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Conceptual Revision and Synthesis of Proximate Factors Associated with Age-Related Improvement in Reproduction

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(Invited Review)

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Abstract

Improvement in reproductive performance with age, up to the point of senescence, is a predominant pattern among vertebrates. Predictions from life-history theory provide a powerful framework for understanding the evolutionary basis of these patterns. However, based on the growing number of publications on this topic, there is increased interest in understanding the proximate causes of age-related improvements in reproductive performance (ARIRP). A formal conceptual framework through which factors related to ARIRP can be examined is lacking. Here, we establish hypotheses with testable predictions for social and ecological factors, including resource quality, mate fidelity, site fidelity, prior breeding experience, and changes in ability to attract mates. We use this conceptual framework to review 55 empirical studies published (between 1900 through 2013) on avian species as birds have the greatest representation in empirical studies of ARIRP. Our synthesis revealed that tests of the breeding experience hypothesis are most prevalent in the literature, whereas tests of the site fidelity hypothesis are least prevalent. Overall, the role of increased mate attraction with age seems to be an important predictor of ARIRP, whereas changes in resource quality with age show the least support among published studies. Because many studies suffered from small sample sizes and did not control for confounding variables, we suggest experimental methodologies for teasing apart hypotheses in empirical investigations and offer statistical approaches for longitudinal datasets. From an ultimate perspective, we also highlight the role of life-history variation, in shaping within-individual improvements. Future work should employ a standardized framework to study patterns of ARIRP, as set forward here, to allow for more quantitative comparison of results across studies.

Introduction

According to life-history theory, there are various reasons why an individual's reproductive performance, defined as the number of offspring produced in each bout of breeding, should be age-related. For example, as an individual ages, the number of opportunities remaining for reproduction decreases and thus an individual is expected to allocate more energy toward reproduction (Roff 1992). The relationship between age and reproduction is hypothesized to be shaped by the threat of mortality and the physiological mechanisms of senescence, leading to a diversity of life-history strategies including a negative relationship between age and performance (e.g., type I survivorship curve), a constant relationship between age and performance (e.g., type II survivorship curve), and a positive relationship between age and performance (type III survivorship curve; Jones et al. 2014). The latter, positive relationship has received attention from biologists, as the pattern has been observed across diverse taxa, including birds, ungulates, and primates (Packer 1979; Forslund & Larsson 1992; Ericsson et al. 2001). To explain these patterns,

Forslund & Pärt (1995) proposed three non-mutually exclusive hypotheses: progressive disappearance of inferior phenotypes (selection), the acquisition of experience (constraint), and unequal investment in reproduction (restraint). Of these three hypotheses, the 'constraint' hypothesis has received strong support, but remains unresolved, as there is currently no framework for discerning which experiences within an individual's lifetime are responsible for such improvements in reproduction (Takagi 2001; González-Solís et al. 2004; Dugdale et al. 2011). To further develop the constraint hypothesis, a framework of testable hypotheses about the proximate mechanisms that predict patterns of age-related improvement in reproductive performance (ARIRP) is required.

The importance of understanding the proximate causes underlying ARIRP is underscored by the increasing number of studies focused on disentangling the effects of different types of experience (Dugdale et al. 2011; Lifjeld et al. 2011; Horie & Takagi 2012). However, because there is little consensus about how to study ARIRP, what proximate factors should be studied, which factors are generally most important across species, and how life-history theory informs predictions about the factors and ARIRP, it is difficult to draw conclusions from the current body of the literature. Furthermore, the literature features a wide variety of employed methodologies, with very few experimental studies. For example, studies examining the relationship between breeding experience, age, and performance may utilize a cross-sectional or longitudinal approach, define breeding experience in different ways, may or may not address potential covarying and confounding variables (such as site or mate fidelity), and employ different types of statistical analyses that may or may not account for repeated measures, random effects, or other statistical concerns. To generate more comparable and definitive datasets about the mechanisms related to ARIRP, a standardized approach to incorporate age into studies of behavior, conservation, and evolution is needed.

In light of these research needs, we here aim to (1) establish a framework to generate hypotheses for social and ecological influences on patterns of within-individual ARIRP with respect to the predominant proximate factors outlined in the literature: resource quality, previous experience at a site through site fidelity, mate-familiarity through mate fidelity, breeding experience, and an increased ability to attract mates (Table 1). We then (2) apply this framework to organize and synthesize the existing empirical literature in avian species as birds comprise the majority of

the empirical literature on age-related reproduction. Because life-history strategy influences the relative importance of a particular factor compared with others, we note whether the importance of each hypothesis likely interacts with lifespan, an important aspect of life-history strategy. For example, long-lived species typically benefit more from experience as they often have numerous opportunities for reproduction as compared to short-lived species (section 'Discussion').

By organizing the literature with respect to a diversity of relevant ecological and social factors, we are able to evaluate the current support and research needs for each potential mechanism underlying ARIRP. When possible, we suggest experimental approaches that can conclusively support or refute each hypothesis and, if several mechanisms are determined to be operating, how to estimate their relative contributions to patterns of ARIRP (section 'Experimental Tests and Teasing Apart Interacting Factors'), and include information for how frequentist and Bayesian statistical approaches can be used to test these hypotheses when confronted with longitudinal datasets (section 'Methodological and Statistical Approaches for Longitudinal DataSets', Fig. 1).

