Cross-seasonal effects and the dynamics of waterfowl populations

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Abstract

Cross-seasonal effects (CSEs) on waterfowl populations link together events and habitats that individuals experience as carry-over effects (COEs) throughout the annual cycle. The importance of CSEs has been recognised since at least the 1950s. Studies of nutrient dynamics beginning in the 1970s, followed by regression analyses that linked production of young to winter habitat conditions, confirmed the importance of CSEs. CSEs have been most apparent in large-bodied waterfowl, but evidence for CSEs in much smaller passerines suggests the potential for CSEs in all waterfowl. Numerous studies have established effects of winter weather on body condition and reproduction in both ducks and geese. Additionally, the ubiquitous use (during laying and incubation) of nutrients stored previously during spring migration suggests that such nutrients commonly influence reproductive success in waterfowl. Carry-over effects from the breeding season to autumn and winter are less well understood, although nutrition during the growth period in geese has been widely demonstrated to influence subsequent survival and reproduction. Only a few studies have examined effects of breeding on reproduction in later years. Because pathogens and parasites can be carried between seasonal habitats, disease represents an important potential mechanism underlying CSEs; so far, however, this role for diseases and parasitism remains poorly understood. CSEs were originally of interest because of their implications for management of seasonal habitats and CSEs represent a fundamental rationale for the habitat joint ventures in North America. Substantial research examining the role of COEs in individual fitness and of CSEs on population dynamics has now been conducted. New techniques (*e.g.* stable isotopes, geolocators) developed over the last decade, combined with more traditional marking programmes have created opportunities to understand CSEs more fully and to inform the management of seasonal habitats for waterfowl.

Key words: carry-over effect, climate, cross-seasonal effect, fitness, population, reproduction, survival.

The concept that variation in habitat quality can influence population dynamics of waterfowl has been established for some time (Lynch 1952). For example, reduced snow accumulation and spring rains in mid-continent prairie-parkland ecosystems result in fewer ponds, which reduces annual production of young ducks (Pospahala *et al.* 1974). Kaminski & Gluesing (1987) extended this notion to include cross-seasonal effects (CSEs) when they showed that the influence of breeding habitat availability on autumn age-ratios (an index of the breeding success of the population) was modified by population density in Mallard *Anas platyrhynchos*. Such density-dependence in the reproductive process is incorporated into models of population dynamics used to manage harvest rates (Johnson *et al.* 1997). For ducks, the number of breeding individuals in the population is influenced by the production of young from the previous breeding season and the number of individuals surviving through winter, so that density-dependent effects on reproduction represent a CSE. Newton (2006) showed how density-dependent mortality operating at different segments of the annual cycle interacted with density-dependent reproduction to regulate population size.

Before the 1970s, attempts to understand waterfowl population dynamics in North America focused largely on habitat conditions in the mid-continent prairie-parkland breeding areas and on the role of harvest as the major drivers of population trends (Johnson *et al.* 1992). The interests of a number of prominent waterfowl scientists in the late 1970s to early 1980s coincided, stimulating discussion and thought on the role of habitats used by waterfowl outside the breeding season in governing their subsequent breeding activity and thus their population dynamics. Ankney & MacInnes (1978) and Raveling (1979) demonstrated that female geese stored nutrients acquired before nesting and used these nutrient reserves during egg laying and incubation. Ankney & MacInnes (1978) further showed that clutch size of Lesser Snow Geese *Chen caerulescens caerulescens* was directly related to their levels of endogenous nutrients. Shortly thereafter, Heitmeyer & Fredrickson (1981) used regression approaches to illustrate that winter wetland indices and winter precipitation predicted age-ratios in Mallard harvested the next autumn in the Mississippi Flyway, suggesting that winter conditions influenced production of young at the population level. Raveling & Heitmeyer (1989) used similar approaches to show that winter habitat conditions in California were important predictors of productivity in Northern Pintail *Anas acuta*, but that importance of winter habitat also depended on population size and breeding habitat conditions. In 1982, 40 waterfowl scientists met in Puxico, Missouri (Anderson & Batt 1983) to identify key aspects of the winter ecology of waterfowl that were still largely unstudied and not well understood. Specifically, this group focused on the potential role of CSEs in governing dynamics of waterfowl populations and proposed fundamental questions and approaches toward an improved understanding of CSEs. There was strong support for hypothesis testing, as well as comparative and experimental approaches to research combined with long-term studies. Participants identified the need to understand a number of basic aspects of waterfowl biology including the extent and basis for philopatry, potential of winter habitats to limit waterfowl populations, the ecology of winter habitats, the bioenergetics of winter moult, the role of flocking behaviour in winter ecology and other biological processes. A number of these questions have been addressed successfully, but more importantly, the questions themselves have evolved as our understanding of CSEs has increased.

Our goals in this paper are to: 1) provide a functional definition of CSEs; 2) discuss how body size and life-histories affect the potential for CSEs; 3) describe mechanisms underlying CSEs; 4) discuss the role of CSEs in management of waterfowl; and 5) propose approaches for detecting, understanding and measuring the magnitude of CSEs.

