esa

ECOSPHERE

CONCEPTS & THEORY

Biological carryover effects: linking common concepts and mechanisms in ecology and evolution

CONSTANCE M. O'CONNOR,[1,4,]† D. RYAN NORRIS,[2] GLENN T. CROSSIN,[3] AND STEVEN J. COOKE[1]

[1]*Fish Ecology and Conservation Physiology Lab, Department of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, Ontario K1S 5B6 Canada*

[2]*Department of Integrative Biology, University of Guelph, 50 Stone Road East, Guelph, Ontario N1G 2W1 Canada*

[3]*Department of Biology, Dalhousie University, 1355 Oxford Street, Halifax, Nova Scotia B3H 4R2 Canada*

Citation: O'Connor, C. M., D. R. Norris, G. T. Crossin, and S. J. Cooke. 2014. Biological carryover effects: linking common concepts and mechanisms in ecology and evolution. Ecosphere 5(3):28. http://dx.doi.org/10.1890/ES13-00388.1

Abstract. The term 'carryover effect' originally arose from repeated measures clinical experiments. However, the term has more recently been applied to ecological and evolutionary studies, often in migratory systems, which has led to an emphasis on non-lethal effects across seasons. In this article, we suggest that ecological carryover effects can also occur between life-history stages, developmental stages, physiological states, or social situations, and each will be associated with a discrete time-scale. Therefore, we propose the working definition: *In an ecological context, carryover effects occur in any situation in which an individual's previous history and experience explains their current performance in a given situation*. This concept of carryover effects provides an explicit but highly flexible context for examining the mechanisms that drive non-lethal interactions between distinct periods of an organism's lifetime, and unites the currently disparate fields investigating these effects in ecological systems. Greater communication among research fields and identifying mechanisms of carryover effects at different time scales will ultimately lead to a better understanding of the factors influencing variation in individual fitness.

Key words: carry over effect; delayed effect; latent effect; life-history trade-off; maternal effect; reproductive trade-off.

Received 13 December 2013; accepted 17 December 2013; final version received 11 February 2014; **published** 13 March 2014. Corresponding Editor: D. P. C. Peters.

[4] Present address: Aquatic Behavioural Ecology Lab, Department of Psychology, Neuroscience and Behaviour, McMaster University, 1280 Main Street West, Hamilton, Ontario L8S 4K1 Canada.

† **E-mail:** coconn@mcmaster.ca

INTRODUCTION

One common goal for ecologists is to understand the factors that influence the fitness of wild organisms (Pough 1989, Spicer and Gaston 1999). In pursuing this goal, researchers have long recognized that neither individuals nor environments are static, which complicates efforts to track individuals across life-history stages and through complex spatial and temporal landscapes. Historically, our ability to resolve the environmental factors that influence the fitness of wild organisms has been constrained by a lack of appropriate tracking and monitoring technologies (Feder and Block 1991). It has only been more recently that advances in electronic tracking and biologging technologies have allowed researchers to investigate hitherto untestable questions about fitness-related processes operating at broad spatial and temporal scales in wild

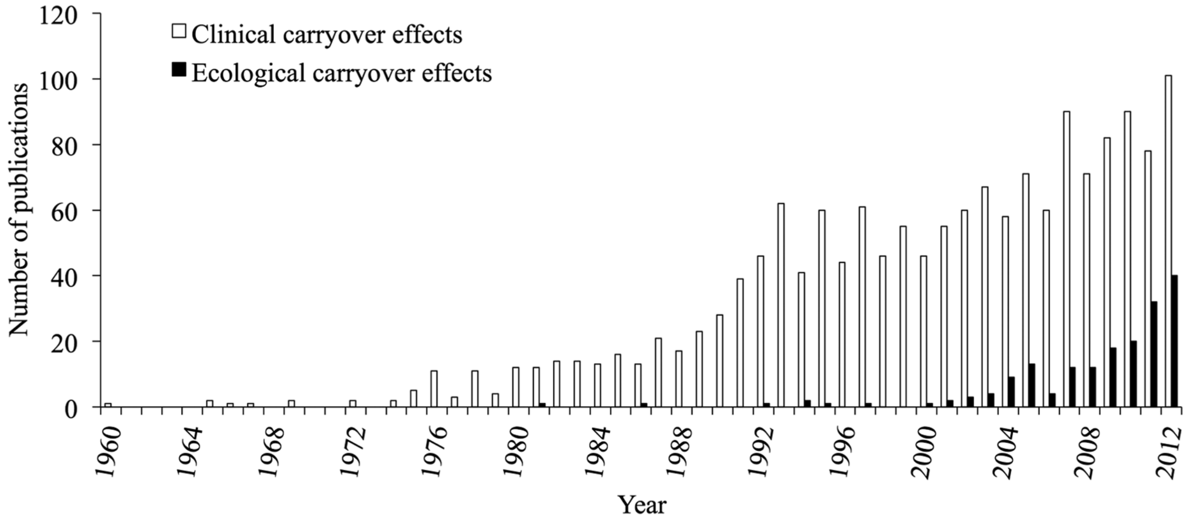

Fig. 1. Temporal trends of the use of the 'carryover effect' term based on a Web of Science search using the keywords "carryover effect*" or "carry over effect*" or "carry-over effect*", conducted on October 1 2013. Only original articles or reviews were included. A clinical article covered medical, dental, veterinary, agricultural, biochemical, microbiological and psychological literature, and including publications devoted to statistics and methods to deal with carryover effects in a clinical context. In this context, the carryover effect was generally viewed as a potential concern for a repeated measures experimental design, and was not the main effect investigated in the article. For ecological papers, the carryover effect was generally the main effect of interest.

individuals and populations (Webster et al. 2002, Rubenstein and Hobson 2004, Block 2005).