By delineating this framework for studying within-individual ARIRP and evaluating the abundant literature in avian species, we aim to (1) highlight research needs in regard to avian ARIRP so that more formal comparative studies may be possible and (2) set forth an experimental and statistical methodology for studying ARIRP across species.
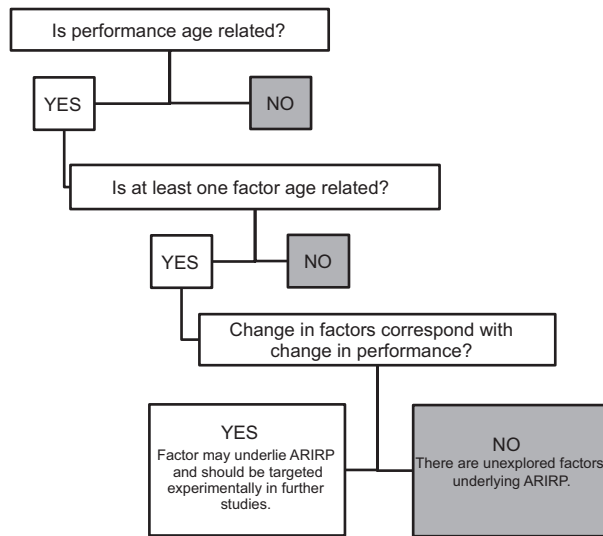
Methods

We compiled a database of published articles using a Web of Science search with the keywords: 'age-related; reproduction; reproductive performance; reproductive success,' for all papers published from 1900, the beginning of the indexing coverage of the Web of Science, through 2013. We define reproductive 'performance' or 'success' as measures of seasonal breeding success, including clutch size, hatching success, offspring production, and offspring survival. For species that exhibit extra-pair mating or do not form pair bonds, reproductive performance may be measured as total number of sired young or total number of successful fertilizations in a given breeding season or year.

There were three criteria for inclusion in our study: (1) each paper must include a test of at least one of the ecological and social factors in our framework (Table 1), (2) the test used by the study must measure

Table 1: Definitions, predictions, and their tests for hypotheses related to age-related reproductive performance. See Fig. 1 for statistical implementation scheme suggested for testing these factors

Hypothesis	Definition	Factor(s) to measure	Prediction	Ways to test
Resource Quality	Quality of territory, nest site, food	Food availability (Bunce et al. 2005) Predation risk (Pärt 2001) Nest site suitability (Horie & Takagi 2012)	Ability to obtain resources increases with age and predicts reproductive performance (RP)	Experimentally limit resources (Pärt 2001); older individuals should be better at obtaining them when compared to younger individuals. Alternatively, increase resource availability so that all ages have equal access (Williams & Christians 2003)
Site Fidelity	Returning to the same breeding site for consecutive years	Number of years an individual has returned to a site (Lombardo & Thorpe 2010)	Previous experiences (e.g., foraging and nest building) at a particular breeding location predict future success at that site; individuals increase site fidelity with age	Force breeding individuals to disperse at a time during the season in which individuals will not lose breeding experience (e.g., remove nest boxes, translocate individuals; Komdeur 1995) and compare to individuals who are site faithful; dispersed individuals should have lower performance when compared to same-aged site-faithful birds. Alternatively, consider 'natural experiments' resulting from habitat fragmentation.
Mate Fidelity	Mating with the same partner for consecutive years	Number of years individuals have bred together (Bradley et al. 1995)	Previous experience with the same mate predicts future success; individuals increase fidelity with age	Use translocations (Komdeur 1995) or mate removals (van de Pol 2006) to simulate a divorce scenario and compare same-age individuals that divorce and those that are allowed to remain mate-faithful; mate-faithful individuals should have higher performance when compared to same-aged divorced individuals.
Breeding Experience	Number of previous breeding experiences	Number of successful previous experiences mating or rearing offspring (Cichoň 2003)	Previous breeding experience predicts future success; individuals increase experience with age	Experimentally delay experience by simulating egg predation (Cichoň 2003) or temporarily preventing fertilization via 'anticopulation' rings (Michl et al. 2002) and compare delayed individuals with control individuals. Delayed birds should have decreased reproductive performance when compared to birds with breeding experience of the same age
Mate Attraction Cues	Age-related changes in an individual's ability to attract or compete for mates	Traits related to mate attraction (e.g., testes size, Laskemoen et al. 2008; ornament size Lifjeld et al. 2011; song characteristics, Poesel et al. 2006)	Traits change their expression over time, increasing attractiveness as a mate	Manipulate the phenotype of younger individuals to that of older individuals or manipulate older individuals to match that of younger members of the population. In either case, different-age birds with the same trait expression should have equivalent reproductive performance

Fig. 1: Methodological schematic for use with longitudinal data. Note that the process is stepwise, where the appropriateness of analyses is determined by the results from the previous step of analysis (see Section Methodological and Statistical Approaches for Longitudinal Data-Sets).

the importance of the factor with respect to reproductive performance, and (3) the study must feature at least one avian taxon. While there were many studies addressing age and reproduction, relatively few explicitly addressed within-individual improvements and their role in age-related reproduction. Among hundreds of studies that were reviewed, our selection process yielded 55 studies that were included in this synthesis. Of these studies, we found a mix of longitudinal (within-individual over time) and cross-sectional (cohort) studies concluding that there was support for within-individual improvement. Using a standardized template for data collection, we organized the following information from each study: whether the study was observational or experimental, species examined, number of years the researcher(s) had studied the population, factors that the researcher(s) considered, and which hypotheses were supported by their results (Table S1; section 'Discussion'). We also used several longevity databases (Australian Bird Study Association Data; Cornell Lab of Ornithology Birds of North America; Euring; Max Planck Institute for Demographic Research) and published studies (Zann 1996; Møller 2006; Richardson et al. 2007; Nisbet & Dann 2009; Schmoll et al. 2009; Wasser & Sherman 2010) to obtain information on the maximum recorded longevity in the wild per species. This enabled us to assess the potential role of different life-history strategies in the patterns of hypotheses proposed for ARIRP (section 'Discussion').

Below, in section 'Description of Social and Ecological Hypotheses', we describe factors proposed to influence ARIRP. While all factors are at a proximate level of analysis, they represent a mix of the most likely ecological, social, physiological, and behavioral traits that could contribute to ARIRP, as identified in the literature. Each of these factors is delineated as a hypothesis with testable predictions for empirical field studies and meta-analysis, when possible.

