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Age-specific reproduction and survival of individually marked Wood Thrushes, *Hylocichla mustelina*

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Abstract. Several nonexclusive, sometimes contradictory, hypotheses have been employed to explain age-related changes in reproduction and survival among vertebrates. We evaluated these hypotheses with observations collected from a 31-year study of individually marked Wood Thrushes (*Hylocichla mustelina*). Age-specific fledgling production, survival probabilities, and derived life table columns are presented here. Additionally, we report "genetic value," or the number of young remaining to be recruited into the breeding population by individuals of age *x*. Controlling for age of mate, the presence of some individuals in multiple years, and the effect of year of breeding, reproduction and survival peaked in middle-aged birds of each sex and declined later in life for the oldest individuals. We could not exclude the selection hypothesis (removal of inferior individuals) as an explanation for improved female reproduction until middle age. The age at last reproduction was a significant determinant of age-related reproductive success, indicating a disappearance of low-quality individuals. Yearling females that did not successfully reproduce had greater within-season emigration than all other age classes of each sex, regardless of the reproductive success of other classes. For males, we favored the constraint hypothesis (improved reproduction with experience) to explain greater reproductive output with increasing age until at least middle age. For each sex, the age of the mate independently influenced all measures of reproductive performance, but there was generally a linear or quadratic, rather than interactive, effect of the mate's age on reproduction. For both sexes, hypotheses of age-related reproduction were only partially supported because of effects of senescence, or a decline in reproductive output or survival probabilities with increasing age. Senescence may confound attempts to examine or apply general hypotheses of age-related reproduction that assume a monotonic relationship between age and reproduction or survival.

Key words: aging; Hylocichla mustelina; *life history strategies; life tables; reproductive value; senescence; survival; Wood Thrush.*

Introduction

Age- and sex-specific differences in reproduction and survival occur in a diverse variety of taxa (Finch 1990) yet the mechanisms that cause these patterns are not clearly understood (Holmes et al. 2001). For example, middle-aged birds tend to reproduce and survive better than the youngest and oldest individuals (Clutton-Brock 1988, Newton 1989), and one sex may exert a greater influence on reproductive success than the other (Desrochers and Magrath 1993, Green 2001). Several nonexclusive hypotheses have been employed to explain age-related differences in reproductive performance (reviewed by Curio 1983, Forslund and Pärt 1995, Martin 1995). The selection hypothesis assumes greater differential mortality of inferior phenotypes at early ages, resulting in an apparent increase in reproductive success with increasing cohort age. Similarly, the recruitment hypothesis posits delayed breeding as the cause of an apparent increase in age-related reproductive success: some young birds forego breeding opportunities and instead accumulate resources for breeding at a later age. The restraint hypothesis predicts a trade-off between reproduction and survival. If reproductive effort increases with age as reproductive value and the probability of survival decreases, the oldest birds are expected to be the most productive. Lastly, the constraint hypothesis suggests that age-related improvements in breeding competence occur because of experience and enhanced parental skills. Such experience may include improvements in nest-site selection, foraging ability, coordination with a partner, parental care, or defense of young with increasing age (McCleery and Perrins 1988, Desrochers and Magrath 1993, Forslund and Pärt 1995, Martin 1995, Espie et al. 2000, Balbontín et al. 2007).

All of these hypotheses of age-related reproduction predict a linear increase in reproductive success with increasing age but do not account for senescence, defined as a decrease in reproduction or probability of

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survival with increasing age (Partridge 2001). Senescence is widely acknowledged to occur in birds and mammals (Loison et al. 1999, Holmes et al. 2001) and is generally discussed in terms of antagonistic pleiotropy or mutation accumulation (Medawar 1946, Williams 1957, 1966, Partridge 2001). In antagonistic pleiotropy, genes or traits that enhance reproduction early in life may negatively affect later reproduction or survival. Antagonistic pleiotropy is based on the same trade-off between reproduction and survival as the restraint hypothesis (reproductive effort increases as reproductive value decreases) yet predicts the opposite result on reproductive performance in the oldest birds, or a decrease in reproductive output with increasing age.

The mutation accumulation hypothesis recognizes that chance extrinsic forces, such as predation and disease, can cause mortality not attributable to aging effects. Individuals carrying deleterious mutations expressed later in life are likely to die from these extrinsic causes before such mutations are apparent. Consequently, deleterious mutations will accumulate over time and be expressed in those individuals that reach an advanced age, resulting in lowered reproduction and survival probabilities. High levels of extrinsic mortality should result in fewer individuals achieving older ages, and therefore weaker selection on traits expressed at those ages (Partridge 2001). Changes in reproductive output with increasing age also may affect the strength of selection acting on age-specific traits.

Given this wide range of hypotheses regarding age-related fecundity and survival, some of which are contradictory, and general lack of detailed data from natural populations, further empirical observations and theoretical development are needed for a better understanding of variability in life history strategies. Likewise, few explanations exist for sex-specific differences in reproductive effort. Many studies, for logistical reasons, have only been able to measure the reproductive performance of one sex (e.g., most studies in Clutton-Brock 1988, Newton 1989). Little is known about reproductive and survival patterns among monogamous, migratory passerines (Green 2001), and few studies have attempted to investigate the effect of the age of one sex independent of the age of its mate (e.g., McCleery and Perrins 1988, Desrochers and Magrath 1993, Balbontín et al. 2007).

We evaluated the general prediction of each hypothesis of age-related fecundity and survival with age- and sex-specific observations of reproduction and survival collected from a 31-year study of individually marked Wood Thrushes (*Hylocichla mustelina*) breeding in a Delaware forest remnant. We present age- and sex-specific survival probabilities, fledgling production, recruit production, reproductive value, and "genetic value," a measure that incorporates age-specific survival probabilities and the production of recruits into the local population. To our knowledge, genetic value has not been previously described for any species. In addition to the effects of annual fledgling and recruit production on survival, the effects of clutch initiation dates and annual number of nesting attempts on both age-specific reproduction and survival are presented. The age of the mate and the year of breeding are considered in these analyses.

METHODS

Study species and site

Wood Thrushes breed in eastern North America from southern Canada southward to Texas and northern Florida, and winter in Central America. The sexes are of similar appearance and mass and may nest up to five times to produce two broods in a season; rarely, three broods are completed (Brown and Roth 2004). Females build open-cup nests, and pairs are usually seasonally monogamous. See Roth et al. (1996) for details of breeding ecology.

