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AGE-SPECIFIC REPRODUCTION IN THREE SPECIES OF EUROPEAN DUCKS

PETER BLUMS,[1,3] GARY R. HEPP,[2] AND AIVARS MEDNIS[1]

[1] *Institute of Biology, University of Latvia, Miera 3, LV-2169, Salaspils, Latvia; and*

[2] *Department of Zoology and Wildlife Science, Auburn University, Auburn, Alabama 36849, USA*

ABSTRACT.—We tested the effects of female age on reproductive performance of Northern Shovelers (*Anas clypeata*), Tufted Ducks (*Aythya fuligula*), and Common Pochards (*A. ferina*) based on a long-term study (1958 to 1995) at Engure Marsh, Latvia. Yearling females initiated nests later than older (≥2 years) females in each species, but female age explained little of the remaining variation in reproductive performance. Clutch size and brood size of all species declined seasonally. Age-specific increases in reproductive performance were most consistent between 1 and 2 years of age and were more apparent in the diving ducks than in Northern Shovelers. Clutch size, brood size, and duckling mass of yearling Tufted Ducks, and brood size and duckling mass of yearling Common Pochards, were smaller than those of older females. In Northern Shovelers, only duckling mass increased with age of the female. Nesting and hatching success did not vary by age for any species. Among 2-year-old females with and without previous breeding experience, experienced females nested five to six days earlier than inexperienced females in all species. Experienced, 2-year-old Tufted Ducks also had larger clutches and broods than inexperienced females. Effects of breeding experience generally lasted for only a single breeding season. Nesting date and duckling mass of yearling Northern Shovelers did not differ from that of inexperienced 2-year-olds. However, inexperienced 2-year-old Tufted Ducks and Common Pochards nested earlier and produced larger ducklings than did yearling females. Brood size of inexperienced, 2-year-old Common Pochards also was larger than that of yearlings. We found no evidence that age-specific increases in reproductive performance were related to differential survival of good breeders. Reproductive performance was constrained by past breeding experience in Northern Shovelers and by age and experience in Tufted Ducks and Common Pochards. *Received 19 August 1996, accepted 22 May 1997.*

REPRODUCTIVE PERFORMANCE varies with parental age in many species of birds (Sæther 1990). Young birds commonly nest later in the season, produce smaller clutches, and have lower fledging success than older conspecifics (Sæther 1990, Forslund and Pärt 1995, Martin 1995). A better understanding of whether age influences reproduction is important for studies of demography and life-history evolution (Clutton-Brock 1988).

Hypotheses proposed to explain age-specific variation in reproduction have focused on the concepts of constraint and restraint, which are not mutually exclusive (Curio 1983, Rohwer 1992). The constraint hypothesis proposes that young individuals lack some skill essential for high reproductive performance. Developmental or behavioral constraints, for example, may reduce foraging success of young birds (Marchetti and Price 1989), thereby lowering reproductive performance (Desrochers 1992a). The restraint hypothesis suggests that the young are not less skilled than adults, but rather that they increase their probability of future reproduction by limiting current reproduction. This idea is based on life-history theory; i.e. residual reproductive value declines with age because of lower age-specific survival and reproduction (Curio 1983, Stearns 1992). In essence, reproductive events become more valuable with age; hence, older individuals invest more in reproduction than do younger individuals, causing age-specific differences in reproductive performance. Increased age-specific breeding performance also may result from differential survival of the more successful breeders (Clutton-Brock 1988, Rohwer 1992).

We use data from a long-term study of breeding waterfowl on the Engure Marsh in Eastern Europe to examine age-specific (1 to 6 years old) differences in reproductive performance of

[3] Present address: Gaylord Memorial Laboratory, School of Natural Resources, University of Missouri-Columbia, Puxico, Missouri 63960, USA. E-mail: gaylord@sheltonbbs.com

Northern Shovelers (*Anas clypeata*), Tufted Ducks (*Aythya fuligula*), and Common Pochards (*A. ferina*). Northern Shovelers (hereafter "shoveler") are dabbling ducks (tribe Anatini) that forage on the surface or by tipping up in shallow water; they are mostly omnivorous. Common Pochards (hereafter "pochard") and Tufted Ducks (tribe Aythyini) typically dive for their food and also are omnivorous. Most females of each species begin nesting in their first breeding season (Blums et al. 1996). Most nests of pochards and Tufted Ducks at Engure Marsh were built on floating mats of emergent vegetation, and shovelers nested on vegetated islands.