Description of Social and Ecological Hypotheses

Resource Quality

Definitions
'Resource quality' has been previously defined in terms of general resource availability in a location or year (Bunce et al. 2005), resource availability within an individual's territory (Ferrer & Bisson 2003), risk of predation in a territory (Pärt 2001), history of reproductive success in that territory (Penteriani et al. 2003), or time spent foraging (Reid 1988). Here, we define resource quality in terms of the relevant resources needed for reproduction in a territory, with the following categories: (1) the degree of predation in the defended area, measured by a survey of predator abundance in the area, the probability of predation, or diversity of predators relative to other individuals' territories in the population (Pärt 2001), (2) food availability, measured by food item abundance, or nutrient content of available food (Ferrer & Bisson 2003), and (3) suitability of nesting area for reproduction (e.g., degree of protection from climatic variation, Horie & Takagi 2012; number of nest parasites, Safran 2006).

Hypothesis and Predictions

We hypothesize that an individual's resource quality improves with age, and thereby underlies patterns of ARIRP, due to increased ability to both procure and defend resources necessary for reproduction (e.g., resulting from social dominance; Daunt et al. 1999; Pärt 2001). If resource quality underlies ARIRP, we predict that an individual holds successively and predictably higher quality territory with age, leading to increased reproductive performance. In a cross-sectional context, within a cohort of same-aged individuals, the quality of the acquired resource should be about the same within the cohort but have higher quality resource when compared to younger cohorts. Thus, when comparing age groups, older individuals will have higher resource quality, even with variation among individuals within a cohort.

Previous Investigations

Predictions of the resource quality hypothesis have been tested, but in very different contexts and rarely as a function of ARIRP. In eleven studies that investigated the role of resource quality in ARIRP, four studies used 'natural experiments' in which they compared old and young age groups in years with low food abundance and high food abundance; three of these four studies found that older individuals were able to breed successfully in low food abundance better than young individuals (Sydeman et al. 1991; Laaksonen et al. 2002; Bunce et al. 2005; but see Ratcliffe et al. 1998). While these population-level studies indicate that resource quality is age-related, they do not show a relationship between age-related differences in resource quality and age-related differences in reproduction, nor whether there are age-related improvements within individuals. To address this question, three studies used experimental manipulation, two of which supported a role for resource quality in ARIRP. In one of these studies, Pärt (2001) experimentally manipulated territory quality of nesting Wheatears (*Oenanthe oenanthe)* by changing the grass height – an important predictor of predation – between years. Within-individual, longitudinal analyses in these short-lived passerines showed that if territory quality was kept constant between years, there was no increase in reproductive performance; therefore, increases in reproductive performance were primarily due to age-related improvements in territory acquisition (see Daunt et al. 1999; Williams & Christians 2003).

Because there are generally few studies and even fewer manipulative experiments to shed light on the importance of resource quality on patterns of ARIRP, it is unclear whether resource quality is age-related (Table 2). There is also little evidence to suggest that the importance of resource quality is dependent on

life-history strategy (the hypothesis was supported both in long-lived species such as Bonelli's Eagle, *Hieraaetus fasciatus*, Penteriani et al. 2003; and short-lived species such as the Wheatear, Pärt 2001). We suggest additional experimental approaches using the methods suggested below and in sections 'Experimental Tests and Teasing Apart Interacting Factors' and 'Methodological and Statistical Approaches for Longitudinal DataSets' to determine the support for a role of changes in resource quality as a mechanism of ARIRP.

Challenges

Measurement of and definitions for resource quality are highly variable among researchers, making studies related to this factor difficult to compare. While the metrics that individual studies employ to quantify resource quality are, in many cases, appropriately reflective of the biology of those systems, researchers can define their study system's metric within the broad classifications of resource quality measures outlined in this review (e.g., 'grass field height' in the Wheatear translates to the predation risk category of resource quality (Pärt 2001), and can be defined as such to avoid confusion). In doing so, the literature will be more explicitly comparable despite the expected variation in actual metrics used to measure resource quality between species.

Site Fidelity

Definitions

'Site fidelity' has been most commonly defined as the number of years nesting in a particular location (e.g., 'local breeding experience,' Lombardo & Thorpe 2010; or 'prior residency,' Lozano & Lemon 1999). Here, we define site fidelity as the number of successive years an individual has spent in an area (i.e., a

Table 2: Summary of studies in database by hypothesis, including the number of studies investigating the hypothesis, the number, and percentage of studies that supported the hypothesis, the number of cross-sectional (*C*) and longitudinal (*L*) approaches taken by the studies. Note that a study may have taken both a cross-sectional and longitudinal approach. Average maximum lifespan recorded in years (MLR) of the studies addressing the hypothesis is also reported. Numerical study references are provided, which refer to the supplementary file references section

Hypothesis	No. studies	Supporting (no., %)	Study design (*C*, *L*)	Avg. MLR	Studies
Resource quality	11	6, 54.5	10, 2	28.4	8,11,14,21,22,37,38,42,43,47,54
Site fidelity	5	3, 60.0	4, 2	17.3	28,29,35,41,50
Mate fidelity	13	10, 76.9	11, 4	23.22	2,5,6,10,18,19,33,35,41,45,46,49,53
Breeding experience	26	18, 69.2	24, 9	20.01	2,4,6,9,10,12,13,15,16,20,22,23,27,30,32,34,35,36,40,41,44,51,52,54,55
Mate attraction	10	10, 100.0	10, 2	14.65	1,3,7,17,24,25,26,31,39,48

particular breeding location or one very close to it) during the breeding season. For species that do not breed every year or in which chick rearing takes longer than a year, a within-species standardized maximum value metric of site fidelity should be used. This definition does not rule out the confounding effects of other aspects of breeding experience, but see section 'Experimental Tests and Teasing Apart Interacting Factors' for particular methods to distinguish between types of experience.

Hypothesis and Predictions

We hypothesize that as an individual ages, it is more likely to use the same breeding site across breeding bouts, resulting in reproductive advantages for the individual such as familiarity with nesting areas, predator-avoidance strategies, and local climate. The benefits gained by site fidelity will be dictated by the spatial heterogeneity of the nesting areas, predators, and climate of the broader area that the population occupies. Individuals that return to or remain in the same nesting area from year to year should have greater reproductive performance (Lombardo & Thorpe 2010) compared with those that are forced to disperse away from their previous breeding locations during subsequent breeding attempts.