Cross-seasonal effects

We largely subscribe to the definitions of CSEs developed by Norris (2005) and Harrison *et al.* (2011). These definitions attribute lagged population processes in one season to conditions during a previous season. For example, breeding propensity by Mallard in prairie-parkland ecosystems might depend on habitat conditions, feeding opportunities and climate experienced by individuals during the previous winter in the Mississippi Alluvial Valley. We distinguish between CSEs at the population level and carry-over effects (COEs) that operate at the individual level, but the two are linked as population CSEs can result from COEs experienced by individuals. The influence of COEs and CSEs may be modified further by population size and density-dependence (Harrison *et al.* 2011). We exclude from CSEs those environmental or maternal effects experienced early in life on traits such as body size, even though they may influence subsequent survival and reproduction by individuals (*e.g.* Sedinger *et al.* 1995; Cooch 2002), because such effects are relatively permanent and not necessarily subject to modification of individual fitness by events occurring later in life. We allow for COEs on both survival and reproduction with potential lagged effects over multiple seasons, although we exclude direct effects of behaviour or habitat on fitness during the same season. For example, we do not view reduced survival of female ducks associated with nesting (Arnold *et al.* 2010) as a COE but we do consider reduced survival of breeding individuals over the next winter (*e.g.* Daan *et al.* 1996). Similarly, we do not consider reduced within-winter survival associated with occupancy of a particular habitat (Fleskes *et al.* 2007) as a COE, but do include the potential lagged effect of lower survival during spring migration associated with use of a particular winter habitat as a COE.

Generally, we are interested in COEs that influence breeding success as a result of previous events during the same annual cycle (*e.g.* Alisauskas 2002; Bêty *et al.* 2003). Presumably, a COE may extend from one breeding season to the next, although effects extending over a full annual cycle may be mediated by events during intervening seasons (Fig. 1). We are also concerned with factors that affect survival in seasons subsequent to use of particular habitats or

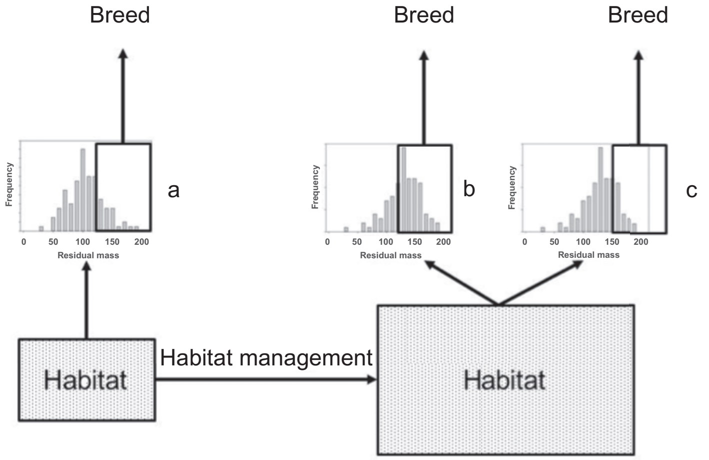

Figure 1. Hypothetical links between habitat availability, nutritional status (measured as body mass) and the probability of breeding. We show increases in mean mass in response to increases in wintering habitat but two different responses to increased mass. In scenario (b), threshold mass required for breeding does not change in response to increased mass, while in scenario (c) threshold mass increases in response to habitat availability, resulting in a similar proportion of individuals breeding before and after habitat enhancement. Under scenario (c), individuals benefit nutritionally from increased food availability but other attributes (potentially latent) prevent many individuals from translating improved nutritional status into increased reproductive success. We do not advocate scenario (c) as the expected response to improved habitat conditions. In fact, numerous examples suggest that individuals respond positively to increased food availability. The intention, here, is to indicate that complexities, including latent attributes of individuals, may influence population level responses to habitat management.

investments in reproduction. In this paper, we consider COEs that have the potential to influence both reproduction and survival. We also explore how COEs that operate at the individual level as precursors may scale up to CSEs at the population level. Such scaling up brings population level processes such as density-dependence into play.

Body size, life-histories and the potential for cross-seasonal effects

Body size is clearly related to the ability to store nutrients in one season for use in another (Alisauskas & Ankney 1992), which results in part from lower mass-specific metabolic rate in larger species (Kleiber 1975). Use of previously stored (endogenous) nutrients for egg formation and incubation generally increases with body size (Alisauskas & Ankney 1992; Meijer & Drent 1999; Alisauskas & DeVink 2015), although details about use of endogenous nutrients for breeding may vary as a function of the ecology or life-histories of individual species (*e.g.* Alisauskas & Ankney 1992; Alisauskas & DeVink 2015). Because greater reliance on endogenous nutrients should increase the potential for

COEs, one might expect that COEs are more common in larger-bodied waterfowl species (but see below). In fact, the largest numbers of examples of CSEs exist for larger bodied waterfowl, especially geese (Table 1), although this may reflect to some extent the greater ease with which individuals of larger-bodied species can be monitored (*e.g.* Ebbinge & Spaans 1995).

Other aspects of life-histories covary with body size and also might be predicted to influence the potential for COEs. For example, duration of maintenance of social bonds within families increases with body size; most geese and swans normally show lifelong monogamy and their young remain in family units through the first winter (with their parents) and sometimes through a second winter (either with parents or solely in sibling groups, *e.g.* Prevett & MacInnes 1980; Scott 1980). Because size of family groups influences social status (Boyd 1953; Raveling 1970; Poisbleau *et al.* 2006), breeding success in one year affects social status in the following winter. Social status related to family size affects dominance and aggressive defence of food resources. Presumably, enhanced access to food improves daily efficiency of nutrient storage during spring hyperphagia as geese travel north to breeding areas. Thus, a series of sequential COEs from the arctic summer, through the following winter and spring migration may influence reproductive investment by individual females in a subsequent breeding season.

