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Authors: Streby, Henry M., Refsnider, Jeanine M., and Andersen, David E.

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PERSPECTIVE

Redefining reproductive success in songbirds: Moving beyond the nest success paradigm

Henry M. Streby,[1]* Jeanine M. Refsnider,[1] and David E. Andersen[2]

[1] Department of Environmental Science Policy and Management, University of California Berkeley, Berkeley, California, USA
[2] U.S. Geological Survey, Minnesota Cooperative Fish and Wildlife Research Unit, St. Paul, Minnesota, USA
* Corresponding author: henrystreby@gmail.com

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ABSTRACT

One of the most commonly estimated parameters in studies of songbird ecology is reproductive success, as a measure of either individual fitness or population productivity. Traditionally, the "success" in reproductive success refers to whether, or how many, nestlings leave nests. Here, we advocate that "reproductive success" in songbirds be redefined as full-season productivity, or *the number of young raised to independence from adult care* in a breeding season. A growing body of evidence demonstrates interdependence between nest success and fledgling survival, and emphasizes that data from either life stage alone can produce misleading measures of individual fitness and population productivity. Nest success, therefore, is an insufficient measure of reproductive success, and songbird ecology needs to progress beyond this long-standing paradigm. Full-season productivity, an evolutionarily rational measure of reproductive success, provides the framework for appropriately addressing unresolved questions about the adaptive significance of many breeding behaviors and within which effective breeding-grounds conservation and management can be designed.

Keywords: avian ecology, breeding behavior, fitness, fledgling stage, full-season productivity, population ecology

Redefinición del éxito reproductivo en las aves canoras: más allá del paradigma del éxito de los nidos

RESUMEN

Uno de los parámetros estimados con mayor frecuencia en los estudios sobre la ecología de las aves canoras es el éxito reproductivo, ya sea como medida de aptitud individual o de productividad poblacional. Tradicionalmente, el "éxito" del éxito reproductivo se refiere a si los pichones dejan el nido y a cuántos lo hacen. Aquí recomendamos que el "éxito reproductivo" de las aves canoras sea redefinido como la productividad de toda la temporada, o *el número de crías que alcanzan la independencia del cuidado parental* en una temporada reproductiva. Un creciente cuerpo de evidencia demuestra dependencia mutua entre el éxito de los nidos y la supervivencia de los volantones, y enfatiza que los datos de cualquiera de las dos etapas de vida por sí solos pueden producir medidas erróneas de la aptitud individual y de la productividad de la población. Por lo anterior, el éxito de los nidos es una medida insuficiente del éxito reproductivo y la ecología de las aves canoras necesita progresar más allá de este paradigma. La productividad de toda la temporada es una medida evolutivamente razonable de éxito reproductivo que brinda el marco para evaluar apropiadamente preguntas no resueltas sobre el significado adaptativo de muchos comportamientos reproductivos, y dentro del cual se pueden diseñar estrategias efectivas de conservación y manejo de las áreas de cría.

Palabras clave: aptitud, comportamiento reproductivo, ecología de aves, ecología de poblaciones, etapa de los volantones, productividad de toda la temporada

INTRODUCTION

A common goal in studies of avian ecology is to measure the reproductive success of individuals and populations. At the individual level, there is an enormous body of literature on the fitness consequences of habitat selection (reviewed by Martin 1992 and by Chalfoun and Schmidt 2012), the phenology of migration and breeding (Price et al. 1988, Norris et al. 2004), mate choice (Griffith et al. 1999, Wolfenbarger 1999, McGraw et al. 2001), and male parental care (reviewed by Ketterson and Nolan 1994). At the population level, many management and conservation-based studies use population reproductive success to assess habitat quality (Van Horne 1983, Johnson 2007, Bakermans et al. 2012), determine management treatment effects (meta-analyzed by Hartway and Mills 2012), monitor source–sink population dynamics (Brawn and Robinson 1996), identify ecological traps (Stracey and Robinson 2012), and predict climate-change impacts (Schaefer et al. 2006).