We separately test the effects of breeding experience and age on reproductive performance. We also examine whether differential survival of successful breeders is responsible for the positive relationship between breeding performance and age by comparing initial reproductive performances of yearling females that survive to the next breeding season with yearlings that do not survive.

STUDY AREA AND METHODS

The study was conducted from 1958 to 1995 on Engure Marsh (35 km^2) located on the east coast of the Baltic Sea (57°15′ N, 23°07′ E) in Latvia, Eastern Europe. The study site is a shallow, permanently flooded palustrine marsh (Cowardin et al. 1979) dominated by robust hydrophytes such as common reed (*Phragmites australis*) and cattail (*Typha* spp.).

Permanent sampling areas from 1958 to 1981 included five natural islands with total surface area at low water of approximately 20 ha. Large portions of these islands were flooded during conditions of high water and were not always suitable for nesting. To maintain more stable breeding conditions, many elevated islands were constructed on the flooded sections of two natural islands from 1981 to1983 (Blums and Mednis 1991). Beginning in 1984, 82 islands with a total area of 14.3 ha were available for nesting within the previous island habitat. In addition to natural and artificial islands, nest searches were expanded beginning in 1972 to include three isolated areas of persistent emergent marsh totaling 111 ha. Thus, permanent sampling areas included natural and artificial islands (1958 to 1995) and emergent marshes (1972 to 1995).

For the last 20 years, Engure Marsh has supported about 2,000 breeding pairs of ducks; pochards, Tufted Ducks, and shovelers comprised 60% of the total pairs. From 1977 to 1993, average numbers of breeding pairs on the entire marsh consisted of the following: 900 pochards (range 560 to 1,640), 280 Tufted Ducks (range 160 to 360), and 33 shovelers (range 19 to 59; Blums et al. 1993). We estimated that approximately 99%, 42%, and 23% of shovelers, Tufted Ducks, and pochards, respectively nested within permanent sampling areas.

Nesting data.—Each year, two to three complete searches for duck nests on permanent sampling areas were conducted between mid-May and late-June. All breeding habitats within permanent sampling areas were systematically searched to locate nests by walking parallel transects. Distances between transects were adjusted from 1.5 to 3.0 m in relation to height and density of vegetation. We believe the effectiveness of nest searches was very high because sampling areas were assigned to biologists who worked on the same areas for 10 to 30 consecutive field seasons and were familiar with potential nest sites. Experimental burns on islands, after last nests hatched, verified that >95% of all nests were found each year. Any scrape with two or more eggs was considered a nest.

Nests were found during egg laying (23%) or after incubation had commenced (77%). At each nest we recorded the date found, location, number of eggs in and out of the nest bowl, and incubation stage of eggs. To determine the day of incubation we initially used the flotation method (Westerskov 1950), which was calibrated for each species (Mihelsons and Blums 1976). Gradually, however, we switched to candling (Sobkowiak and Bird 1984) using guides to aging of embryos (Klett et al. 1986). Nest-initiation dates were estimated by subtracting the sum of the total number of eggs and number of days eggs had been incubated from the date that nests were first discovered. Females of each species generally laid one egg per day, which is consistent with other studies of these species (Bezzel 1969, Bellrose 1976, Alisauskas and Ankney 1992).

Conspecific brood parasitism was common in Tufted Ducks and pochards but rare in shovelers. The following factors, singly or in combination, provided evidence that a nest had been parasitized: laying rate exceeded one egg per day, eggs were different in coloration and shape, incubation stages of eggs were widely different, one or more eggs were found outside the nest bowl, and clutch sizes were ≥14 for shovelers and pochards and ≥15 for Tufted Ducks.

A nest was considered successful if at least one duckling hatched and exited the nest. Hatching success was the percentage of eggs in nests that produced ducklings (Nichols and Johnson 1990). Brood size was the number of ducklings that hatched and exited the nest. From 1978 to 1995, ducklings were weighed (± 1 g) with a 100-g Pesola scale.