Reproductive and survival data were gathered from a population of individually marked Wood Thrushes that bred in the isolated 15-ha University of Delaware Woods (UDW; Appendix A) on the University's Experimental Farm in Newark, Delaware, from 1974 through 2004. Nearly all individuals in the population were uniquely color banded (Brown and Roth 2004), and contents of all nesting attempts were recorded through completion or failure of the nest (see Brown and Roth [2002, 2004] for details of field methodology). The study site was primarily mature upland hardwood forest with a well-developed shrub layer. Relatively recent changes in vegetation because of disease include the decline of dogwoods (*Cornus* spp.) and oaks (*Quercus* spp.). General landscape changes since the study was initiated, both locally and statewide, include continued forest removal and suburban expansion (Environmental Law Institute 1999).

Demography and life table methodology

Reproductive and survival observations from a composite cohort of Wood Thrushes, starting from eggs, are presented in life tables (see Appendix B, Tables 1 and 2). Only data from nest owners that had completed their reproductive life at UDW between 1974 and 2004 were used in life tables and analyses. Additionally, data were from nests known to contain at least one Wood Thrush egg and for which the identity of owners and the number of eggs laid, hatched, and fledged could be determined. No nests were used from 1979, as data were not collected during that year.

Standardized nesting stages, defined by nest contents and parental behavior, were a compromise among temporally changing nest contents, especially a decrease in clutch size (from four eggs to three) over the course of the breeding season (Brown and Roth 2002). Because incubation typically begins with the penultimate egg (Roth et al. 1996), we defined the laying stage as days 0 through 2 of a standardized 29-day nest cycle. Likewise, the end of incubation was defined as the hatching of the

Table 1. A composite cohort life table of female Wood Thrushes at the University of Delaware Woods, 1974–2004.

Female age, *x*†	*S*(*x*)	Fertility schedule		Survivorship schedule, *l*(*x*)	Survival probability, *g*(*x*)	Mean lifetime remaining (yr), *e*(*x*)	Reproductive value, *v*(*x*)	Genetic value, *F*(*x*)
		b(*x*)	SD					
Nest stage (d)								
Eggs (0–2)	1736			1.000	0.89			
Incubation (3–15)	1553			0.894	0.75			
Hatchlings and nestlings (16–29)	1164			0.671	0.69			
Fledglings (30–304)	799			0.460	0.36			
Adults (including immigrants)								
1	286	2.4	2.0	0.165	0.38	0.78	3.49	0.09
2	109	3.1	1.9	0.063	0.68	1.20	5.71	0.14
3	74	3.7	2.2	0.043	0.53	1.01	4.39	0.07
4	39	3.4	2.2	0.022	0.69	1.06	4.68	0.03
5	27	3.8	2.1	0.016	0.56	0.76	2.70	0.05
6	15	2.4	2.0	0.009	0.60	0.57	2.29	0.00
7	9	3.1	2.2	0.005	0.44	0.22	0.58	0.00
8	4	1.3	1.5	0.002	0.00	0.00	0.00	0.00

Notes: Methodology and nomenclature (except genetic value, see *Methods*) follow Gotelli (1995). Net reproductive rate, $R_0 = 0.92$; generation time, $G = 2.30$ yr; corrected $r = -0.036$. See *Methods: Demography and life table methodology* for construction of data set and explanation of terms. $S(x)$ is the number of survivors of age x; fertility schedule is mean number of fledglings/yr; survivorship schedule is the proportion of original cohort surviving to start of age x; survival probability is the probability an individual of age x survives to age $x + 1$; reproductive value is the number of offspring remaining to be born to individuals of age x; genetic value is the number of female recruits to be produced by individuals of age x.

† Days for nest stages, years for adults.

first egg, even though other eggs could hatch over the next 24 hours (Brown and Roth 2004). As incubation averaged 12.7 days, we designated days 3–15 of the nest cycle as the incubation stage. The nestling stage was defined as the difference between the day of first hatch to first fledge, which required 12–15 days. The nestling period, therefore, was standardized as days 16–29 of the nest cycle.

The mean date of fledging for the 713 nests in which it could be determined was 3 July (median 1 July, mode 10 June). Fledging dates ranged from 1 June to 26 August. Based on the approximated mean fledging date, we assigned 1 July as the standardized birth date of all fledglings for the purpose of life table calculations. The earliest recorded date of egg-laying was 4 May. As such, 1 May reasonably represented the start of the breeding season. From 1 July to 30 April of the following year is 304 days, our standardized "fledgling" stage. Mortality from fledging to independence was subsumed by

Table 2. A composite cohort life table of male Wood Thrushes at the University of Delaware Woods, 1974–2004.

Male age, *x*†	*S*(*x*)	Fertility schedule		Survivorship schedule, *l*(*x*)	Survival probability, *g*(*x*)	Mean lifetime remaining (yr), *e*(*x*)	Reproductive value, *v*(*x*)	Genetic value, *F*(*x*)
		b(*x*)	SD					
Nest stage								
Eggs (0–2)	1856			1.000	0.89			
Incubation (3–15)	1654			0.891	0.75			
Hatchlings and nestlings (16–29)	1237			0.666	0.68			
Fledglings (30–304)	843			0.454	0.30			
Adults (including immigrants)								
1	254	2.4	1.9	0.137	0.55	1.07	4.69	0.11
2	140	3.0	2.0	0.075	0.62	1.14	5.24	0.13
3	87	3.1	2.0	0.047	0.63	1.02	5.08	0.14
4	55	3.7	2.4	0.030	0.60	0.81	4.10	0.11
5	33	3.5	2.4	0.018	0.52	0.59	3.16	0.11
6	17	3.9	1.9	0.009	0.47	0.41	2.04	0.08
7	8	3.3	1.5	0.004	0.38	0.19	0.92	0.02
8	3	2.3	2.1	0.002	0.00	0.00	0.00	0.00

Notes: Methodology and nomenclature (except genetic value; see *Methods*) follow Gotelli (1995). Net reproductive rate, $R_0 = 0.92$; generation time, $G = 2.50$ yr; corrected $r = -0.033$. See *Methods: Demography and life table methodology* for construction of data set and explanation of terms. $S(x)$ is the number of survivors of age x; fertility schedule is mean number of fledglings/yr; survivorship schedule is the proportion of original cohort surviving to start of age x; survival probability is the probability an individual of age x survives to age $x + 1$; reproductive value is the number of offspring remaining to be born to individuals of age x; genetic value is the number of male recruits to be produced by individuals of age x.