Common among many individual- and population-level studies of songbird ecology is a response variable that is some measure of "reproductive success." In individual-level studies, "reproductive success" is generally used as a proxy for fitness, whereas in population-level studies it is used as an indicator of population productivity, which is essentially the mean fitness of all individuals in the population. Importantly, in both types of studies, "reproductive success" is traditionally defined as either the number of nestlings that fledge from nests or whether any nestlings fledge. Here, we advocate that "reproductive success" in both types of studies be redefined as full-season productivity, or *the number of young raised to independence from adult care* in a breeding season. Full-season productivity is a more accurate and meaningful measure of both individual fitness and population productivity than whether or how many nestlings fledge from nests, and, because individual fitness drives the behavior and activity of birds, it is the parameter of greatest interest in much of songbird ecology. Necessitating this redefinition are recent studies demonstrating that nest success (i.e. the probability that a nesting attempt produces young that fledge) and fledgling survival (i.e. the probability that a fledgling survives to independence) are interdependent, integral components of individual fitness (e.g., Streby et al. 2014) and of population productivity (e.g., Streby and Andersen 2011, Peterson 2014). Therefore, data from either life stage considered in isolation produce, at best, an incomplete measure or, at worst, a misleading measure of reproductive success. The answers to many unresolved questions about apparently maladaptive behaviors and incongruent relationships between productivity and habitat quality lie in a paradigm shift toward a more evolutionarily rational measure of reproductive success.

The concept that reproductive success relies on life stages past that of the nest is not unique to songbirds (see Refsnider and Janzen 2010). Perhaps the strongest argument for a paradigm shift in songbird reproductive ecology from nest-centric proxies of reproductive success toward full-season productivity is that, in other taxa, conflicting selection pressures on multiple life stages influence the evolution of breeding behaviors in general and of nest-site choice in particular (reviewed by Refsnider and Janzen 2010). There is abundant evidence that individuals prioritize juvenile survival over nest survival when choosing nest sites in insects (Rausher 1983, Vacek et al. 1985, Heard 1994, Sadeghi and Gilbert 1999, Pöykkö 2006), fishes (Johannes 1978, Bilkovic et al. 2002, Charteris et al. 2003), amphibians (Resetarits and Wilbur 1989, Halloy and Fiano 2000, Matsushima and Kawata 2005), and nonavian reptiles (Drummond 1983, Kamel and Mrosovsky 2004, Lohmann et al. 2008). In bird populations, population growth rates can be more sensitive to variation in juvenile survival during brood rearing than to variation in nest success in waterfowl (Amundson et al. 2013), Galliformes (Clark et al. 2008), and even in songbirds (Streby and Andersen 2011). Selection pressure to maximize maternal survival also influences nest-site choice in many taxa (Refsnider and Janzen 2010), including some birds (Low et al. 2010, Arnold et al. 2012). However, maternal survival at nest sites tends to be high in songbirds (Streby et al. 2014); therefore, we focus here on survival of nests and fledglings.

Past Tradition: The Nest-Success Paradigm

Traditional proxies for "reproductive success" in studies of songbird ecology include a variety of terms, some of which have multiple definitions and some of which are used interchangeably. The more commonly used terms include daily survival of nests (e.g., Johnson 1979), nest success (e.g., Mayfield 1961), fledging success (e.g., Gates and Gysel 1978), fledgling success (Stevenson and Bryant 2000), and nest productivity (e.g., Kight et al. 2012). The statistical methods for estimating parameters of "reproductive success" from nest-monitoring data have improved considerably since the Mayfield (1961) exposure method was introduced (reviewed by Johnson 2007), and several authors (e.g., Flaspohler et al. 2001, Thompson et al. 2001) have emphasized the importance of incorporating renesting attempts and fledged brood size in such estimates. However, even estimates of the number of young fledged from nests over an entire season (i.e. seasonal or annual "reproductive success"; Zanette et al. 2006, Stracey and Robinson 2012) assume that fledging young from a nest is "success." For simplicity we will use "nest success" hereafter to encompass all such nest-centric proxies for reproductive success. In addition, we use "full-season productivity" only to emphasize the inclusion of nest and fledgling data, and not to introduce yet another term to an already crowded field; ideally, full-season productivity will eventually be referred to simply as "productivity" or "reproductive success."

