The Canadian Field-Naturalist

Timing of pair formation and male acquisition of alternate plumage by three wintering dabbling ducks

Rodger D. Titman[1,*], Elise A. Titman[2], and Shawn R. Craik[3]

[1]Department of Natural Resource Sciences, McGill University, Ste-Anne-de-Bellevue, Quebec H9X 3V9 Canada
[2]68 Somerset, Baie-d'Urfé, Quebec H9X 2V9 Canada
[3]Département des Sciences, Université Sainte Anne, Pointe de l'Église, Nova Scotia B0W 1M0 Canada
[*]Corresponding author: rodger.titman@mcgill.ca

Titman, R.D., E.A. Titman, and S.R. Craik. 2021. Timing of pair formation and male acquisition of alternate plumage by three wintering dabbling ducks. Canadian Field-Naturalist 135(1): 39–46. https://doi.org/10.22621/cfn.v135i1.2547

Abstract

Pair formation in ducks is thought to be influenced by the acquisition of breeding plumage, the occurrence of courtship display, or both. We examined the frequency of pair formation in Mallard (*Anas platyrhynchos*), Green-winged Teal (*Anas crecca carolinensis*), and Northern Shoveler (*Spatula clypeata*) in the central valley of California in relation to the frequencies of male attainment of breeding plumage and courtship display. Predictions related to two hypotheses are: (1) the timing of pair formation is directly related to the attainment of breeding (definitive alternate) plumage by males, and (2) frequencies of courtship display are highest during pair formation. Most female Mallard were paired by the end of October, with >80% in pairs by early December. Of Northern Shoveler, 90% were paired by early January and 90% of female Green-winged Teal were paired by early February. The highest rates of courtship display by Mallard were observed during October through November, by Northern Shoveler in November, and by Green-winged Teal in November through January. Courtship display was, therefore, relatively frequent at the same time as pair formation for all three species. Northern Shoveler spent less time in courtship display than the other two species. Most (90%) male Mallard had acquired alternate plumage by mid-November, Northern Shoveler by early February, and Green-winged Teal by mid-December. Thus, timing of pair formation coincided with timing of attainment of breeding plumage in Mallard and Green-winged Teal but not Northern Shoveler.

Key words: Pair formation; alternate plumage; winter; courtship; Northern Shoveler; *Spatula clypeata*; Green-winged Teal; *Anas crecca carolinensis*; Mallard; *Anas platyrhynchos*

Abrégé

On considère que la formation de couples chez les canards est influencée par l'acquisition du plumage de reproduction et le comportement social. Deux hypothèses découlent : (1) la chronologie de la formation des couples est directement lié à l'acquisition du plumage nuptial (alternatif définitif) par les mâles; (2) la fréquence de la parade nuptiale est particulièrement élevé pendant la formation des couples. Dans la vallée centrale de la Californie, une majorité de femelles du canard colvert (*Anas platyrhynchos*) ont été accouplées à la fin du mois d'octobre, et > 80 % au début du mois de décembre. Chez le canard souchet (*Spatula. clypeata*), 90 % des femelles ont été appariées au début de janvier et 90 % des femelles sarcelle d'hiver (*Anas crecca carolinensis*) été en couple au début de février. Les taux les plus élevés de parade nuptiale ont été observés chez le canard colvert en octobre et novembre, en novembre pour le canard souchet et durant la période de novembre à janvier pour la sarcelle d'hiver. La parade nuptiale a donc eu lieu en même temps que la formation des couples chez les trois espèces. Le souchet a passé moins de temps en parade nuptiale que les deux autres espèces. Quatre-vingt-dix pour cent des mâles du canard colvert avaient acquis leur plumage alternatif à la mi-novembre, au début de février pour le canard souchet et à la mi-décembre pour la sarcelle d'hiver. Ainsi, la formation des couples a eu lieu au même temps que l'acquisition du plumage nuptial, sauf pour le canard souchet.

Mots clefs: formation de couples; plumage nuptial; hiver; parade nuptiale; canard souchet; *Spatula clypeata*; sarcelle d'hiver; *Anas crecca carolinensis*; canard colvert; *Anas platyrhynchos*

Introduction

Studies of waterfowl biology show events on the wintering grounds influence breeding success and population dynamics (Raveling 1970; Fretwell 1972; Tamisier 1972, 1976; Paulus 1983; Sedinger and Alisauskas 2014). Acquisition and storage of energy for reproduction occurs in waterfowl in late winter and early spring and can impact reproductive success (Krapu 1981; Devries *et al.* 2002). Pair formation occurs during the winter among most dabbling ducks.