Timing of pair formation in ducks is a function of body size. For example, larger bodied Mallard form pair bonds in early autumn, while small-bodied Blue-winged Teal *Anas discors* and Green-winged Teal *A. crecca* may not be paired until later in the year (MacKinney 1986). Additional energy demands of males from larger species associated with maintenance of pair bonds throughout autumn and winter might increase the potential that males of larger species are more influenced by habitat quality in winter than is the case for smaller bodied species. Alternatively, costs of delayed pairing by females of larger bodied species, and associated reduced access to food resources from intra- and interspecific competition, might interact disadvantageously with habitat quality to create greater potential for COEs in females of larger-bodied species.

Despite the clear logic underlying the linkage between body size and potential for COEs, there may be species-specific deviations from this general pattern in waterfowl. Examples from non-waterfowl species indicate that some caution is warranted when considering such relationships. Variation in quality of wintering habitat, and its influences on reproductive performance by American Redstarts *Setophaga ruticilla* is a very clear illustration of COEs (Marra *et al.* 1998), and there exist numerous other examples from small passerines and shorebirds (Norris & Marra 2007). Body size is probably too small in these passerine and shorebird examples for substantial mass to be carried between sequentially used seasonal habitats. So, the existence of COEs in such small birds suggests that mechanisms underlying COEs may involve complexities beyond nutritional dynamics. We address some of these potential mechanisms below.

Cross-seasonal effects in waterfowl

Evidence of CSEs transmitted from wintering areas to breeding is extensive (Table 1). Studies based on regression of population age ratios in post-breeding censuses against precipitation in the previous winter, demonstrate ecological links between landscapes separated sometimes by lengthy time lags of several months or great distances of thousands of kilometres. For example, winter precipitation can influence habitat, and thus feeding conditions for wintering waterfowl that in turn affect the production of young at the population level as indexed by age ratios during the following hunting season (Heitmeyer & Fredrickson 1981; Raveling & Heitmeyer 1989). Boyd *et al.* (1982) found that winter precipitation in the U.S. along the Gulf of Mexico affected the number of adult Lesser Snow Geese and their breeding success to a greater extent than spring temperatures and precipitation in the Dakotas and southern Manitoba, which are used during spring migration. More recently, winter climate has been related to age-ratios in Barnacle Geese *Branta leucopsis* (Trinder *et al.* 2009), pre-breeding body mass of Common Eiders *Somateria mollissima* (Descamps *et al.* 2010), as well as their breeding propensity (Jónsson *et al.* 2009) and breeding success (Lehikoinen *et al.* 2006). Correlations between expansion of cereals and other agricultural crops in both North America and Europe, and the growth of goose populations on both continents, support inferences from earlier regression-based studies about the importance of food supply to population growth. Finally, capture-mark-recapture (CMR) studies which demonstrate that quality of wintering locations influences breeding probability (*e.g.* Sedinger *et al.* 2011) provide additional evidence for the impact of winter habitats on production of offspring. Evidence for CSEs currently appears stronger for geese than for ducks (Table 1), but we suspect that this in part represents the greater ability to monitor individual geese throughout the annual cycle than is the case for ducks.

Evidence for CSEs linking spring migration and breeding are especially strong (Table 1). Studies using stable isotopes demonstrate that nutrients acquired away from breeding areas contribute to egg production in numerous species of ducks and geese (Table 1). In some cases contributions of endogenous nutrients to eggs were relatively modest (< 30% of the total). Such modest contributions to egg formation may, however, provide essential supplements to dietary nutrients if the latter are insufficient to meet the daily needs of females for egg production. Such needs can be substantial during early clutch formation, when yolk and albumin formation overlap (Alisauskas & Ankney 1992). Drent & Daan (1980) considered variation in reliance on nutrient reserves for egg formation along a capital-income continuum. Some studies have characterised egg formation as income-based if more than half of egg nutrients supplied were exogenous. However, the pervasiveness of nutrient reserve use (particularly of fat) in waterfowl (Ankney & Alisauskas 1991; Alisauskas & Ankney 1992) suggests to us that usage of nutrient reserves might be largely obligatory, or at least highly adaptive, and so *any* usage

Table 1. Examples of cross-seasonal and carry-over effects in waterfowl. These examples are restricted to cases where one of two conditions was met: 1) investigators demonstrated a direct link between individual state in one season and individual demographic rates in a subsequent season; or 2) investigators demonstrated a relationship between habitat conditions or average state at the population level and population demographic rates in a subsequent season.

Carry-over effect	Species	Reference
Individual level effects		
Breeding propensity and clutch size lower in springs with hunting on staging area	Greater Snow Goose	Mainguy *et al.* 2002
Females with greater fat before spring migration laid earlier and larger clutches	Greater Snow Goose	Bêty *et al.* 2003
Endogenous reserves provided > 20% of egg nutrients based on stable isotopes	Greater Snow Goose	Gauthier *et al.* 2003
Increased lipid stores on spring staging area and population increase associated with increased corn production	Greater Snow Goose	Gauthier *et al.* 2005
Positive correlation between endogenous lipid and protein on arrival and clutch size	Lesser Snow Goose	Ankney & MacInnes 1978
Endogenous nutrients provided 55% of nutrients in eggs based on stable isotopes	Lesser Snow Goose	Hobson *et al.* 2011
Endogenous nutrients provided 25–36% of nutrients in eggs based on stable isotopes	Lesser Snow Goose	Sharp *et al.* 2013
Earlier hatching goslings are larger and are recruited at a higher rate	Lesser Snow Goose	Cooke *et al.* 1984; Cooch *et al.* 1991a; Aubry *et al.* 2013
Migration strategy and condition during spring related to production of offspring	Pink-footed Goose	Madsen 2001

Table 1 (*continued*).

