AGE-DEPENDENCE AND INDIVIDUAL HETEROGENEITY IN REPRODUCTIVE SUCCESS OF GREATER SAGE-GROUSE

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ABSTRACT

Research on iteroparous species has shown that reproductive success may increase with age until the onset of senescence. However, from the population perspective, increased reproductive success with age could be a consequence of within-individual variation (e.g., ageing, breeding experience, foraging ability hypotheses), between-individual variation (e.g, individual heterogeneity, frailty, selection, delayed breeding hypotheses), or a combination thereof. We evaluated within- and between-individual variation in reproductive success of greater sage-grouse (*Centrocercus urophasianus*; sage-grouse), a galliforme of conservation concern throughout western North America. We monitored female reproductive activity from 1998–2010 and used generalized linear mixed models incorporating within-subject centering to evaluate and separate within- and between-individual effects. We detected positive effects of within-individual variation on nest initiation and success where ageing increased the likelihood of both parameters, which appears to support the breeding experience and/or foraging ability hypotheses. However, nest initiation was also affected by between-individual variation whereby the likelihood of initiation was higher for individuals with higher mean age (i.e., survived longer), as is predicted by the frailty and selection hypotheses. Our results indicate both within- and between-individual variation affect reproductive output of sage-grouse, but the effects of each varied by measure of reproductive output. Our results corroborate previous findings that suggest population age parameters (i.e., cross-sectional) should be interpreted with caution due to potential entanglement of within- and between-individual processes. Moreover, the relative role and strength of within- and between-individual processes appeared to vary by measure of reproductive output in our results, which further

emphasizes the need for longitudinal analysis of age effects, even in relatively short-lived iteroparous animals, to adequately interpret biological processes.

KEY WORDS *Centrocercus urophasianus*, frailty hypothesis, generalized linear mixed model, greater sage-grouse, phenotypic plasticity, selection hypothesis, within-subject centering.

INTRODUCTION

Age is an important biological parameter and has received considerable attention in models of survival and reproduction for many species (e.g., Rockwell et al. 1993; Robertson et al. 1994, Blomqvist et al. 1997; Angelier et al. 2007; Low et al. 2007). Positive effects of age on reproduction (Forslund and Pärt 1995) and survival (Martin 1995) are common for avian taxa, until the onset of senescence when reproductive success declines in some species (e.g., Rockwell et al. 1993). Numerous hypotheses have been proposed to explain age related variation in survival and reproduction (see Forslund and Pärt 1995), which can be more broadly categorized as the result of within-individual processes (e.g., ageing, breeding experience, foraging ability hypotheses) or between-individual processes (e.g, individual heterogeneity, frailty, selection, delayed breeding hypotheses). Age-specific variation in life history traits can be obscured by individual heterogeneity, whereby observed population-level patterns result from hidden processes specific to subpopulations (Cam and Monnat 2000) or a latent distribution in individual quality. Consequently, population-level age effects may confound within- and between-individual effects and can thereby represent individual heterogeneity effects rather than changes within individuals. For example, subpopulation effects can appear to be the result of the age of individuals within the population when less fit individuals are frail and regularly exit the population earlier (i.e., have higher mortality rates) than less frail individuals (i.e., frailty hypothesis: Vaupel et al. 1979; Vaupel and Yashin 1985). This process has also been referred to as the selection hypothesis (Forslund and Pärt 1995). In avian taxa, individual heterogeneity in reproductive output and cost of reproduction appears common (e.g., Aubry et al. 2009; Aubry et al. 2011; Cam et al. 2013; Caudill et al. 2014). As such, within- and between-

individual effects should be separated to accurately assess the effect(s) of age, and the hypotheses contained therein (e.g., breeding experience, selection, delayed breeding, frailty hypotheses).

Greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) are sagebrush (*Artemisia* spp.) dependent galliformes (Patterson 1952; Dalke et al. 1963; Zablen et al. 2003; Connelly et al. 2011) of conservation concern throughout their endemic range due to habitat loss/degradation and subsequent population declines (Connelly et al. 2004; Schroeder et al. 2004; Connelly et al 2011; Garton et al. 2011; Miller et al. 2011). Numerous studies on sage-grouse report age as an important parameter for both survival and reproduction (e.g., Connelly et al. 1993; Zablan et al. 2003; Gregg et al. 2006; Davis et al. 2014; see Connelly et al. 2011). However, most studies on sage-grouse, as well as various other species, implicitly incorporate both within- and between-individual effects of age, but interpret the parameter as though only within-individual effects (e.g., ageing) are present. When support is assumed for only one of the hypotheses entangled in age parameters (e.g., ageing), conclusions and resulting predictions could be misguided, because competing hypotheses (e.g., individual heterogeneity) are left unaccounted for. Accurate knowledge of population regulation and ecology is imperative to maximize the fectiveness of management actions on species conservation, particularly for declining species.

The purpose of our research was to estimate within- and between-individual effects of age on greater sage-grouse reproductive success. We hypothesize: 1) Within-individual effects of age are positively related to reproductive success (e.g., ageing, breeding experience, foraging ability hypotheses); 2) Between-individual effects exist in nest and

brood success (i.e., individual heterogeneity, selection, frailty hypotheses). We did not hypothesize individual heterogeneity for nest initiation, because previous research has indicated that sage-grouse, in our system, enter the breeding season with adequate resources to attempt reproduction (i.e., Caudill et al. 2014).

METHODS

Habitat

Our study was conducted in south-central Utah on Parker Mountain, a high elevation plateau (2,200–3,000 m) which lies at the southern extent of the sage-grouse range (Schroeder et al. 2004). Parker Mountain is typified by 65–80 frost-free days per year and annual precipitation totals of 40–50 cm, predominately as snow (60%) during the dormant season (Jaynes 1982). Vegetation across the site is predominantly mountain big sagebrush (*Artemisia tridentate tridentate*) in swales and black sagebrush (*A. nova*) on ridges. Limited quaking aspen (*Populus tremuloides*) and pinyon pine/juniper (*Pinus edulis/Juniperus* spp.) stands occur at higher and lower elevation sites, respectively.

Field methods

We captured female sage-grouse at roost sites proximal to breeding grounds (i.e., leks) using spotlights and long handled nets (Giesen et al. 1982; Wakkinen et al. 1992) during March and April 1998–2009. Individuals were fitted with 15–19g necklace-style radio transmitters (Advanced Telemetry Systems, Isanti, MN, USA 1998–2004; Holohil Systems, Carp, Ontario, Canada in 2005–2009). Females were classified as second year (SY) or after second year (ASY) based on wing characteristics (Beck et al. 1975) and condition of the outer primaries (Dalke et al. 1963). Beginning in May, radio marked females were located at least once every 5 days to document the onset of incubation. Hens were not

intentionally flushed due to the species' propensity to abandon nests if disturbed (Holloran et al. 2005; Baxter et al. 2008). Nesting was confirmed visually and status was checked every 1–2 days to determine fate. Broods were monitored using two techniques dependent upon year. From 1998–2004 and in 2010, radio marked brood hens were located every 3 days to determine brood fate, and non-brood hens were located every 5 to 7 days. From 2005–2009 chicks of radio marked hens were marked with 1.5 g backpack-style radio transmitters (Advanced Telemetry Systems, Insanti, MN, USA in 2005; Holohil Systems, Carp, Ontario, Canada in 2006-2008; American Wildlife Enterprises, Monticello, FL, USA in 2009). In these years, broods were captured within 1 week of hatch (most within 48 hours of hatch), transmitters were attached with 2 sutures (Burkepile et al. 2002), and chicks were located every other day. Broods success, regardless of monitoring technique, was measured using direct observations and apparent success.

