trol of pairing in most waterfowl species (Trivers 1972; McKinney 1986; Black and Owen 1988; Oring and Sayler 1992). However, because female migratory ducks are thought to benefit from early pair formation, it has been assumed that they should be willing to pair whenever males are energetically capable, and thus *ipso facto* the control of the timing of pairing devolves to the males (Rohwer and Anderson 1988). The current body size) and early pairing among North American dabbling ducks lend some support (Rohwer and Anderson 1988). However, most data are inconsistent with the hypothesis: timing of pairing is not correlated with body size inter-specifically among Western Palearctic dabbling ducks (Rohwer and Anderson 1988) nor among North American Mergini (Coupe and Cooke 1999); male courtship is often intense for extended periods before pair formation occurs; pair bonds in some small-bodied species (e.g., Hooded Merganser *Lophodytes cucullatus*; Dugger *et al.* 1994; Coupe and Cooke 1999) are formed during mid-winter when time and energy constraints should be most severe; and paired males frequently participate in social courtship groups (Hepp and Hair 1983; Williams 1983; McKinney 1992) indicating that energetic costs of mate defense are not limiting. Studies comparing time budgets of the timing of pairing, and 2) that it is necessary to incorporate the process of choosing a partner as well as the state of being paired.

site. The mutual-choice hypothesis thus predicts that re-uniting pairs will pair earliest, as measured by pair-date, while young individuals will require time for mate sampling and pair later. Experienced birds that have lost a mate will pair at intermediate dates because mate sampling for them likely involves some form of information updating (McNamara and Houston 1980) and they should require less time for mate assessment than naive birds. The corollary to this prediction is that court-time will be greatest for young birds and least for re-uniting birds.

What are the predictions of the male-costs hypothesis in relation to individual experience? Young females with poorer foraging skills likely have most to gain from mate defense and will want to pair as early or earlier than experienced females, while young males will pair later than experienced males because they are less able to afford the costs of mate defense. The trend for males would translate into a similar trend for females if sex ratios are balanced and mating is assortative. However, when sex ratios are male biased, there should be a pool of previously paired males, whose mates have died, that are as equally capable of pairing early to young females as those that are re-pairing or re-uniting with surviving, experienced females. Thus, the male-costs hypothesis predicts that young females will pair earlier or at the same time as experienced females when sex ratios are male biased. All studies that have investigated age-related differences in pairing chronology have found that young females pair later than older females, even in species with amount of time per day that they allocate to courtship and mate sampling. The male-costs hypothesis predicts the same relationship for males but not females, because all females should be willing to pair as early as males are capable.

Once a pair bond has been formed, the male-costs hypothesis assumes that males will incur most of the cost of defense, whereas the mutual-choice hypothesis expects variation among pairs in the relative share that males and females engage in aggression and defense of the pair bond, and predicts that a male will assume a greater share of defense when paired to a relatively high than low quality female. As mentioned above, studies show that females may perform as much or more pair-bond maintenance and defense as males (Weller 1967; Anderson 1984; Lovvorn 1989) and relative amounts have been related to mate quality (Rodway 2004).

Social and Ecological Factors

ations suggest that if environmental conditions or differences in habitat use reduce the phenotypic quality of potential mates in an area then pairing will be delayed because individuals will find it more costly to satisfy their mate preferences and may be unwilling to pair if there are better options elsewhere or at a later date. Also, individual decisions about habitat use and timing of pairing are likely inter-related and should be considered together (Rodway 2006).

COMPARATIVE DATA AND THE S

Table 1. Variables used to analyze differences in the timing of pair formation [illegible] species of the subfamily Anatinae.