The development of new tracking technologies has resulted in a surge of studies demonstrating that long-term processes, including carryover effects, can influence fitness. More recently, experimental studies in the lab have demonstrated that non-lethal carryover effects have influence long-term population dynamics (Betini et al. 2013*a*, *b*). Norris (2005) defined carryover effects as "events in one season that produce residual effects on individuals the following season". Harrison et al. (2011) modified this definition slightly to: "events and processes occurring in one season that result in individuals making the transition between seasons in different states (levels of condition) consequently affecting individual performance in a subsequent period." It is important to emphasize that both definitions focus on the non-lethal effects on individuals across seasons. However, the concept of carryover effects predates these ecologically centered studies by almost 30 years, to the early 1960s when clinicians became aware that effects can 'carry over' from one treatment to another in repeated measures experimental designs (Wallenstein and Fisher 1977). The use of the term in the biomedical realm still dominates the literature, but studies of carryover effects in ecological contexts have been steadily increasing since the early 2000s (Fig. 1). Although these studies are among the first to describe how carryover effects can operate in ecological settings, we suggest that the seasonal requirement is unnecessarily restrictive, and risks precluding events that operate over shorter or longer time scales from consideration as legitimate carryover effects. In this article, we therefore propose a more inclusive definition of carryover effects: *In an ecological context, carryover effects occur in any situation in which an individual's previous history and experience explains their current performance in a given situation*. This general definition allows one to identify carryover effects in a broad range of situations, e.g., within and across life-history stages, seasons, years, or experimental settings, and is useful because it is consistent with, and therefore embraces, the traditional use of the term 'carryover effects'. Most importantly, it is also general enough to apply to a wider set of scientific disciplines, research questions, and experimental or field contexts. We contend that a more general and inclusive definition will increase clarity and communication among the various fields already investigating these effects in ecological systems. We further propose that this definition can be applied to classic concepts of life-history trade-offs and costs of reproduction, which may potentially be viewed as special types of carryover effects. The overall aim of this article is to present an overview of the current state of knowledge about carryover effects, and to propose a concise definition that can be applied consistently across many different fields of study. We highlight new research that suggests that common mechanisms might underlie carryover effects, trade-offs and costs of reproduction, and encourage future research on the mechanisms driving carryover effects.

Why Do We Need a New Definition of Carryover Effects?

The concept of carryover effects was first recognized in repeated measures clinical trials, where certain factors could 'carry over' from one treatment to another in laboratory studies (e.g., Wallenstein and Fisher 1977). A Web of Science search using the keywords 'carryover effect*' or 'carry over effect*' or 'carry-over effect*' identified over 200 articles that directly discuss methods for controlling and accounting for carryover effects in clinical trials, as well as several hundreds of papers that consider carryover effects more generally in clinical contexts (search date October 1 2013; see Fig. 1).

Recently, the study of carryover effects in ecology has been increasing (Fig. 1), primarily through mathematical modeling studies (e.g., Norris 2005, Runge and Marra 2005, Norris and Taylor 2006) and empirical research on birds (e.g., Myers 1981, Marra et al. 1998, Gill et al. 2001, Norris et al. 2004, Inger et al. 2010, Legagneux et al. 2011, Sedinger et al. 2011). These studies have examined carryover effects through the lens of migration biology, which has led carryover effects being tightly linked to a phenomenon that occurs across seasons (sensu Norris and Marra 2007, Harrison et al. 2011). We argue that this seasonal component is unnecessarily restrictive, and excludes the years of previous research on carryover effects in other disciplines, including a significant body of literature on what could be considered carryover effects that occur across life-history stages (e.g., Marshall et al. 2008, Marshall and Morgan 2011). This definition has also unintentionally generated confusion in the literature about the very nature of carryover effects and which phenomena qualify as such (reviewed by Norris and Marra 2007, Harrison et al. 2011). A definition of carryover effects that embraces the historical use of the term and is without arbitrary time scale restrictions is therefore needed to provide some measure of consistency for all previous and current studies of carryover effects, and to provide a conceptual framework for future studies.

What is a Carryover Effect?

In the clinical context, a carryover effect occurs when an initial treatment 'carries over' to influence a subject's response to a secondary treatment. For example, consider an experiment testing two drugs, 'X' and 'Y'. Both drugs have the effect of raising plasma concentrations of testosterone. If subjects are administered 'X' and then 'Y', 'X' results in circulating testosterone concentrations of 5 ng ml^{-1}, and 'Y' results in circulating testosterone concentrations of 8 ng $m1^{-1}$. However, if subjects are administered 'Y' and then 'X', 'Y' still results in circulating testosterone concentrations of 8 ng ml^{-1} but 'X' results in circulating testosterone concentrations of 16 ng ml^{-1} (see Fig. 2A for illustration). In this example, there is a drug interaction, and 'Y' has a carryover effect on 'X'. (For a full description of drug interaction carryover effects, see Nix and Gallicano 2001.)