Analysis

To isolate the effect of female age on reproductive parameters we subset the data to only include known-age individuals (i.e., SY at capture). We used generalized linear mixed models implemented with the "glmer" function from the lme4 package (Bates et al. 2014) in program R 3.1.1 (R Core Team 2014) for all analyses. We used within-subject centering (see also within-group centering) to separate within-subject (i.e., individual) from between-subject effects (van de Pol and Wright 2009). We applied each of the three models outlined by van de Pol and Wright (2009) and labeled parameters accordingly. Model 1 (Table 1) is the standard mixed effects model with age at observation modeled as a fixed effect (i.e., x_{ij}; combined within- and between-subject effects) and the individual included as a random effect (i.e., random individual intercept). Subscripts refer to the data structure, where x_{ij} is

the x value of measurement i from subject j. Model 2 (Table 1) separates within- (i.e.,

$x_{ij} - \overline{x}_j$) and between-subject (i.e., $\overline{x}_j$) effects, whereby within-subject effects are within-

subject centered (i.e., the subject's mean value is subtracted from each observation) and

between-subject effects are the subjects' mean values. Model 3 (Table 1) is an alternative

formulation of model 2 that allows for testing differences in the effects (i.e., slopes) of

within- and between-subject effects (van de Pol and Wright 2009). Separate modeling

procedures were implemented to evaluate the effects of female age on nest initiation, nest

success, and brood success. Data for nest success and brood success models was subset to

isolate the direct effect of each parameter (i.e., only data from individuals that actually

attempted the parameter was used in the analyses). Nest success was defined as

successfully hatching a nest, given a nest was initiated. Because sage-grouse are precocial,

brood success was defined as ≥ 1 chick survived to ≥ 50 or ≥ 42 days post-hatch for 1998–

2004 and 2005–2010, respectively, given a successful nest attempt. For all modeling

procedures, we used a binomial distribution, a logit link, and fit models using an adaptive

Gaussian Hermite approximation procedure.

RESULTS

We marked 248 hens, monitored 313 nests, and tracked 142 broods from 1998–2010. Nest

initiation models were based on 233 observations of 147 individuals. Nest success models

were based on 154 observations of 105 individuals. Brood success models were based on

88 observations of 72 individuals. Due to the nature of our field methods (i.e., transmitter

battery life ~ 2.5 years) and grouse biology (i.e., mean longevity within the taxon typically

under 2.5 years for females; Johnsgard 1983) our age comparison was primarily between

age classes 2nd and 3rd year (Table 1), which also limited our ability to consider more

complex model structures (i.e., quadratic trend in within-individual process of ageing) to further evaluate senescence. Even when both within- and between-individual effects were entangled (model structure 1) we detected effects of female age on both nest initiation ($\beta_1 = 0.91$, SE = 0.29, p < 0.01) and nest success ($\beta_1 = 0.48$, SE = 0.26, p = 0.06), in contradiction with Caudill et al. (2014). Consequently, aggregations of adults (i.e., comparisons of SY vs. ASY; *sensu* Taylor et al. 2012; Caudill et al. 2014; Davis et al. 2014) could obscure within- and between-individual effects in the aggregate adult class (e.g., ASY).

Our results indicate that within-individual variation (e.g., ageing, breeding experience hypotheses) was present in nest initiation (Model 2: $\beta_W = 0.84$, SE = 0.33, p ≤ 0.01) and success (Model 2: $\beta_W = 0.81$, SE = 0.31, p = 0.01) where the likelihood of reproductive success increased with ageing. Between-individual variation (e.g., individual heterogeneity, frailty, selection hypotheses) was detected in nest initiation (Model 2: $\beta_B = 1.05$, SE = 0.44, p = 0.01) where individuals with higher mean age (i.e., survived longer) were more likely to initiate nests. However, for nest initiation the difference in the slopes of within- and between-individual effects were not significantly different (Model 3: $\beta_B - \beta_W = 0.21$, SE = 0.46, p = 0.63); although, both were additive positive effects on production (Table 1). The effect size of between-individual effects (e.g., individual heterogeneity) was numerically larger than that of within-individual effects (e.g., ageing) for nest initiation (Tables 1 and 2). We did not detect significant within- or between-individual age effects for brood success, but our results could have been influenced by sample sizes. Because we used two monitoring methods for brood success we evaluated a

fixed effect of monitoring type, which did not appear to affect success ($p = 0.41$, 0.51, and

0.51 for model structures 1, 2, and 3, respectively).

