Timing of Pairing in Waterfowl I: Reviewing the Data and Extending the Theory

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Abstract.—The current *male-costs hypothesis* to explain variation in the timing of pairing in waterfowl acknowledges that relative parental investment and intra-sexual competition among males place females in control of pairing in most species. However, because females may benefit from early pair formation, it assumes that they should be willing to pair whenever males are energetically capable, and thus predicts that timing of pairing depends on decisions made by males. A compilation and review of available data on pairing behavior in waterfowl found little support for this hypothesis and considerable data that were inconsistent with its predictions. The *mutual-choice hypothesis* extends the male-costs hypothesis by incorporating cost-benefit trade-offs to females as well as males, and by giving more consideration to the various components of the pairing process, including time and energy invested into mate choice, the quality of mate chosen, and the state of being paired, including possible benefits of time spent gaining familiarity with a partner before breeding. This hypothesis differs from the male-costs hypothesis in two essential points: 1) that decisions by females rather than males primarily determine 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. The new hypothesis was supported by available data and by results of preliminary, comparative analyses, and provides a theoretical structure to describe phylogenetic trends in pairing behavior. However, critical testing of many predictions is currently hampered by a lack of longitudinal data on age- and sex-specific pairing chronologies using individual-based measures of pairing chronology. *Received 13 November 2006. accepted 26 May 2007.*

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Several aspects of the sexual behavior of waterfowl (Anatidae) are unusual and, despite long-term interest (Darwin 1871; Heinroth 1910, 1911; Lorenz 1941; Johnsgard 1965; Lack 1968), remain poorly understood (McKinney 1986). Most migratory ducks lack paternal care, yet contrary to theoretical expectations that such male emancipation should lead to polygynous mating systems (Orians 1969; Emlen and Oring 1977), most ducks are seasonally or perennially monogamous. Though socially monogamous, the degree of sexual dimorphism is more typical of lek-mating species with pronounced polygyny (Skutch 1992; Johnsgard 1994). One of the most intriguing questions is why pair bonds in many species are formed well in advance of the actual period of fertility (Bluhm 1988), often several months or even years prior to breeding (Lack 1968), and why the timing of pairing varies among and within waterfowl species (Weller 1965; Paulus 1983; Wishart 1983). Though a variety of hypotheses have been generated and the topic has motivated numerous studies (reviewed in Rohwer and Anderson 1988; Oring and Sayler 1992), many phenotypic, social, and ecological factors that likely influence pairing chronology have not been adequately considered and progress in understanding the behavior has been slow. The objectives in this paper are to 1) demonstrate the limitations of current hypotheses to explain variation in the timing of pairing, 2) extend current theory by incorporating previously ignored components of the pairing process, and 3) compile available data on pairing chronology in waterfowl to assess the state of our knowledge, test predictions of current and new hypotheses, and relate new theory to the possible phylogeny of pairing behavior.

CURRENT THEORY: THE MALE-COSTS HYPOTHESIS

Recent authors agree that relative parental investment and intra-sexual competition among males for females place females in control 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 *male-costs hypothesis* suggests that early pairing benefits females (through increased foraging efficiency and survival due to male defense and vigilance) and males (through mate acquisition and improved female condition) but is constrained by costs to males of courtship, mate defense, and vigilance (Rohwer and Anderson 1988; Owen and Black 1990; Oring and Sayler 1992).

The main premise of the male-costs hypothesis, that females gain benefits of increased foraging efficiency by being paired, is poorly founded. The premise derives from pivotal studies demonstrating that mate guarding and vigilance by their partner may increase foraging efficiency for paired females by protecting them from harassment and reducing their need for vigilance (Milne 1974; Ashcroft 1976; Scott 1980; Sorenson 1992). However, these studies did not compare paired and unpaired females but investigated differences in mate performance among paired females, showing that feeding rate of paired females was higher and number of interactions with other birds was lower when males were close than far away. These studies provide evidence for differences in mate quality and indicate likely benefits of mate choice rather than benefits of being paired *per se*. The male-costs hypothesis predicts that paired females will spend more time feeding, suffer less harassment, and spend less time in vigilant behavior than unpaired females. Studies comparing time spent in these activities during winter by paired and unpaired females report little difference (Jorde 1981; Paulus 1984; Paulus 1988a, b; Rave and Baldassarre 1989; Migoya *et al.* 1994; Lee 1997; Nakamura and Atsumi 2000; Torres *et al.* 2002; Guillemain *et al.* 2003).