A successful reproductive attempt for a pair of songbirds includes laying eggs, incubating eggs, and rearing hatched young until they are independent from adult care (Figure 1). Young that survive to independence spend some time in the nest (i.e. as nestlings, a period roughly half of the nesting stage) and some time outside the nest (i.e. the fledgling stage). The temporal ratio of the nesting and fledgling stages varies among species (Martin 2014), with different temporal ratios among species likely having evolved in response to predation pressure on each stage; often the fledgling stage is similar to or longer than the nesting stage (e.g., Streby 2010). Historically, studies of songbird reproductive success were limited to measuring nest success due to the near impossibility of monitoring survival of secretive and mobile fledglings. However, radio-

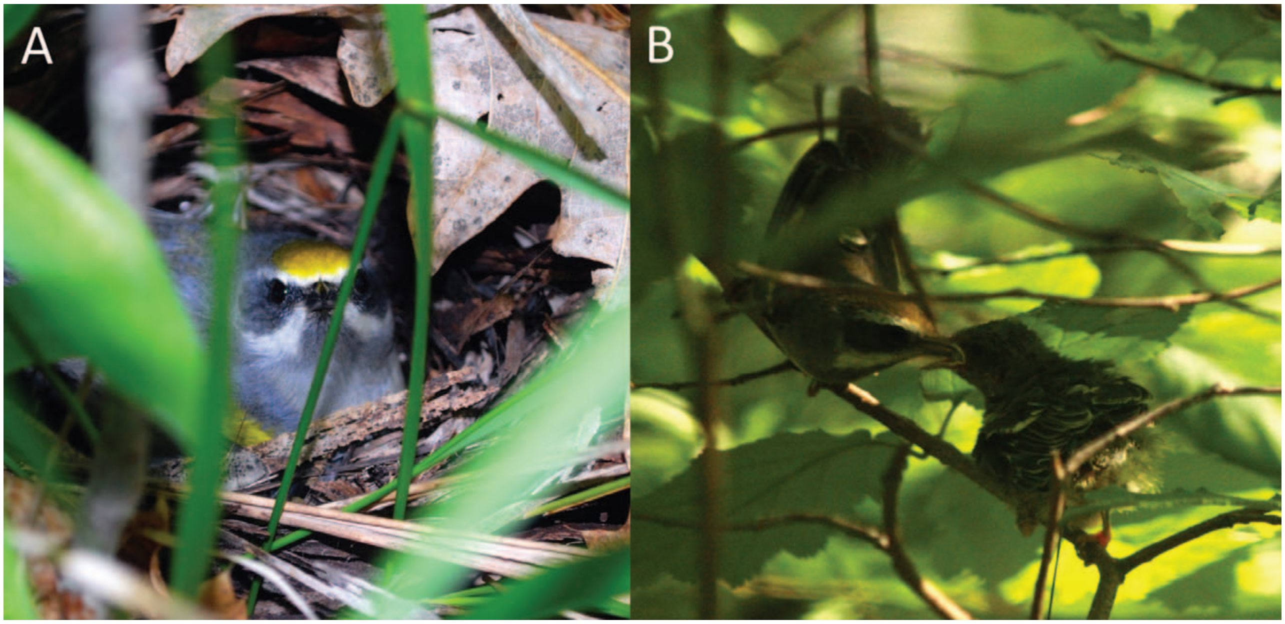

FIGURE 1. A successful reproductive attempt for songbirds includes (**A**) nesting and (**B**) raising fledglings to independence from adult care. A growing body of published evidence for interdependent differences between these stages indicates that data from either stage alone can produce misleading measures of individual fitness and population productivity. Here, we argue that a redefinition of songbird reproductive success to the number of young raised to independence from adult care is necessary to provide the framework within which questions about the adaptive significance of breeding behaviors can be appropriately addressed, and within which effective breeding-grounds conservation and management can be designed. Photo credits: (**A**) H. Streby and (**B**) B. Vernasco