Carry-over effect	Species	Reference
More than 50% of nutrients in eggs from endogenous sources based on stable isotopes	Canada Goose	Sharp *et al.* 2013
Larger goslings survive autumn migration at a higher rate	Barnacle Goose	Owen & Black 1989
Greater nutrient reserves and earlier migration positively related to reproductive success	Barnacle Goose	Prop *et al.* 2003
Heavier females on arrival to breeding area laid more eggs and were more attentive to nests	Barnacle Goose	Tombre *et al.* 2012
Females with greater nutrient reserves in spring produced more offspring	Dark-bellied Brent	Ebbinge & Spaans 1995
Endogenous nutrients used during egg laying and incubation	Dark-bellied Brent	Spaans *et al.* 2007
Earlier hatching goslings survive better and are recruited at a higher rate	Black Brant	Sedinger & Flint 1991; Sedinger *et al.* 1995; Sedinger & Chelgren 2007
Increased sea surface temperatures on wintering area reduced breeding propensity	Black Brant	Sedinger *et al.* 2006
Winter location affected breeding propensity and timing of nesting	Black Brant	Sedinger *et al.* 2011; Schamber *et al.* 2012
Breeding affected quality of wintering area	Black Brant	Sedinger *et al.* 2011
Use of particular brood rearing areas affects breeding probability the next year	Black Brant	Nicolai & Sedinger 2012
Females that hatch earlier are recruited at a higher rate	Mallard	Dzus & Clark 1998

Table 1 (*continued*).

Carry-over effect	**Species**	**Reference**
Females with greater nutrient reserves on arrival had greater breeding propensity, nested earlier and laid larger clutches	Mallard	Devries *et al.* 2008
Females fasted in winter were heavier but laid fewer eggs	Black Duck	Barboza and Jorde 2002
>30% of protein in eggs from endogenous source in one of three years	Lesser Scaup	Cutting *et al.* 2011
Endogenous nutrients used for maintenance during egg laying	Redhead	Hobson *et al.* 2004
Immunosuppression by low body mass females. Females that abandoned broods and had low lymphocyte levels had lower return rates the next year	Common Eider	Hanssen *et al.* 2003
Increased incubation demand reduced immune function and clutch size the next year	Common Eider	Hanssen *et al.* 2005
Wintering location related to timing of nesting and weakly to clutch size	King Eider	Mehl *et al.* 2004
Endogenous nutrients contributed significantly to egg production based on stable isotopes	King Eider	Oppel *et al.* 2010
Population level effects		
Increased commodity acreage correlated with increased population size	Lesser Snow Goose	Abraham *et al.* 2005
Autumn age-ratios positively related to mean body mass and fat in spring	Lesser Snow Goose	Alisauskas 2002
Smaller clutches fewer young breeders in years with drought on spring staging areas	Lesser Snow Goose	Davies & Cooke 1983
Estimated number of adults and young correlated with previous winter weather	Lesser Snow Goose	Boyd *et al.* 1982

Table 1 (*continued*).

Carry-over effect	**Species**	**Reference**
Increased disturbance reduced nutrient reserves during spring staging and age-ratios following breeding	Pink-footed Goose	Drent *et al.* 2003
Increased age-ratios with increased availability of agricultural foods on wintering areas	Greenland White-fronted Goose	Fox *et al.* 2005
Age ratios positively correlated with winter temperature	Barnacle Goose	Trinder *et al.* 2009
Winter precipitation positively related to age ratios the next autumn	Mallard	Heitmeyer & Fredrickson 1981
Winter precipitation positively related to age ratios the next autumn	Northern Pintail	Raveling & Heitmeyer 1989
Plumage quality during pair formation varied among moulting areas	Green-winged Teal	Legagneaux *et al.* 2012
Winter index of North Atlantic Oscillation positively correlated with body mass of adult females at hatch, and subsequent age ratios	Common Eider	Lehikoinen *et al.* 2006
More females nested following warm-wet winters	Common Eider	Jónsson *et al.* 2009
NAO positively related to prenesting body condition in two separate nesting populations	Common Eider	Descamps *et al.* 2010
More females nested following warm-wet winters	Common Eider	Jónsson *et al.* 2009

might be properly considered as a capital breeding strategy.

Numerous studies have shown that nutritional state in spring affects success in producing offspring (Table 1). Similarly, earlier migrants typically are more likely to produce offspring (*e.g.* Prop *et al.* 2003). Because these studies were without experimental manipulation and so primarily observational, we cannot rule out the potential for spurious correlation between condition, or timing of migration, and reproductive success; that is, other unmeasured variables may have been associated with both nutritional status and production of offspring, but without the former variate directly influencing the latter. Two kinds of experiments, however, suggest that nutritional status can have an important influence on reproductive success in waterfowl. First, implementation of a spring hunt on a major spring staging area for Greater Snow Geese *C. caerulescens atlanticus*, reduced nutritional status of staging geese, associated with increased disturbance (Féret *et al.* 2003), and reduced the proportion of females that attempted to nest and reproductive investment by those females that did nest (Mainguy *et al.* 2002; Bêty *et al.* 2003). Second, reduced availability of agricultural habitats for Pink-footed Geese *Anser brachyrhynchus* during spring migration in Norway reduced both nutritional status of migrating geese and their subsequent reproductive success (Drent *et al.* 2003).