Foraging efficiency may also improve for paired females (and males) because they can gain access to higher quality food patches due to the increased behavioral dominance of paired to unpaired birds, as has been frequently demonstrated in geese (Black and Owen 1989; Hupp *et al.* 1996; Siriwardena and Black 1998; Stahl *et al.* 2001). In ducks, the hypothesis that increased dominance status provides access to preferred food supplies or results in improved body condition for paired birds has been postulated frequently (Paulus 1983; Baldassarre and Bolen 1986; Heitmeyer 1988; Pattenden and Boag 1989; Hanson *et al.* 1990; Demarest *et al.* 1997), but has little support (Combs 1987; Hepp 1989; Hohman 1993; Hohman and Ankney 1994; Hohman and Weller 1994; Marsden and Sullivan 2000).

These data in relation to the foraging benefits of being paired reveal two important points. For northern, migratory ducks, there is as yet no evidence that females gain nutritional benefit during the winter by becoming paired, either through male protection or through increased dominance status of the pair. Benefits of increased foraging efficiency is not supported as an explanation for early pair formation in these species. In contrast, single geese are lowest in dominance hierarchies (Boyd 1953; Raveling 1970) and young birds could benefit from becoming paired after leaving their family or sibling groups. That most yearling and many two to three year-old geese remain single in winter flocks, even after they have begun courting and have had temporary liaisons with prospective partners (Raveling 1969; Prevett and MacInnes 1980), indicates that increased dominance status and access to better food supplies provides insufficient benefit to young, single birds to select for acceleration of the mate-choice process.

The other main premise of the male-costs hypothesis, that energy constraints on males influence timing of pairing, also has little support. Evidence that males in better condition or at better food supplies pair earlier than conspecifics in poorer condition (Wishart 1983; Brodsky and Weatherhead 1985; Hepp 1986), and a positive correlation inter-specifically between body size (assuming greater energy constraints with smaller 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 paired and unpaired males during the winter pair formation period have shown little difference in time spent feeding, and a trend for unpaired birds to allocate more time to courtship and agonistic behavior than paired males spend in mate defense (Jorde 1981; Paulus 1984, 1988a, b; Rave and Baldassarre 1989; Migoya *et al* 1994; Torres *et al.* 2002; Rodway 2007).

If females are willing to pair early, as is assumed by the male-costs hypothesis, then the fitness costs to males of obtaining a low-quality mate, or, in male-biased duck populations, of failing to obtain a mate, should result in all males attempting to pair as early as possible unless they are absolutely time or energy limited (Oring and Sayler 1992). Also, as male time constraints increase, then harassment by courting males and thus the costs to paired males (and benefits to females) of mate-defense should decrease. This makes it difficult to predict how the cost-benefit balance will change. In addition, females may perform as much or more pair-bond maintenance and defense as males (Weller 1967; Anderson 1984; Lovvorn 1989), and females often are unreceptive to male advances (Johnsgard 1960a; Weller 1965; Hepp and Hair 1983), suggesting that there must be trade-offs of early pairing for females as well as males.

In summary, many available data are inconsistent with the male-costs hypothesis and limited tests of some aspects of the theory have largely been unsupportive. The hypothesis is inadequate because little consideration has been given to cost-benefit trade-offs and decision-making by females, nor to the actual process of mate choice, and how different social and ecological factors may affect that process to result in variation in the timing of pairing.

EXTENDING THE THEORY: THE MUTUAL-CHOICE HYPOTHESIS

Three components of the pairing process are important to consider in order to extend the theory: the process of choosing a mate, the mate chosen, and the state of being paired. The first two components correspond, respectively, to choosiness and preference functions in mate choice theory (Jennions and Petrie 1997). The third component partially reflects the realized fitness benefits of a particular mate choice, but also may function to enhance the benefits of that choice through experience and familiarity gained with a partner (Rowley 1983; Ens *et al.* 1996; Black 2001). Individuals will want to pair when the combined fitness benefits of these three components are maximized. Variation in the timing of pairing then depends on variation in and trade-offs among the benefits and costs of the three components, and results from variation in individual life-history decisions about the allocation of time and energy to the mate-choice process, i.e., when to begin, how much time and energy to allocate to search and assessment, and when to make the choice. Female and male interests necessarily interact and likely partially conflict (Trivers 1972), and optimal decisions on the timing of pairing will depend on the behavior of others due to competition and changes in mate availability as pairing occurs (Real 1991; Johnstone 1997). This state-dependent, game-type theory, that will be referred to as the *mutual-choice hypothesis,* differs from the male-costs hypothesis in two essential points: 1) that decisions by females rather than males primarily determine 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.