telemetry microtechnology (e.g., Wikelski et al. 2006) removed the logistical constraints of studying the fledgling stage two decades ago (e.g., Powell et al. 2000). Anders et al. (1997) published the first telemetry-based estimate of fledgling songbird survival, in which they touted the development as opening the door to improved estimates of reproductive success. However, contemporary research in songbird reproductive ecology continues to focus on nest success (Anders and Marshall 2005), which suggests paradigm stagnation. For nest success to be an accurate proxy for reproductive success, one of two assumptions must be met: either (1) fledgling survival must correlate positively with nest success (i.e. what's good for nests is good for fledglings), or (2) fledgling survival must be entirely independent of nest success. Recent studies of fledgling survival and of full-season productivity suggest that neither assumption is valid (Cohen and Lindell 2004, Jackson et al. 2013, Streby and Andersen 2013a, Streby et al. 2014).

A New Direction: Putting the Fledgling Back into Reproductive Success

The past 20 years have produced a steady increase in studies of the fledgling stage (reviewed by Cox et al. 2014). Unfortunately, rather than improving estimates of reproductive success, studies of fledgling ecology have instead been treated as a new and separate area of research. This may be a consequence of "nest success" and "reproductive success" being used synonymously in the literature, which is unfortunate because studies of the fledgling stage have provided evidence that nest success and fledgling survival are not independent, but in fact are strongly interdependent. First, habitat used during the fledgling stage is often different from that used for nesting at multiple spatial scales (Cohen and Lindell 2004, King et al. 2006, Streby and Andersen 2013b), and habitat characteristics associated with high fledgling survival often differ from those associated with high nest success (Cohen and Lindell 2004, Jackson et al. 2013, Streby and Andersen 2013a). Second, nests and fledglings can experience predation, the primary cause of nest failure and fledgling mortality (Martin 1993, Cox et al. 2014), by different predator suites, and those predator suites can interact with each other, which can result in high nest success associated with low fledgling survival, and vice versa (e.g., Streby 2010). Third, the effects of insect parasites (Streby et al. 2009), avian brood parasites (Payne and Payne 1998, Peterson et al. 2012), and anthropogenically increased predator abundance (Shipley et al. 2013) can be strong and direct on fledgling survival, even when they have no apparent effect on nest success. Finally, the strongest predictors of fledgling survival often are habitat characteristics associated directly with the nest location (Cohen and Lindell 2004, Jackson et al. 2013, Streby and Andersen 2013a), and these can be the same characteristics that affect nest success differently, suggesting that any one nest location is unlikely to maximize survival of both the nest and the fledglings that might fledge from it.

Full-Season Productivity and Individual Fitness

Studies of the fledgling stage and of the full breeding season in songbirds have provided considerable evidence that nest and fledgling survival are interdependent (e.g., Streby et al. 2014). In some cases, there may even be tradeoffs in factors that are most beneficial for each stage. Because birds are ultimately attempting to maximize their individual fitness through their breeding decisions (e.g., timing, location, mate choice, and clutch size), they may respond to tradeoffs between life stages in ways that appear suboptimal or even maladaptive if individual life stages are considered separately (Tarwater and Beissinger 2013, Martin 2014, Streby et al. 2014). However, it is important to recognize that even though nest success and fledgling survival each are important components of individual fitness, neither is an accurate measure of fitness on its own when the stages are interdependent. To fully understand breeding decisions made by birds and the implications of those decisions for fitness, it is not sufficient to rely only on nest success or fledgling survival—it is necessary to consider full-season productivity of individuals.