A contribution towards the cost of this publication has been provided by the Thomas Manning Memorial Fund of the Ottawa Field-Naturalists' Club.

Various hypotheses have been proposed to explain the prevalence of pair formation before breeding season, including possible benefits associated with familiarity of a breeding partner, opportunity to test a bond and assess mate quality, and male protection of a female allowing her to feed, avoid disturbance from predators or conspecifics, and accumulate nutrient and energy reserves (Milne 1974; Paulus 1983; Rohwer and Anderson 1988).

Field data on the timing of pair formation in North American ducks are rather limited, although their courtship displays are well documented (Lorenz 1971; Johnsgard 1960, 1965; McKinney 1992). Some rough counts of the frequency of paired wintering Mallard (*Anas platyrhynchos*) and Green-winged Teal (*Anas crecca carolinensis*) are cited by Palmer (1976) and Bellrose (1976) and information about timing and displays is given for six species of dabblers in North Carolina, including Northern Shoveler (*Spatula clypeata*) and Green-winged Teal (Hepp and Hair 1983).

We examined the timing of pair formation over winter in three species of dabbling ducks in the central valley of California, United States, to determine the association of alternate plumage acquisition and the performance of courtship display. We chose to study Northern Shoveler, Green-winged Teal, and Mallard based on their close taxonomic relationship, their range in body size, and abundance in the study area during winter.

We assume that alternate plumage (Howell *et al.* 2003) occurs to enhance a male's acquisition of a mate (McKinney 1992). As such, pair formation could be dependent on male attainment of alternate plumage. This hypothesis predicts that paired males have already acquired their alternate plumage; the contrasting null prediction is that pairs occur at high frequency without the male having attained this plumage. Thus, individual males in more advanced plumage should be paired more frequently than those that have not yet attained alternate plumage, and, conversely, those not yet in alternate plumage should be unpaired more frequently than those in alternate plumage. Weller (1965) suggested that the timing of plumage acquisition evolved simultaneously with early pair formation in *Aythya,* an idea that has not been evaluated in dabbling ducks. Another hypothesis concerning the timing of pair formation is that courtship display has a major influence (McKinney 1992). Prediction 2 is that pair formation should be associated with increases in the frequency of courtship display. Courtship display should thus be correlated with pair formation.

Methods

Study area

The central valley of California is a major overwintering area for waterfowl that breed in the northern portions of the central and Pacific flyways (Bellrose 1976). We conducted our study by observing ducks on the flooded impoundments in the Suisun Marsh, Grizzly Island, and Joyce Island Wildlife Areas (38.1724°N, 121.9644°W) near Fairfield, California, and the Gray Lodge Wildlife Area (39.3727°N, 121.7060°W) near Gridley. Vegetation grew along the dikes; although there were some patches of emergent vegetation, extensive open water facilitated observation.

Observations

We observed the birds using a spotting telescope or binoculars and measured activity with scan sampling, recording instantaneous behaviour of individuals alone, paired, or in flocks at timed intervals using a metronome (Altmann 1974). Scans typically surveyed flocks ranging from 40 to 600 individuals. For each observation, we recorded the species, sex, and pair status of the bird. The timing of scans was systematically assigned to cover all daylight hours. Attempts to view animal activity at night with a night vision telescope failed. We compiled frequencies for 10 different behaviours. Courtship display included burp, introductory shake, grunt-whistle, head-up-tail-up, down-up, bill-up, turn-back-of-the-head, bridling, nod-swim, swim, preen, maintenance, and inciting; the other nine categories were not related to courtship (Lorenz 1971; Johnsgard 1965). We determined whether a female and a male were paired based on behaviour toward each other and proximity. Females of all three species are known to breed in the first year after hatching, although factors may influence whether they attempt to breed (Devries *et al.* 2008; Drilling *et al.* 2020; DuBowy *et al*. 2020; Johnson *et al.* 2020).