However, carryover can also occur irrespective of treatment group. As an example, consider a repeated measures experiment used to test the effect of exposure to music on memory. In this experiment, subjects would initially be subjected to either a white noise or music, and asked to complete a memory task. Later, the subjects would be given the reverse treatment and asked to complete a similar memory task. If all subjects showed higher scores on the second memory task, regardless of treatment order, this improvement would be considered a carryover effect (see

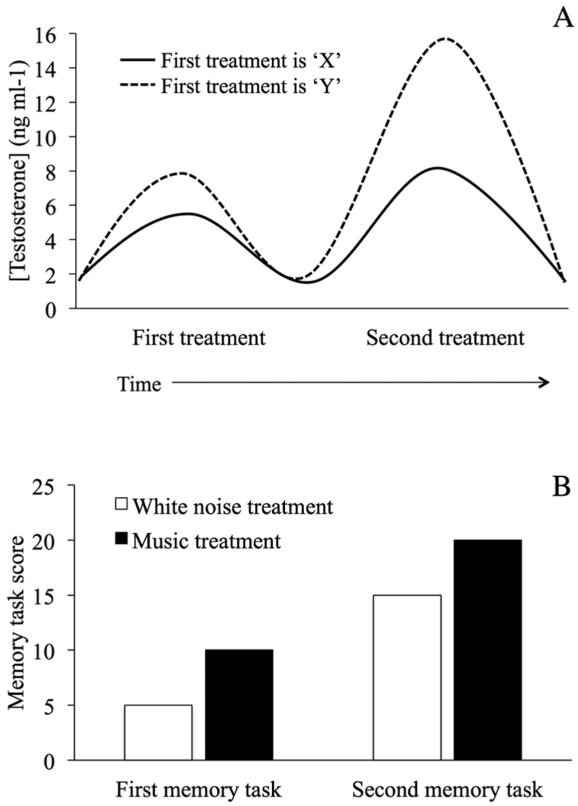

Fig. 2. An illustrative example of carryover effects. In (A), a drug interaction causes a carryover effect. In this example, two drugs are administered sequentially, both of which raise circulating testosterone concentrations. The solid line represents a case where drug 'X' is administered during a first treatment phase, and after a short recovery period, drug 'Y' is administered during a second treatment phase. The dashed line represents a case where drug 'Y' is administered first, and drug 'X' is administered second. Regardless of treatment order, drug 'Y' has the same effect on circulating testosterone concentrations. However, there is a carryover effect of drug 'Y' on drug 'X'. Administering drug 'Y' prior to administering drug 'X' increases the potency of drug 'X'. In (B), there is a learning carryover effect. Regardless of treatment, all subjects perform better on a memory task after practice.

Fig. 2B for illustration). The practice and learning that occurred during the first task 'carried over' and affected scores on the second task, regardless of the treatment. (For a full description of practice and fatigue carryover effects, see Greenland 1996.) Thus, in its most generic form, a carryover effect occurs when a past experience has an effect on a current outcome. Furthermore, total measured effects can often be partitioned into current treatment effects and carryover effects from previous experiences. In the musical example, there was an effect of music treatment, but also an effect of practice, on memory scores (Fig. 2B).

If we consider an ecological context, carryover effects will occur in any situation where an individual's previous history and experience explains their current performance in a given situation. In this case, 'performance' is a broad term that encompasses the action or process of performing a function, and can occur over a range of different time-scales (Fig. 3). In statistical terms, ecological carryover effects, as a clinical carryover effects, occur when a measurable and statistically significant proportion of current variation is explained by a previous experience. The classic example of a seasonal carryover effect comes from studies of migratory birds, where birds overwintering in high quality habitats have higher reproductive success than birds overwintering in less desirable habitats, although the quality of the breeding habitat is the same for both groups (see review by Harrison et al. 2011). These effects have also been referred to as a type of seasonal interaction (Myers 1981, Norris and Marra 2007), which can encompass phenomena such as seasonal density dependence (Ratikainen et al. 2008, Betini et al. 2013*a*).

However, carryover effects should be considered a more general phenomenon. First, as recognized by several studies already, seasonal carryover effects can occur without a requirement for migration. For example, non-migratory fish experiencing high stress in spring show differences in growth rates through the summer (O'Connor et al. 2011), while the same stress experienced in the autumn generates differences in winter behavior and survival compared to fish experiencing less stress (O'Connor et al. 2010), thus demonstrating a seasonal carryover effect within a restricted spatial scale. In birds, Robb et al. (2008) found that supplemental feeding during the winter advanced breeding date and increase the number of young raised in resident blue tits (*Cyanistes caeruleus*) the following breeding season, while in mammals, Cook et al.