Previous Investigations

In the body of literature surveyed, five observational studies addressed site fidelity's role in ARIRP. Of these, four found that site fidelity is age-related, where older individuals tend to accumulate more experience at a site (this relationship was found for both long- and short-lived species; for example, Fulmar, *Fulmar glacialis*, Ollason & Dunnet 1978; Tree Swallow, *Tachycineta bicolor*, Lombardo & Thorpe 2010). However, the effect of site fidelity on ARIRP was not universal, where in long-lived species changes in nesting site (i.e., less site fidelity) were favored and tended to be adaptive, (i.e., changes in nest site are predicted by previous success or failure; e.g., female Lesser Snow Geese, *Chen caerulescens*, Rockwell et al. 1993; Lanyu Scops Owl, *Otus elegans*, Bai & Severinghaus 2012). In contrast, short-lived species tend to benefit from repeated experiences at a site (Tree Swallow, Lombardo & Thorpe 2010). However, the relationship between lifespan and the benefit of site fidelity may be driven by other life-history parameters such as the function of the breeding territory itself. For example, some species use the breeding area as an all-purpose territory, whereas in other

species, the breeding area contains only a nest location. Additionally, because all studies on this topic are observational, there are many probable confounding factors, such as concomitant mate fidelity and site fidelity, which warrants further experimental investigation into the role of site fidelity on ARIRP to establish both the overall age-relatedness of site fidelity and the life-history variation in its importance to ARIRP.

Challenges

The benefits of site fidelity have not been well-established experimentally. The only way to experimentally test this hypothesis, to our knowledge, is to perform translocations of individuals within same-age groups. Although translocations have been implemented successfully in some species (Komdeur 1995; Bell & George 2012), there are likely significant costs imposed by translocation other than those related to site unfamiliarity and requires that resource quality is controlled for between the original and translocated sites. It is also important to standardize and/or control for mate status of translocated individuals, categorized as unpaired, paired but translocated without their mate, or paired and translocated with their mate (see '*Mate Fidelity*' below, section 'Experimental Tests and Teasing Apart Interacting Factors'). Additionally, for species that breed in discrete locations, such as nest cavities or boxes, it might be possible to experimentally manipulate the ability to return to the same breeding location. In such species, the scale over which the dispersion is forced will influence whether or not the translocation and thus site fidelity impacts reproductive success. Therefore, studies should determine the relevant scale over which a translocation should be carried out, which could be found by comparing reproductive performance between locations while controlling for individual differences as a proxy for site differences. For large-scale study populations, researchers should look out for 'natural experiment' opportunities, which may influence return rates, such as new development or habitat fragmentation which may lead to an individual needing to move to a new breeding location.

Mate Fidelity

Definitions

Mate fidelity is understood as an individual repetitively mating with an individual across breeding seasons or years (Bradley et al. 1990; Nisbet & Dann 2009). There are many potential benefits to remating

with the same individual, which may differ across mating systems, such as coordination of parental duties (Ens et al. 1993), decreased mate-search effort, and earlier breeding times. The alternative to mate fidelity is divorce or mating alternatively, where both individuals survive for another breeding season and are present in the population yet pair or mate with different individuals (Bradley et al. 1990). We assume that mate loss is not a true alternative to mate fidelity, as there is no individual choice involved with a mate's death.

Hypothesis and Predictions

We hypothesize that mate fidelity across consecutive breeding seasons is beneficial to reproductive performance due to advanced breeding times, decreased search effort, or coordination of parental duties (Bradley et al. 1995). We predict that individuals are more likely to be faithful to their mates as they age and that faithful individuals have higher reproductive performance, and is thus implicated in ARIRP. However, it might be important to take into account that members of the pair bond are not the same age and are senescing at different rates, which could lead to adaptive patterns of divorce or pair-bond maintenance.

Previous Investigations

Of thirteen studies of this hypothesis, nine found that some degree of mate fidelity benefited reproductive performance (Table 2). In short-lived species, such as the Barn Swallow, *Hirundo rustica*, mate fidelity was implicated in patterns of ARIRP (Balbontín et al. 2007). In long-lived species, mate fidelity is beneficial for reproductive performance, but only up to a point, after which mate fidelity leads to a decline in reproduction (e.g., Short-tailed Shear Water, *Puffinus tenuirostris*, Bradley et al. 1990, Cassin's Auklet, *Ptychoramphus aleuticus*, Pyle et al. 2001). However, only two of the eleven studies (both in long-lived species) teased apart the effect of breeding experience and mate fidelity using experimental and statistical approaches. For example, van de Pol (2006) examined pair-bond duration in the monogamous Eurasian Oystercatcher (*Haematopus ostralegus*) by experimentally removing the mate (the sex of the removed mate was determined randomly) of 20 randomly chosen pairs and then tracking the remaining mates of those pairs for the following 4 yr. They found that although the pairs had the same number of breeding experiences as pairs that remained together and were the same age, individuals that formed a new pair-bond had decreased

egg survival and later breeding compared with those with intact pair-bonds in the year following the experiment. The results of this elegant experiment suggest that mate fidelity has a positive effect on reproductive performance in a monogamous long-lived species and highlight the need for further study to determine the effect of life-history variation in mate fidelity and ARIRP, especially across a greater diversity of mating systems.

Challenges

Because mate fidelity often covaries with other factors, such as site fidelity or breeding experience, confounding variables are a challenge (Naves et al. 2007). While multivariate models can account for many of these issues (see section 'Methodological and Statistical Approaches for Longitudinal DataSets'), sample sizes may prohibit their application. In these circumstances, homogenous comparison groups should be made in terms of age group or breeding experience accumulated before estimating the effect of mate fidelity (Naves et al. 2007).

For experimental studies, the mate removal protocol developed by van de Pol (2006) will allow researchers to control for covarying factors and isolate the effects of mate fidelity, although this is certainly not feasible in all study systems. In those cases, longitudinal analyses are recommended (see section 'Methodological and Statistical Approaches for Longitudinal DataSets').