CSEs on adults from breeding to autumn or winter are generally less well understood than those linking other seasons. Limitations in our understanding reflect the difficulty of monitoring highly mobile individuals outside the breeding season and the difficulty of monitoring non-breeding individuals that typically migrate away from breeding areas to moult. Nevertheless, there are *a priori* reasons to expect that such CSEs exist and empirical evidence exists for such CSEs.

Female waterfowl invest substantial nutrients into both egg formation and incubation (Alisauskas & Ankney 1992; Afton & Paulus 1992; Alisauskas & DeVink 2015) and these nutrients must be replenished before autumn migration (Sedinger & Bollinger 1987). Post-breeding storage of nutrients occurs simultaneously with brood rearing and moult. Increased vigilance and attentiveness of adults toward their offspring may be at the expense of reduced foraging effort (Schindler & Lamprecht 1987; Sedinger & Raveling 1990; Sedinger *et al.* 1995), potentially reducing nutrient intake. The simultaneous need to grow feathers and restore nutrient reserves has the potential to reduce feather quality, rate of restoration of nutrient reserves or both. Schmutz & Ely (1999) and Eichholz (2001) each found that autumn survival was related to nutritional status, so the ability of adults to restore nutrients after hatch has implications for fitness later in the year.

Breeding success in geese can also influence events during the non-breeding season because family cohesion persists for a full year after hatch and family groups are dominant to pairs without young or singles (Raveling 1970; Prevett & MacInnes 1980; Lamprecht 1986; Poisbleau *et al.* 2006). Social status is related to position in foraging flocks and food intake (Boyd 1953; Gregoire & Ankney 1990; Black *et al.* 1992); thus, successful reproduction has the potential to influence nutrient dynamics the following winter through its effect on social status. Consistent with this hypothesis, Sedinger *et al.* (2011) showed that Black Brant *B. bernicla nigricans* that bred tended to shift to higher quality wintering areas the following winter. Similar mechanisms could occur in ducks if more "attractive" individuals pair earlier in autumn and experience enhanced social status as a result. Gregoire & Ankney (1990) also noted that family structure varied by winter habitat, so that any COEs of nutrition related to previous breeding success and resulting family size during winter on subsequent breeding may interact with the types of winter habitats occupied.

Finally, numerous studies have demonstrated COEs based on experience during their first summer for young waterfowl, especially geese. Growth conditions during the first summer influence survival during the next autumn (Owen & Black 1989; Hill *et al.* 2003; Sedinger & Chelgren 2007; Aubry *et al.* 2013) and ultimately, recruitment into the breeding population (Cooke *et al.* 1984; Sedinger *et al.* 2004). An important determinant of survival probability for goslings over the year after they fledge is phenology of hatch, both within years and between years (Cooch 2002; Slattery & Alisauskas 2002; Aubry *et al.* 2013). Slattery & Alisauskas (2002) found that dispersal distance by goslings after hatching influenced their subsequent survival probability over the next year. Dzus & Clark (1998) showed that hatch date influenced recruitment in Mallard, and Alisauskas & Kellett (2014) found a negative effect of relative initiation date of nests that produced King Eider *S. spectabilis* ducklings, with equivocal support for an additive negative influence of spring thaw date on the age that ducklings were recruited as breeders. Both studies support the notion that events early in life can influence recruitment and lifetime reproductive success.

Investments in breeding by female waterfowl may result in lagged trade-offs with subsequent breeding or with other life-history traits. Viallefont *et al.* (1995) demonstrated that Lesser Snow Geese breeding for the first time were less likely to breed the following year, suggesting the existence of costs associated with these first breeding attempts. Specific brood-rearing areas used by female Black Brant influenced their likelihood of breeding the next year (Nicolai & Sedinger 2012). Assessment of breeding costs is complicated by heterogeneity in individual quality (van Noordwijk & de Jong 1986) and variation in the probability of breeding among individuals (Sedinger *et al.* 2008; Hoye *et al.* 2012). Additionally, as noted above, successful breeding by geese enhances their social status (Poisbleau *et al.* 2006), which may compensate for some of the costs of breeding (*e.g.* Sedinger *et al.* 2011). Leach & Sedinger (unpubl. data) manipulated brood size and found that removing broods can negatively affect probability of breeding the following year, but increasing brood size can also reduce breeding the following year for larger initial brood sizes. These results are generally consistent both with the social advantages of breeding in geese, and the idea that successful breeding can induce costs for future breeding.

Drake (2006) experimentally manipulated nest success of Ross's Geese *C. rossii* and found that survival of successful nesters was consistently lower than those with destroyed nests, and that the strength of this effect varied among years, consistent with COEs of successful breeding on subsequent survival. However, we note that there is a general paucity of studies of CSEs on the survival of breeding adults, and suggest that the lack of such results reflects logistical or technical difficulties in assessing the survival of adults in breeding *versus* non-breeding states. Because non-breeding waterfowl typically undergo moult migrations to areas remote from breeding habitats (Hohman *et al.* 1992), it is uncommon that samples of both breeders and non-breeders are monitored simultaneously. As illustrated by Drake (2006), this can be remedied to a certain extent by experimentation. The limited evidence for absence of evidence for CSEs on survival should, thus, be viewed as an absence of appropriate data, rather than an absence of such CSEs.