Frequencies of males in three plumage classes were made during the scans. The plumage classes were based on completion of the pre-alternate moult as shown by new colouration on the head, breast, and flank regions: A = full alternate plumage, B = 50–95% complete, and C = <50% complete. Six arbitrary time periods were designated to examine changes in plumage and behaviour over the study period (15 October 1981 to 10 April 1982): 15 October–14 November; 15 November–12 December; 13 December–9 January; 10 January–6 February; 7 February–6 March; and 7 March–10 April.

Measurements at hunter check stations

Sex, age, and plumage score (as above) were recorded at hunter check stations in the Wildlife Areas for 656 Green-winged Teal, 846 Northern Shoveler,

and 526 Mallard during the legal hunting season from 17 October 1981 to 17 January 1982 (periods 1 through early 4). With the aid of legal volunteers, R.T. collected additional specimens under scientific permits during periods 5 and 6. Hunters were also asked whether a given bird was part of a pair when shot. We judged whether answers were credible based on hunter experience, description of events including consideration of proximity, and behaviour of birds toward each other when they were shot. We did not include pair status information in analysis if answers were not deemed credible.

Analysis

Our data consist of four observational variables collected for three species during up to six periods over winter: (1) percentages of females paired, considering that because of a male-biased sex ratio this represents a reliable indication of pair formation (Hepp and Hair 1983) and, alternatively, (2) percentages of paired and unpaired males; (3) percentages of males in alternate plumage; and (4) percentages of individuals observed in courtship. Prediction 1 and corollaries were tested by comparing frequencies of pairs formed over time with frequencies of males having attained full alternate plumage over time as well as comparing paired versus unpaired males with attainment of alternate plumage using χ^2 tests (Zar 1974). For prediction 2, we compared frequencies of courtship behaviour with frequencies of pairs over time using Scheffe's test and Spearman rank correlations (Zar 1974) using SAS (SAS Institute Inc., Cary, North Carolina, USA). All tests were two tailed.

Results

Pair formation and male alternate plumage acquisition

Most female Mallard (61%) were already paired when we began our observations in October (Table 1; Figure 1), whereas significantly lower proportions of female Green-winged Teal ($\chi^2_1 = 257.5$; $P < 0.001$) and Northern Shoveler ($\chi^2_1 = 372.5$; $P < 0.001$) were paired during the first observation period. It took until January (period 4) for over 90% of Northern Shoveler to be paired and another month for this proportion to be achieved by Green-winged Teal.

Alternate plumage in males was acquired earlier in Mallard and Green-winged Teal than in Northern Shoveler. Behavioural scans showed that 97% and 92% of combined paired and unpaired male Mallard and Green-winged Teal had full breeding colours by mid-November (i.e., end of period 1), compared with 9% of Northern Shoveler (Table 2; Figure 1). Analyses of plumage class from hunter-collected males during period 1 yielded a somewhat similar result to that of scan samples, although the proportion of male Green-winged Teal that attained alternate plumage was lower for the former (55%; Figure 2). Nearly all hunter-collected Mallard and Green-winged Teal had alternate plumage by mid-December (i.e., period 2), whereas most Northern Shoveler did not have alternate plumage until early January.

Only 13.9% of paired male Northern Shovelers observed during scan samples for period 1 had acquired alternate plumage (Table 2, Figure 1). By period 2, nearly 95% of paired male Northern Shoveler had acquired alternate plumage in contrast with only 21% of unpaired males. Analyses of hunter-collected birds supported scan sample observations: all three paired males collected during period 1 did not have alternate plumage, whereas 10 of 16 (63%) paired males collected during period 2 had acquired alternate plumage (Figure 2). Thus, female Northern Shoveler paired early in the season chose males that had yet to acquire full breeding colours; this was not the case for Mallard and Green-winged Teal. Most female Green-winged Teal were not paired before early February (period 4), so pair formation in this species occurred after males had attained full alternate plumage.

Pair formation and courtship display

The percentages of female Northern Shoveler and Green-winged Teal that were paired did not correlate significantly with courtship ($r_s = 0.71$, $P = 0.11$; $r_s = 0.49$, $P = 0.33$, respectively), although there was a general tendency for the percentage of paired females of both species to increase with courtship activity

TABLE 1. Paired female Northern Shoveler (*Spatula clypeata*), Green-winged Teal (*Anas crecca carolinensis*), and Mallard (*Anas platyrhynchos*) observed in northern California during six periods in winter 1981–1982, determined from behavioural scan samples (including adult and juvenile birds).