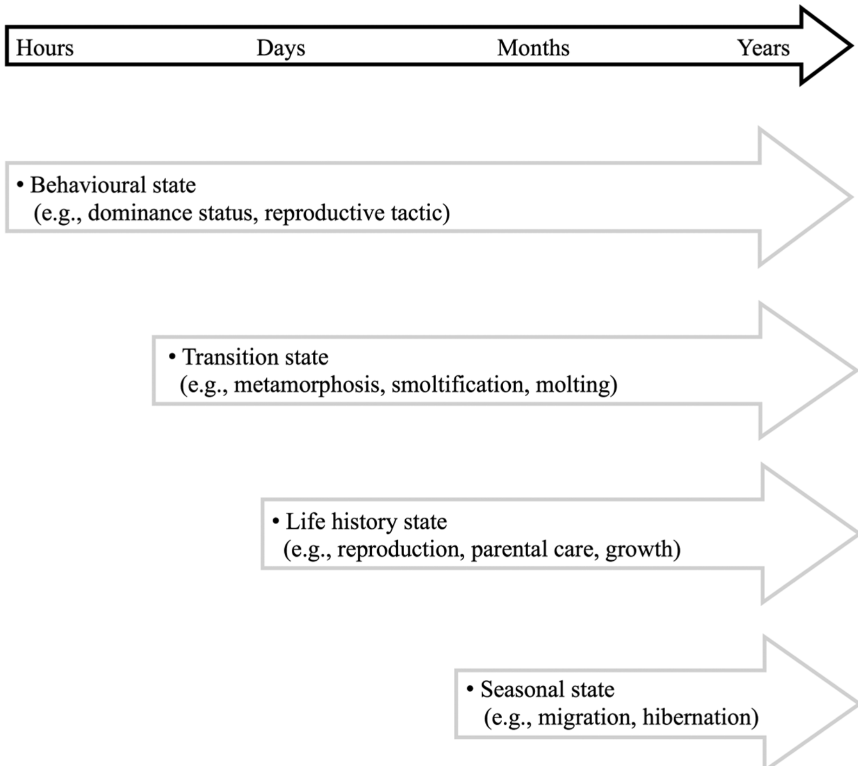

Fig. 3. Ecological carryover effects occur when experiences in one state influence performance in a subsequence state. This Fig. provides instances of different individual states where ecological carryover effects could occur, and the time scales over which they could operate.

(2004) found that nutrition during the summer and autumn had an influence on conception rates and timing of parturition in captive elk (*Cervus elaphus*) herds.

Second, carryover effects need not be limited to non-lethal effects that occur between two seasons, per se. In other organisms, transitions between physiological states can occur within a single season, as in birds and insects that undergo a period of fattening and muscle build-up in advance of breeding (e.g., Blem 1990, Witter and Cutchill 1993). Similarly, carryover effects can constrain aspects of reproductive endocrinology and egg production in female seabirds over short time frames in the spring (Crossin et al. 2010, 2012, 2013). Carryover effects have been demonstrated across metamorphic stages in insects (e.g., De Block and Stoks 2005), amphibians (e.g., Vonesh 2005, Touchon et al. 2013), marine fish (e.g., Johnson 2008), and marine invertebrates (e.g., Marshall et al. 2008, Marshall and Morgan 2011), all of which can occur within a single season and over comparatively short time periods.

Carryover effects can also be considered to occur across multiple seasons. For example, a study of *Spartina alterniflora* salt marshes demonstrated that the effects of a single enrichment of nitrogen persisted for up to three years, affecting plant primary productivity long after the nitrogen supplement has been exhausted (Gratton and Denno 2003). In another plant example, the forest fires were shown to have multi-year carryover effects on growth and recruitment of *Adenstoma* and *Ceanothus* spp. shrubs (Moreno et al. 2012). Interestingly, social carryover effects have been demonstrated in long-tailed manakins (*Chiroxiphia linearis*), where male reproductive success is not determined by a male's current social status, but instead is higher in males that establish strong social connections with other males years earlier (McDonald 2007). Finally, an example of a carryover effect not necessarily linked to migration or seasonality is the carryover effect following compensatory growth in Atlantic salmon (*Salmo salar*; Morgan and Metcalfe 2001) and brown trout (*Salmo trutta*; Johnsson and Bohlin 2006). During periods of food shortage, starved fish will reduce their growth rates, and will be smaller than fish with abundant food. When more food becomes available, the previously starved fish are able to compensate and 'catch up' with their well-nourished cohort, but this compensatory growth has a long-term cost; fish that undergo food deprivation and subsequent compensatory growth ultimately show decreased performance and increased mortality over long time scales (Morgan and Metcalfe 2001, Johnsson and Bohlin 2006, Lee et al. 2013).

This overview of studies is not meant to be a synthetic review of all carryover effect research to date. (For recent reviews in invertebrates, see review by Marshall and Morgan 2011; for recent reviews in vertebrates, see reviews by Webster and Marra 2005, Norris and Marra 2007, Harrison et al. 2011.) Our aim is to provide examples of situations where past experience explains current performance in wild biota, at temporal and spatial scales that are not necessarily linked to seasonality or migration (Fig. 3). Interestingly, in collecting these examples we note that there is far less research in mammalian systems relative to other animal taxa. This may be due to the difficulties associated in tracking mammals across broad temporal and spatial scales (Bolger et al. 2008) or perhaps that the genesis of the ecological carryover effect term was in avian research (Myers 1981, Marra et al. 1998).

Thus far, we have explained how carryover effects were first identified and described in clinical studies, and that the basic concept is highly relevant to ecological studies. One important distinction to make, however, is that, in clinical studies, carryover effects occur between discrete experimental treatments with consequences for group outcomes (or means; Fig. 2), but that, in ecological studies, carryover effects can be observational or experimental. For example, ecological studies of carryover effects can be experimental, with discrete treatment types, as demonstrated in the stress treatment and survival studies of fish mentioned above (O'Connor et al. 2010, 2011) and a recent study on the effects of condition during migration on reproductive performance in greater snow geese (*Chen caerulescens*; Legagneux et al. 2011). However, carryover effects in an ecological context can also emerge between discrete life-history stages or social situations where there is not necessarily a discrete treatment that is under study. These stages and states are analogous to clinical treatments, but with the statistical distinction that in observational studies, carryover effects can be interpreted from individual variation in some response variable rather than from differences in group means. As an example, Sorensen et al. (2009) documented migratory carryover effects in Cassin's auklets (*Ptychoramphus aleuticus*) using individual variation in isotopic signatures of blood, which related to individual differences in winter foraging with consequences for breeding performance. There was no experimental treatment applied, but individual variation in the isotopic response variable emerged between winter foraging and spring reproduction. In this sense, there was a carryover effect between discrete time-periods and life-history stages. Thus, ecological carryover effects occur over an experimental treatment, or analogous temporal or life-history transition.