Mechanisms for cross-seasonal effects

The most direct mechanism underlying CSEs in waterfowl, especially those linking winter and spring migration areas to breeding, relates directly to nutritional state, and is, therefore, related to individual abilities to store more nutrients earlier than others (Prop *et al.* 2003; Drent *et al.* 2003). Individual variation in schedules of nutrient storage induces and governs variation in departure phenology. For example, Alisauskas (1988) found that Lesser Snow Geese constituting the northernmost vanguard of the mid-continent Lesser Snow Goose population during spring migration were fatter than conspecifics farther south at the same calendar date. Earlier arrival during migration increases the potential for protracted residency at each staging area, which may permit greater nutrient acquisition (Drent *et al.* 2003). The result is that individuals that store high levels of nutrients early at any staging area tend to maintain this advantage throughout spring migration, resulting in higher probability of early arrival onto nesting areas, earlier breeding and larger clutches (Prop *et al.* 2003; Drent *et al.* 2003; Bêty *et al.* 2003).

It is unlikely that the same nutrients stored in winter or early in migration actually contribute directly to reproduction because the substantial energy costs of long-distance migratory flight result in a major turnover of nutrients throughout spring migration. Although most assessments of the contribution of endogenous nutrients to egg production distinguish between body reserves acquired by the female before arrival on the breeding grounds (*i.e.* "capital" breeders) and food acquired locally on or near the breeding territories (for "income" breeders: Drent & Daan 1980; Gauthier *et al.* 2003; Hobson *et al.* 2004; Cutting *et al.* 2011), they do not assign a geographic origin to endogenous nutrients. As suggested by Klaassen *et al.* (2006), it is important to distinguish between distant *versus* local capital breeding (*i.e.* whether intensive feeding in preparation for breeding is a few kilometres from the breeding areas or at more distant sites), in addition to determining whether the birds use capital or income breeding strategies.

The substantial investments required for egg-laying by waterfowl create the potential for COEs, yet few examples of such COEs exist. We exclude costs of breeding, such as reduced survival, that occur during the breeding season (Madsen *et al.* 2002; Arnold *et al.* 2010) because such trade-offs, while real, do not represent COEs. Clearly, the ability of breeding adults to restore nutrients depleted during breeding may influence fitness during seasons following breeding. Several studies document a relatively slow replenishment of nutrients before the post-breeding moult (*e.g.* Ankney & MacInnes 1978; Ankney 1984; Fox *et al.* 2013). Non- and failed-breeding Black Brant gained more mass before moult than did adults with broods (Fondell *et al.* 2013), suggesting the possibility that mass gain following nesting might be constrained by competing demands of tending broods. Virtually all species lose mass during moult (Hohman *et al.* 1992), and while there is debate about whether such mass loss is adaptive (*e.g.* Fox & Kahlert 2005), adult waterfowl do not restore nutrient reserves at this time of year. Thus, investments in reproduction, combined with constraints on the ability to replenish these nutrients following breeding, have the potential to influence fitness in seasons following breeding.

Waterfowl undergo complete remigial moult and become flightless at the same time that they are restoring nutrients depleted during breeding, which has the potential to influence feather quality as well as somatic nutrient levels. Both moult location (Norris *et al.* 2007) and competing nutritional demands during moult (Norris *et al.* 2004) influence feather colour in passerines. Legagneaux *et al.* (2012) demonstrated that the iridescent colouration in Green-winged Teal was influenced by the location where individuals moulted, consistent with the hypothesis that nutrient availability influenced feather quality and perhaps attractiveness to mates. Feathers of yearling Black Brant during their second summer are highly degraded relative to those of adults (J. Sedinger pers. obs.). Because development of these feathers occurred during the growth period, when nutrient availability is typically limiting tissue production (*e.g.* Sedinger 1984; Sedinger *et al.* 2001), the poor quality of feathers on yearling geese is consistent with the notion that nutrient availability could influence feather quality, as is the case in other birds (Butler *et al.* 2008). Absence of data on feather quality and the relationship between feather quality and fitness in waterfowl have hindered assessment of linkages between feather quality and fitness (COE) or population dynamics (CSE) of waterfowl. We suggest that such research is warranted.

Immune function and associated disease status both provide mechanisms that could facilitate CSEs. Long-distance migrants appear to be more exposed, or more susceptible, to parasitic infection (Figuerola & Green 2000). Two studies demonstrate that parasite load during brood-rearing has a negative influence on the survival of young after fledging (Slattery & Alisauskas 2002; Souchay *et al.* 2013). Nematode levels were negatively associated with lipid levels for Lesser Snow Geese during spring migration (Shutler *et al.* 2012). The authors could not differentiate between the hypotheses that:

1) nematode infestation inhibited lipid deposition; 2) some individuals were chronically infected, which reduced the size of nutrient stores; and 3) individuals that invested more in lipid storage and less in immune function were more susceptible to nematode infection. The first two hypotheses would be consistent with COEs associated with disease.

Cholera *Pasturella multicida* has been known for some time to cause substantial mortality on both breeding and wintering areas (Rosen & Bischoff 1949; Wobeser *et al.* 1983). The dynamics of Cholera transmission are not well understood but evidence suggests that individuals serve as carriers (Samuel *et al.* 1999, 2004, 2005), creating the potential that exposure of individuals in one seasonal habitat can lead to disease transmission and mortality in another season, with possible population level consequences. Sub-lethal roles of disease beyond immediate mortality effects are also not well understood. Infection by low-pathogenic avian influenza has been associated with less efficient feeding and delayed migration in Bewick's Swans *Cygnus columbianus bewickii* (van Gils *et al.* 2007). Latorre-Margalef *et al.* (2009) found that Mallard infected with avian influenza had lower body mass during migration, which could influence timing of migration and investment in reproduction. The association between the timing of migration and reproductive success (see above) suggests that infection could cause lower productivity. Such sub-lethal effects are likely to be of broader importance in waterfowl, especially when individuals are concentrated because wintering or migration habitat is limited (Galsworthy *et al.* 2011; Gaidet *et al.* 2012).