Breeding Experience

Definitions

Breeding experience is the most widely studied factor in analyses related to ARIRP. Yet, there are many ways in which breeding experience is defined, including the number of successful breeding attempts accumulated until current reproductive effort (Blas et al. 2009), total breeding attempts (Limmer & Becker 2010), number of breeding partners (Bradley et al. 1990), or whether an individual has parental experience as a helper though not a breeder (Komdeur 1995). Here, we simply define breeding experience as the number of years that an individual successfully mates (relevant in sexes or species that do not participate in raising chicks), rears young to independence, or has experience with parental care either as a parent or as a helper (i.e., in cooperatively breeding species). The definitions of parental care may be more or less inclusive of all the stages of the production of offspring, including incubation duties as well as feeding

young after hatching as breeding experience can be gained at any of these stages.

Hypothesis and Predictions

The breeding experience hypothesis states that an individual's increasing ability to successfully mate, care for and provision young, build nests, and defend nests underlies patterns of ARIRP (Komdeur 1995; Horie & Takagi 2012). We predict that by having previous experiences, whether as a successful mate, parent, or cooperative breeder, individuals will have higher reproductive performance than individuals who do not have prior breeding experience. Accordingly, when an individual is kept from gaining additional experiences and breeding experience is held constant, individuals should not show patterns of ARIRP over time (see section 'Experimental Tests and Teasing Apart Interacting Factors' for suggestions in implementing this approach experimentally). For studies able to employ longitudinal analyses, a primary prediction is that among individuals similar in age yet variable in accrued experience, those with greater breeding experience should have higher reproductive performance than those with less experience (van de Pol 2006).

Previous Investigations

Breeding experience is both the most studied and most supported factor in studies of ARIRP (Table 2); of 26 studies, 18 supported a positive role of breeding experience in age-related reproductive performance. Many of these studies featured long-lived species (13 of the 18 studies; e.g., Kittiwake, *Rissa tridactyla*, Desprez et al. 2011; Common Tern, *Sterna hirundo*, Limmer & Becker 2010). Although short-lived species are less studied with regard to this factor, there appears to be a general positive effect of breeding experience on reproduction (seven of the 20 studies; e.g., Collared Flycatcher, *Ficedula albicollis*, Cinchoñ 2003, Seychelles Warbler, *Acrocephalus sechellensis*, Komdeur 1995). It is important to note that very few of the studies in both long- and short-lived species teased apart confounding factors, such as mate fidelity and site fidelity. Of the 26 studies, only four experimentally manipulated breeding experience, all with short-lived species, three of which supported a positive effect of breeding experience (Collared Flycatcher, Pärt 1995 and Cinchoñ 2003; Seychelles Warbler, Komdeur 1995) and one that did not (Zebra Finch, *Taeniopygia guttata*, Williams & Christians 2003); see section 'Experimental Tests and Teasing

Apart Interacting Factors' for experimental approaches.

Challenges

The evidence for the breeding experience hypothesis is robust (i.e., the age-related accumulation of breeding experiences appear to improve reproductive performance; see Table 2). However, studies that partition breeding experience from the benefits acquired from mate and site fidelities with age are difficult to perform, as finding adequate experimental methods to test the breeding experience hypothesis can be difficult (see section 'Experimental Tests and Teasing Apart Interacting Factors' for possible avenues to prevent acquisition of breeding experience). In species that cooperatively breed, helpers with different degrees of helping experience may also be compared (e.g., Western Bluebird, *Sialia mexicana*; Guinan et al. 2008). Life-history theory predicts that breeding experience should operate differently in short- versus long-lived species, where long-lived species benefit from experiences across their lifetime up until a peak of reproductive performance and short-lived species improve after initial experience but do not benefit from experience thereafter. Therefore, first teasing apart breeding experience from other factors is extremely important to generate data for more formal analysis of the effect of life-history strategy on the importance of breeding experience.

Mate Attraction Cues

Definitions

Mate attraction cues in the context of ARIRP include traits obtained after subadult growth has been completed, including primary sexual traits, such as testes size (Laskemoen et al. 2008) and secondary sexual traits implicated in courtship and mate selection, such as feather iridescence (Komdeur 2005) or song characteristics (Poesel et al. 2006). Often these traits are underlaid by changes in reproductive physiology via hormones such as prolactin or testosterone. Here, we define the mate attraction cue as any physiological (e.g., concentrations of reproductive hormones), morphological (e.g., feather color), or behavioral (e.g., acoustic signals) trait that influences mating success, via inter- and intrasexual selection.

Hypothesis and Predictions

The mate attraction cue hypothesis states that the ability to attract or compete for access to mates

changes over time, such that individuals improve reproductive performance up to a point of senescence. This hypothesis predicts that older individuals have higher reproductive performance due to these age-related changes in traits related to mate attraction.

Previous Investigations

While this factor has been well studied in the sexual selection literature (Lifjeld et al. 2011), there are few studies that specifically address how age-related changes in mate attraction cues influence ARIRP relative to the other social and ecological hypotheses. Ten studies addressed the role of changing mate attraction in ARIRP, and all found that age, a trait related to mate attraction, and reproductive performance were intercorrelated. For example, Budden & Dickinson (2009) investigated the role of blue and rufous patches in male Western Bluebirds and found that males with brighter plumage patches were older and in better condition, producing more fledglings compared with younger males (also see Komdeur 2005; Alonso et al. 2010; Freeman-Gallant et al. 2010). Generally, most studies feature short-lived species (nine of 10 studies featured short-lived species such as the Barn Swallow, Lifjeld et al. 2011) and the Blue Tit, *Cyanistes caeruleus* (Poesel et al. 2006). However, one study on long-lived species found support for the mate attraction hypothesis via increases in body size (Great Bustard, *Otis tarda*; Alonso et al. 2010). While the unanimous support for this hypothesis is compelling, few of the ten studies utilize within-individual analyses or models that eliminate confounding variables that may be driving the effect (Table 2). Therefore, it remains unclear whether there are tangible within-individual changes over time and whether mate attraction cue changes underlie patterns of ARIRP (section 'Experimental Tests and Teasing Apart Interacting Factors'; Table 1).