Species[a]	Mass (g) Male	Mass (g) Female	Female survival (%)	Sex ratio[c]	Latitude (°N)	Migr.[d]	Sex segr.[e]	Pair bonds >1 yr	Court start	80% paired	Court time (mo.)	Sources[g]
North America												
Anatini												
Aix sponsa	680	671	48	2.67	37	Y	N	Y	SEP	JAN	4	15, 18, 25, 32
Mareca strepera	966	835	56	1.36	35	Y	N	N	SEP	NOV	2	15, 20, 21, 32
M. americana	792	719	58	1.85	35	Y	N	N	SEP	NOV	2	20, 21, 32, 39
Anas rubripes	1,252	1,111	51	1.32	35	Y	N	N	SEP	OCT	1	15, 20, 21, 32
A. platyrhynchos	1,247	1,107	55	1.33	42	N	N	N	SEP	JAN	4	5, 15, 32
A. fulvigula	1,134	1,048	46	1.07	30	Y	N	N	AUG	OCT	2	15, 22, 32
A. discors	463	376	52	1.50	17	Y	N	N	DEC	APR	4	1, 15, 32
A. clypeata	680	635	46	2.02	35	Y	N	N	DEC	FEB	2	15, 20, 21, 32
A. acuta	1,025	866	65	1.81	35	Y	Y	N	DEC	JAN	1	15, 20, 21, 32
A. carolinensis	322	308	47	2.82	35	Y	Y	N	DEC	FEB	2	15, 20, 21, 32
Aythyini												
Aristonetta valisineria	1,252	1,157	56	1.94	37	Y	Y	N	FEB	MAY	3	7, 15, 17, 32
A. americana	1,107	971	50	1.50	26	Y	Y	N	DEC	—	—	7, 8, 15, 19
Aythya collaris	744	671	50	1.59	30	Y	Y	N	JAN	MAY	4	7, 15, 19, 32
A. affinis	826	748	46	2.40	42	Y	N	N	MAR	MAY	2	7, 15, 19, 33
Mergini												
Histrionicus histrionicus	638	569	76	1.51	49	Y	N	Y	SEP	MAR	6	31, 38, 42, 43, 44
Melanitta perspicillata	1,050	900	77[b]	2.31	49	Y	Y	Y	OCT	—	—	34, 41, 45
M. deglandi	1,722	1437	77	1.50	52	Y	Y	Y[f]	—	MAY	—	23, 30, 32
M. americana	1,117	987	77	1.67	49	Y	Y	Y[f]	OCT	—	—	13, 15, 28, 45
Clangula hyemalis	932	814	72	0.79	43	Y	Y	Y	OCT	MAY	7	12, 14, 39

[a] Classification after Livezey 1997.

[b] Estimated from other scoters.

[c] Ratio of males to females during midwinter (Nov.-Jan.) or when the birds were present at the study site. Taken from Bellrose 1980 if not measured at the study site.

[d] Study population was part of a migratory population.

[e] Study population was part of a sexually segregated population.

[f] Long-term bonds not confirmed; inferred from other Mergini species.

[g] (1) Bennett 1938, (2) Lebret 1950, (3) Carter 1958, (4) Bezzel 1959, (5) Johnsgard 1960b, (6) Lebret 1961, (7) Weller 1965, (8) Weller 1967, (9) Nilsson 1970, (10) Erskine 1972, (11) Gorman 1974, (12) Alison 1975, (13) Palmer 1976b, (14) Cramp and Simmons 1977, (15) Bellrose 1980, (16) Gray 1980 *in* Johnsgard and Carbonell, (17) Nichols and Haramis 1980, (18) Armbruster 1982, (19) Alexander 1983, (20) Hepp and Hair 1983, (21) Hepp and Hair 1984, (22) Paulus 1988b, (23) Brown and Fredrickson 1989, (24) Choudhury and Black 1991, (25) Hepp and Hines 1991, (26) Gauthier 1993, (27) Dugger *et al.* 1994, (28) Bordage and Savard 1995, (29) Eadie *et al.* 1995, (30) Brown and Fredrickson 1997, (31) Gowans *et al.* 1997, (32) Krementz *et al.*1997, (33) Austin *et al.* 1998, (34) Savard *et al.* 1998, (35) Coupe and Cooke 1999, (36) Mallory and Metz 1999, (37) Titman 1999, (38) Cooke *et al.* 2000, (39) Dunning 2000, (40) Eadie *et al.* 2000, (41) Iverson 2002, (42) Rodway *et al.* 2003a, (43) Rodway *et al.* 2003b, (44) Rodway 2004, (45) MSR unpublished.