† Days for nest stages, years for adults.

mortality from fledging to return. No corrections were made for a 3-ha portion of UDW not studied from 1980–1983, which may have influenced survival probabilities of individuals present in that area during those years. Recapture probabilities determined for the entire study (Brown and Roth 2004) also were influenced by omitting this portion of the study site during that time and are therefore conservative.

Only data from males and females that completed their reproductive life at UDW from 1974 through 2004 were used for adult-related life table entries and survival analyses (i.e., no censored data were used in any analysis). Nesting and banding data from 2005 and 2006 were examined to verify that these birds were no longer in the population. Given the high probabilities of recapture in this study (97% for males, 92% for females [Brown and Roth 2004]) and the observation that only three individuals in the 31 years of the study were not present one year and reappeared in the population the following year (Brown and Roth 2002), we assumed here that an individual had died if it was not later observed.

Before 1994, all immigrant adults were aged as after-hatching year (AHY birds). Beginning in 1994, immigrants were aged as second-year (SY) or after second-year (ASY) birds based on flight feather patterns (Weinberg and Roth 1994). As there was no basis for redistributing the sample of individuals before 1994 into these refined age classes, and most immigrants between 1994 and 2004 were SY birds (124 out of 140, or 89%; R. R. Roth, *unpublished data*), all immigrant adults in all years were considered here to be SY birds, or yearlings.

Assuming rates of immigration equaled rates of emigration (Newton and Rothery 1997), we treated immigrant birds as if they were produced at UDW. This methodology allowed for a composite cohort of eggs to be followed through adulthood and provided survival estimates for all stages of the life cycle. Data were used to compute separate cohort life tables for males, females, and for all adults combined. For sex-specific life tables, different numbers of male and female owners were identified from the total sample of nests (254 males and 286 females); this difference was due at least in part to SY females being less philopatric than SY males (Weinberg and Roth 1998, Brown and Roth 2002).

We constructed life tables using the methodology and nomenclature of Gotelli (1995). A new column of information, genetic value, was added to life tables based on methods for determining reproductive value. Reproductive value, $v(x)$, is defined as the relative number of offspring that remain to be born to a given individual of age x (Gotelli 1995). We used the discrete-time version of this equation (Gotelli 1995):

$$v(x) = \frac{e^{rx}}{l(x)} \sum_{y=x}^{k} e^{-ry} l(y) b(y) \qquad (1)$$

to calculate reproductive value for individuals of age x. For the above formula, y is all the ages that individuals pass through until the ultimate age of consideration, or k; $l(y)$ is the survivorship schedule for individuals of age y, $b(y)$ is the fertility schedule for individuals of age y, and r is the intrinsic rate of increase, determined separately for each sex (see Tables 1 and 2) and for all adults combined (Appendix B).

TABLE 3. The chi-square contingency table that was used to determine if the distribution of all possible age-class pair combinations of Wood Thrushes was random.

Female age class	No. age class pairings	Male age class			Totals
		1	2	3	
1	observed	139	114	6	259
	expected	104	143	12.6	
	cell χ^2	11.9	5.7	3.4	
2	observed	72	160	18	250
	expected	100	138	12.1	
	cell χ^2	8.0	3.6	2.80	
3	observed	4	21	2	27
	expected	10.8	14.9	1.3	
	cell χ^2	4.3	2.5	0.4	
Totals		215	295	26	536

Notes: Age classes were defined as follows: age class 1 = yearlings, class 2 = 2–5 years, and class 3 = 6–8 years. Younger birds paired with each other at a greater frequency than expected by chance; older individuals paired with younger birds less frequently than expected. Data are from the University of Delaware Woods, 1974–2004, and reflect the age of each bird's partner during the first annual nesting attempt. Overall $\chi^2 = 42.7$, $P < 0.0001$, df = 4.

For each age class, we also determined the number of fledglings produced per individual in year t that recruited into the study population in year $t + 1$. Recruits were substituted for fledglings in Eq. 1 to provide an estimate of genetic value, $F(x)$, for each sex and age class. This genetic value refers to local, site-specific recruitment only and should not be construed to represent recruitment of young into the broader population elsewhere. Sex-specific genetic value, reported in the sex-specific life tables (see Tables 1 and 2) was determined as the number of same-sex fledglings that remain to be recruited into the local population. Note that recruitment rates varied substantially among years (Brown and Roth 2004).

Age-related pairing

As both males and females fell into three age classes based on similar reproduction or survival estimates—yearlings, two- to five-year-olds, and those greater than five years old (see *Results*)—we performed a chi-square contingency analysis to determine the significance of age-related assortative pairing. Because pairings were not random (Table 3), we retained these age classes to examine the effect of measures of reproductive output on male and female survival.

Statistical analyses

Reproduction.—There are several methods for analyzing long-term reproductive data that address confounding between cross-sectional and longitudinal data (e.g.,

TABLE 4. Results of hierarchical linear models of the effects of age and the age of the mate on measures of reproductive output.