Challenges

Although mate attraction has generally been well studied and well characterized in the sexual selection literature, there is little formal study of the mate attraction hypothesis in an ARIRP context. As a result, there are relatively few studies that investigate this hypothesis in concert with other hypotheses or that control for other age-related factors, as detailed in this review. Additionally, quantification of some mate attraction traits, such as testes size, requires destructive or invasive sampling, which is prohibitive for the large sample sizes required for within-individual

analyses. However, cross-sectional studies of ARIRP are acceptable when appropriate controls are utilized (Naves et al. 2007).

Experimental Tests and Teasing Apart Interacting Factors

After outlining and reviewing the research available for each hypothesis, we offer several experimental tests for teasing them apart (Table 1). To maximize the insights produced by experimental tests in any system, correlations between each factor and reproductive performance should be investigated (using predicted associations in Table 1 and scheme presented in Fig. 1). However, because many of these factors may covary (e.g., mate and site fidelity), we provide additional discussion on potential experimental tests to distinguish between these potentially interactive hypotheses, as well as correlational approaches for longitudinal analyses (although statistical analyses are discussed in more detail in section 'Methodological and Statistical Approaches for Longitudinal Data-Sets'). While the interacting factors are presented in this section as competing, it is possible that the factors may be simultaneously acting in ARIRP. In these cases, we suggest estimating effect sizes of the relative contributions of each factor to patterns of ARIRP.

Mate and Site Fidelity

The mate and site fidelity hypotheses may be difficult to tease apart because mate fidelity is often driven by site fidelity (Dubois & Cézilly 2002). To differentiate between site fidelity driven mate fidelity and independent mate- and site-fidelities, Llambías et al. (2008) utilized a multistep correlational approach, in which they determined (1) the extent to which mate fidelity impacted reproductive performance in successive years for Tree Swallows, (2) whether breeding success increased with a new mate, and (3) if mate retention rates were lowest in the cohorts that showed the lowest site fidelity (i.e., young females). Because they found that mate fidelity had no impact on breeding success, and mate fidelity was lowest in cohorts that displayed low site fidelity, Llambías et al. (2008) concluded that mate fidelity was indeed driven by site fidelity. This approach can also be adopted experimentally. For example, the Eastern Bluebird *(Sialia sialis)*, which nests in the same nest box repeatedly from season to season (Gowaty & Plissner 1998), could be used in an experiment in which the effects of mate fidelity and site fidelity are partitioned. In an area where researchers have access to two

meta-populations that are sufficiently far apart, one population can be forced to relocate by removing nest boxes and blocking access to natural cavities. If a primary benefit to site fidelity in this species is conservation of energy via avoiding costly territorial interactions when settling in the new location, it would be sufficient to simply set up new nest boxes for the relocating meta-population in their current area to create these disputes, representing the cost of relocation. For the mate fidelity component of the experiment, mate removals can be performed in both populations following van de Pol (2006). In this way, four treatment groups are created: relocated and mate removed; relocated and mate remains; site undisturbed and mate removed; and undisturbed and mate remains. The relative influence of each effect can be estimated by the differences between each treatment group; if site or mate fidelity has a dominant effect, individuals with that fidelity will have the greatest performance regardless of their fidelity in the other category. Because average meta-population fecundity is a potential confounding variable, populations should be monitored prior to the experiment to determine baseline reproduction (i.e., average reproduction and variance in reproduction across multiple years, assuming that there is variation between years). Differences in baseline reproduction can be accounted for using statistical controls, which are possible in mixed models (see section 'Methodological and Statistical Approaches for Longitudinal DataSets'). Additionally, the populations should be monitored over time to determine the duration of the effect of the mate removal (*sensu* van de Pol 2006) and site relocation.

Mate Fidelity and Breeding Experience

As the duration of mate fidelity is usually a strong predictor of breeding experience (Komdeur 1995), these two hypotheses may be highly correlated and thus difficult to discriminate between. With a longitudinal dataset, the correlative approach adopted by Naves et al. (2007) may prove useful, where homogenous comparison groups are made, such that, for example, comparisons to evaluate mate fidelity are made between individuals that are the same age and have the same amount of breeding experience. This approach can also be utilized experimentally, such as the experiment conducted by Komdeur (1995) to examine breeding experience in the cooperatively breeding in the Seychelles Warbler by comparing same-aged individuals with and without helping experience their first year of reproduction. However, molecular analyses must be used to

verify that helping individuals are not cobreeders, as was determined of some Seychelles Warbler helpers in a later study (Komdeur & Richardson 2007). Other cooperative breeders and possible experimental species to tease apart these hypotheses include the Western Bluebird, the Brown Headed Nuthatch (*Sitta pusilla*; Slater et al. 2013) and the Bushtit (*Psaltriparus minimus*; Sloane 2001). In a species without cooperative breeding, this approach may be taken by preventing a pair from gaining breeding experience (e.g., anticopulatory rings for the males, where a rubber ring is attached to the cloacal protuberance (Michl et al. 2002; White et al. 2008) and egg removal with plastic egg replacement (Cichoň 2003) and compare the inexperienced birds with experienced birds in the second year of reproduction. However, this experiment depends on an informed knowledge of the salient aspects of breeding experience, which as noted in the breeding experience section, may include a broad range of behaviors (e.g., incubation or territory defense). For this experiment to be successful in bird species that exhibit extra-pair mating, both the anticopulatory ring (described above, or other method of restricting fertilization such as removing the gonads or ovaries, *sensu* Cox et al. 2009) and plastic egg replacement must be used. Although the male is unable to fertilize his mate's eggs, other males may not be under the same treatment and extra-pair fertilization is likely to occur. Thus, eggs should be removed so they do not hatch. Plastic eggs should be used to replace the clutch, as the removal of the eggs will be perceived as predation and will typically induce females to initiate replacement clutches (Safran et al. 2005).

Methodological and Statistical Approaches for Longitudinal DataSets

One of the reasons for the increasing number of studies on ARIRP is the prevalence of extensive longitudinal datasets, especially for bird populations that have been sampled for many years. The convenience of utilizing existing datasets is important to note, and as such we suggest practical statistical solutions to performing comparable studies with these datasets.