Bucephala albeola	465	337	64	1.50	51	Y	N	Y	OCT	APR	6	10, 26
B. clangula	1,120	710	61	1.60	45	Y	Y	Y[f]	—	MAR	—	3, 29
B. islandica												

that courtship began (population court-start), the calendar date that 80% of females were paired (population pair-date), and the length of time between those two dates (population court-time).

The start of courtship, pair-date, and court-time differed significantly among tribes (Table 2). Anatini and Mergini species began courtship earlier than Aythyini and Oxyurini species, and Anatini species paired earlier than Aythyini and Mergini species, resulting in longer court-times for Mergini than either Anatini or Aythyini species. Results suggest that phylogenetic relationships account for a substantial proportion of the variation in pairing chronologies among species of northern Anatinae.

Data were re-analyzed by adding other variables to ANOVA models to determine what other factors may contribute to the differences seen among tribes. Analyses based on these data must be considered exploratory because of the lack of independence in data for related species (Felsenstein 1985; Harvey and Pagel 1991), because where there were several studies of a particular species, one was subjectively chosen to include, and because with such a small sample size it was necessary to use a stepwise procedure to determine the relative importance of the different explanatory variables. No other variables added significantly to explained variation for court-start or pair-date if effects of tribe were included. Analyses without tribe in the model indicated that start of courtship ($F_{1,28}$ = 12.6, P = 0.001) and pair-date ($F_{1,25}$ = 4.5, P = 0.04) were later with increasing male-bias in the sex ratio as predicted by the mutual-choice hypothesis. Body mass was not related to measures of pairing chronology, contrary to predictions of the male-costs hypothesis. Delayed start of courtship and pair-date in species' populations with more male-biased sex ratios reinforces the evidence discussed above indicating that male-male competition is not an important determinant of pairing chronology.

For court-time, a model including only the effect of long-term pair bonds (r^2 = 0.61, $F_{1,27}$ = 44.4, P < 0.001) was superior to the one with tribe (Table 2). No other variables added significantly to explained variation for court-time if effects of long-term pair bonds were included, but court-time was positively related to female annual survival (r^2 = 0.26, $F_{1,24}$ = 9.7, P = 0.005) if pair-bond duration was excluded from the model. These results provide tentative support for predictions of the mutual-choice hypothesis that court-time will be greater with increasing survival and duration of pair bonds. Court-time averaged 2.4 ± 0.3 months (N = 19) and 5.4 ± 0.4 months (N = 9) for species with annual and long-term pair bonds, respectively. This conclusion is tentative because it was assumed that all Mergini species have long-term pair bonds, and this has only been confirmed in some species (Bengtson 1972; Allison 1975; Spurr and Milne 1976; Savard 1985; Gauthier 1987; Savard *et al.* 1998) and suspected in others (Eadie *et al.* 1995; Brown and Fredrickson 1997; Mallory and Metz 1999). Also, most Anatini and Aythyini were considered to have annual pair bonds, even though instances of long-term bonds have been confirmed (Lebret 1961; Dwyer *et al.* 1973; Palmer 1976a, p. 338; Bluhm 1985; Mielstad and Saetersdal 1990; Losito and Baldassarre

Table 2. D ffe ce a c a a e f be e bfa A a ae e e e e. a ca af e L e e (1997). M a be ed e e e f J J e, ec e Mea SE a d ANOVA a ed, a d a e e (be f ec e) a e a e e .