What is not a Carryover Effect?

In this article, we have defined carryover effects as any situation where an individual's previous history and experience explains a significant proportion of their current performance in a given situation. As noted, we find this a particularly useful and inclusive definition. However, under our definition, it could be argued that almost any measureable phenomenon across any time scale could qualify as a carryover effect. To counter this, we emphasize that the conceptual framework that unifies carryover effects necessitates that a clear transitional period separates cause from effect. While clinical carryover effects occur across treatment periods, ecological carryover effects must be linked to a measurable and quantifiable biological phenomenon, such as a distinct life-history transition or different physiological states.

This raises a more complex question: do developmental effects, such as maternal effects or latent effects, qualify as carryover effects? Maternal effects arise when the experience of the mother is manifested in the offspring (see reviews by Mousseau and Fox 1998, Wolf and Wade 2009). For example, female rats that frequently lick and groom their offspring induce epigenetic changes in the endocrine stress response of their offspring (e.g., Weaver et al. 2004). Offspring from particularly doting mothers will have lower stress responses and show differences in stress-related and reproductive behaviors throughout their lives (e.g., Champagne and Curley 2009). Latent effects are similar, although the term is more common in invertebrate literature, and arise when early developmental experiences cause differences between individuals at later metamorphic stages (see review by Pechenik 2006). Such effects are clearly similar in concept to carryover effects.

Ecological carryover effects are typically considered those effects mediated through reversible mechanisms such as changes in energetic state, with either positive or negative effects on a measured outcome (see review by Harrison et al. 2011), and therefore distinct from irreversible, early-life organizational effects such as maternal or latent effects. However, while the current distinction between early developmental effects and carryover effects is useful in defining ecological carryover effects, it raises the important issue that our current understanding of the mechanisms driving carryover effects is limited. Few studies have identified specific mechanisms underlying carryover effects, and when mechanisms have been identified, it remains largely unknown whether or not these effects are reversible. For example, even brief elevations of corticosteroid stress hormones have been shown to cause within-season carryover effects on responses to secondary challenges (McConnachie et al. 2012) and long-term seasonal carryover effects on growth and mortality rates (O'Connor et al. 2010, 2011). While carryover effects in these cases are mediated by the endocrine system, it is unknown whether changes in the regulation of genes associated with the stress axis are involved, or whether these changes are reversible. In other cases, reversible processes, such as energetic state, can cause carryover effects across irreversible life-history transitions, such as metamorphoses. For example, body condition in the larval stage influenced growth rate following subsequent metamorphoses in marine mussels (Phillips 2002).

Therefore, while the current distinction between early developmental effects and carryover effects is useful, the current paucity of information regarding the mechanisms underlying carryover effects makes it difficult to unequivocally separate maternal or latent effects from carryover effects based on mechanistic underpinnings. In order to encourage communication and knowledge transfer among sub-disciplines, we therefore encourage researchers to consider both similarities and differences between early-life organizational effects, and potentially reversible later-life ecological carryover effect. We also encourage the study of mechanisms underlying all types of carryover effects. A better understanding of underlying mechanisms in ecology will highlight similarities among previously distinct research fields, and help us better recognize distinct biological phenomena.

Carryover Effects: Uniting New Research with Old Concepts

Under our inclusive definition of carryover effects, it can be argued that carryover effects have been studied in ecological contexts long before the concept was formally recognized and defined. This has occurred largely through the study of life-history trade-offs (Stearns 1992). The concept of life-history trade-offs is a pillar of modern ecological and evolutionary research, and posits that organismal traits do not evolve independently but within a matrix of correlations. Negative relationships that occur between traits thus form the basis for most trade-offs, which involve differential investment in one trait at the expense of another, opposing trait. This concept was presented, discussed, and refined throughout the 20th century (for highlights, see Stearns 1976) and remains a productive area of investigation. Many life-history trade-offs can be viewed within the framework of carryover effects and common physiological mechanisms may underlie both processes (Williams 2012). For example, one of the most well studied life-history trade-offs is that between current and future reproduction, which is based on the premise that reproduction is associated with costs that diminish future reproductive opportunities (Williams 1966). High investment in current reproduction will therefore reduce potential investment available for future reproduction or survival (see reviews by Stearns 1989, 1992, Roff 2002). A physiological mechanism linking current reproduction to future survival in birds was demonstrated by Dawson et al. (2000) and involved a cost of reproduction on feather quality, which carried over to affect winter survival. As another example, in bighorn sheep (*Ovis canadensis*), reproduction is associated with reduced mass, and subsequent reduced future reproductive success, particularly in high densities (Festa-Bianchet et al. 1998). While most recent research on carryover effects has largely focused on the long-term effects of overwintering habitat and migration on reproduction (reviewed by Norris and Marra 2007, Harrison et al. 2011), trade-offs and costs of reproductive effort also represent carryover effects, although they have rarely been framed as such.