The interacting components of the pairing process indicate that we need better, individual-based measures of the timing of pairing before we can develop predictions and further evaluate the hypotheses. In their review, Rohwer and Anderson (1988) defined timing of pairing as the winter month when a majority of birds (75-80%) are observed in conspicuous pair bonds. There are four problems with this kind of measure. First, no distinction is made among individuals of different status. The benefits, costs, and tactics of mate choice leading to pair formation likely differ among individuals that are re-uniting, re-pairing (*sensu* Rowley 1983), or forming their first pair bond. Demographics also are important to consider in this regard. If young birds generally pair later than older birds, then species or populations with higher mortality rates will appear to pair later only because of the greater proportion of new recruits. Second, no consideration is given to when individuals pair relative to when they begin breeding. This is especially relevant to long-lived birds that may form initial pair bonds one or more years before they first breed, and to non-migratory and tropical species that may breed at irregular times. Third, no measure of the process of pair formation is included. If individuals of one species are more choosy (*sensu* Jennions and Petrie 1997) in selecting a mate, then they may pair later even though they may have begun courtship and mate sampling at the same or even earlier time than a less choosy species. Finally, pair bonds may not always be conspicuous (Armbruster 1982; Green and Hamzaoui 2000). Costs may outweigh the benefits to paired birds of maintaining a pair-bond structure through the winter, for example in diving species that forage in dense flocks.

Five measures are recommended: 1) the age at which young individuals first begin courtship (court-age), 2) the number of days or months that newly-pairing or re-pairing individuals are engaged in courtship activity and mate sampling, including trial liaisons, before pairing (court-time), 3) the amount of time per day allocated to courtship (court-rate), 4) the calendar date that pairing occurs (pair-date), and 5) the number of days or months between pair formation and nesting (pair-time). These measures may be subject to different selection pressures and require different hypotheses to explain their inter- and intra-specific variation.

Predictions in Relation to Phenotypic Traits

Theoretical models of optimal sampling tactics and decision rules used by individuals choosing mates (Janetos 1980; Wittenberger 1983; Real 1990; Johnstone 1997) lead to a number of testable predictions about how timing of pairing in waterfowl will vary in response to variation in phenotypic, social, and ecological factors. Under time constraints and competition for mates, and assuming *a priori* perfect knowledge of the distribution of mate qualities, models of mutual choice predict that high-quality individuals will pair earliest and that mating will be closely assortative early in the season, unless costs are high, and less assortative later (Real 1990; Johnstone 1997). It thus may pay low-quality individuals to delay pairing because they may be accepted by higher-quality mates towards the end of the season when higher-quality individuals can no longer afford to be choosy. Models of Johnstone (1997) assume a 1:1 sex ratio, and benefits of delaying pairing by low-quality individuals will be greater for the limiting sex when sex ratios are biased. In waterfowl, the assumption that individuals have *a priori* knowledge is likely most true for previously paired individuals that have been through the mate-choice process at least once, and least true for young, newly pairing birds. Models of adaptive search predict that naive individuals will spend considerable time gaining information about mate-quality distribution before beginning to select a mate (Dombrovsky and Perrin 1994). If individuals that are re-uniting represent the highest-quality mate for each other (Rowley 1983; Black 1996), then they should pair as soon as they re-encounter each other (Johnstone 1997), assuming mutual philopatry to a wintering 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 male-biased sex-ratios (Stotts 1958; Stotts and Davis 1960; Spurr and Milne 1976; Blohm 1982; Wishart 1983; Heitmeyer 1988, 1995).

Early authors suggested that possible benefits of early pairing were to give birds time for mate testing (Weller 1967; McKinney 1975; Afton and Sayler 1982; Wishart 1983) or to gain familiarity with a partner (Gorman 1970; Milne 1974; Choudhury *et al.* 1996). Rohwer and Anderson (1988) rejected mate testing as a hypothesis to explain variation in timing of pairing because they reasoned it predicted early pairing for all birds. However, the benefits of mate testing likely vary in relation to relative parental investment by the two sexes and duration of the pair bond. More importantly, if mate testing is viewed as part of the mate-choice process, then extended periods required for mate testing may delay rather than accelerate pairing chronology. Variance in male mate quality increases with increasing paternal care, favoring greater choosiness by females and males (Parker 1983). The benefits of choosiness also likely increase for both sexes with increasing duration of the pair bond because the fitness benefits of mate choice accrue over multiple breeding seasons. The mutual-choice hypothesis thus predicts greater investment in the mate-choice process (higher court-time and/or court-rate) with increasing paternal care or increasing duration of the pair bond. Pair-time also should increase with increasing paternal care because the benefits of mate co-ordination are likely greater when parental care is shared. Though individuals may have to trade off benefits of increased court-time and increased pair-time if constrained by an approaching breeding season, both measures can be increased by beginning the pairing process earlier in the non-breeding season or at a younger age, or by deferring breeding one or more years, as do swans and geese with biparental care, and most other species of waterfowl with long-term pair bonds.