Tradeoffs between nest success and fledgling survival in individuals. Studies in which nest success and fledgling survival both have been investigated provide increasing evidence for interdependence between these parameters. Despite this, few studies have included both of these life stages along with an examination of factors, including habitat characteristics, that may affect nest success and fledgling survival. One of the few studies that has done so found that female Golden-winged Warblers (*Vermivora chrysoptera*) face opposing selection pressures to maximize nest success versus fledgling survival when choosing nest sites with respect to distance to forest edge (Streby et al. 2014). Golden-winged Warbler nest success is highest in shrublands and lowest in forest, but fledgling survival is highest from nests in forest and lowest from nests in shrublands. Both the nest and fledgling stages have moderate survival when nests are near forest–shrubland edge. Golden-winged Warblers choose nest sites close to forest–shrubland edge, balancing the opposing selection pressures to maximize the number of young raised to independence. Furthermore, there is a time-dependent switch in nest-site choice by individual Golden-winged Warblers to prioritize fledgling survival early in the season and nest success later in the season, indicating that nest-site choice is not only influenced by fledgling survival, but that fledgling survival can be prioritized over nest success in nest-site choice (Streby et al. 2014).

Nest distance to edge is only one of many habitat variables that can affect nest success and fledgling survival differentially; in other systems, nest height, nest concealment, and other environmental factors that affect nest success will likely be found to affect fledgling survival differently. Moreover, the selection pressures acting on nest-site choice to maximize nest success versus fledgling survival may be nonlinear, further complicating the relationship between nest-site choice and individual fitness. Regardless, in any case where selection pressures are dissimilar between life stages, neither stage alone is an accurate proxy for fitness.

The misleading nature of nest success of individuals. Golden-winged Warblers change nest sites within the breeding season in a switch of priorities between maximizing fledgling survival and maximizing nest success (Streby et al. 2014). Had Streby et al. (2014) studied only nest success, they could have erroneously concluded that their observations supported many nest-centric hypotheses posited to explain the mismatch between nest-site choice and nest success. For example, they could have concluded that Golden-winged Warblers follow a win–stay:lose–switch rule, in which nest-site choice is performance-based (i.e. performance of the nest) and birds change nest locations after initial nest failure (e.g., Chalfoun and Martin 2010). In addition, had Streby et al. (2014) studied only nests, their results could have provided clear, but erroneous, evidence for the hypothesis of prospecting behavior. Prospecting birds choose nest sites in areas where there is evidence of conspecific nest success (e.g., Betts et al. 2008). Without consideration for fledgling survival, Streby et al. (2014) might have concluded that Golden-winged Warblers that failed when nesting in forest switched nest sites to shrublands because the birds observed signs of successful nesting by conspecifics in shrublands. Finally, had they studied only nest success, Streby et al. (2014) might have concluded that nest-site choice is maladaptive in Golden-winged Warblers, because birds chose nest sites relatively close to forest edges despite experiencing the highest nest success farther into shrublands. Ultimately, the problem with the win–stay:lose–switch, prospecting, and maladaptive behavior hypotheses is the assumption that nest success is the sole objective of nest-site choice. It is not. A successful nest is not a win, nor is a failed nest necessarily a loss, in the context of producing fledglings to independence over the course of a breeding season. This is not to say that relatively complex hypotheses for explaining breeding behaviors will not bear out in some or many systems. However, it does demonstrate that redefining reproductive success to full-season productivity has the potential to provide a simpler explanation.

Full-season productivity explains the adaptive significance of nest-site choice in songbirds. The reader might be asking, "If nest success is such a poor proxy for fitness, why do so many nest-success studies report that nest-site choice is adaptive?" A small number of high-profile nest-success studies have demonstrated that nest-site choice is adaptive (e.g., Southwood 1977, Martin 1998). However, two exhaustive literature reviews on the adaptive significance of nest-site choice in songbirds have concluded that the relationship between nest-site choice and nest success is inconsistent and unclear (Martin 1992, Chalfoun and Schmidt 2012). Chalfoun and Schmidt (2012) summarized 200 accounts of 19 hypothesized explanations for the mismatch between nest success and nest-site choice, including the win–stay:lose–switch, prospecting behavior, and maladaptive behavior hypotheses discussed above. A more parsimonious explanation for the extensive reporting of mismatches between nest success and nest-site choice in the published literature is that nest success is not a proxy for individual fitness, which is the parameter that birds are attempting to maximize through their nest-site choices. If birds select nest sites to maximize the survival of fledglings, or if there are tradeoffs between sites that maximize nest success vs. those that maximize fledgling survival, nest-site choice is unlikely to predict nest success because birds are not choosing nest sites based on (or solely on) potential nest success.