As mentioned above with reference to early-life developmental effects, the most valuable benefit of recognizing the potential connection between life-history trade-offs, costs of reproduction, and carryover effects is that integration will improve our understanding of the mechanisms driving these processes, and we will likely discover that the three are mediated by similar physiological mechanisms. Indeed, the macro- and micro-nutrient limitations proposed as mechanisms of seasonal carryover effects by Harrison et al. (2011) mirror many of the mechanisms thought to drive life-history trade-offs and costs of reproduction (Stearns 1992). There has also been recent interest in endocrine mechanisms (Zera and Harshman 2001, Ricklefs and Wikelski 2002) and oxidative stress (Monaghan et al. 2009) as mechanisms driving life-history trade-offs, and it is probable that these mechanisms are equally important in driving seasonal carryover effects, as well as carryover effects at different time scales. Finally, there is a recent and growing recognition that life-history trade-offs and carryover effects need not be based on energy or resource allocation tactics alone (Zera and Harshman 2001, Dowling and Simmons 2009, Williams 2012). Indeed, the physiological systems that directly control reproduction might generate trade-offs and long-term carryover effects (Barnes and Partridge 2003, Partridge et al. 2005, Williams 2005, Harshman and Zera 2006, Williams 2012).

Integrating research on carryover effects with existing research on life-history trade-offs and costs of reproduction has the potential to improve our understanding of both carryover effects and the physiological mechanisms controlling life-history trajectories. A more comprehensive understanding of mechanisms driving carryover effects will in turn help us better understand factors affecting variation in fitness and population dynamics in the wild. Moreover, with growing human development and disturbance, the concept of carryover effects could be used to better understand the long-term fitness and population consequences of animal-human interactions (e.g., bycatch, habitat alteration, noise disturbance) that in the short-term may be viewed as inconsequential (Cooke and O'Connor 2010, Cooke et al. 2013).

Conclusion

Based on the information we review in this article, we propose the following working definition for carryover effects: *In an ecological context, carryover effects occur in any situation in which an individual's previous history and experience explains their current performance in a given situation*. By defining carryover effect in this way we hope to offset any potential confusion that may arise from a definition constrained by strict temporal requirements. We believe this working definition to be sufficiently flexible to allow researchers to address any number of relevant scenarios where carryover effects might occur, ranging from transitions between life-history stages or developmental states, to seasonal interactions and inter-annual costs of reproduction. We further suggest that recent research on carryover effects represents an important contribution towards the study and unification of life-history trade-offs and costs of reproduction. Recognizing this relationship progresses our understanding of physiological mechanisms driving carryover effects at different time scales, and will ultimately led to a better understanding of the factors that influence individual fitness in both theoretical and applied contexts.

Acknowledgments

Support was provided by an Ontario Graduate Scholarship (C. M. O'Connor), Carleton University (C. M. O'Connor), NSERC (S. J. Cooke, D. R. Norris), the Canada Research Chairs program (S. J. Cooke), and the University of Guelph Research Chair program (D. R. Norris).

Literature Cited

Barnes, A. I. and L. Partridge. 2003. Costing reproduction. Animal Behavior 66:199–204.

Betini, G. S., C. K. Griswold, and D. R. Norris. 2013*a*. Carry-over effects, sequential density-dependence and the dynamics of populations in a seasonal environment. Proceedings of the Royal Society B 280:1759.

Betini, G. S., C. K. Griswold, and D. R. Norris. 2013*b*. Density-mediated carry-over effects explain variation in breeding output across time in a seasonal population. Biology Letters 9:20130582.

Blem, C. R. 1990. Avian energy storage. Current Ornithology 7:59–133.

Block, B. A. 2005. Physiological ecology in the 21st century: advancements in biologging science. Integrative and Comparative Biology 45:305–320.

Bolger, D. T., W. D. Newmark, T. A. Morrison, and D. F. Doak. 2008. The need for integrative approaches to understand and conserve migratory ungulates. Ecology Letters 11:63–77.

Champagne, F. A. and J. P. Curley. 2009. Epigenetic mechanisms mediating the long-term effects of maternal care on development. Neuroscience and Biobehavioral Reviews 33:593–600.

Cook, R., J. G. Cook, and L. D. Mech. 2004. Nutritional condition of Northern Yellowstone elk. Journal of Mammalogy 85:714–722.

Cooke, S. J. and C. M. O'Connor. 2010. Making conservation physiology relevant to policy makers and conservation practitioners. Conservation Letters 3:159–166.

Cooke, S. J., L. Sack, C. E. Franklin, A. P. Farrell, J. Beardall, M. Wikelski, and S. L. Chown. 2013. What is conservation physiology? Perspectives on an increasingly integrated and essential science. Conservation Physiology 1(1):cot001.

Crossin, G. T., R. A. Phillips, P. N. Trathan, D. S. Fox, A. Dawson, K. E. Wynne-Edwards, and T. D. Williams. 2012. Migratory carryover effects and endocrinological correlates of reproductive decisions and reproductive success in female albatrosses. General and Comparative Endocrinology 176:151–157.

Crossin, G. T., R. A. Phillips, K. A. Wynne-Edwards, and T. D. Williams. 2013. Post-migratory body condition and ovarian steroid production predict breeding decisions by female gray-headed albatrosses. Physiological and Biochemical Zoology 86:761–768.