Here, we emphasize the importance of distinguishing between population-level and within-individual analyses. There is evidence suggesting that, in some species, associations between age and improved reproductive performance are due to the progressive disappearance of inferior phenotypes, not because of within-individual ARIRP (presented as competing

hypotheses in Forslund & Pärt 1995; also see Bowen et al. 2006; van de Pol & Verhulst 2006; Brown & Roth 2009). Therefore, cross-sectional analyses will not always yield an accurate representation of the relationship between age, factor, and reproductive performance (as discussed in the *Previous Investigations* for each factor above; van de Pol & Verhulst 2006). Longitudinal data are thus a pre-requisite to understanding within-individual ARIRP (van de Pol 2006; van de Pol & Verhulst 2006).

Prior to directly analyzing relationships between factors and reproductive performance, preliminary stepwise analyses must be conducted to determine first whether there is ARIRP in the population (Step 1, Fig. 1). To ensure that within-individual change is being measured, data should be collapsed into 'change' in performance or factor between two time points; for example, to find whether within-individual ARIRP exists in a population, model the change in performance as predicted by the change in age. If the change in performance for an age group is significantly different than zero, after standardizing baseline performance, then individuals on average change performance over time, and there is evidence for ARIRP. Likewise, if rates of change in performance are significantly different between groups, ARIRP is likely to occur in the population. Standardizing baseline performance may be performed simply by including 'year' as a random effect in a mixed model (discussed in more detail below) or using a Z transformation for each year, where each sample is standardized by the mean for the year.

If there is ARIRP in the population, then age-relatedness of factors should be determined in the same way as described above with regard to 'change' in the factor modeled by change in age (Step 2, Fig. 1). Only factors that are age-related can be examined with regard to ARIRP in Step 3 of the stepwise analysis (Step 3, Fig. 1), in which the change in reproductive performance and each age-related factor are explicitly analyzed. Significant associations indicate that this factor may underlie ARIRP and should be targeted in the future with experimental approaches (Fig. 1). There may also be multiple factors that contribute to ARIRP. In these cases, as noted in section 'Experimental Tests and Teasing Apart Interacting Factors', we suggest estimating effect sizes to determine the relative contribution of each factor. Below, we present two possible ways to perform the stepwise analysis that allow flexibility for differing data structures and confounding variables common to longitudinal datasets (e.g., differences between sampling sites or years, repeated measures).

General Linear Mixed Models

General linear mixed models (GLMMs) are increasingly popular in the literature (Bolker et al. 2009) and are excellent tools to analyze ARIRP. GLMMs accommodate random effects (i.e., the variation due to measurable differences in sampling sites or years) before estimating the effect of fixed variables (e.g., pair status or site familiarity) on reproductive performance. With these models, one can then isolate the effect of the factor of interest on reproductive performance, while controlling for so-called nuisance variables (e.g., change in reproductive performance predicted by change in factor, controlling for differences between individuals, sites, and years; this approach can be applied to Steps 1–3). While GLMMs by default determine a linear relationship between the fixed and response variables, curvilinear and interactive terms can be specified in the model using syntax appropriate to the statistical environment (Zuur et al. 2009, 2012; Crawley 2012).

These models allow for categorical and continuous fixed effects; this flexibility is convenient as some factors are continuous, such as morphological measurements, and other are categorical, such as whether a bird re-mated with the same individual. The distribution from which the response variable is drawn can be specified with GLMMs, (e.g., Gaussian, Zero-inflated, Poisson, and Binomial distributions), along with the link functions appropriate for the data (e.g., logit or probit links) and the structure of the random effects. Information for applying these techniques can be found for multiple statistical environments (Bolker et al. 2009; Zuur et al. 2009, 2012) and is increasingly featured in statistical and ecological literature.

Bayesian Approaches

While GLMMs are very useful and relatively easy to implement, they do not allow analyses to incorporate prior information and are dependent on large sample sizes (Kéry 2010). Additionally, in Bayesian approaches, analyses do not merely yield point estimates, but posterior distributions of the variables of interest are generated, including distributions of variables such as change in performance (Step 1, Fig. 1), change in factors (Step 2, Fig. 1), and the covariance of change in performance and change in factors (Step 3, Fig. 1). These posterior distributions are generated by 'updating' a prior distribution, which may range from an uninformative prior distribution (i.e., uniform) to a more informative distribution, which is

based on previous information or biological constraints (e.g., positive values only).

For example, when considering Step 1 in ARIRP (Fig. 1), in which the relationship between change in age and change in performance is determined, a Bayesian approach could be implemented as follows: (1) specify the model, where each observation of the change in performance [y] is modeled by a simple linear equation with an intercept, slope, change in age [x], and error. The complexity of the model can be increased by adding additional predictors and random effects. (2) Next, prior distributions for the intercepts, slopes, and properties of the distribution of the y variable are specified. Values for these may be found in published studies or preliminary data (e.g., for average change in performance [y] found in a previous study, the prior distribution may be described by a normal distribution with mean $\bar{x}$ and standard deviation σ.) (3) Lastly, this information is incorporated into a likelihood function that compares the collected data to simulated data over a range of variable values. This process produces a posterior distribution of values for each variable in the model. For the purposes of Step 1 (Fig. 1), these posterior distributions measure the mean relationship between change in age and change in performance (slope), whether the change in performance was tangible (i.e., if the credible interval does not include zero), and other derived quantities that can be built into the likelihood function.

These analyses can be conducted in several programs, such as WinBUGS, an R-compatible interface for Bayesian analysis, which has several accessible accompanying texts (Bolker et al. 2009; Kéry 2010.). While this approach relies on the explicit expression of the model and appropriate prior distributions, there are many benefits to conducting Bayesian analysis. These benefits include the ability to incorporate previous information via prior distributions, the generation of posterior distributions instead of point estimates, and adequacy of small samples, making Bayesian approaches an important, albeit thus far underutilized, tool for analyzing the dynamics of ARIRP.