Breeding females.—We captured females on nests during the last week of incubation using drop-door traps (Blums et al. 1983) or dip nets; unmarked females were banded with conventional leg bands. Female body mass was measured to the nearest 10 g with 1,000-g or 1,500-g Pesola scales (1978 to 1995). Body masses were corrected to the third (shoveler) or fourth day (diving ducks) before hatching (ducklings in the nest), when the greatest proportion of females were captured, by regressing female body mass against day of incubation (n = 483 shovelers, 2,096 Tufted Ducks, and 3,572 pochards).

We obtained a sample of known-age females using two methods. First, day-old ducklings were captured at nests in 1958 to 1995 and individually marked with plasticine-filled leg bands (Blums et al. 1994). Subsequent recaptures of these birds allowed us to assign them an exact age. Second, beginning in 1976, unmarked females captured during incubation were aged as either yearlings (i.e. ca. 1 year old) or adults ($\geq$2 years old) using wing-feather characteristics (i.e. shape and coloration of greater secondary coverts; Blums et al. 1996). In addition, eye color was used to age female Tufted Ducks (see Trauger 1974, Blums et al. 1996:63), although some overlap in color existed between yearlings and older females. Females aged as yearlings with these techniques provided us with another group of known-age individuals.

Data analysis.—Analyses of age-specific variation in reproductive performance were restricted to data from 1978 to 1995, because body mass of incubating females and their ducklings were not measured before 1978. Analyses that did not use duckling mass or female mass included data from earlier in the study period. Nest-initiation date, clutch size, brood size, mean duckling mass, nesting success, and hatching success were used as measures of reproductive performance. In all analyses, unless noted otherwise, we used the first nesting attempts of the season and restricted our analyses of clutch size, brood size, mean duckling mass, and hatching success to nonparasitized nests. One-way analysis of covariance (ANCOVA) was used to test effects of female age (1 to 6 years) on clutch size, brood size, mean duckling mass, and hatching success. Date (either standardized nest initiation date or standardized hatching date) and adjusted female body mass were used as covariates. One-way ANCOVA with female body mass as the covariate was used to test the effect of female age on standardized nesting date. Nest-initiation date and hatching date were standardized to control for annual variation by expressing them as deviations from initiation and hatching dates of the first 10% (Tufted Duck and pochard) or 30% of nests (shoveler) each year. We tested whether slopes were homogeneous for all ANCOVAs and used Tukey-Kramer multiple comparisons tests to separate significant age effects (Day and Quinn 1989). Because the probability of nest abandonment was significantly higher for nests with more than six parasitic eggs (Dugger 1996), we excluded such nests before using likelihood-ratio tests to examine the association between nesting success and female age (Sokal and Rohlf 1981).

We used t-tests to compare breeding performance of 2-year-old females with and without previous breeding experience (the breeding experience hypothesis), and to compare reproductive performance of yearlings with 2-year-olds nesting for the first time (the age hypothesis). The sample of inexperienced females was limited to individuals that were marked as ducklings in permanent plots. We eliminated 2-year-old females that were not marked as ducklings at permanent plots because these individuals may have nested elsewhere as yearlings and then moved to permanent plots in their second year. Changing nesting areas is known to delay initiation of nests in some ducks (Hepp and Kennamer 1992), and we wanted to reduce this source of variation. We also used t-tests to examine the differential survival hypothesis by comparing reproductive performance of yearling females that survived to the next breeding season with that of yearlings that did not survive. Earlier analyses of band recoveries and capture-recapture data indicated that permanent emigration was virtually nonexistent (see Blums et al. 1996).

Results

Age-specific differences.—Clutch size and brood size of shovelers did not vary with female age (Table 1), but yearling females produced smaller ducklings and nested later than older females (Table 2, Fig. 1). Clutch size and brood size of shovelers declined as the season progressed, and heavy females produced larger ducklings than did light females (Tables 1 and 2). All measures of reproductive performance varied with age of female Tufted Ducks, but the covariates, nesting date and female body mass, explained more variation than did female age (Table 1 and 2). Clutch size and brood size declined as the nesting season progressed, and heavy females produced larger ducklings and nested earlier in the season than did light females. Clutch size of pochards did not vary with female age, but older females produced larger broods and ducklings, and initiated nests earlier than young females (Tables 1 and 2). As with Tufted Ducks, nesting date and female body mass explained most of the variation in reproductive performance. Clutch size and brood size were larger early in the season, and heavy female pochards produced larger broods and larger ducklings than did light females.