Because court-time and court-rate are component measures of the total time invested into courtship and mate sampling, we might expect an inverse relationship between them prior to pairing if the optimal level of investment into courtship was similar for all individuals. More likely, optimal time investment differs among individuals, and higher quality individuals may be able to afford a higher court-rate, as suggested by Rohwer and Anderson (1988). However, this would still result in an inverse relationship between court-time and court-rate if individuals begin courtship at the same time and if high-quality individuals pair earliest as predicted by Johnstone (1997). The mutual-choice hypothesis thus predicts that court-time and pair-date of females, but not necessarily males, will be negatively related to the 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

Previous theories on the timing of pairing that focused on trade-offs to males (Afton and Sayler 1982) predicted that greater male-biased sex ratios would lead to earlier pairing because of increased male-male competition (Rohwer and Anderson 1988). The mutual-choice hypothesis makes the opposite prediction. The degree of female or male control of pairing chronology will vary depending on the relative benefits and costs of mate choice, particularly opportunity costs, to each sex or individual. Individuals may incur opportunity costs of losing access to high-quality mates by exercising choice and delaying pairing. Male-biased sex ratios reduce opportunity costs to females, resulting in greater female control and choosiness (Real 1990; Jennions and Petrie 1997) and thus greater investment in courtship and mate sampling, and, for species on similar seasonal cycles, later pair dates, with increasing male bias in the sex ratio. Hepp and Hair (1984) found just such a relationship in their study of six Anatini species. Opportunity costs to males will increase with increasing male bias in the sex ratio, and contrary to the male-costs hypothesis, the mutual-choice hypothesis predicts that males and not females will want to pair as early as possible in most male-biased duck populations.

Studies demonstrating that decreased food availability and increased energetic costs due to cold weather delay pairing chronology (Brodsky and Weatherhead 1985; Hepp 1986; Pattenden and Boag 1989; Demarest *et al.* 1997) generally have been interpreted as support for the male-costs hypothesis (Rohwer and Anderson 1988). As pointed out by Pattenden and Boag (1989), an alternative explanation is that decreased food availability affects pairing because males in poorer body condition are less attractive to females choosing mates. This would explain why pair formation in Mallards *Anas platyrhynchos* and Black Ducks *Anas rubripes* was later and more liaisons were temporary for birds on restricted than *ad libitum* diets even though the amount of courtship by males did not differ (Hepp 1986; Pattenden and Boag 1989), a finding inconsistent with the male-costs hypothesis.

Sex-segregation at local or latitudinal scales due to behavioral dominance (Gauthreaux 1978; Alexander 1983) or habitat specialization (Marsden and Sullivan 2000; Iverson 2002) has been considered as a reason for late pairing in some waterfowl species (Oring and Sayler 1992; Kahlert *et al.* 1998; Coupe and Cooke 1999). However, sex-segregation is never complete and we need an explanation for why pairing does or does not occur among the males and females that do winter together. Differences in male quality may occur whenever habitat or latitudinal segregation occurs (Anderson and Timken 1972; Nichols and Haramis 1980; Nichols *et al.* 1983; Hepp and Hines 1991) and may partly explain why pairing chronology was delayed and dominance relations were reversed, with females dominant to males, for dabbling ducks wintering at milder, southern latitudes (Thompson and Baldassarre 1992). This does not explain why, in some Aythyini and Mergini species, males and females in northern areas also pair late (Weller 1965; Kahlert *et al.* 1998; Coupe and Cooke 1999), a question I will return to in the light of comparative data. In general, the above considerations 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 STATE OF OUR KNOWLEDGE

Inter-specific Comparisons

Available data on waterfowl pairing behavior were compiled to further test predicted relationships between pairing chronology and a number of variables discussed above (Table 1). This compilation also served to assess the state of our knowledge about timing of pairing in waterfowl and to direct us to future research needs. Data were compiled by searching BIOSIS Previews 1969-2007, and by tracking down published and unpublished literature referenced within major works on the subject and within those found by searching BIOSIS. Few quantitative data on pairing chronology for southern hemisphere species were found and thus only northern hemisphere species are represented. When there were multiple studies of a species, one was chosen where several species were compared (e.g., Hepp and Hair 1983) or that was considered the most complete (i.e., presented information on both courting and pairing times).