	Anatini	Aythyini	Mergini	Oxyurini	r^2	*F*	*P*
Court-start[a]	3.9 ± 0.4 (15)	7.5 ± 0.4 (6)	4.7 ± 0.4 (14)	10.0 (1)	0.51	13.0	0.000
Pair-date[b]	6.5 ± 0.5 (16)	10.3 ± 0.4 (6)	9.9 ± 0.3 (9)	11.0 (1)	0.55	13.4	0.000
Court-time[c]	2.6 ± 0.4 (15)	2.8 ± 0.3 (6)	5.7 ± 0.4 (7)	1.0 (1)	0.54	12.0	0.000

[a] Calendar month that courtship began.

[b] Calendar month when 80% of females were paired.

[c] Number of months between start of courtship and pair-date.

1996) or suspected (Bezzel 1959; Paulus 1988b) in some northern hemisphere species and are more common in tropical or southern hemisphere Anatini species (Sorenson 1991; Williams and McKinney 1996; Port 1998). However, high mortality rates (Table 1) likely constrain the possible frequency of multi-year pair bonds and the proportion of birds possibly involved would be small in most northern, migratory and hunted Anatini species (e.g., Losito and Baldassarre 1996). Pair-date also was later for species with long-term pair bonds ($F_{1,25} = 5.1$, $P = 0.03$, when tribe was excluded), suggesting that greater court-time was associated with later pair-date in these species.

Secondary analyses suggested that sexual segregation delayed pairing; court-start ($F_{1,28} = 7.6$, $P = 0.01$) and pair-date ($F_{1,25} = 10.2$, $P = 0.004$) were later for sexually segregated species. However, effects of sexual segregation are difficult to interpret. Much of this effect was likely due to later pairing in Mergini, which as discussed above was probably mostly a function of prolonged court-time. Most Aythyini show sexual segregation during winter, but there is little evidence of segregation in Lesser Scaup, the latest pairing species. Better sampling of pairing behavior throughout the winter range of segregated and non-segregated species is needed before we can evaluate the importance of this factor. Inconsistent latitudinal trends among species discussed above, and inter-annual variation in pairing chronology within species possibly due to changing climatic conditions and habitat quality (Raitasuo 1964; Wishart 1983; Migoya *et al.* 1994; Kozulin 1995; Johnson and Rohwer 1998; Ganter *et al.* 2005) emphasize the importance of adequate sampling in different parts of a species' range and over several years.

Phylogenetic Trends

Likely evolving from an ancestral mating system of biparental care and perennial monogamy, the family Anatidae now exhibits a diverse range of mating systems (Kear 1970; Oring and Sayler 1992). If we seek an adaptive explanation for variation in timing of pairing among waterfowl, it is appropriate to begin with consideration of pairing behavior in species whose behavior most resembles the likely ancestral condition. In geese and swans, young birds generally begin the mate-choice process and engage in trial liaisons by the spring or summer of their first year, form permanent pair bonds by the time they are two or three, and first breed at the age of two to four (Raveling 1969; Minton 1968; Owen 1980; Prevett and MacInnes 1980; Owen *et al.* 1988; Warren *et al.* 1992; Cooke *et al.* 1995; Mowbray *et al.* 2000). Geese that have lost or divorced a mate usually take three to nine months to re-pair (Owen *et al.* 1988). One-or-more-year intervals between the beginning of mate sampling and pairing, and between pairing and nesting, implicate benefits of both a prolonged period for mate selection and for gaining familiarity and experience with the chosen partner. The relative impor-

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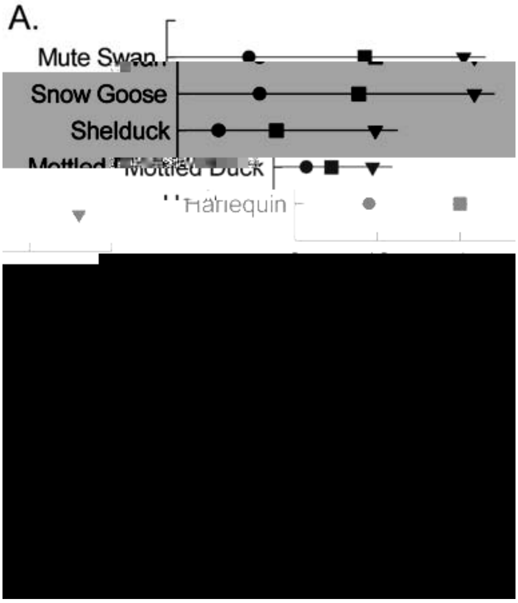
when there was selection for later age of first breeding.