Nesting success was not associated (likeli-

TABLE 1. One-way analysis of covariance testing effects of female age (1 to 6 years) on clutch size, brood size, and duckling mass for three species of European ducks. Date and female body mass are used as covariates.

	Clutch size			Brood size			Duckling mass		
Source	F	df	P[a]	F	df	P	F	df	P
Northern Shoveler									
Age	0.6	5, 366	NS	0.7	5, 345	NS	2.7	5, 321	*
Date[b]	76.2	1, 366	***	18.6	1, 345	**	3.4	1, 321	NS
Female body mass	13.7	1, 366	**	4.1	1, 345	*	27.4	1, 321	***
R^2		0.28			0.11			0.14	
Tufted Duck									
Age	3.6	5, 1,170	**	9.8	5, 930	**	3.5	5, 994	**
Date	165.3	1, 1,170	***	9.4	1, 930	**	2.1	1, 994	NS
Female body mass	0.4	1, 1,170	NS	1.3	1, 930	NS	88.3	1, 994	***
R^2		0.25			0.12			0.15	
Common Pochard									
Age	1.7	5, 1,571	NS	5.2	5, 1,167	***	19.8	5, 1,296	***
Date	546.1	1, 1,571	***	90.7	1, 1,167	***	0.8	1, 1,296	NS
Female body mass	1.8	1, 1,571	NS	5.6	1, 1,167	*	35.2	1, 1,296	***
R^2		0.38			0.21			0.17	

[a] NS, $P > 0.05$; *, $P < 0.05$, **, $P < 0.01$; ***, $P < 0.0001$.

[b] Standardized nest initiation date for clutch size and standardized hatching date for brood size and duckling mass.

hood-ratio tests; all $Ps > 0.05$) with female age for any of the species. Overall ANCOVA models testing the relationship between hatching success and female age also were not significant (all $Ps > 0.05$) for any species.

Experience, age, and differential survival.—Only reproductive variables that we found to be age-specific were tested to evaluate the relative influences of female breeding experience, female age, and differential survival on reproduction. Reproductive performance of 2-year-old females that nested as yearlings (experienced) were compared with those of 2-year-old females that did not nest as yearlings (inexperienced). Experienced 2-year-old female Tufted Ducks nested earlier and produced larger clutches and broods than did inexperienced 2-year-old females (Table 3). Duckling mass and female body mass, however, did not differ ($P > 0.05$) between experienced and inexperienced females (Table 3). Experienced 2-year-old pochards nested about five days earlier than inexperienced 2-year-old females, but brood size, duckling mass, and body mass did not differ ($P > 0.05$) between experienced and inexperienced females (Table 3). Experienced 2-year-old shoveler females nested approximately five days earlier than inexperienced females ($P = 0.0001$), but body mass of inexperienced (499 g) and experienced (499 g) females did not differ ($P = 0.55$). Experienced shovelers also did not produce larger ducklings than did inexperienced females (27.2 vs. 27.3 g, $P = 0.87$).

To determine how long the effects of breeding experience persisted, we used a subset of inexperienced and experienced 2-year-olds that also nested as 3-year-olds (Table 3). Effects of early breeding experience did not carry over and influence nest-initiation dates of 3-year-old Tufted Ducks, pochards, and shovelers, or

TABLE 2. Analysis of covariance testing effects of female age (1 to 6 years) on nesting date of three species of European ducks. Female body mass at the end of incubation is used as the covariate.

	Nesting date		
Source	F	df	P[a]
Northern Shoveler			
Age	11.2	5, 373	***
Female body mass	1.8	1, 373	NS
R^2		0.17	
Tufted Duck			
Age	127.0	5, 1,246	***
Female body mass	6.4	1, 1,246	*
R^2		0.39	
Common Pochard			
Age	161.5	5, 1,681	***
Female body mass	0.4	1, 1,681	NS
R^2		0.36	

[a] NS, $P > 0.05$; *, $P < 0.05$; *** $P < 0.0001$.

clutch size of Tufted Ducks (Table 3). However, female Tufted Ducks that nested as yearlings had larger broods at 3 years of age than did females that did not nest as yearlings.