Different studies of the same species often showed considerable latitudinal variation in pairing chronologies, and a different choice of studies to include may have yielded different conclusions. However, intra-specific trends by latitude were inconsistent. In North America, studies indicated earlier pairing at higher latitudes for Northern Shoveller (*Anas clypeata*; Hepp and Hair 1983; Thompson and Baldassarre 1992), Northern Pintail (*Anas acuta* Hepp and Hair 1983; Miller 1985), Green-winged Teal (*Anas carolinensis*; Hepp and Hair 1983; Miller *et al.* 1988; Rave and Baldassarre 1989; Johnson and Rohwer 1998), and Canvasback (*Aristonetta valisineria*; Smith 1946; Weller 1965), later pairing at higher latitudes for Black Duck (*Anas rubripes*; Johnsgard 1960b; Hepp and Hair 1983), Mallard (*Anas platyrhynchos*; Johnsgard 1960b; Heitmeyer 1988; Johnson and Rohwer 1998), and Redhead (*Aristonetta americana*; Low 1945; Weller 1965), and no difference by latitude for Gadwall (*Mareca strepera*; Hepp and Hair 1983; Paulus 1983) and Lesser Scaup (*Aythya affinis* Weller 1965; Austin *et al.* 1998). For American Wigeon (*Mareca americana*), two studies conducted at middle latitudes showed that 80% of females were paired by November (Hepp and Hair 1983; Heitmeyer 1995), while three other studies conducted at more southern and northern latitudes showed that 80% of females were not paired until March or later (Soutiere *et al.* 1972; Wishart 1983; Thompson and Baldassarre 1992). In the western Palearctic, Mallard also paired later at higher (Raitasuo 1964; Jonsson and Gardarsson 2001) and lower (Green and Hamzaoui 2000) latitudes than at middle latitudes (Bezzel 1959; Lebret 1961). Eurasian Widgeon (*Anas penelope*) paired later at higher latitudes (Bezzel 1959; Jonsson and Gardarsson 2001), while Eurasian Green-winged Teal (*Anas crecca*) showed little difference by latitude (Bezzel 1959; Lebret 1961; Green and Hamzaoui 2000; Jonsson and Gardarsson 2001). Studies of American Wigeon in North America and of Mallard in Europe suggest that pairing may be earlier in the middle of a species' range and later at both southern and northern extremes.

Age- and sex-specific pairing chronologies were available for few species (see below). The paucity of such data precludes definitive tests of many predictions and represents a major gap in our knowledge. Population-level patterns of pairing measured within a single wintering season were available for 26 North American and twelve Western Palearctic species of waterfowl in the subfamily Anatinae (Table 1). Data were sufficient data to test for differences among four waterfowl tribes in the calendar date

Table 1. Variables used to analyze differences in the timing of pair formation among northern hemisphere species of the waterfowl subfamily Anatinae.

	Mass (g)											
Species[a]	Male	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.