Full-season productivity may also explain the adaptive significance of other breeding behaviors. Nest-site choice is not the only breeding behavior that evolutionary theory predicts should be adaptive, but for which nest-success studies fail to provide consistent support (e.g., Price et al. 1988, Ketterson and Nolan 1994). As with nest-site choice, some nest-success studies provide evidence that female mate choice (e.g., McGraw et al. 2001), breeding phenology (e.g., Norris et al. 2004), and male parental care (e.g., Sasvari 1986) are adaptive. However, as with nest-site choice, many other studies and some literature reviews report a general incongruity between nest success and each of these behaviors. For example, when plumage coloration of male mates is not found to correlate linearly with female "fitness" (i.e., nest success), complicated explanations about variation and plasticity in female mate choice are invoked (e.g., Chaine and Lyon 2008). Similarly, strong directional selection for earlier nesting dates is commonly reported in nest-success studies (e.g., Price et al. 1988, Norris et al. 2004), and heritability for breeding date is moderate to high (Price et al. 1988), yet evolution of earlier nesting generally has not occurred (Price et al. 1988). Finally, in the case of male parental care, female songbirds usually fledge most or all of their nestlings even when male mates are experimentally removed, leading to confusion about the adaptive significance of male parental care (Wolf et al. 1988, Ketterson and Nolan 1994). To our knowledge, subsequent fledgling survival has been considered in only one of these cases and it has provided considerable insight. Ketterson and Nolan (1994) provided evidence in Dark-eyed Juncos (*Junco hyemalis*) that the consequences of male parental care are direct and immediate during the typically unstudied fledgling stage. It is likely that consideration for fledgling survival will clarify additional unanswered evolutionary questions about songbird reproductive ecology. Indeed, the relative developmental stage at which nestlings fledge, and the resultant relative fledgling mobility, has recently inspired a new conceptual framework for the evolution of clutch size in songbirds (Martin 2014), the testing of which will require intensive study of both nests and fledglings.

Full-Season Productivity: Improving Measures of Population Productivity

It is important to distinguish between the evolution of traits related to individual reproductive success, or fitness, and population reproductive success, or population productivity. Studies of evolutionary selection pressures focus on relative fitness of individuals within a population, which is by definition independent of overall population trends. In contrast, population-level studies focus on the total or mean productivity of a group of individuals, often without concern for underlying evolutionary mechanisms causing variation within the group. Interestingly, interdependent relationships between nest success and fledgling survival have also been demonstrated in population-level studies, wherein low nest success is accompanied by high fledging survival and high nest success is accompanied by low fledgling survival (e.g., Cohen and Lindell 2004, Streby and Andersen 2011, Peterson 2014).

Interdependence of nest success and fledgling survival in populations. The interdependence between nest success and fledgling survival is apparent at the population level (e.g., Streby and Andersen 2011, Peterson 2014). For example, variation in fledgling survival can offset and even overwhelm variation in nest success among years, thereby making nest success a misleading indicator of full-season productivity in Ovenbirds (*Seiurus aurocapilla*; Streby and Andersen 2011). In addition, although Ovenbirds often have reduced nest success near forest edges (e.g., Manolis et al. 2002), increased fledgling survival from nests near forest edges can result in relatively high full-season productivity near edges (Streby and Andersen 2011). Similarly, in Golden-winged Warblers, nest success and fledgling survival respond differently at the population level to variation in landscape composition (Peterson 2014). Using a novel, spatially explicit model of full-season productivity, Peterson (2014) demonstrated that forested landscapes with the highest full-season productivity for Golden-winged Warblers are not the landscapes that host either the highest nest success or the highest fledgling survival, but rather are the landscapes that host moderate levels of both.