Next, we compared the reproductive performance of inexperienced, 2-year-old females with that of yearlings. These tests controlled for differences in breeding experience (both groups of females were inexperienced) while testing for the effects of female age on reproduction. Clutch size and brood size of Tufted Ducks did not differ between inexperienced 1- and 2-year-old females (Table 4). However, inexperienced, 2-year-olds nested earlier, produced larger ducklings, and weighed more than did yearlings (Table 4). For pochards, all measures of reproductive performance were greater for inexperienced, 2-year-olds than for yearlings (Table 4). Nesting date and duckling mass of yearling and inexperienced 2-year-old shovelers did not differ ($P > 0.05$), but body mass of inexperienced, 2-year-olds was greater than that of yearlings (Table 4).

To test the differential survival hypothesis, reproductive performance of yearling females that survived to the next breeding season (year $t + 1$) was compared with that of yearling females that did not survive to year $t + 1$. Greater reproductive performance of surviving females would give support to the hypothesis. There was no evidence ($P > 0.05$) for any species that yearling females surviving to year $t + 1$ had larger clutch size, larger brood size, larger duckling mass, larger body mass, or nested earlier than did yearlings that did not survive.

Discussion

Age-specific differences.—We have shown that older females (i.e. ≥2 years old) of three species of ducks initiate nests earlier than yearlings. Measures of reproductive performance, such as

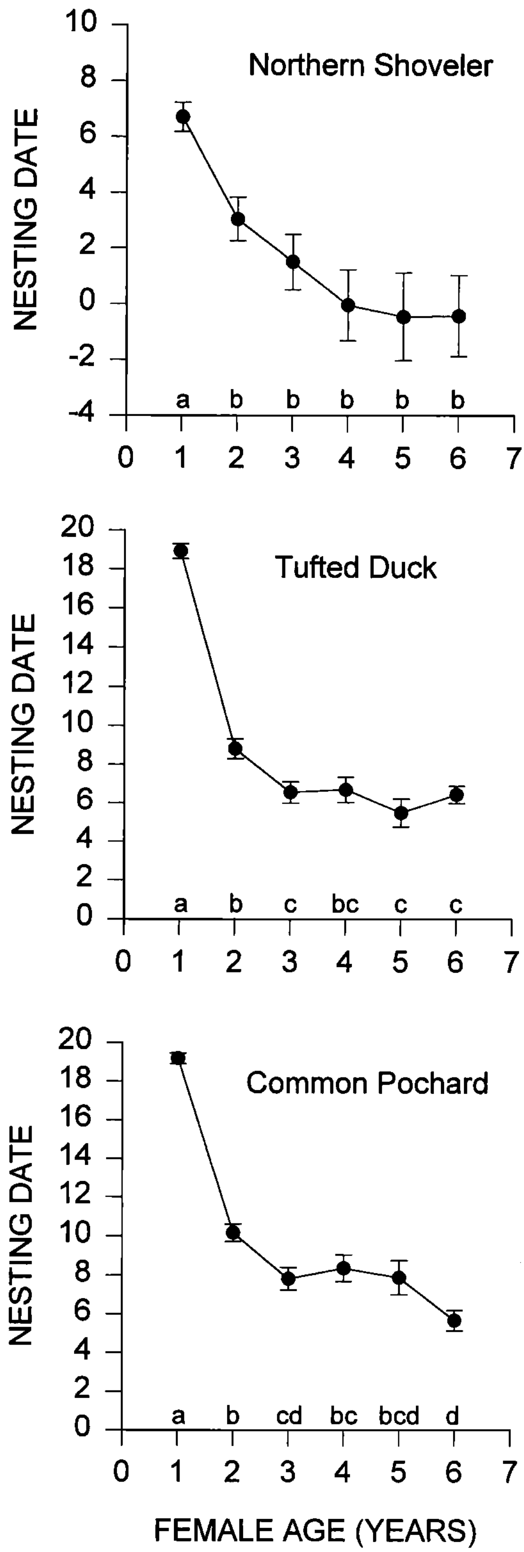

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FIG. 1. Age-specific least-squares means (± SE) of standardized nesting date for three species of ducks breeding at Engure Marsh, Latvia. Individual nesting dates were standardized as deviations from the 10th percentile (Tufted Duck and Common Pochard) or the 30th percentile (Northern Shoveler) of nests each year. Mean nesting dates denoted by different letters above the x-axis are significantly different ($P \leq 0.05$).