Measure of reproductive output	Females					
	Effect	Estimate	SE	F	df	P
Fledglings	Intercept	1.23	0.37	11.2	1, 25.7	0.0009
	Male age	0.58	0.21	8.1	1, 537	0.005
	Male age^2	−0.05	0.03	3.1	1, 536	0.08
	Female age	0.58	0.21	8.0	1, 523	0.005
	Female age^2	−0.07	0.03	5.9	1, 513	0.02
Recruits	Intercept	0.02	0.05	0.1	1, 16	0.70
	Female age	0.09	0.04	6.0	1, 532	0.01
	Female age^2	−0.01	0.01	5.9	1, 526	0.01
Clutch initiation	Intercept	21 May	0.84	>1000	1, 102	<0.0001
	Female age	−2.00	0.46	19.1	1, 390	<0.0001
	Female age^2	0.21	0.07	10.6	1, 383	0.001
	Male age	−2.25	0.46	23.7	1, 400	<0.0001
	Male age^2	0.22	0.07	10.7	1, 405	0.001
Nest attempts	Intercept	1.42	0.14	96.4	1, 130	<0.0001
	Female age	0.45	0.10	19.3	1, 517	<0.0001
	Female age^2	−0.06	0.01	18.5	1, 500	<0.0001
	Male age	0.45	0.10	6.7	1, 447	0.01

Notes: Full models were fitted with male and female age, quadratic age terms for both sexes, and two-way interactions of male and female age terms as explanatory variables. Variables were retained if P values were $\leq$0.10. Random effects included those listed in Table 5. Male age did not affect recruitment. Male and female models did not differ for fledgling production or date of clutch initiation. Data sources and sample sizes are indicated in Table 5. See Fig. 1 for a graphical presentation of these results.

Cam et al. 2002, Reid et al. 2003, van de Pol and Verhulst 2006, McMahon and Diez 2007). Here, we used a modified form of the mixed-model approach suggested by van de Pol and Verhulst (2006), in which we introduce a quadratic age term into all models to account for potential reproductive senescence. Further, year of breeding, individual females, individual males, and year × individual interactions were included as random effects in these models. Hierarchical linear models (HLM; see McMahon and Diez 2007) account for the repeated appearance (nonindependence) of reproductive data from the same individuals among years and age groups. Because Wood Thrushes begin breeding as yearlings (Roth et al. 1996), it was not necessary to incorporate terms to examine the selective appearance of individuals into the breeding population. We examined the age of last reproduction (ALR), however, to determine if there was selective disappearance of low quality individuals from the population.

Evidence of reproductive senescence in each sex was examined by fitting linear and quadratic HLM to age-specific reproductive data using restricted maximum likelihood for estimating the fixed effects of age and the random variance components listed above (PROC MIXED [SAS Institute 2003]). These tests included sex- and age-related trends in the number of fledglings and recruits produced each year, the date of clutch initiation, and the number of nesting attempts per season. We also tested if the date of first clutch initiation and annual number of nesting attempts affected annual fledgling production using HLM methodology.

As reproductive success may depend on the age of the mate, and the opposite sex may experience senescence, we included linear and quadratic terms for the age of the mate and tested for interactive effects of the age of each pair member in separate HLM of fledgling and recruit production, date of clutch initiation, and annual nesting attempts. Year of breeding and individual pair members were included as random terms. These models tested the significance of sex and age in the presence of the partner on measures of reproductive success, as well as determined if there was an interactive effect of the age of the mate on reproductive success.

Survival.—As our data contained only individuals that had completed their reproductive life, we did not model censored or right-skewed survival data (see McDonald et al. 1996). Nonetheless, observations were not independent as the oldest individuals were measured repeatedly during their life span and represent a longitudinal data structure. Additionally, the year(s) of breeding may affect survival propensity. To account for the correlated nature of the data, we used a generalized linear model design for univariate responses (McCullagh and Nelder 1989) implemented by generalized estimating equations (Liang and Zeger 1986) to model actuarial senescence in each sex based on linear and quadratic age terms, a binomial distribution of the response, and a logit link function. Individuals and year × individual interactions were specified as repeated effects (PROC GENMOD [SAS Institute 2003]).

Relationships between date of clutch initiation, fledgling production, recruit production, and annual nesting attempts—measures of reproductive output—on male and female survival were investigated using generalized linear mixed models with binomial error and a logit link function (GLIMMIX macro [Littell et al. 1996, SAS Institute 2003]). Independent variables were considered as fixed effects and were evaluated for significance using Type III estimable functions; year of breeding and individuals were included as random terms. Survival

TABLE 4. Extended.

Males					
Effect	Estimate	SE	F	df	P
Intercept	1.23	0.37	11.2	1, 25.7	0.0009
Male age	0.58	0.21	8.1	1, 537	0.005
Male age^2	−0.05	0.03	3.1	1, 536	0.08
Female age	0.58	0.21	8.0	1, 523	0.005
Female age^2	−0.07	0.03	5.9	1, 513	0.02
Intercept	0.11	0.03	13.4	1, 44.6	0.0004
Male age	0.005	0.01	0.2	1, 561	0.62
Intercept	21 May	0.84	>1000	1, 102	<0.0001
Female age	−2.00	0.46	19.1	1, 390	<0.0001
Female age^2	0.21	0.07	10.6	1, 383	0.001
Male age	−2.25	0.46	23.7	1, 400	<0.0001
Male age^2	0.22	0.07	10.7	1, 405	0.001
Intercept	1.64	0.13	166.9	1, 130	<0.0001
Male age	0.09	0.03	13.2	1, 447	0.0003
Female age	0.26	0.09	8.7	1, 517	0.003
Female age^2	−0.04	0.01	8.3	1, 500	0.004

was indicated as returning to breed the following year. As annual recapture probabilities were near 1.0, we assumed that marked individuals not present in the population had died and were not breeding elsewhere.

The effects of date of clutch initiation, number of fledglings produced, number of recruits, and number of nesting attempts on survival were evaluated for all birds of each sex, then for individuals divided into three age classes (yearlings, two- to five-year-olds, and those greater than five years old). Given that tests were repeated on the same set of data, potentially affecting Type I error rates, we controlled the false discovery rate (FDR) at the 0.05 level (García 2004; PROC MULTTEST [SAS Institute 2003]) and report both raw P values and FDR-corrected P values for each measure of reproductive output.

RESULTS

Demography

For the sexes combined, reproduction, probability of survival, mean lifetime remaining, reproductive value, genetic value, and survival nominally increased and then decreased as Wood Thrushes aged (Appendix B). The net reproductive rate of 0.92 indicated that production did not meet the replacement needs necessary to maintain a stable population. Accordingly, r was negative (Appendix B). Net reproductive rate and other values were determined for the entire 31-year period, however, and the result of a negative r should be cautiously interpreted. As this population has fluctuated in abundance over the course of the study (Appendix C), different r values can be determined if data from different time periods are used (e.g., 1975–1983 vs. 1985–1990).