Period	Northern Shoveler, no. (%)	Green-winged Teal, no. (%)	Mallard, no. (%)
15 Oct.–14 Nov.	2318 (15.6)	526 (10.0)	353 (61.2)
15 Nov.–12 Dec.	1763 (64.3)	541 (28.4)	563 (77.4)
13 Dec.–9 Jan.	2083 (86.8)	238 (58.4)	75 (85.4)
10 Jan.–6 Feb.	2041 (94.3)	1126 (78.2)	497 (95.9)
7 Feb.–6 Mar.	4562 (97.9)	935 (94.5)	181 (99.4)
7 Mar.–7 Apr.	2482 (98.8)	1748 (98.7)	388 (99.7)

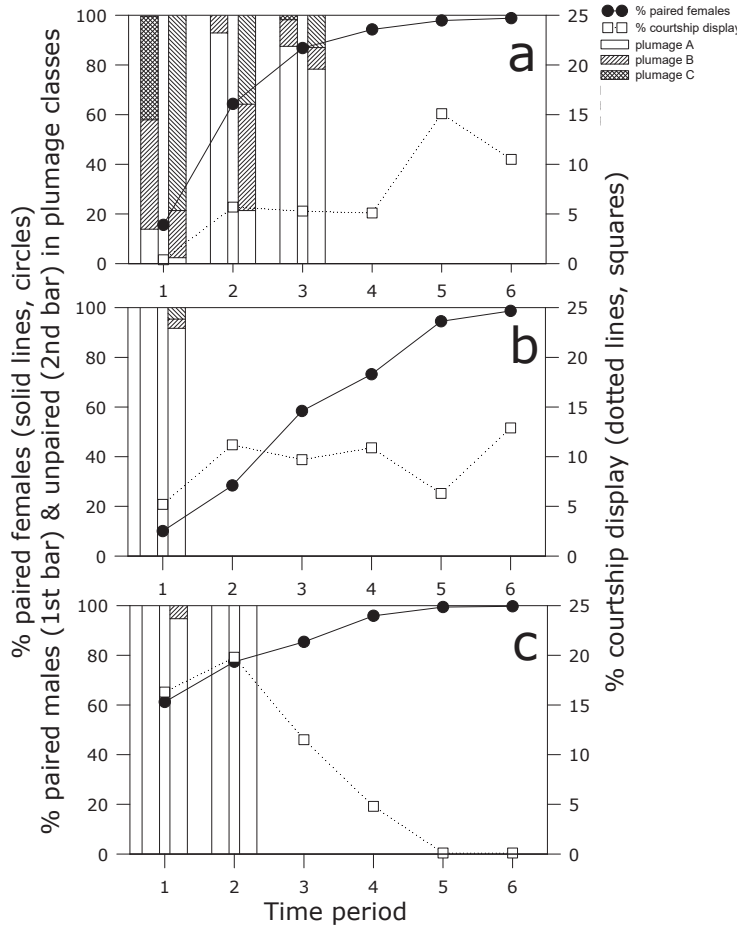

FIGURE 1. Relation between acquisition of alternate plumage by male ducks with pairing and courtship display: a. Northern Shoveler (*Spatula clypeata*), b. Green-winged Teal (*Anas crecca carolinensis*), and c. Mallard (*Anas platyrhynchos*) during six observation periods, winter 1981–1982 in California State Wildlife Areas of northern California, USA. Plumage class A = full alternate plumage, B = 50–95% of pre-alternate moult complete, C = <50% complete. Period 1 = 15 October to 14 November, period 2 = 15 November to 12 December, period 3 = 13 December to 3 January, period 4 = 10 January to 6 February, period 5 = 7 February to 6 March, and period 6 = 7 March to 7 April. Plumage data were obtained from separate purposeful scans at close distance where pair status and plumage condition were readily apparent; however, adults could not be distinguished from juveniles (see Table 2 for sample sizes). Sample sizes for counts assessing frequency of courtship display in periods 1 to 6 are: Northern Shoveler: 164, 138, 120, 155, 114, 106; Green-winged Teal: 77, 116, 112, 158, 96, 103; Mallard:109, 101, 106, 112, 64, 78.