TABLE 3. Mean values (n) of reproductive performance of 2- and 3-year-old female Tufted Ducks and Common Pochards that did not nest as yearlings (I, inexperienced) or nested as yearlings (E, experienced). If there were no differences for individual parameters among 2-year-olds, no further comparisons were conducted. P-values are from t-tests comparing inexperienced vs. experienced females within age classes.

	Tufted Duck			Common Pochard		
	2-year-olds	2-year-olds[a]	3-year-olds	2-year-olds	2-year-olds[a]	3-year-olds
			Clutch size			
I	8.6 (46)	8.4 (25)	9.5 (25)	—	—	—
E	9.3 (225)	9.3 (95)	9.7 (95)	—	—	—
P[b]	**	**	NS	—	—	—
			Brood size			
I	8.1 (39)	7.3 (19)	8.2 (19)	7.3 (64)	—	—
E	8.6 (186)	8.9 (72)	9.3 (72)	7.7 (180)	—	—
P	*	**	**	NS	—	—
			Duckling mass (g)			
I	33.8 (33)	—	—	44.0 (56)	—	—
E	38.9 (132)	—	—	44.7 (183)	—	—
P	NS	—	—	NS	—	—
			Nesting date[c]			
I	13.1 (51)	12.4 (28)	6.7 (28)	14.1 (91)	14.0 (22)	6.5 (22)
E	7.4 (219)	7.1 (103)	5.5 (103)	8.4 (219)	10.9 (51)	6.7 (51)
P	**	**	NS	***	NS	NS
			Body mass (g)[d]			
I	630 (43)	—	—	777 (108)	—	—
E	630 (196)	—	—	784 (306)	—	—
P	NS	—	—	NS	—	—

[a] Subset of inexperienced and inexperienced 2-year-old females that also were recaptured during nesting when they were 4-years old, so any long-term effects of breeding experience effects (i.e. not nesting as yearlings) could be determined.
[b] NS, $P > 0.05$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.0001$.
[c] Nesting date of first nests standardized to the first 10% of nests each year.
[d] Female body mass at the end of incubation.

clutch size, often decline over the course of a breeding season (Klomp 1970, Hochachka 1990, Winkler and Allen 1996). After statistically controlling for differences in nesting date, female age explained little of the variation in reproductive performance; however, age-specific differences occurred more consistently for Tufted Ducks and pochards than for shovelers.

Investigations of most species of birds (Sæther 1990), including waterfowl (Afton

TABLE 4. Mean values (n) of reproductive performance of 1-year-old and 2-year-old female Northern Shovelers, Tufted Ducks, and Common Pochards. Two-year-old females had no previous breeding experience; comparisons control for differences in breeding experience while testing effects of female age on reproductive performance. Data are from first nests of the season. P-values are from t-tests comparing 1-year-olds and 2-year-olds within species.

	Northern Shoveler			Tufted Duck			Common Pochard		
	1-year-olds	2-year-olds	P[a]	1-year-olds	2-year-olds	P	1-year-olds	2-year-olds	P
Clutch size	—	—	—	8.2 (581)	8.6 (45)	NS	—	—	—
Brood size	—	—	—	7.6 (481)	8.0 (38)	NS	6.5 (744)	7.3 (62)	**
Duckling mass (g)	26.7 (177)	27.3 (26)	NS	37.6 (289)	38.8 (33)	**	43.1 (607)	44.0 (56)	**
Nesting date[b]	7.7 (280)	6.2 (54)	NS	18.6 (606)	13.4 (50)	***	19.0 (1,020)	14.2 (86)	***
Body mass (g)[c]	490 (187)	501 (30)	*	613 (399)	630 (43)	**	762 (959)	778 (102)	**

[a] *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.0001$.
[b] Nesting date was standardized to the first 10% (Tufted Duck and Common Pochard) and 30% (Northern Shoveler) of nests each year to control for annual variation.
[c] Female body mass at the end of incubation.