Crossin, G. T., P. N. Trathan, R. A. Phillips, A. Dawson, F. Le Bouard, and T. D. Wlliams. 2010. A carry-over effect of migration underlies individual variation in reproductive readiness and extreme egg size dimorphism in macaroni penguins (*Eudyptes chrysolophus*). American Naturalist 176:357–366.

Dawson, A., S. A. Hinsley, P. N. Ferns, R. H. Bonser, and L. Eccleston. 2000. Rate of moult affects feather quality: a mechanism linking current reproductive effort to future survival. Proceedings of the Royal Society B 267:2093–2098.

De Block, M. and R. Stoks. 2005. Fitness effects from egg to reproduction: bridging the life history transition. Ecology 86:185–197.

Dowling, D. K. and L. W. Simmons. 2009. Reactive oxygen species as universal constraints in life-history evolution. Proceedings of the Royal Society B 276:1737–1745.

Feder, M. E. and B. A. Block. 1991. On the future of animal physiological ecology. Functional Ecology 5:136–144.

Festa-Bianchet, M., J.-M. Gaillard, and J. T. Jorgenson. 1998. Mass- and density-dependent reproductive success and reproductive costs in a capital breeder. American Naturalist 152:367–379.

Gill, J. A., K. Norris, P. M. Potts, T. G. Gunnarsson, P. W. Atkinson, and W. J. Sutherland. 2001. The buffer effect and large-scale population regulation in migratory birds. Nature 412:436–438.

Gratton, C. and R. F. Denno. 2003. Inter-year carryover effects of a nutrient pulse on *Spartina* plants, herbivores, and natural enemies. Ecology 84:2692–2707.

Greenland, S. 1996. Confounding and exposure trends in case-crossover and case-time-control designs. Epidemiology 7:231–239.

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.

Harshman, L. G. and A. J. Zera. 2006. The cost of reproduction: the devil in the details. Trends in Ecology and Evolution 22:80–88.

Inger, R., X. Harrison, G. D. Ruxton, J. Newton, K. Colhoun, G. A. Gudmundsson, G. McElwaine, M. Pickford, D. Hodgson, and S. Bearhop. 2010. Carry-over effects reveal reproductive costs in a long-distance migrant. Journal of Animal Ecology 79:974–982.

Johnson, D. W. 2008. Combined effects of condition and density on post-settlement survival and growth of a marine fish. Oecologia 155:43–52.

Johnsson, J. I. and T. Bohlin. 2006. The cost of catching

up: increased winter mortality following structural growth compensation in the wild. Proceedings of the Royal Society B 273:1281–1286.
Lee, W. S., P. Monaghan, and N. B. Metcalfe. 2013. Experimental demonstration of the growth rate-lifespan trade-off. Proceedings of the Royal Society B 280:20122370.
Legagneux, P., P. L. F. Fast, G. Gauthier, and J. Bêty. 2011. Manipulating individual states during migration provides evidence for carry-over effects modulated by environmental conditions. Proceedings of the Royal Society B 279:876–883.
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.
Marshall, D. J., R. M. Allen, and A. J. Crean. 2008. The ecological and evolutionary importance of maternal effects in the sea. Oceanography and Marine Biology: An Annual Review 46:203–250.
Marshall, D. J. and S. G. Morgan. 2011. Ecological and evolutionary consequences of linked life-history stages in the sea. Current Biology 21:R718–R725.
McConnachie, S. H., C. M. O'Connor, K. M. Gilmour, G. K. Iwama, and S. J. Cooke. 2012. Supraphysiological cortisol elevation alters the response of wild bluegill to subsequent stressors. Journal of Experiment Zoology A 317:321–332.
McDonald, D. B. 2007. Predicting fate from early connectivity in a social network. Proceedings of the National Academy of Sciences USA 104:10910–10914.
Monaghan, P., M. B. Metcalfe, and R. Torres. 2009. Oxidative stress as a mediator of life history trade-offs: mechanisms, measurements and interpretation. Ecology Letters 12:75–92.
Moreno, J. M., I. Torres, M. B. Luna, W. C. Oechel, and J. E. Keely. 2012. Changes in fire intensity have carry-over effects on plant responses after next fire in southern California chaparral. Journal of Vegetation Science 24:395–404.
Morgan, I. J. and N. B. Metcalfe. 2001. Deferred costs of compensatory growth after autumnal food shortage in juvenile salmon. Proceedings of the Royal Society B 268:295–301.
Mousseau, T. A. and C. W. Fox. 1998. Maternal effects as adaptations. Oxford University Press, New York, New York, USA.
Myers, J. P. 1981. Cross-seasonal interactions in the evolution of sandpiper social systems. Behavioural Ecology and Sociobiology 8:195–202.
Nix, D. E., and K. Gallicano. 2001. Design and data analysis of drug interaction studies. Pages 483–506 *in* S. C. Piscitelli and K. A. Rodvold, editors. Drug interactions and infectious diseases. Humana Press, New York, New York, USA.
Norris, D. R. 2005. Carry-over effects and habitat quality in migratory animals. Oikos 109:178–186.
Norris, D. R. and P. P. Marra. 2007. Seasonal interactions, habitat quality and population dynamics in migratory birds. Condor 109:535–547.
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 B 271:59–64.
Norris, D. R. and C. M. Taylor. 2006. Predicting the consequences of carry-over effects for migratory populations. Biology Letters 2:148–151.
O'Connor, C. M., K. M. Gilmour, R. Arlinghaus, C. T. Hasler, D. P. Philipp, and S. J. Cooke. 2010. Seasonal carryover effects following the administration of cortisol to a wild teleost fish. Physiological and Biochemical Zoology 83:950–957.
O'Connor, C. M., K. M. Gilmour, R. Arlinghaus, S. Matsumura, C. D. Suski, D. P. Philipp, and S. J. Cooke. 2011. The consequences of short-term cortisol elevation on individual physiology and growth rate in wild largemouth bass (*Micropterus salmoides*). Canadian Journal of Fisheries and Aquatic Sciences 68:693–705.
Partridge, L., D. Gems, and D. J. Withers. 2005. Sex and death: What's the connection? Cell 120:461–472.
Pechenik, J. A. 2006. Larval experience and latent effects: metamorphosis is not a new beginning. Integrative and Comparative Biology 46:323–333.
Phillips, N. E. 2002. Effects of nutrition-mediated larval condition on juvenile performance in a marine mussel. Ecology 83:2562–2574.
Pough, F. H. 1989. Organismal performance and Darwinian fitness: approaches and interpretations. Physiological Zoology 62:199–236.
Ratikainen, I., J. Gill, T. Gunnarsson, W. Sutherland, and H. Kokko. 2008. When density dependence is not instantaneous: theoretical developments and management implications. Eology Letters 11:184–198.
Ricklefs, R. E. and M. Wikelski. 2002. The physiology/life-history nexus. Trends in Ecology and Evolution 17:462–468.
Robb, G. N., R. A. McDonald, D. E. Chamberlain, S. J. Reynolds, T. J. E. Harrison, and S. Bearhop. 2008. Winter feeding of birds increases productivity in the subsequent breeding season. Biology Letters 4:220–223.
Roff, D. A. 2002. Life history evolution. Sinauer, Sunderland, Massachusetts, USA.
Rubenstein, D. R. and K. A. Hobson. 2004. From birds to butterflies: animal movement patterns and stable isotopes. Trends in Ecology and Evolution 19:256–263.
Runge, M., and P. P. Marra. 2005. Modelling seasonal interactions in the population dynamics of migratory birds. Pages 375–389 *in* R. Greenberg and P. P.