How have these patterns of pair formation changed in other waterfowl groups? Data were adequate to estimate timing of first pairing for females from representative species of five tribes (Fig. 1a). Comparisons revealed markedly similar patterns among these species. Differences were related primarily to differences in age of first breeding. Similar pairing chronologies when standardized to age of first breeding (Fig. 1b) suggest that selection has acted primarily to accelerate life history events related to pair formation. Mergini species with long-term pair bonds have maintained the ancestral pattern, as have some Anatini species (Fig. 1). Divergence may then have occurred within the Anatini and Aythyini, that form pair bonds shortly before or during migration to the breeding ground (T



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the Oxyurini, that form weak pair bonds or lack pair bonds entirely (Siegfried 1976; Johnsgard and Carbonell 1996). This evolutionary sequence is supported by the apparent primitive position of long-term pair bonds and bi-parental brood care in Anatini (Livezey 1991). Similar court-time but later pair-date in Aythyini than Anatini (T suggest that selection has acted to shorten relative pair-time but not court-time in Aythyini. This also appears to be true for late-pairing Anatini species. Both court-time and pair-time have been reduced in Oxyurini, but again the greatest relative decrease has been in pair-time, especially in promiscuous species (Johnsgard and Carbonell 1996), suggesting that time to become familiar with a mate is less important in these species.

A clear understanding of inter-specific differences in court-time and pair-time, however, awaits detailed studies of marked, known-age birds. For example, Lesser Scaup (*Aythya affinis*) are one of the latest of the northern, migratory Anatinae to form pair bonds (Austin *et al.* 1998), and it again appears that selection has acted to reduce pair-time. However, most Lesser Scaup females probvGly pair in their first year but do not breed until their second year (T Johnsgard 1978). What happens to pair associations made in the first year? Are they maintained or renewed? Could they account for the small percentage of females that are paired during mid-winter (W long before most females appear paired? Until we can answer these questions we cannot determine just how the pairing pattern in such species deviates from the likely ancestral pattern.

Results support previous perceptions that diving ducks pair later than dabbling ducks (Rohwer and Anderson 1988), but suggest that the reasons for later pairing in diving ducks differ between Aythyini and Mergini. Late pairing in Mergini is associated with an early start to courtship and an extended court-time. Extended courtship probvGly relates to their higher survival, delayed maturity, and long-term pair bonds, and meets predictions of the mutual-choice hypothesis that birds with long-term pair bonds will invest more in the mate-choice process. However, if most Mergini maintain long-term pair-bonds and the majority of pairs re-unite early in the winter, then late pairing simply reflects the time when young females form their first pair bonds and is an artifact of using the time when 80% of females are paired as the measure of pairing date. If most Mergini follow the pattern determined for Harlequin Ducks (*Histrionicus histrionicus*), then young females are engaged in courtship and trial liaisons for a year or more before they pair, while older females are re-uniting or re-pairing more rapidly (Rodway 2007). This emphasizes the need for individual-based measures of pairing chronology.