after period 1 (i.e., mid-November). The frequency of courtship activity in Northern Shoveler was highest in periods 5 and 6 ($P < 0.001$, Scheffe's test) just as the frequency of pairs began exceeding 95%. Courtship activity for Green-winged Teal was greatest in mid-winter, as most pair formation was occurring. The percentage of paired female Mallard declined with greater courtship activity ($r_s = -0.71$, $P = 0.008$). A high proportion of females was paired by mid-October when migrants were arriving on the wintering area to meet local breeders (Drilling *et al.* 2020); then, an increase in courtship display, often associated with copulation, occurred just before departure of migrants and local breeders. Frequencies of courtship display were relatively high until pair bonds were formed (Table 1, Figure 1).

Discussion

Earlier studies indicate that female ducks use plumage as a criterion for choosing one male among many displaying to them (Weller 1965; McKinney 1992). This was likely true during fall and winter in northern California for female Mallard and Green-winged Teal, as they appeared to have a good choice

TABLE 2. Pair status and frequency of plumage class of paired and unpaired male Northern Shoveler (*Spatula clypeata*), Green-winged Teal (*Anas crecca carolinensis*), and Mallard (*Anas platyrhynchos*) over three periods of early winter 1981–1982 in northern California.

Period	Species/pair status (*n*)	Frequency (%) of plumage class*		
		A	B	C
1. 15 Oct.–14 Nov.	Northern Shoveler			
	Paired (144)	13.9	44.0	41.7
	Unpaired (126)	2.4	19.0	78.6
	Green-winged Teal			
	Paired (7)	100.0	0.0	0.0
	Unpaired (108)	91.7	3.7	4.6
	Mallard			
	Paired (17)	100.0	0.0	0.0
	Unpaired (19)	94.7	5.2	0.0
2. 15 Nov.–12 Dec.	Northern Shoveler			
	Paired (71)	92.9	7.0	0.0
	Unpaired (70)	21.4	42.8	35.7
	Mallard			
	Paired (15)	100.0	0.0	0.0
	Unpaired (29)	100.0	0.0	0.0
3. 13 Dec.–3 Jan.	Northern Shoveler			
	Paired (56)	87.5	10.7	1.8
	Unpaired (23)	78.3	8.7	13.0

*Plumage class A = full alternate plumage, B = 50–95% of pre-alternate moult complete, C = <50% complete. These frequencies were obtained from separate purposeful scans at close distances where pair status and plumage condition were readily apparent, yet one could not distinguish adults from juveniles.

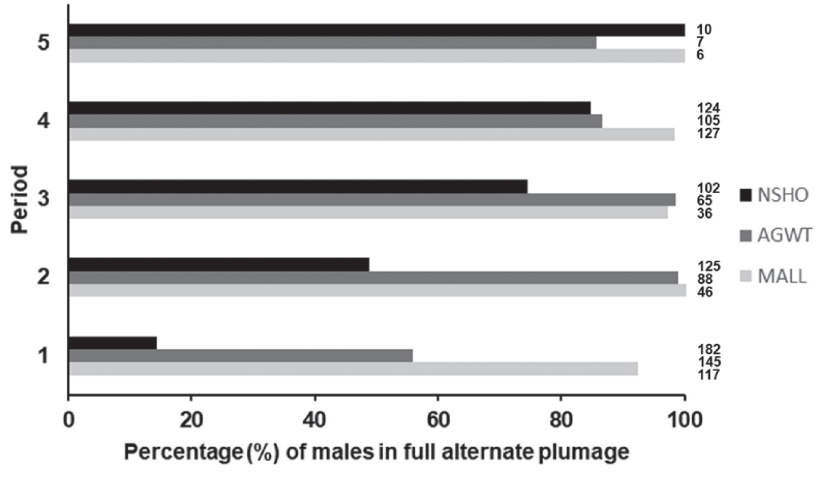

FIGURE 2. Proportion of males in full alternate plumage over five periods for Northern Shoveler (*Spatula clypeata*, NSHO), Green-winged Teal (*Anas crecca carolinensis*, AGWT), and Mallard (*Anas platyrhynchos*, MALL) at hunter check stations and collected under permit in state wildlife areas of northern California in 1981–1982. Includes both adults and juveniles. Period 1 = 15 October to 14 November, period 2 = 15 November to 12 December, period 3 = 13 December to 3 January, period 4 = 10 January to 6 February, and period 5 = 7 February to 3 April. Sample sizes are given for each bar.

of males already in full alternate plumage; Northern Shoveler males at differing stages of moult displayed to females during October–November. This suggests that a unifying set of hypotheses explaining timing of pair formation in dabbling ducks may be complex and elusive.