The misleading nature of nest success in populations. Population-level interdependence between nest success and fledgling survival means that conclusions derived about population productivity based only on nest-success data can be erroneous. In full-season studies of Ovenbirds (Streby and Andersen 2011) and Golden-winged Warblers (Peterson 2014), data on nest success without data on subsequent fledgling survival would have produced erroneous conclusions about relative growth among populations, habitat quality, and edge effects, and would have led to incorrect habitat management recommendations. Importantly, data from fledgling survival alone also would have resulted in incorrect conclusions about full-season productivity for both species. We do not contend that nest success is always relatively high when fledgling survival is relatively low, and vice versa. Rather, we emphasize the empirical evidence that the stages can be interdependent, and that therefore it should not be assumed that a treatment maximizing one stage or the other maximizes full-season productivity. In many systems, conclusions about population productivity based solely on data from only the nest or the fledgling stage may require reconsideration.

At the population level, fledgling survival has recently been proposed as a possible explanation for mismatches between breeding density and nest success (e.g., Cunningham and Johnson 2012, Boves et al. 2013). Some authors of singing-bird-survey and nest-success studies have speculated that unexpectedly high breeding densities near edges of preferred nesting habitat (Cunningham and Johnson 2012), and unexpectedly low nest success following habitat management (Boves et al. 2013), might be explained by yet-unidentified benefits to fledgling survival. Unfortunately, however, this speculation is often discounted because "the influence of breeding habitat on these future components of fitness [i.e. fledgling survival] may be relatively indirect and is currently unclear, while the influence of breeding habitat on nest success and fledgling production is direct and obvious" (Boves et al. 2013:10). In direct contrast to the conclusion of Boves et al. (2013), the literature on fledgling survival in general, and the full-season studies on Ovenbirds (Streby and Andersen 2011) and Golden-winged Warblers (Streby et al. 2014, Peterson 2014) in particular, demonstrates that fledgling survival is not only directly influenced by breeding habitat choice, but that fledgling survival can be prioritized over nest success when birds choose breeding habitat.

Full-season productivity implications for habitat management. Identifying population-level interdependence between nest success and fledgling survival is critical for informing management designed to increase songbird population productivity. If habitat management based on the results of nest-success research is successful at increasing nest success, as it tends to be (meta-analysis by Hartway and Mills 2012), it is possible that tradeoffs in reduced fledgling survival will result in no net gain, or even a decrease, in full-season population productivity. Similarly, conclusions of failed management efforts based on increased breeding density and reduced nest success (e.g., Boves et al. 2013) may be premature without knowledge of fledgling survival and full-season productivity. In general, conclusions that songbird breeding density is a misleading indicator of habitat quality in songbirds (e.g., Van Horne 1983) may need to be reassessed: When full-season productivity is accurately measured, breeding density may turn out to be a good indicator of habitat quality after all. It seems clear that managing a landscape to maximize full-season productivity, rather than any one component thereof, is the most evolutionarily rational path forward for songbird breeding-grounds management and population conservation. Therefore, to the inevitable protest that the addition of fledgling survival to songbird productivity research is too costly, we argue that the increased cost of data collection must be weighed against the far greater cost of implementing counterproductive management actions.

Conclusions

The redefinition of songbird reproductive success from nest success to full-season productivity, or young raised to independence from adult care over a breeding season, is a necessary step forward in songbird ecology research. For simplicity, we presented the need for this redefinition in the context of multinesting, single-brooded species. The implications for multibrooded species (i.e. those that can successfully fledge more than one brood from $\geq$1 nest in a single season; e.g., Powell et al. 1999) are more complicated. However, the same general concept applies: The number of young raised to independence in a breeding season is a better measure of individual and population-level productivity than the number of young fledged from nests in both single- and multi-brooded species. Similarly, individual behaviors like nest-site choice will likely be better understood when considered in the context of full-season productivity (i.e. all the young raised to independence) in multibrooded species. Finally, studies using full-season productivity as the measure of reproductive success could provide clearer answers to questions about brood parasitism, postfledging brood splitting, cooperative breeding, and other behaviors not discussed here. A paradigm shift in the definition of reproductive success will provide the framework for appropriately addressing unresolved questions about the adaptive significance of many breeding behaviors and within which effective breeding-grounds conservation and management can be designed. Redefining reproductive success in songbirds is an evolutionarily rational progression beyond the nest-success paradigm, and is a timely and necessary advance in ornithology.

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