DISCUSSION

Positive relationships between age and reproductive performance are common for avian

taxa (Forslund and Pärt 1995), including grouse species (e.g., Willebrand 1992; Gregg et al.

2006; Connelly et al. 2011). For sage-grouse, both within- and between- individual effects

of age appeared to manifest early (e.g., nest initiation) in a reproductive attempt, but not in

later stages (e.g., brood success). The within-individual process of ageing (e.g., breeding

experience, foraging ability hypotheses) increased both nest initiation rates and nest

success. However, between-individual variation also influenced nest initiation such that

individuals with higher mean age (i.e., higher apparent survival) initiated nests more often,

which supports the frailty and selection hypotheses. We found both within- and between-

individual processes simultaneously influencing the propensity to even attempt

reproduction (i.e., nest initiation), where ageing (i.e., breeding experience, foraging ability

hypotheses) aided even inherently fecund individuals (i.e., Mauck et al. 2012). The role of

within- and between-individual processes also appeared to vary by component of a

reproductive event for sage-grouse, which supports the notion that multiple factors can

simultaneously affect age related patterns in reproduction of birds (Forslund and Pärt

1995). Moreover, our findings indicate between-individual variation can manifest via

multiple pathways and could require multiple measures to detect. Regardless, individual

heterogeneity in cost of reproduction and reproductive output seems prevalent in avian taxa

(e.g., Aubry et al. 2009; Aubry et al. 2011; Cam et al. 2013; Caudill et al. 2014), and

consequently evaluation of age effects should attempt to disentangle within- and between-

individual effects. Decoupling of within- and between-individual effects is of particular importance because they reflect different underlying processes (e.g., breeding experience vs. individual heterogeneity hypotheses) and other important processes (e.g., senescence) could be masked when age effects are entangled (Cam and Monnat 2000; van de Pol and Verhulst 2006).

Our findings indicated age related effects occur primarily towards the beginning (i.e., nest initiation and success) of a reproductive attempt. However, an opposite relationship has been documented between reproductive trade-offs and output whereby trade-offs manifested in later stages of reproduction, but were undetected in early stages (Caudill et al. 2014). Accordingly, reproduction in sage-grouse appears to initially be affected by within-individual variation (i.e., ageing) and transitions to reproductive trade-offs in later stages (Caudill et al. 2014), while between-individual variation (i.e., individual heterogeneity, selection, frailty hypotheses) influences both ends of a reproductive attempt (i.e., nest initiation from our results and brood success from Caudill et al. 2014). We documented within-individual variation (i.e., breeding experience, foraging ability hypotheses) in nest success, but did not detect individual heterogeneity (i.e., between-individual effects). Costs of reproduction also appear to affect sage-grouse nest success; however, similar to our results, individual heterogeneity was seemingly absent (Caudill et al. 2014). Bergerud (1988) postulated that nest spacing drives success and recruitment in grouse, which leads to the hypothesis that when nests are evenly distributed across a landscape predation should be a random event (i.e., evenly distributed nests in homogeneous habitat have equal likelihood of predation). Both our analysis and Caudill et al. (2014) estimated the random individual intercept variance essentially at zero (i.e., < 1e-

13) for nest success which could lend support to the hypothesis that sage-grouse nests on our study site were predated at random, possibly as a result of nest spacing (i.e., evenly distributed).