1984, Dow and Fredga 1984, Rockwell et al. 1993), have reported that reproductive performance increases with parental age. However, studies like ours that have controlled for factors normally associated with parental age (e.g. nesting date) have reported a reduction or elimination of age-specific differences. In Barnacle Geese (*Branta leucopsis*), for example, the number of young fledged by parents was associated more directly with nesting date and clutch size than with parental age (Forslund and Larsson 1992). Clutch size and brood size of Wood Ducks (*Aix sponsa*; Hepp and Kennamer 1993) and clutch size of Redheads (*Aythya americana*; Serie et al. 1992) and Marsh Tits (*Parus palustris*; Smith 1993) also were not associated with female age but were higher in females that nested early in the breeding season. For most birds, parental age has its greatest effect on nesting date (Sæther 1990), which in turn may influence other reproductive parameters. For example, females of all ages may lay smaller clutches late in the season in response to declining probabilities of successfully raising young (e.g. Perrins 1970, Toft et al. 1984, Winkler and Allen 1996).

Experience, age, and differential survival.—In addition to female age, we examined the effects of breeding experience and differential survival of good breeders on reproductive performance to better understand the relative importance of age in explaining differences that were present. For each species, previous breeding experience was important. Among 2-year-old females with and without breeding experience, experienced females nested five to six days earlier than inexperienced females. Nesting delays of inexperienced females represented 7 to 8% of the nesting season (P. Blums unpubl. data) and were similar to delays (12 of 157 days; 8%) shown by inexperienced 2-year-old Wood Ducks (Hepp and Kennamer 1993). For all three species, inexperienced and experienced females produced ducklings that did not differ in mass, but experienced 2-year-old Tufted Ducks had larger clutches and broods than did inexperienced ones.

The few studies of reproductive performance that have separated the effect of parental age from that of breeding experience have produced mixed results (Forslund and Pärt 1995). In anatids (Gauthier 1989, Hepp and Kennamer 1993, this study), previous breeding experience consistently influenced nesting date; experienced females initiated nests earlier than inexperienced ones. It is not clear how breeding experience helped these females to establish nests early in the season. Greater familiarity with nesting areas and with selecting nest sites certainly may assist females in selection of and competition for nest sites (Greenwood and Harvey 1982). In cavity-nesting ducks, even among experienced females, those using the same nest site in successive years nested earlier than females that changed nesting locations (Dow and Fredga 1983, Gauthier 1990, Hepp and Kennamer 1992). Females in the genus *Bucephala* also acquire information about potential nest sites prior to the next breeding season by visiting nest sites (i.e. nest prospecting) near the end of the current season (Eadie and Gauthier 1985, Zicus and Hennes 1989). Female Common Goldeneyes (*Bucephala clangula*) apparently use this information to select nest sites where nests are less likely to be destroyed by predators (Dow and Fredga 1985). Experienced females also may become familiar with locations of good feeding sites that may help them acquire the nutrients needed for breeding. Anderson (1985), for example, reported that the same foraging sites often were used by female Canvasbacks (*Aythya valisineria*) in successive breeding seasons.

The effects of breeding experience on our ducks generally lasted for only a single breeding season. These results are similar to those for female Western Gulls (*Larus occidentalis*), in which the greatest improvement in reproductive performance occurred between the first and second breeding attempts (Pyle et al. 1991, Sydeman et al. 1991). However, in Buffleheads (*Bucephala albeola*), nesting date improved steadily over the first three breeding seasons (Gauthier 1989). The short-term effects of breeding experience in the species we studied suggest that reproductive differences were caused by variation in experience rather than by differences in phenotypic quality between females that delayed nesting until they were 2 years old and females that nested as yearlings (see Forslund and Pärt 1995). However, the most appropriate test of this hypothesis would involve experimentally manipulating female breeding experience.

When we controlled for differences in breeding experience, age of females influenced reproductive performance of Tufted Ducks and pochards but not of shovelers. Compared with dabbling ducks (Anatini), female diving ducks (Aythyini) more commonly delay nesting until after their first year (Bengston 1972, Afton 1984, Johnson et al. 1992). Breeding may be more constrained in young diving ducks because of slower physical and physiological maturation, or because foraging skills may take longer to develop. In birds, adults typically forage more successfully than young individuals (Marchetti and Price 1989), and age-specific differences in the ability to acquire nutrients may partly explain the lower reproductive performance of young birds (Martin 1987). For example, yearling Great Tits (*Parus major*) and European Blackbirds (*Turdus merula*) given supplemental food began nesting at the same time as adults (Källander 1974, Desrochers 1992a). Studies of captive Mallards (*Anas platyrhynchos*) and Northern Pintails (*A. acuta*), both species of dabbling ducks, indicated that yearlings fed an *ad libitum* diet were physiologically capable of the same reproductive performances as adults (Batt and Prince 1978, Duncan 1987). In temperate-nesting waterfowl, females of many species acquire lipid reserves after arriving at breeding areas and use these stored nutrients to help offset the high costs of egg production (Alisauskas and Ankney 1992). Because of the importance of nutrient reserves to reproduction, a threshold level of reserves may have to be reached by females before they begin egg development (see Alisauskas and Ankney 1992). Individuals capable of accumulating nutrients more quickly (i.e. adults), perhaps by foraging more efficiently or by having better access to food, will be the first to reach the nutrient threshold. How quickly female ducks acquire nutrient reserves, together with their past breeding history, will help determine nesting dates.