Ostensibly, the safest nesting stage was the laying stage, with 89% of eggs surviving to hatch (Appendix B, Tables 1 and 2). On a daily basis, however, this stage experienced the greatest losses, with 3.5% of eggs lost per day. The lowest percentage of eggs lost per day occurred during incubation, with 1.9% lost. Overall, the period between fledging and return as a yearling exhibited the lowest survival probability from one stage to the next. This survival estimate included unknown dispersal of surviving individuals (assumed here to have died) and the assumption that all immigrant adults were yearlings produced at UDW; note that this assumption affects survival estimates from fledging to return as yearlings, not survival estimates of adults. Males had a noticeably lesser probability of survival as fledglings than females did, but had a much greater probability of survival as yearlings. From age 6 onward, males produced more fledglings than females (Tables 1 and 2). These relatively large discrepancies in survival between the sexes may be due to differences in selection pressure and inherent faults in the assumptions of life table methodology (see *Discussion*). Female genetic value peaked at age 2 and quickly declined (Table 1). Male genetic value remained fairly constant until age 6 or 7 and was 2–3 times greater than that of females from age 3 onward. That is, males had more same-sex offspring recruit into the breeding population than females did (Table 2). Very similar patterns were found if recruits of both sexes were used (not shown), partly reflecting the male bias to annual recruitment rates (see Brown and Roth 2002).

Reproduction

Yearlings paired with each other more frequently than expected due to chance, as did older birds (Table 3). For all pairs, fledgling production was positively related to the number of annual nesting attempts (0.48 ± 0.09 [mean ± SE], $F_{1,570} = 25.5$, $P < 0.0001$) and negatively related to the date of clutch initiation (–0.11 ± 0.02, $F_{1,424} = 25.7$, $P < 0.0001$). The number of nesting attempts was negatively related to the date of clutch initiation (–0.05 ± 0.01, $F_{1,413} = 27.9$, $P < 0.0001$).

For females, pairing with a middle-aged male resulted in greater fledgling production than pairing with a yearling or the oldest males, regardless of the age of the female (Table 4, Fig. 1). Reproductive differences were slight, however, if the male was aged 4 or older. There was not an interactive effect of female age and male age on fledgling production. Production of recruits peaked at age 3 before decreasing in older females (Tables 1 and 4) and did not covary with male age class.

The selection hypothesis was addressed by including the age of last reproduction (ALR), including ALR^2, of each sex in models of age-related fledgling production. The significance of female ALR terms (Table 5) demonstrated an effect of the disappearance of low quality females from the population on fledgling production. Male ALR terms were not significant.

Clutch initiation was earliest among middle-aged females and co-varied with the age of the mate: at any age, pairing with a middle-aged male resulted in an earlier date of clutch initiation than pairing with the