Accurate knowledge and perception of population ecology is vital to optimize the efficacy of management actions on species conservation, particularly for declining species. Sage-grouse population growth meta-analysis has postulated that increased survivorship and reproductive success should be the focus of conservation efforts (Johnson and Braun 1999; Taylor et al. 2012). However, in studies of many species, including sage-grouse (e.g., Johnson and Braun 1999; Gregg et al. 2006; Taylor et al. 2012; Davis et al. 2014), age parameters are typically interpreted as though only within-individual effects (e.g., ageing or breeding experience hypothesis) occur, yet within- and between-individual effects may actually be entangled. In many instances data are collected in a form that could be structured longitudinally to disentangle within- from between-individual processes. Hence, when age is hypothesized to affect a biological parameter, evaluation should include longitudinal analysis to disentangle and elucidate the underlying effects. Our results demonstrate that when only an entangled parameter is considered, the resulting predicted effects could be erroneous in either directions (i.e., over or underestimated). For example, when the effects of age on sage-grouse nest initiation were disentangled the within-individual effect was slightly smaller than the entangled effect and a numerically larger, than either, between-individual effect became apparent (Table 1). Conversely, the disentangled within-individual effect of age on nest success was 1.7 times larger than the entangled effect in the standard fixed effect model (Table 1). Consequently, if longitudinal analyses are impossible then inference should be limited to acknowledge that multiple

competing hypotheses may be entangled (e.g., breeding experience vs. individual heterogeneity hypotheses), which could limit the ability to predict age related improvements in reproductive success.

ACKNOWLEDGMENTS

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Table Legends

Table 1. Effect of age on greater sage-grouse (*Centrocercus urophasianus*) reproductive parameters on Parker Mountain, Utah, USA, 1998–2010.

Model and Parameter	Nest Initiation	Nest Success	Brood Success
Model 1: $y_{ij} = \beta_0 + \beta_1 x_{ij} + u_{0j}$			
β_0 (intercept)	-1.41 ± 0.68 [††]	-0.52 ± 0.67	1.4 ± 1.08
β_1 (combined within- and between-subject effect)	0.91 ± 0.29 [†††]	0.48 ± 0.26 [†]	-0.09 ± 0.35
$\sigma^2_{u_{0j}}$	0.67 ± 0.07	0 ± 0	1.56 ± 0.15
Deviance (-2 * log likelihood)	282.9	191.6	105.5
Model 2: $y_{ij} = \beta_0 + \beta_W (x_{ij} - \overline{x}_j) + \beta_B \overline{x}_j + u_{0j}$			
β_0 (intercept)	-1.76 ± 1.04 [†]	0.77 ± 0.94	-0.44 ± 1.81
β_W (within-subject effect)	0.84 ± 0.33 [†††]	0.81 ± 0.31 [†††]	-0.56 ± 0.56
β_B (between-subject effect)	1.05 ± 0.44 [††]	-0.03 ± 0.37	0.71 ± 0.77
$\sigma^2_{u_{0j}}$	0.68 ± 0.07	0 ± 0	1.98 ± 0.17
Deviance (-2 * log likelihood)	282.7	187.9	103.8
Model 3: $y_{ij} = \beta_0 + \beta_W x_{ij} + (\beta_B - \beta_W) \overline{x}_j + u_{0j}$			
β_0 (intercept)	-1.76 ± 1.04 [†]	0.77 ± 0.94	-0.44 ± 1.81
β_W (within-subject effect)	0.84 ± 0.33 [†††]	0.81 ± 0.31 [†††]	-0.56 ± 0.56
$\beta_B - \beta_W$ (within- versus between-subject difference)	0.21 ± 0.46	-0.84 ± 0.44 [†]	1.27 ± 1.11
$\sigma^2_{u_{0j}}$	0.68 ± 0.07	0 ± 0	1.98 ± 0.17
Deviance (-2 * log likelihood)	282.7	187.9	103.8
Age class sample sizes			
2nd year class	146	82	43
3rd year class	68	57	35
4th year class	15	12	8
5th year class and older	4	3	2

Significance codes: 0.1 [†]; 0.05 [††]; 0.01 [†††]

Table 2. Odds ratios for age effects on greater sage-grouse (*Centrocercus urophasianus*) reproductive parameters on Parker Mountain, Utah, USA, 1998–2010.

Reproductive Parameter	Effect	Odds Ratio	90% CI
Nest Initiation	Within-subject	2.32	1.39–4.1
Nest Initiation	Between-subject	2.87	1.46–6.41
Nest Success	Within-subject	2.25	1.37–3.87