We found no evidence that yearling females that survived to the next breeding season had higher reproductive performance than yearlings that did not survive. Thus, increases in reproductive performance with female age cannot be attributed to the differential survival (selection) of good breeders. Most studies have reported similar results (Forslund and Larsson 1992, Perdeck and Cavé 1992, Hepp and Kennamer 1993, Desrochers and Magrath 1993; but see Nol and Smith 1987).

Constraint, restraint, and time of breeding.— Age-specific differences in avian reproduction apparently are produced by constraints rather than by restraint (Sæther 1990, Rohwer 1992, Forslund and Pärt 1995, Martin 1995). Young individuals of some long-lived species may display reproductive restraint (e.g. Pugesek 1981); however, testing whether restraint is responsible for age-specific variation in reproduction has been difficult because of problems inherent with measuring reproductive effort. An important assumption of the restraint hypothesis, that survival rates decline with increasing age (i.e. adults put more into reproduction because chances of surviving to the next breeding season are low), has been examined but with mixed results. There was no evidence that survival rates decreased with age for Song Sparrows (*Melospiza melodia*; Nol and Smith 1987), Eurasian Coots (*Fulica atra*; Perdeck and Cavé 1992) and Wood Ducks (Hepp and Kennamer 1993), but survival rates decreased with age in Black-capped Chickadees (*Parus atricapillus*; Loery et al. 1987) and Short-tailed Shearwaters (*Puffinus tenuirostris*; Bradley et al. 1989). The greatest improvement in reproductive performance occurred between the first and second breeding seasons in the three species we studied, and this pattern is typical of many other avian species (Martin 1995). This pattern of reproductive improvement cannot be attributed to increased reproductive effort caused by declining adult survival, because adult survival rates were the same or higher than those of yearlings (Blums et al. 1996). No evidence exists for a senescent decline in survival rates of Common Pochards (Nichols et al. 1997), and data are insufficient for similar tests in Northern Shovelers and Tufted Ducks.

Reproductive performance of the three anatids we studied was constrained by age and/or breeding experience of females. However, we were unable to determine the specific mechanisms responsible for these differences. Experimental studies are needed to distinguish among various alternative hypotheses (e.g. foraging ability, physiological maturation, and competition for food or nesting space). Studies that test whether age-specific differences in foraging ability exist and are responsible for variation in female reproductive performances are especially needed (e.g. Desrochers 1992a,b).

Age had its greatest effect on nesting dates of the species we studied, which agrees with other studies where differences occurred more frequently early in the breeding cycle (Martin 1995). These differences may be cumulative and strongly affect subsequent reproductive success, or they may disappear. In Black Brant (*Branta bernicla nigricans*) and Lesser Snow Geese (*Anser caerulescens caerulescens*), early hatching goslings grew faster and developed into larger adults than those hatching late in the season (Cooch et al. 1991, Sedinger and Flint 1991, Sedinger et al. 1995); these differences may have subsequent life-history consequences (Sedinger et al. 1995). Young hatched early in the season frequently survive better than those hatching later (Dow and Fredga 1984, Cooke et al. 1995, Blums et al. unpubl. data), but there are exceptions. In South Carolina, Wood Ducks hatching early were not recruited at higher rates than those hatching later (Hepp et al. 1989), but adult females that nested early hatched more young from successful nests, were at less risk from predators, and were more likely to initiate second nests than females nesting later (Hepp and Kennamer 1993). In many species of birds, older, more experienced females generally are better able to meet the demands of reproduction and initiate nests early. Clearly, timing of nesting can be a critical element in determining subsequent reproductive success.

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