In contrast, Aythyini species have annual pair bonds, generally pair in their first year, and invest less time than Mergini in the mate-choice process. However, as noted above for Lesser Scaup, the mate-choice process may be more protracted for some young females, especially when breeding conditions are unfavorable (Austin *et al.* 1998). Also, pair-formation behavior of pochards has rarely been investigated at northern latitudes early in the winter and thus we still need to know whether females wintering in northern parts of a species' range begin the mate-choice process earlier than those in more southern areas. For example, over 70% of the Atlantic Flyway population of Canvasbacks winter in the Chesapeake Bay area (Lovvorn 1989), but we have little data on pairing activities in that area through the winter. Prolonged court-time in Canvasbacks may be expected given their high selectivity in choosing a mate (Bluhm 1985). Weller (1965) made a visit to Chesapeake Bay in February and observed much more courtship activity by Canvasbacks there than in Texas, and M. Anderson (pers. comm.) reported some (<10%) Canvasbacks paired there at that time. Canvasbacks arrive paired at their breeding grounds (Anderson 1985) and estimates that the majority of females pair during migration are difficult to interpret without winter data from areas where large proportions of their populations occur. Changes in proportions of females paired at migratory stopovers (Smith 1946) could occur because females are pairing at these sites at these times or could be due to differential arrival of paired and unpaired birds from different wintering areas. The latter scenario may more easily explain observed changes in proportions paired from 10% to 65% to 18% within a one-week interval during the passage of about 50,000 Canvasbacks (Smith 1946).

CONCLUSION

Previous hypotheses that focused primarily on cost-benefit trade-offs of being paired for males were inadequate to explain variation in the timing of pairing in waterfowl. Consistent, empirical support for the mutual-choice hypothesis confirms the value of greater focus on female perspectives and strengthens the main premise that timing of pairing is primarily determined by female mate-choice decisions. The process of mate choice, how the interactions of phenotypic, social, and ecological conditions affect that process, and how individuals integrate that process with other requirements of their life history are essential to consider in order to understand variation in the timing of pairing events. Male and female interests necessarily interact and a comprehensive theory to predict variation in pairing behavior requires consideration of benefits, costs, and conflicts of interest among individuals engaged in pairing decisions (McKinney 1986; Rohwer and Anderson 1988; Oring and Sayler 1992; Choudhury 1995; Brown *et al.* 1997).

Further testing predictions of the mutual-choice hypothesis is currently hampered by a lack of data on age- and sex-specific pairing chronologies. We need longitudinal studies of marked, known-age individuals from a variety of waterfowl species differing in age of maturity, pair-bond duration, parental care patterns, winter grouping behavior, and degree of sexual segregation on wintering grounds. Comparative studies under different ecological conditions of multiple wintering populations of migratory species, especially sexually-segregated species, and of sedentary and southern hemisphere species are also needed. Coincident time-activity budget analyses are required to interpret pairing behavior using measures of individual pairing chronology as recommended in this study, and to investigate cost-benefit trade-offs to individuals making pairing decisions. In many non-waterfowl species, individuals with multi-year pair bonds separate for some portion of the non-reproductive season, and assumptions that paired waterfowl maintain close proximity and defend pair bonds throughout the winter need to be questioned, especially for densely-flocking species with high survival rates such as scoters. Further developing a generalizable theory to explain variation in temporal patterns of mate choice and pairing will require broadening our consideration to other groups of birds (e.g., some penguins, corvids, parids) that also form and maintain pair bonds well in advance of breeding and often during non-reproductive periods.

Such a theory would be a valuable complement to hypotheses regarding temporal, life-history decisions on the age of maturity and the timing of reproduction (Rohwer 1992). Winter pairing in waterfowl may have been selected because of the benefits of prolonged periods for mate assessment and for improving mate co-ordination. The benefits and costs of protracted periods for mate-choice and co-ordination with a mate prior to breeding have yet to be considered in relation to, and ultimately must entail trade-offs with other reproductive decisions. Direct fitness consequences of mate choice and familiarity likely affect the costs of reproduction and thus may contribute to variation in the age of first breeding and the seasonal timing of nest initiation, that are incompletely explained by survival-fecundity trade-offs (Roff 1992) and food limitation hypotheses (Lack 1954; Perrins 1970). In waterfowl, mature females that are not allowed free choice of a mate may not breed, instead deciding to defer breeding even though possible mates are available (Bluhm 1985). Effects of constrained mate choice in wild birds are unknown. Thus, a worthy aim is an integration of hypotheses to explain variation in the timing of pairing, the age of first breeding, and the timing of reproduction.

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