Our prediction 1 (males acquire alternate plumage before forming a pair bond) held for Mallard and Green-winged Teal but not for Northern Shoveler. Full breeding plumage is not necessary for pair formation to occur in Northern Shoveler; however, males that were more advanced in their pre-alternate molt appeared to be paired earlier than others (R.D.T. pers. obs.). A corollary to prediction 1 is that pair formation is ordered according to the sequence of male alternate plumage acquisition. Some male Mallard had acquired alternate plumage before our first observations; all were in full alternate plumage by period 1 and they were paired first. In contrast, Green-winged Teal acquired their alternate plumage by period 2 (November), and over 90% were not paired until period 5. Over 90% of Northern Shoveler were paired by period 3 (December) when 15–25% of males had yet to acquire full alternate plumage (Table 2, Figures 1, 2). Therefore, the evidence above leads us to reject prediction 1 only for Northern Shoveler. Dubowy *et al*. (2020: 9) stated: "Only males in Alternate plumage display to females wintering in North Carolina", but this was certainly not the case for Northern Shoveler in our study in California.

The late acquisition of breeding plumage in Northern Shoveler coupled with their early pairing schedule tends to suggest that selection has favoured individuals with full alternate plumage arriving on the breeding ground over having this plumage earlier for mate acquisition. Perhaps the most important function of alternate plumage is for territorial advertisement and defense. Northern Shovelers are very strongly territorial while breeding when the males have their brightest and most conspicuous alternate plumage. Display, plumage quality, and other aspects of morphology can influence mate choice (Klint 1980). For example, Omland (1996) found that female Mallard selected males based on bill characteristics and plumage ornamentation. Is it not possible that female Northern Shoveler can use other cues, such as condition or bill characteristics or colouration, to select mates? This also begs the question: why do Northern Shovelers not act as do Mallards and Green-winged Teal which keep their alternate plumage from fall through to the breeding season? Is this related to nutrient availability or perhaps feather wear caused by Northern Shovelers' habit of ploughing with their head through water and floating vegetation? Hohman *et al*. (1992: 136) have stated that "waterfowl are able to make physiological adjustments to meet the energy/nutrient demands of molt when presented with seasonal constraints or variation in food resources".

Mallards engage in courtship display during fall staging and migration when pair formation begins with intensity (Drilling *et al.* 2020). Increased courtship display was followed by an increase in the frequency of pairs. Mallard courtship display peaked in period 2 (late November/early December) and this was the first of the three species to pair at a high level. Green-winged Teal courtship peaked in period 6 (April), but showed high levels of courtship in periods 2, 3, and 4 (November through January); this was the last of the three species in timing of pairing. Northern Shoveler courtship peaked in period 5 (February/March), but this species showed increasing courtship display in periods 2, 3, and 4 and was the second in order of pairing. Together, these observations are consistent with prediction 2 (frequencies of courtship display are highest during pair formation), but correlation tests were not significantly positive for any of the three species. Once pairs have formed, the frequency of courtship display declines. It reached zero in Mallards in the last two periods of winter. A significant negative correlation for Mallards may reflect that courtship is no longer necessary once pairs are formed.

Neither peak courtship display nor peak acquisition of alternate plumage in Green-winged Teal coincided with high frequencies of pairs, although trends toward these coalescing were observed. Early high frequencies of courtship display were noted. It was difficult to distinguish first-year males (juveniles) from adults, which most likely influenced the results. It is reasonable to expect that adults should attain full alternate plumage earlier and, therefore, court and pair earlier than juveniles, but we could not determine this. However, one cannot discount the possibility of other factors, such as hormone levels and condition, influencing aggressive tendencies in males, making dominant individuals more attractive apart from plumage and displays (Davis 2002; Devries *et al.* 2008). We cannot claim that either plumage acquisition or courtship display is the definitive influence on pair formation in Green-winged Teal, but they do affect the timing of pair formation.