Discussion

Across disparate taxa, empirical data reveal a pattern in which individuals increase in reproductive performance as they age, up to a point of senescence, although the rate of this increase and the timing of the onset of senescence varies across species (Roff 1992). Studies related to the proximate underpinnings of age-related reproductive performance are increasing in the literature, yet there is no unified framework in which

to explore these patterns. Here, we present a framework of hypotheses for testing the relative importance of social and ecological factors on patterns of ARIRP, which we then apply to organize the current literature on ARIRP in avian taxa. Using this approach, we identify the many potential confounding variables present in the literature and suggest experimental field studies and statistical approaches that will reduce or eliminate these difficulties, enabling researchers to distinguish which factors may contribute to ARIRP.

In the studies we reviewed, there were some hypotheses that have been investigated extensively (breeding experience, mate fidelity) and others that have not (resource quality, site fidelity, mate attraction; also see Table 2). This may be because the hypotheses have not been defined clearly with experimental designs and methods that allow them to be tested in a broad group of organisms. Additionally, some hypotheses (e.g., mate attraction and resource quality) are more difficult to adequately address in some study systems because they depend on well-characterized natural history of the species, as well as large amounts of difficult-to-obtain data (e.g., quantifying patterns of morphological change over time may be considerably more difficult than counting the number of years of prior breeding experience). Despite the disparity in the number of publications between hypotheses, most studies found supporting evidence for the hypothesis in question (all hypotheses each received support from at least half of the studies we reviewed; see Table 2), which may indicate that the factors are all important, but may reflect a publication bias or artefactual collinearity between factors for studies collecting data on only one factor in the ARIRP framework. By studying factors in combination, the likelihood of reporting a false positive for a particular factor's role in ARIRP decreases and also allows estimation of effect sizes among age-related factors. If published studies employ this framework and test factors in combination, greater resolution on ARIRP will be gained and a broader, more formal analysis may be possible. It is also important to note that sample sizes are often low in these analyses, as measuring an individual across multiple years for multiple variables is a challenge. In these cases, which comprise a significant portion of studies of ARIRP, caution in interpretation and use of statistical inference should be exercised.

There are also fascinating patterns that remain to be explored with respect to variation in lifespan. Life history predicts that lifespan is related to the probability of extrinsic mortality, where short-lived species face a higher probability of mortality from factors such as

predation or starvation, and long-lived species experience less risk of mortality (Austad & Fischer 1991). Therefore, for short-lived species, individuals are predicted to begin breeding earlier in life and become competent breeders quickly, compared with long-lived species. When considering ARIRP, this indicates that the benefit of experiences for short- versus long-lived species will differ, where short-lived species benefit from experiences early in life but not later, and long-lived species benefit from experience throughout life (Lombardo & Thorpe 2010).

For example, in the studies included in this review, the influence of mate fidelity in generating patterns of ARIRP has been studied in both long- and short-lived avian species, but seems to benefit only long-lived avian species. There are also some factors that have been exclusively addressed in either long- or short-lived species; mate attraction and its role in ARIRP has been primarily considered in short-lived species, whereas the influence of resource quality on ARIRP has only been robustly studied in long-lived species. While this review is restricted to avian species, our findings regarding life-history variation and ARIRP and consideration of the ARIRP literature across more diverse taxa suggests that the viability and prediction of a given hypothesis varies by life-history strategy. For example, female Grey Seals *Halichoerus grypus*, which live to approximately 40 years of age, tend to increase the weight of their pups (an important indicator of survivorship) with each episode of breeding experience (Bowen et al. 2006). In contrast, in the European Corn Borer, *Ostrinia nubilalis*, which lives only for a few days, females suffer decreased lifetime fecundity and longevity when mating with males that have previous mating experience (Milonas et al. 2011). Comparing these markedly different species caricatures how breeding experience can impact patterns of ARIRP differently by life-history strategy. In this example, long-lived species benefit from experiences, while short-lived species that breed maximally for a short time will not benefit from increased experience. Life-history strategy also dictates which hypotheses may underlie ARIRP. For example, the mate attraction hypothesis must be considered when evaluating patterns of male ARIRP in African Elephants (*Loxodonta africana*; Hollister-Smith et al. 2007). Because females group independently from males, males must expend energy in mate-search efforts (Hollister-Smith et al. 2007). The search effort is mediated by the age-related expression and duration of musth, the period of increased testosterone, aggression and sexual activity, making the mate attraction hypothesis of primary interest when considering ARIRP (as

considered in Hollister-Smith et al. 2007). Despite this fascinating variation in factors' directionality of effect on ARIRP and the relative relevance of a particular factor, the intersection of life history and ARIRP remains understudied but is an exciting avenue of inquiry.

While investigations on the proximate predictors of age-related performance are in their early stages, the information that they may reveal will have broad implications and applications in other fields. For example, the role of age on ornamentation may be underestimated in sexual selection, given the preliminary evidence that mate attraction is not only individual-dependent, but also age-dependent (e.g., Barn Swallow, Lifjeld et al. 2011; Bighorn Rams, *Ovis canadensis*, Coltman et al. 2002; Jamaican Field Crickets, *Gryllus assimilis*, Bertram & Rook 2011). While a particular trait related to mate attraction within a species will reflect individual variation, there are measurable differences in these traits after subadult growth has been completed that are due to age. These differences can be accounted for by controlling for age in experiments (Freeman-Gallant et al. 2010; Lifjeld et al. 2011). By examining these proximate factors, morphological variation can be partitioned by age- and condition dependence, which may explain signal content of these sexual signals, as well as inform our understanding of how selection is acting on the signals (Freeman-Gallant et al. 2010; Evans et al. 2011). In order to ensure that progress continues to be made in understanding ARIRP, future research efforts should consider multiple ARIRP hypotheses, control for confounding variables via statistical tools, and utilize experimental methodologies to support longitudinal study findings.

Acknowledgements

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Supporting Information

Additional supporting information may be found in the online version of this article at the publisher's web-site:

Table S1: Database of species studied and findings in the 55 studies examined.