Marra, editors. Birds of two worlds: the ecology and evolution of temperate-tropical migration systems. Johns Hopkins University Press, Baltimore, Maryland, USA.

Sedinger, J. S., J. L. Schamber, D. H. Ward, C. A. Nocolai, and B. Conant. 2011. Carryover effects associated with winter location affect fitness, social status, and population dynamics in a long-distance migrant. American Naturalist 178:110–123.

Sorensen, M. C., J. M. Hipfner, T. K. Kyser, and D. R. Norris. 2009. Carry-over effects in a Pacific seabird: stable isotope evidence that pre-breeding diet quality influences reproductive success. Journal of Animal Ecology 78:460–467.

Spicer, J. I. and K. J. Gaston. 1999. Physiological diversity and its ecological implications. Blackwell Science, Malden, Massachusetts, USA.

Stearns, S. C. 1976. Life-history tactics: A review of the ideas. Quarterly Reviews in Biology 51:3–47.

Stearns, S. C. 1989. Trade-offs in life-history evolution. Functional Ecology 3:259–268.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford, UK.

Touchon, J. C., M. W. McCoy, J. R. Vonesh, and K. M. Warkentin. 2013. Effects of plastic hatching timing carry over through metamorphosis in red-eyed treefrogs. Ecology 94:850–860.

Vonesh, J. R. 2005. Sequential predator effects across three life stages of the African tree frog, *Hyperolius spinigularis*. Oecologia 143:280–290.

Wallenstein, S. and A. C. Fisher. 1977. The analysis of the two-period repeated measurements crossover design with application to clinical trials. Biometrics 33:261–269.

Weaver, I. C. G., N. Cervoni, F. A. Champagne, A. C. D'Alessio, S. Sharma, J. R. Secki, S. Dymov, M. Szyf, and M. J. Meaney. 2004. Epigenetic programming by maternal behavior. Nature Neuroscience 7:847–854.

Webster, M. S., and P. P. Marra. 2005. The importance of understanding migratory connectivity and seasonal interactions. Pages 199–209 *in* R. Greenberg and P. P. Marra, editors. Birds of two worlds: the ecology and evolution of temperate-tropical migration. John Hopkins University Press, Baltimore, Maryland, USA.

Webster, M. S., P. P. Marra, S. M. Haig, S. Bensch, and R. T. Holmes. 2002. Links between worlds: unraveling migratory connectivity. Trends in Ecology and Evolution 17:76–83.

Williams, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's Principle. American Naturalist 100:687–690.

Williams, T. D. 2005. Mechanisms underlying costs of egg production. BioScience 55:39–48.

Williams, T. D. 2012. Physiological adaptations for breeding in birds. Princeton University Press, Princeton, New Jersey, USA.

Witter, M. S. and I. C. Cutchill. 1993. The ecological costs of avian fat storage. Philosophical Transactions of the Royal Society B 340:73–92.

Wolf, J. and M. J. Wade. 2009. What are maternal effects (and what are they not)? Philosophical Transactions of the Royal Society B 364:1107–1115.

Zera, A. J. and L. G. Harshman. 2001. Physiology of life history trade-offs in animals. Annual Review of Ecological Systems 32:95–106.