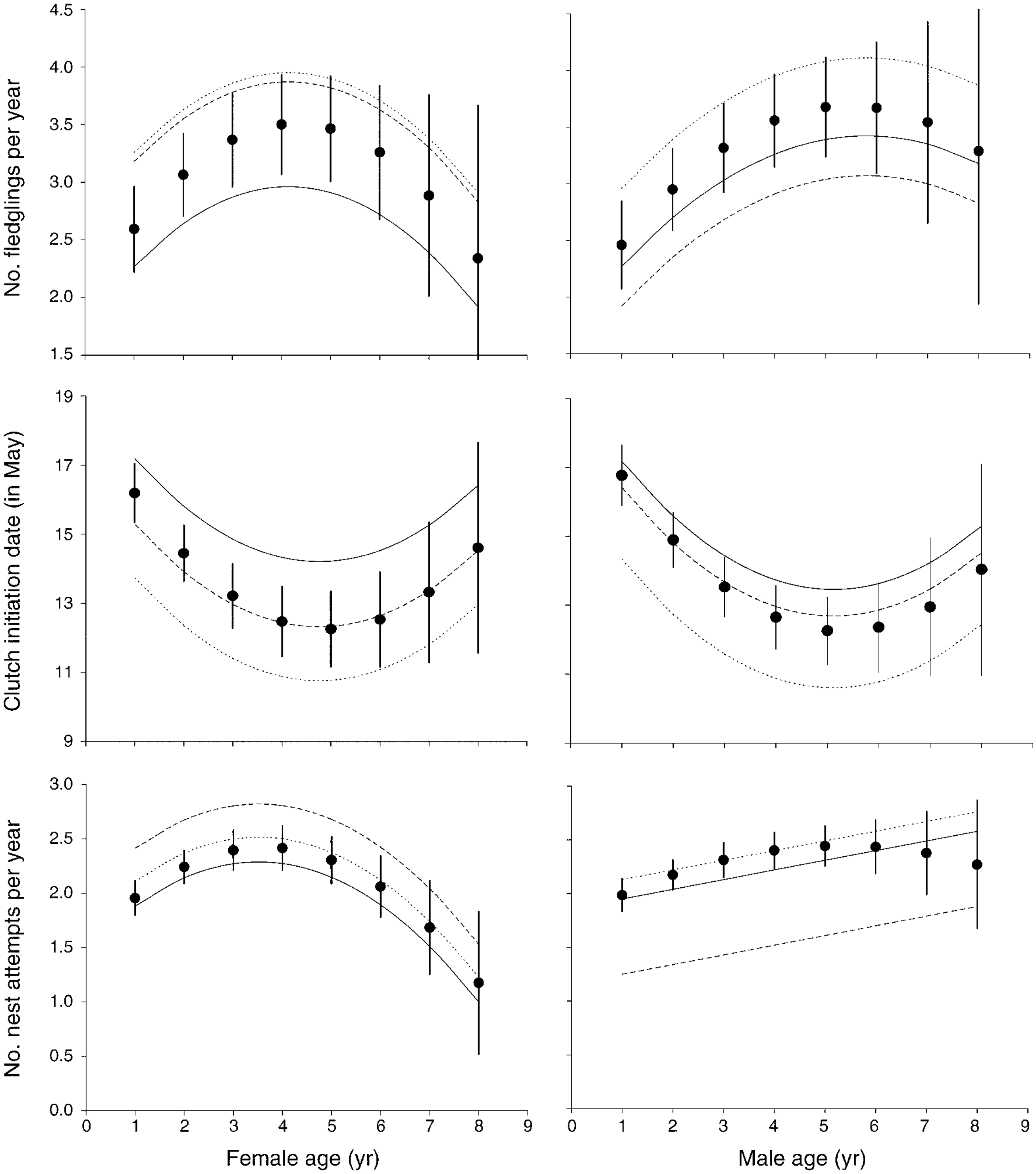

FIG. 1. Age- and sex-specific fledgling production, date of clutch initiation, and annual number of nesting attempts based on hierarchical linear models. Solid circles and SE bars represent sex-specific results when the age of the mate was not included in the model; individual pair members, year of breeding, and individual × year interactions were specified as random terms. When entered, the age of the mate significantly influenced all models. To illustrate the effect of the age of the mate, solid lines represent modeled results when the mate was a yearling, dotted lines indicate four-year-old mates, and dashed lines represent results when the mate was eight years old (results are not shown for every possible age of the mate). There was a quadratic effect of the age of the mate on fledgling production and clutch initiation dates. Male age had a linear effect on the annual number of female nesting attempts, whereas female age had a quadratic effect on the annual number of male nesting attempts. See Table 4 for relevant statistics.

youngest or oldest males (Table 4, Fig. 1). The number of annual nesting attempts followed a pattern inversely related to that of clutch initiation: middle-aged females had more nest attempts than the youngest and oldest females (Table 4, Fig. 1). Unlike fledgling production and date of clutch initiation, there was a linear effect of male age on the annual number of nesting attempts by females. Females of any age that paired with the oldest males attempted more nests per year than females paired with younger males (Table 4, Fig. 1).

TABLE 5. The effect of the age of last reproduction (ALR) on age-specific fledgling production in Wood Thrushes.

Effects	Estimate	SE	df	F	P
Random					
Male	0.02				
Female	0				
Year	0.15				
Male × female	0				
Year × male	0.43				
Year × female	0				
Residual	0.34				
Fixed					
Intercept	−0.95	0.85	1, 370	23.5	<0.0001
Female age	0.2	0.12	1, 467	2.8	0.09
Female age^2	−0.02	0.02	1, 471	1.7	0.19
Male age	0.3	0.1	1, 464	9	0.003
Male age^2	−0.03	0.01	1, 471	3.7	0.05
Female ALR	0.17	0.1	1, 472	2.8	0.09
Female ALR^2	−0.02	0.01	1, 472	3.7	0.05

Notes: Hierarchical linear models with random effects were built with male and female age, ALR, and interactions of these terms as explanatory variables. Only significant terms are presented, except for the quadratic pattern of female age on fledgling production, which was retained. The significance of the female ALR terms indicates that inferior females disappeared from the population. Data are from the University of Delaware Woods, 1974–2004, and include 576 nesting attempts of known-age pairs.

There was a quadratic effect of female age on male reproductive success. At any age, males that paired with the youngest or oldest females produced fewer fledglings than those paired with a middle-aged female (Table 4, Fig. 1). If only linear terms were used in the model (see McCleery and Perrins 1988), only male age influenced fledgling production; female age and the interaction term were not significant (not shown). There was no age-related pattern of recruit production in males (Table 4).

The date of clutch initiation was earliest in middle-aged males and included a quadratic effect of female age on the relationship (Table 4, Fig. 1). That is, middle-aged males paired with middle-aged females nested earlier in the season than any other combination of age pairings.

There was a quadratic effect of female age on the annual number of nests attempted by males (Table 4, Fig. 1). At any age, pairing with a middle-aged female resulted in the greatest number of annual nest attempts. Although the oldest males were predicted to have the greatest number of nesting attempts (Table 4), there was no difference in this measure among males older than four years of age (examined separately).

Survival

For females, the probability of annual survival, indicated by returning to breed the following season, fluctuated with no clear age-related pattern (Fig. 2). Although a quadratic logistic regression using maximum likelihood estimates and random effects seemingly modeled this response, a poor goodness-of-fit statistic rendered the model unacceptable (Hosmer-Lemeshow goodness of fit = 12.6, df = 5, $P = 0.03$). For males, the observed pattern of an increase, then decrease, in survival probability with increasing age was successfully modeled (Fig. 2).

Based on P values not corrected for Type I error rate, the production of Wood Thrush fledglings had a positive effect on female survival, particularly yearling females, and the number of nesting attempts positively influenced the survival of middle-aged males (Table 6). No other measures of reproductive output examined positively or negatively influenced the survival of either sex. Different results were obtained if year of breeding and individual females were not specified as random effects in these models; individual males had little effect on results. After correcting for potential Type I errors using the false discovery rate method (García 2004), no relation-

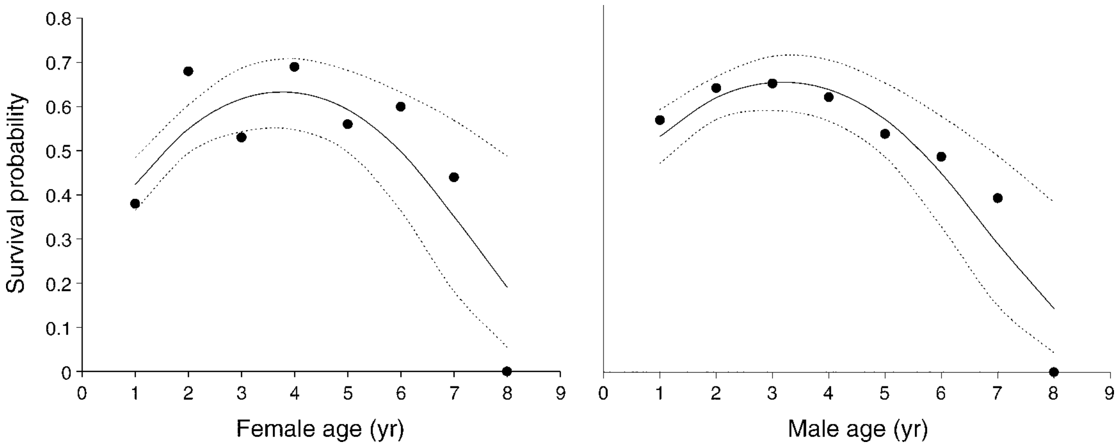

FIG. 2. Age-specific survival probabilities of male and female Wood Thrushes that bred in the University of Delaware Woods, 1974–2004. Generalized estimating equations were used to control for the covariance of survival with year, individual, and year × individual effects. For females, the apparent fit of a quadratic model to survival observations was nullified by a poor goodness-of-fit statistic. For males, the probability of survival increased and then decreased with increasing age. Dashed lines represent 95% confidence intervals.