Table 1. (Continued) Variables used to analyze differences in the timing of pair formation among northern hemisphere species of the waterfowl 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]
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	1,130	751	66	1.17	49	Y	N	Y	NOV	MAR	4	40
Lophodytes cucullatus	680	540	74	1.85	49	Y	N	Y[f]	OCT	—	—	15, 27, 35, 39
Mergus merganser	1,651	1,238	60	1.94	—	Y	Y	Y[f]	DEC	—	—	13, 15, 36
M. serrator	1,158	925	—	1.62	—	Y	Y	Y[f]	NOV	APR	5	37
Oxyurini												
Oxyura jamaicensis	590	499	—	4.10	42	Y	N	N	APR	MAY	1	16, 39
Western Palearctic												
Anatini												
Mareca strepera	966	835	56	1.42	48	Y	N	N	JUL	SEP	2	4, 15, 32
M. penelope	819	724	53	1.08	48	Y	N	N	—	JAN	—	4, 14, 39
Anas platyrhynchos	1,247	1,107	55	1.47	48	Y	N	N	SEP	OCT	1	4, 15, 32
A. acuta	1,025	866	65	1.37	48	Y	Y	N	DEC	FEB	2	2, 4, 9, 15, 32
A. crecca	364	318	49	1.84	48	Y	Y	N	OCT	MAR	5	2, 4, 14, 39
Aythyini												
Aristonetta ferina	849	807	59	1.53	48	Y	Y	N	FEB	MAY	3	4, 14, 24, 32
Aythya fuligula	654	597	71	1.78	48	Y	Y	N	JAN	MAR	2	4, 9, 14, 32
Mergini												
Somateria mollissima	2,218	1,915	90	—	57	Y	N	Y	SEP	APR	7	11, 15, 32, 39
Bucephala clangula	1,120	710	77	0.53	48	Y	Y	Y[f]	NOV	—	—	4, 9, 29, 32
Mergellus albellus	—	—	—	—	52	Y	Y	Y[f]	FEB	—	—	6, 9
Mergus merganser	1,651	1,238	60	—	52	Y	Y	Y[f]	NOV	APR	5	6, 9, 13, 15
M. serrator	1,158	925	—	—	52	Y	Y	Y[f]	DEC	—	—	6, 37

[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.

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. Differences in pairing chronology among waterfowl tribes in the subfamily Anatinae in the northern hemisphere. Classification after Livezey (1997). Months are numbered one to twelve for July to June, respectively. Means ± SE and ANOVA results are listed, and sample sizes (number of species) are given in parentheses.

	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 importance of these two aspects of pairing will likely predict the relative investment in court-time and pair-time, and likely also relates to whether or not pair bonds are maintained from year to year.

Pairing behavior in geese suggests that beyond the one- to two-year intervals spent choosing and becoming familiar with a mate, additional investment in court-time has greater fitness returns than additional investment in pair-time. Court-time varies more than pair-time among individuals and some females have been known to take 14 or 15 years to find a suitable mate (Choudhury *et al.* 1996; Banko *et al.* 1999). Such delays in breeding after finding a mate are unknown. This reveals the importance and perhaps partially stochastic nature of the mate-choice process and suggests that, within species, court-time will be more responsive than pair-time to variation in social and environmental conditions. This appears to be true for Snow Geese *Chen caerulescens.* Wrangell Island birds delay pairing and breeding one to two years compared to mid-continent birds, possibly due to more severe nesting conditions and greater costs of early reproduction at high- than low-arctic colonies (Ganter *et al.* 2005). Thus it appears that these birds extended court-time rather than pair-time 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 (Table 1), and within 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 (Table 2) 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.

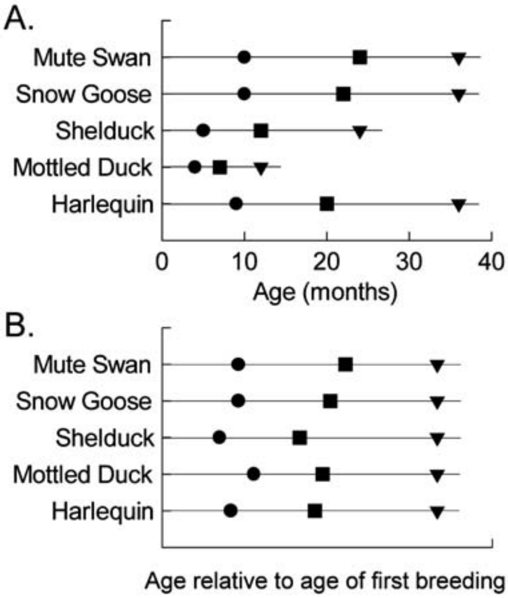

Figure 1. Comparison of absolute (a) and relative (b) ages when females first begin courtship (circles), median age of first pairing (squares), and median age of first breeding (triangles) among representative species of waterfowl tribes Cygnini (Mute Swans *Cygnus olor*), Anserini (Snow Geese *Anser caerulescens*), Tadornini (Paradise Shelducks *Casarca variegata*), Anatini (Mottled Duck *Anas fulvigula*), and Mergini (Harlequin Duck *Histrionicus histrionicus*). Data from Minton (1968) and Wood and Gelston (1972), Prevett and MacInnes (1980), Williams (1979), Paulus (1988b), and Rodway (2004), respectively, and classification from Livezy (1997).

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 probably pair in their first year but do not breed until their second year (Trauger 1971; 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 (Weller 1965), 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 probably 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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