Investment in reproduction can reduce immune function in waterfowl (Hanssen *et al.* 2003, 2005) and other birds (Deerenberg *et al.* 1997; Schmidt-Hempel 2003), with the potential for lower survival or reduced reproductive success in the future. Immune challenges in Mallard (post-fledging) influences colour preference and response to novel environments (Butler *et al.* 2012), as well as the ability to mount an immune response as adults (Butler & McGraw 2012). Although Norris & Evans (2000) demonstrated that investment in breeding affected immune function, which in turn influenced infection rate and reduced fitness, such studies are rare. The presence of complex sequential causative events relating individual variation in immune function to variation in fitness could translate to population level effects if pervasive. We believe studies that address such mechanisms underlying CSEs in waterfowl may be relevant to a full understanding of population dynamics.

Implications of cross-seasonal effects for management

The potential for CSEs was implicit in the development of winter habitat joint ventures in North America during the 1980s, as suggested by references to specific links between habitat and waterfowl population objectives in joint venture documents (*e.g.* Central Valley Habitat Joint Venture 1990). In some cases, specific mechanisms behind assumed CSEs were not made explicit until sometime later (Koneff

2006 unpublished letter to the North American Waterfowl Management Plan evaluation team). Establishment of the joint ventures stimulated substantial new research into dynamics of food availability in both wetlands (Naylor 2002; Hagy & Kaminski 2012a,b; Leach *et al.* 2012) and agricultural habitats (Stafford *et al.* 2010; Foster *et al.* 2010), which typically demonstrated the potential for food to become limiting by December and January (Naylor 2002; Foster *et al.* 2010). These modern studies built on earlier estimates of food abundance and carrying capacity of winter habitats for waterfowl in Europe (Ebbinge *et al.* 1975; Owen 1977) and North America (Givens *et al.* 1964). Demonstration of winter food depletion, combined with increases in many goose populations associated with increased availability of agricultural foods (Abraham *et al.* 2005; Fox *et al.* 2005; Gauthier *et al.* 2005), indicate that agroecosystems or direct management of winter habitats for waterfowl has great potential to influence dynamics of their populations. Refining winter habitat management will require improved understanding of the interplay among winter food abundance, winter population density, COEs, availability of breeding habitat and breeding population density (*e.g.* Runge & Marra 2005; Norris & Marra 2007). We contend that methods now exist to improve our understanding of all of these questions (see below).

Disease transmission increases at higher densities (Rosen & Bischoff 1949; Gaidet *et al.* 2012), so the availability of winter habitat can potentially influence rates of infection at the population level. Infection may influence survival rates (*e.g.* Slattery & Alisauskas 2002) and migration behaviour (van Gils *et al.* 2007; Latorre-Margalef *et al.* 2009). Thus, availability of winter habitat not only has the potential to influence CSEs, but habitat management on the wintering grounds could influence disease processes and so affect the dynamics of waterfowl populations.

Harvest pressure influences behaviour (Fox & Madsen 1997; Webb *et al.* 2011) and habitat use (Béchet *et al.* 2003; Moore & Black 2006), which in turn can affect nutritional status and investment in breeding, at least in geese (Mainguy *et al.* 2002). Direct effects of harvest on mortality rates and population dynamics vary as a function of body size (Rexstad 1992; Sedinger *et al.* 2007; Sedinger & Herzog 2012; Péron *et al.* 2012). Indirect effects of harvest acting through nutrient dynamics are poorly understood for ducks and most populations of geese (but see Pearse *et al.* 2012). Nevertheless, examples cited here indicate that the effects of harvest are likely to be more complex in all waterfowl than are currently assumed.

Density-dependent effects on recruitment are well established in both ducks (Kaminski & Gleussing 1987) and geese (Loonen *et al.* 1997; Lake *et al.* 2008) although mechanisms are less well understood for ducks. In geese, a substantial proportion of density-dependence occurs through food limitation during growth (Cooch *et al.* 1991b; Sedinger *et al.* 1998) and reduced survival during the first year associated with small body size (Sedinger & Chelgren 2007; Sedinger & Nicolai 2011). Thus, density-dependent effects on recruitment in geese reflect a CSE/COE effect on each year's cohort of young. A number of years of predator removal in the North American prairies has resulted in substantially increased nest success (Pieron & Rohwer 2010). Increased production of ducklings, however, has not produced any increase in local densities (Amundson *et al.* 2013). A reasonable hypothesis for the lack of a population response to increased duckling production is that increased brood densities, resulting from higher nest success, increased competition for food, and slower growth and lower post-fledging survival of ducklings, similar to mechanisms reported for geese.

Remaining issues and approaches to estimating cross-seasonal effects

Much of our understanding of CSEs is based on individual responses to an interplay between physiological states and environmental conditions (Table 1). An understanding of how individual effects translate into population level responses will require an appreciation of how population density feeds back on individual responses (Runge & Marra 2005; Norris & Marra 2007). Higher density could, for instance, induce shifts in the mean and variance of individual states (Fig. 1). An important determinant of whether individual response has relevance to population level effects is the degree to which heterogeneity exists in response to population density. For example, Lindberg *et al.* (2013) did not detect a relationship between the proportion of "low quality" individuals in Black Brant cohorts and *per capita* food abundance. Thus, it seems that populations may include a relatively fixed proportion of "low quality" individuals, incapable of response to density-dependent habitat conditions.