TABLE 6. The effect of four measures of reproductive output on the survival (a binary term) of age classes of male and female Wood Thrushes.

		Female survival						Male survival					
Measure of reproductive output	Ages (yr)	Estimate	SE	df	*F*	Raw *P*	FDR-corrected *P*	Estimate	SE	df	*F*	Raw *P*	FDR-corrected *P*
Clutch initiation	All	0.01	0.01	1, 203	0.6	0.44	0.72	0.00	0.01	1, 268	0.1	0.74	0.85
	1	−0.01	0.01	1, 228	1.9	0.18	0.64	0.01	0.01	1, 196	1.7	0.20	0.64
	2–5	0.01	0.01	1, 87	0.4	0.51	0.74	−0.01	0.01	1, 127	1.0	0.31	0.72
	6–8	−0.03	0.05	1, 6	0.3	0.58	0.74	−0.03	0.04	1, 10	0.6	0.46	0.72
Wood Thrush fledglings	All	0.09	0.05	1, 211	4.1	0.04	0.47	0.06	0.04	1, 282	2.2	0.14	0.56
	1	0.19	0.07	1, 263	0.8	0.01	0.16	0.02	0.07	1, 205	0.1	0.77	0.85
	2–5	0.00	0.06	1, 89	0.0	0.97	0.97	0.09	0.06	1, 133	2.4	0.12	0.56
	6–8	0.32	0.24	1, 7	1.7	0.23	0.64	−0.18	0.24	1, 10	0.6	0.46	0.72
Recruits	All	0.19	0.26	1, 211	0.6	0.46	0.72	0.14	0.24	1, 282	0.3	0.57	0.74
	1	0.16	0.41	1, 236	0.2	0.70	0.83	0.32	0.37	1, 205	0.7	0.40	0.72
	2–5	−0.15	0.36	1, 89	0.2	0.67	0.83	−0.02	0.34	1, 133	0.0	0.95	0.97
	6–8	1.10	1.11	1, 7	1.0	0.36	0.72	0.69	1.10	1, 10	0.4	0.55	0.74
Nesting attempts	All	0.16	0.11	1, 192	2.2	0.14	0.56	0.15	0.10	1, 281	2.2	0.14	0.56
	1	0.20	0.17	1, 193	1.4	0.24	0.64	−0.27	0.17	1, 205	2.5	0.12	0.56
	2–5	0.03	0.16	1, 77	0.0	0.85	0.91	0.41	0.14	1, 132	8.4	0.004	0.13
	6–8	0.42	0.49	1, 5	0.8	0.43	0.72	−0.38	0.51	1, 10	0.6	0.47	0.72

Notes: Year of breeding and individual pair members were prescribed as random effects to account for nonindependence of data. Given that these results include repeated tests of the same data, both raw *P* values and *P* values in which the false discovery rate (FDR) was controlled at the 0.05 level are reported for each measure of reproductive output.

ships among measures of reproductive output and survival remained significant (Table 6).

DISCUSSION

Senescence was evident in all measures of reproductive output. Patterns of age-related reproduction and survival differed between the sexes, however, and were not completely accommodated by any of the hypotheses examined. Among available hypotheses, we prefer the selection hypothesis as an explanation for improved reproductive output and survival probabilities with increasing female age, at least until middle age. Accounting for the random effects of individuals and year(s) of breeding, the age of last reproduction in females influenced age-related fledgling production of the cohort, indicating the loss of inferior phenotypes over time. Survival probabilities among age classes also support our preference for the selection hypothesis: SY females, especially, were less likely to return to a site after a failed nesting attempt (Weinberg and Roth 1998, Brown and Roth 2002). Additionally, SY females had a lesser rate of return the following season than any other sex- or age-class; no differences in survival existed among SY males, ASY males, and ASY females (Brown and Roth 2002). Survival estimates, generally recognized to include components of both actual survival and post-season emigration, may be further confounded by dispersal during the breeding season (see Weinberg and Roth 1998, Brown and Roth 2002). Why SY female Wood Thrushes may be more likely than other age groups to disperse after a nest failure (or why the inverse may be true) remains to be determined.

Related to intra-seasonal dispersal, survival probabilities of fledglings and yearlings reported in the life tables are biased by the assumption that emigration equals immigration. The life tables (see Tables 1 and 2) indicated that female fledglings survived better than male fledglings but that SY females survived less well than SY males. These perceived discrepancies may be due, in part, to greater SY female emigration and replacement during the breeding season. Some turnover also occurred with SY males, but probably to a lesser extent (Weinberg and Roth 1998, Brown and Roth 2002). Because greater SY female turnover resulted in a greater count of SY females than SY males, it seemed that fledgling females had a greater rate of survival than fledgling males. Likewise, greater turnover of SY females will give the appearance of greater SY male survival to age 2. Sex-specific differences in survival based on life table values are largely because of differential dispersal or survival between SY females and all other groups.

There was no supporting evidence for other hypotheses related to improvements in reproductive success with increasing female age until middle age. Although reproductive effort is difficult to define and measure on the scale of the individual, obvious measures such as date of clutch initiation, number of nesting attempts, number of fledglings, and number of recruits per season indicate that the oldest females are not exerting greater reproductive effort later in life, nor were these variables related to survival probabilities. Reproductive output did not influence the probability of male survival, either. In particular, the restraint hypothesis suggests that reproductive effort increases with age because reproductive value declines. There was a positive correlation between reproductive value and annual fledgling production among Wood Thrushes, however, which does not follow the prediction of this hypothesis.

We prefer the constraint hypothesis, in which reproduction increases with age because of greater breeding competence or experience, to explain an increase in reproduction in male Wood Thrushes with increasing age. Many studies favor the constraint hypothesis to explain age-related improvements in reproduction (Desrochers and Magrath 1993, Espie et al. 2000, Green 2001, Murphy 2004, Balbontín et al. 2007), yet experience may be confounded with age-dependent effects. The influence of age persisted in those studies that experimentally manipulated breeding experience, with older birds outperforming younger birds of similar experience (Martin 1995). ASY males had greater nest success than SY males at UDW, which was related to greater success during the laying stage (Brown and Roth 2002). Differential nest attendance or defense might cause reproductive differences between experienced and inexperienced birds (Green 2001), or SY birds and all others in this instance.

