pacific Black Brant. *Journal of Field Ornithology* 78:74–82.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd ed. Springer-Verlag, New York.
- LINDBERG, M. S., J. S. SEDINGER, AND P. L. FLINT. 1997. Effects of spring environment on nesting phenology and clutch size of Black Brant. *Condor* 99:381–388.
- BOTH, C., AND M. E. VISSER. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature* 411:296–298.
- DICKEY, M.-H., G. GAUTHIER, AND M.-C. CADIEUX. 2008. Climatic effects on the breeding phenology and reproductive success of an Arctic-nesting goose species. *Global Change Biology* 14:1973–1985.
- LEGAGNEUX, P., P. L. F. FAST, G. GAUTHIER, AND J. BÊTY. 2012. Manipulating individual state during migration provides evidence for carry-over effects modulated by environmental conditions. *Proceedings of the Royal Society of London, Series B* 279:876–883.
- WARD, D. H., T. L. TIBBITTS, A. MORTON, E. CARRERA-GONZÁLEZ, AND R. KEMPKA. 2004. Use of digital multispectral

- videography to assess seagrass distribution in San Quintín Bay, Baja California, Mexico. *Ciencias Marinas* 30:47–60.
30. MOORE, J. E., AND J. M. BLACK. 2006. Slave to the tides: Spatio-temporal foraging dynamics of spring staging Black Brant. *Condor* 108:661–677.
31. CABELLO-PASINI, A., R. MUÑIZ-SALAZAR, AND D. H. WARD. 2004. Biochemical characterization of the eelgrass *Zostera marina* at its southern distribution limit in the North Pacific. *Ciencias Marinas* 30:21–34.
32. GREEN, M., AND T. ALERSTAM. 2000. Flight speeds and climb rates of brent geese: Mass-dependent differences between spring and autumn migration. *Journal of Avian Biology* 31: 215–225.
33. FLINT, P. L., AND J. S. SEDINGER. 1992. Reproductive implications of egg size variation in Black Brant. *Auk* 109:896–903.
34. SEDINGER, J. S., AND D. G. RAVELING. 1986. Timing of nesting by Canada Geese in relation to the phenology and availability of their food plants. *Journal of Animal Ecology* 55:1083–1102.
35. COOCH, E. G., D. B. LANK, A. DZUBIN, R. F. ROCKWELL, AND F. COOKE. 1991. Body size variation in Lesser Snow Geese: Environmental plasticity in gosling growth rates. *Ecology* 72:503–512.
36. SEDINGER, J. S., AND P. L. FLINT. 1991. Growth rate is negatively correlated with hatch date in Black Brant. *Ecology* 72:496–502.
37. LARSSON, K., AND P. FORSLUND. 1991. Environmentally induced morphological variation in the Barnacle Goose, *Branta leucopsis*. *Journal of Evolutionary Biology* 4:619–636.
38. FRANCIS, C. M., M. H. RICHARDS, F. COOKE, AND R. F. ROCKWELL. 1992. Long-term changes in survival rates of Lesser Snow Geese. *Ecology* 73:1346–1362.
39. SEDINGER, J. S., AND N. D. CHELGREN. 2007. Survival and breeding advantages of larger Black Brant goslings: Within and among cohort variation. *Auk* 124:1281–1293.
40. BARRY, T. W. 1962. Effect of late seasons on Atlantic Brant reproduction. *Journal of Wildlife Management* 26:19–26.
41. REYNOLDS, C. M. 1972. Mute Swan weights in relation to breeding. *Wildfowl* 23:111–118.
42. RAVELING, D. G. 1978. Dynamics of distribution of Canada Geese in winter. *Transactions of the North American Wildlife and Natural Resources Conference* 43:206–225.
43. VICKERY, J. A., W. J. SUTHERLAND, A. R. WATKINSON, S. J. LANE, AND J. M. ROWCLIFFE. 1995. Habitat switching by dark-bellied brent geese *Branta b. bernicla* (L.) in relation to food depletion. *Oecologia* 103:499–508.
44. SUMMERS, R. W., L. G. UNDERHILL, R. J. HOWELLS, J. A. VICKERY, AND R. P. PRYCS-JONES. 1996. Phenology of migration and use of wintering sites by the increasing population of dark-bellied brent geese *Branta bernicla bernicla*. *Journal of Zoology (London)* 239:197–208.
45. WARD, D. H., A. REED, J. S. SEDINGER, J. M. BLACK, D. V. DERKSEN, AND P. M. CASTELLI. 2005. North American Brant: Effects of changes in habitat and climate on population dynamics. *Global Change Biology* 11:869–880.

Associate Editor: M. T. Murphy