Assessment of most habitat joint ventures has been based on waterfowl response in the season for which a specific habitat is managed. For winter habitat joint ventures, effectiveness is often measured in predicted "use-days", based on measures of food abundance and models of nutritional requirements (*e.g.* Stafford *et al.* 2006). Alternatively, nest success is used to assess habitat programmes on breeding areas (*e.g.* Stephens *et al.* 2005). These approaches cannot assess the true value of habitat in the context of the complete annual cycle of waterfowl, however, because they do not account for CSEs, which may modulate the response of individual birds to concurrent habitat conditions. Moreover, an understanding of the role that CSEs play in the dynamics of waterfowl populations requires knowledge about proportional habitat use by specific populations at any point in the year, and how this varies over the annual cycle. Although challenging, such information would permit an assessment of the reproductive success of individuals in relation to management actions on previously used wintering areas. The situation may be reinforced by individuals that fledged in a particular breeding habitat migrating to, and also wintering in, the same habitats that had a role in their production. It is unclear how such COEs may have influenced the evolution of both breeding and winter philopatry, but the adaptiveness of occupying high quality habitats which enables pre-breeding ducks to improve their condition probably also has relevance for the survival of the new recruits to the population and the likelihood of them joining the breeding cohort in due course. Such a scenario may have played a role in the evolution of persistent family bonds in geese.

As mentioned above, spring phenology of arctic snow melt governs the timing of nesting, hatch and gosling growth for all arctic-nesting geese and also for many of the sea duck species. High plasticity in growth rates is an apparent adaptation to high variability in nutritional supply to goslings both within and among years, permitting nutritional flexibility in years of nutritional stress, although at the cost of reduced survival and adult body size when nutrients are limited during the growth period. Such intraspecific variation in body size and morphology influences not only subsequent survival, but can influence habitats and broad-scale landscapes occupied during the following winter. Alisauskas (1998) found that Lesser Snow Geese in their traditionally used coastal marsh habitats during winter were larger than conspecifics from inland agricultural landscapes associated with rice agriculture, both of which, were larger than Lesser Snow Geese wintering farther north near the Missouri River Valley of Iowa and Nebraska. Alisauskas (1998) suggested that perhaps large scale expansion of winter range associated with the correlation between body size and bill morphology may have been coupled with density-dependent morphological change on breeding areas. Thus winter range dynamics appear to result from an interplay of winter food distribution and density-dependent effects expressed on the lifelong morphology of geese from events experienced as growing goslings in the arctic.

Studies of geese have been especially successful in identifying cross-seasonal and cross-ecosystem linkages because of the relative ease of marking and observing them at multiple sites throughout the year. Ross's Geese and Snow Geese are highly gregarious, very abundant and occur at very high densities throughout the year, which poses great challenges in marking sufficient numbers so that individuals can be detected and studied. Ring recoveries provide a mechanism for linking together breeding, migration and wintering habitats (*e.g.* Alisauskas *et al.* 2011). We believe that many waterfowl scientists assume similar approaches are not possible for diving or dabbling ducks (genera *Aythya* and *Anas*) for a number of reasons, including insufficient site fidelity and the difficulty of using markers that can be detected at a distance. In our view, this is too pessimistic. Several studies of marked ducks on breeding areas demonstrated excellent success at re-encountering breeding females marked in earlier years (Sowls 1955; Arnold & Clark 1996; Anderson *et al.* 2001; Blums *et al.* 2002), indicating substantial fidelity to relatively small, well-defined breeding areas. We acknowledge it may be difficult or impossible to encounter individuals from these kinds of studies on migration or at wintering sites, as has been undertaken for geese. The emergence of new technologies should, however, improve the ability to identify links between breeding, staging and wintering areas. Stable isotopes in tissues grown during known time periods provide one mechanism for assigning individuals to habitats remote from the breeding range (Hobson *et al.* 2004; Clark *et al.* 2006), or winter areas (Mehl *et al.* 2005). This approach can take advantage of specific feather tracts moulted outside the breeding season (Smith & Sheeley 1993; Combs & Fredrickson 1996) or toe nails which are grown continuously (Clark *et al.* 2006). Geolocators, which record the timing of sunrise and sunset, to allow reconstruction of latitude and longitude, provide an alternative approach (*e.g.* Eichhorn *et al.* 2006). Both geolocators and stable isotopes require that individuals be captured but the studies cited demonstrate that large numbers of breeding females can be captured during nesting. The addition of either geolocators or stable isotope methods to traditional marking and recapture on long-term study sites could enhance substantially knowledge of CSEs for species other than geese.

Our understanding of the role of CSEs in both the dynamics of populations and fitness of individuals has increased dramatically over the past three decades. This information and new technologies are now sufficiently developed to allow more detailed assessments of the role of seasonal habitats in the dynamics of specific populations. We believe it is now possible to use modern methods in the context of CSEs to improve and prioritise management of seasonal habitats. We also believe it is now possible to incorporate events and decisions throughout the complete annual cycle into our understanding of life-history strategies. We are beyond the demonstration phase; we suggest that it is now time to move waterfowl biology forward.

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Photograph: Mallard benefitting from wetlands in Maryland, by Ron Nichols/USDA Natural Resources Conservation Service.