Neither the selection hypothesis nor the recruitment hypothesis (the appearance of delayed breeders causing an increase in age-specific reproduction) was supported by results for males. Although delayed breeding was not explicitly studied in this species, 89% of immigrants were SY birds (see *Methods*), which bred at that age. Any previous reproductive attempts by immigrant ASY birds could not be determined. The recruitment hypothesis has received little empirical support outside of studies on long-lived seabirds (e.g., Mauck et al. 2004, but see Reid et al. 2003).

As with females, we found no support for the restraint hypothesis in males. This hypothesis predicts greater reproductive effort at advanced ages because of a lesser probability of survival (Williams 1957, 1966). The restraint hypothesis may instead apply at any age when prospects of survival are relatively low. For example, SY Wood Thrushes had lesser survival estimates than all but the very oldest individuals; the oldest birds were the first to complete the breeding season and may be the first to leave the breeding grounds (Brown and Roth 2002). SY birds at UDW have nested later into the breeding season than ASY birds, when nests were more successful, but may trade off greater late-season reproductive success against a lesser probability of survival during migration or winter (Brown and Roth 2002).

Few other studies have examined the independent effects of male and female age on reproduction and the effect of male age is not well documented in general (McCleery and Perrins 1988, Daunt et al. 1999, Green 2001). Although some studies found that only female age influenced fledging success (e.g., Lessels and Krebs 1989, Reid et al. 2003), fledging success in Brown Thornbills (*Acanthiza pusilla*), as well as fledgling survival to independence, was dependent only on the age of the male. The ability to deter predators, and be less conspicuous to predators, may increase with male age in Thornbills (Green 2001). Similarly, older male Great Tits (*Parus major*) hold larger territories than younger males and may reduce predation through the increased spacing of nests. Older male Great Tits also may be better at providing food for their newly fledged offspring (McCleery and Perrins 1988). ASY male European Blackbirds (*Turdus merula*) are better providers than SY males (Desrochers 1992), but we do not know how provisioning ability changes with age for Wood Thrushes. The issue of territory size and food availability has not been explored at UDW but is likely irrelevant given the size of the remnant (~15 ha) and rather high density of breeding Wood Thrushes; active nests were occasionally located within 25 m of each other, sometimes closer (W. P. Brown and R. R. Roth, *personal observation*). Familiar neighbors also may cooperate in nest defense and increase reproductive success among participants (Beletsky and Orians 1989). There is a male bias to the social structure of the Wood Thrush (see genetic value, Tables 1 and 2), as in most passerines (Greenwood and Harvey 1982), but the extent of defensive cooperation among relatives or neighbors is not known. The oldest male Wood Thrushes should have the greatest number of relatives concurrently breeding in the study population, especially if this is a cumulative phenomenon. It remains to be determined if there is a reproductive advantage to individual Wood Thrushes conferred by familiar neighbors or proximity to relatives.

Senescence

Hypotheses of age-specific reproduction only apply until antagonistic pleiotropy or mutation accumulation (Medawar 1946, Williams 1966) takes effect. This point is not explicit in reviews on the subject, in which only monotonic relationships between age and reproduction are considered. For females, reproductive success and survival probabilities began declining at approximately age 6. Male reproductive performance increased or leveled out with increasing age, whereas the probability of survival peaked in middle-aged males before declining in the oldest individuals. Thus, both sexes exhibited senescence. Evolutionary theories of senescence predict that if extrinsic causes of mortality are high there is stronger selection on early reproduction and weaker selection for survival and reproductive success later in life (Williams 1957). Both sexes peaked in reproductive output in middle age, which is not consistent with these hypotheses. Causes of extrinsic mortality may not be independent from the genetic composition and developmental state of individuals, however, which further complicates interpretations of mechanisms related to reproduction and survival. Young, old, or infirm individuals may experience elevated rates of depredation relative to other members of the population (Longland and Jenkins 1987).

Why were there age-specific differences in reproduction among Wood Thrushes? In previous analyses

(Brown and Roth 2002), a greater proportion of recruits were produced from early nests, yet early nests failed at a greater rate than later nests. This finding suggests an ultimate reason for why early nesting is important, despite the greater predation costs. The disproportionate failure of early season nests was due to greater depredation of nests belonging to SY pairs. Additionally, SY pairs suffered greater rates of partial loss of nest contents from early season nests and were more likely to fail in the laying stage than older pairs (Brown and Roth 2002). Thus, age-related effects were strongest early in the breeding season, with the potential for differences to accumulate or to attenuate over the course of the season. Older birds that begin breeding sooner may produce larger clutches, have more opportunities for re-nesting attempts, and be better able to re-nest after failure (Desrochers and Magrath 1993, Martin 1995, Balbontín et al. 2007). In this study, both the youngest and oldest Wood Thrushes started nesting later in the season and had fewer nest attempts per year than individuals at their peak of reproduction. These proximate mechanisms account for an increase in reproductive success until middle age, but also account for the patterns of reproductive senescence observed here. Differences between the sexes can be explained by disproportionate SY female emigration, turnover, or survival.

None of the hypotheses of age-related reproduction examined, all of which predict an increase in reproductive output with increasing age, was fully supported by our data. The effects of senescence, including independent patterns of senescence in the opposite sex, may confound attempts to examine or apply general hypotheses of age-related reproduction that assume a monotonic relationship between age and reproduction or survival.

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APPENDIX A

A map of the 15-ha University of Delaware Woods, surrounding forest cover, and road system in New Castle County, Delaware, as of 1997 (*Ecological Archives* E090-014-A1).

APPENDIX B

The number of breeding female and male Wood Thrushes per year at the University of Delaware Woods, 1974–2004 (*Ecological Archives* E090-014-A2).

APPENDIX C

A composite cohort life table of all Wood Thrushes at the University of Delaware Woods, 1974–2004 (*Ecological Archives* E090-014-A3).