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RESEARCH ARTICLE

Evidence of phenotypic plasticity of penis morphology and delayed reproductive maturation in response to male competition in waterfowl

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ABSTRACT

Ducks are an excellent group to study avian genital evolution. Penis morphology of ducks is diverse, and penis length and elaboration are positively correlated with levels of male competition resulting from forced extra-pair copulations, and with female genital elaboration resulting from sexual conflict. Here we examined whether penis morphology is affected by social environment. We found experimental evidence that in a male-biased social environment, consisting of several males and fewer females, the penis in Lesser Scaup (*Aythya affinis*) grew longer in 2 separate years, than in males housed in pairs, as predicted if male–male competition influences penis morphology. In Ruddy Ducks (*Oxyura jamaicensis*), males instead showed evidence of reproductive delays that were explained both by a male's size and his social environment: most males in social groups exhibited shorter penises, variable onset and duration of genital maturation, and faster penis growth rate. These 2 species have different levels of post-copulatory competition in nature, with Ruddy Ducks having more extreme penis sizes and more promiscuity than Lesser Scaup. The results suggest that waterfowl can exhibit complex, socially dependent phenotypic plasticity and reproductive maturation that can generate intraspecific variation in their genitalia.

Keywords: duck reproduction, genital evolution, sexual conflict, social plasticity, vertebrate genitalia

Evidencia de plasticidad fenotípica en la morfología del pene y retraso en la maduración reproductiva en respuesta a la competencia entre machos en las aves acuáticas

RESUMEN

Los patos son un grupo excelente para estudiar la evolución de los genitales en las aves. La morfología del pene de los patos es diversa, y el largo del pene y la elaboración están positivamente correlacionados con los niveles de competencia entre machos resultante de copulaciones forzadas extra-pareja y con la elaboración de los genitales de las hembras resultante de los conflictos sexuales. Aquí examinamos si la morfología del pene es afectada por el ambiente social. Encontramos evidencia experimental de que en un ambiente social sesgado hacia los machos, consistente en varios machos y menos hembras, el pene en *Aythya affinis* creció más largo en dos años separados, que en machos alojados en pareja, como se predijo si la competencia macho-macho influencia la morfología del pene. En *Oxyura jamaicensis*, los machos en cambio mostraron evidencia de retrasos reproductivos que fueron explicados tanto por el tamaño del macho como por su ambiente social: la mayoría de los machos en grupos sociales exhibieron penes más cortos, inicio y duración variable de la maduración de los genitales y tasa de crecimiento más rápida del pene. Estas dos especies tienen diferentes niveles de competencia post-copulatoria en la naturaleza, con *O. jamaicensis* presentando tamaños más extremos del pene y más promiscuidad que *A. affinis*. Estos resultados sugieren que las aves acuáticas pueden exhibir plasticidad fenotípica y maduración reproductiva compleja dependiente del entorno social, que puede generar variación intraespecífica en sus genitales.

Palabras clave: conflicto sexual, evolución de los genitales, genitales en vertebrados, plasticidad social, reproducción en patos

INTRODUCTION

Male genitalia are diverse and highly variable among species (Eberhard 1985). Male–male competition, female choice, and sexual conflict are likely the main evolutionary forces that have shaped male genital traits (Eberhard 1985, Hosken and Stockley 2004, Arnqvist and Rowe 2005). However, the role of phenotypic plasticity (i.e. the capacity to express different phenotypes in response to variations in the environment) in generating phenotypic diversity in genitalia has been little explored, and it can have important evolutionary consequences. Phenotypic plasticity can be an important source of intraspecific variation in genital morphology that has been largely overlooked. Phenotypic plasticity may increase fitness in changing environments, so that plasticity may be adaptive and subject to selection (West-Eberhard 2003). Not only can phenotypic plasticity theoretically generate variation upon which selection can act (West-Eberhard 2003), but understanding how plasticity influences the expression of reproductive traits and the mechanisms that underlie their maintenance and expression is crucial in understanding the processes that influence sexual strategies (Cornwallis and Birkhead 2008).

Many studies have demonstrated that investment in male reproductive traits should respond to social information about sex ratio, group size, and density and therefore the likely strength of male–male competition in birds (e.g., Brown and Brown 2003; Cornwallis and Birkhead 2007, 2008; Immler et al. 2009) and many other groups. However, to our knowledge only one study has demonstrated phenotypic plasticity in genitalia in response to social environment in any organism. In the sessile hermaphroditic acorn barnacle (*Semibalanus balanoides*), phallus size is *inversely* correlated with breeding density (Hoch 2008), because their penis is longer when colonies are less dense so they can reach a neighbor in order to copulate (Hoch 2008). We were therefore interested in examining whether social environment would influence the morphology of duck genitalia seasonally.