Pair formation for all three species increased with time over the winter until the proportion of females that were paired reached ~90% in early February. This rate of pair formation may have been prevented from increasing more rapidly by the deaths of members of pairs (Ackerman *et al*. 2006), especially males. Our hunter bag checks until the end of the hunting season revealed that males were shot more frequently than females (proportion of males harvested: Northern Shoveler = 63%, Green-winged Teal = 62%, Mallard = 61%).

We examined the influence of two proximate factors on the timing of pair formation without considering important ultimate factors, such as availability and use of nutrient resources and predation (risk

aversion). Over the winter, considerable body moult occurred in the ducks we examined (R.D.T. unpubl. data). Protein from invertebrates is needed to build the keratin constituting feathers during moult for each of the three species in our study, and exogenous contributions from daily diet are a major source of protein for this moult (Hohman *et al*. 1992). In winter, Northern Shovelers feed primarily on nektonic invertebrates with some seeds (Dubowy *et al.* 2020), Green-winged Teal diet is 62% seeds and 38% animal matter (Johnson *et al*. 2020), and Mallards eat 88% plant material and 12% animal matter (Hohman *et al*. 1992) to acquire this protein. Since our study, habitat manipulation in Suisun Marsh that particularly improved seed availability has resulted in greater body mass of dabbling ducks, except Green-winged Teal (Fleskes *et al*. 2016). This change in body condition could reflect changes in nutrients affecting moult and behaviour and, thus, the timing of pair formation. Further observations at our study site are warranted, including determining whether Northern Shoveler pairing without achieving full alternate plumage still prevails. The fact that our study area was highly desired and managed for hunting has further impact on aspects, such as risk aversion and other behaviour (e.g., mate guarding) that may also influence pair formation (Ackerman *et al*. 2006). Thus, beyond the plumage characteristics and courtship we studied, there are other factors requiring further examination in the context of pair formation.

We conclude that timing of pair formation in Northern Shoveler, Green-winged Teal, and Mallard is closely tied to frequency of courtship display, whereas our results, especially for Northern Shoveler, show that timing of pair formation is not consistently related across species to attainment of male breeding plumage. Further consideration of other factors driving timing of pair formation, some of which we have discussed above, may help develop a more effective set of hypotheses that apply across more duck species.

Author Contributions

Writing – R.D.T.; Writing – Review & Editing: R.D.T. and S.R.C., Conceptualization: R.D.T., Investigation: R.D.T. and E.A.T.; Methodology: R.D.T.; Formal Analysis: R.D.T. and S.R.C.; Funding Acquisition: R.D.T.

Acknowledgements

This research was conducted in adherence to guidelines of the University of California-Davis and McGill University in 1981 and 1982. Permits to conduct the research on National Wildlife Refuges in California from 1 November 1981 to 30 June 1982 were issued by the U.S. Department of the Interior, Fish and Wildlife Service, for observation – Special Use – permit no. 054, for Scientific Collection – permit no. PRT-2-2657-SC and the State of California, Department of Fish and Game, Scientific Collector's Permit no. 0272 1982. R.D.T. and E.A.T. are grateful to the late Dennis Raveling who was our gracious host and facilitated jumping through the many administrative and logistical hoops while R.D.T. was on a sabbatical leave in the Department of Wildlife and Fisheries Biology at the University of California, Davis. H.A. George and R.B. Reno, California Department of Fish and Game, were helpful in granting access to wildlife areas. We are grateful for advice and assistance provide by M.R. Miller and D.S. Gilmer, United States Fish and Wildlife Service and M.R. McLandress of the University of California. M.A. Fanous provided statistical advice. At hunter check stations, G. Nolan, R. Presley, D. Grider, H.S. Castillo, E. Nagel, H. George, and R.B. Reno were very hospitable and helpful to us. Editorial and critical review of an earlier draft by M.G. Anderson, K. Elliott, D.A.W. Lepitzki, and D.C. Tozer is much appreciated as well as D.A.W. Lepitzki's inspired creation of Figure 1. Financial support was provided by the Natural Sciences and Engineering Research Council of Canada. McGill University provided computer time.

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Received 10 May 2020
Accepted 9 March 2021
Associate Editor: D.C. Tozer