Birds are ideal subjects to study genital evolution because they have the most extreme penis morphology of any vertebrate, ranging from the longest vertebrate penis corrected from body size in the Lake Duck (*Oxyura vittata*; >40 cm; McCracken et al. 2001), to a complete absence of the penis in over 97% of avian species (Briskie and Montgomerie 1997). Among the avian species that have retained the ancestral amniote penis, the penis can be intromittent (long enough to enter the female vagina) or non-intromittent (just long enough to enter the cloaca) (Brennan et al. 2008). All avian penises function with a lymphatic rather than blood vascular erection mechanism (Brennan and Prum 2011).

Waterfowl (Order Anseriformes), have spiral-shaped intromittent penises (Briskie and Montgomerie 1997). In

Mallards (*Anas platyrhynchos*), penis length increases at the beginning of the spring and decreases in late summer; these changes are correlated with androgen hormones (Hohn 1960, Brennan and Atkins-Regan 2014). Erection in Muscovy Ducks (*Cairina moschata*) is explosively rapid after accumulation of lymph at the base of the penis (Brennan et al. 2010).

The morphology of the penis in ducks (Family Anatidae) is correlated with their social behavior. Although most species of ducks form socially monogamous pairs, post-copulatory competition is widespread in this group because males in many species routinely perform forced extra-pair copulations (FEPCs) on females who are already paired (McKinney et al. 1983). Females strongly resist these FEPCs, and they are often injured and even killed by males in the process (McKinney et al. 1983, McKinney 1985, McKinney and Evarts 1998). Among duck species, male penis length is positively correlated with levels of FEPCs, so that in species where these are rare or absent, the penis is short and simple, whereas in species where FEPCs are frequent, the penis is long and elaborate (Coker et al. 2002, Brennan et al. 2007).

Forced copulations, however, are costly for females, creating sexual conflict over mating and fertilization (McKinney et al. 1983, Brennan et al. 2007, Adler 2010, Brennan et al. 2010, Brennan and Prum 2012). Female genital morphology in ducks has diversified by sexually antagonistic coevolution with male genitalia (Brennan et al. 2007, Brennan et al. 2010, Brennan and Prum 2012). In species of ducks and geese where risk of FEPCs is low and male penises are short, female vaginas are simple tubes, whereas in species with frequent FEPCs and long male penises, the female vagina is convoluted and has distinct pouches near the cloacal entrance (Brennan et al. 2007). Elaborations in the female vagina can prevent full intromission of the penis, forcing males to deposit their sperm closer to the cloacal entrance and further from the sites of sperm storage and fertilization (Brennan et al. 2010). Males who perform FEPCs gain little paternity compared to the female's mate, despite the relatively high frequency of FEPCs (Brennan and Prum 2012). In duck species where FEPCs are frequently observed (30–40% of all copulations), only 2–5% of offspring are not sired by the female's mate (Evarts 1990, Dunn et al. 1999, Peters et al. 2003). The female's mate often copulates immediately after FEPCs take place (Brennan and Prum 2012). Waterfowl male genitalia are therefore under selection from intra-sexual competition (via FEPCs) and sexual conflict (via antagonistic coevolution with females).

Here we investigated whether the social environment, in particular male-biased sex ratio and higher density, would affect penis morphology in adult waterfowl. We tested the hypothesis that differences in the social environment (density, group size, and sex ratio) that translate into

higher male–male competition would positively affect penis length *within* species in waterfowl, under the assumption that longer genitalia increase male reproductive success when post-copulatory competition occurs (e.g., Wenninger and Averill 2006 in beetles, van Lieshout and Elgar 2011 in earwigs, but untested in waterfowl). For this reason, we predicted that the penis length of males housed in groups with other males (experimental groups), where they had to compete for access to females, would be larger when compared to males that were housed in pairs with a single female (control). The null hypothesis (H_0) would be that if phenotypic plasticity does not exist, we should find no differences in the penis length of males in these 2 different social environments. According to the prediction that phenotypic plasticity itself is shaped by selection (e.g., Pigliucci 2005, Pfennig et al. 2010), we also predicted that there would be differences between species in the magnitude of genital phenotypic plasticity due to their evolved differences in the intensity of male–male competition. Therefore, we tested 2 species of ducks that differ in breeding system. Lesser Scaup (*Aythya affinis*) form seasonal pair bonds, have intermediate levels of FEPCs, and relatively short penises (Austin et al. 1998, Coker et al. 2002), whereas Ruddy Ducks (*Oxyura jamaicensis*) are highly promiscuous, do not form pair bonds, have very long penises, engage in direct combat over mating, and only a small percentage of males copulate with females (Gray 1980, Brua 2002, Coker et al. 2002). Male–male competition is therefore predictably stronger in Ruddy Ducks than in Lesser Scaup, and Ruddy Ducks could be expected to have a greater magnitude of phenotypic response to male-biased sex ratios and higher male density. However, Ruddy Ducks also appear to have been under strong directional selection for long penis length, and some theory predicts that directional selection can result in lower levels of plasticity (Scheiner 1993).

METHODS

Study Species

Lesser Scaup males compete for access to females during the early spring when seasonal pair bonds are formed (Austin et al. 1998). Actual copulation and egg laying begin several weeks later in May–June (Austin et al. 1998). Breeding pairs do not defend strict territories, but have a flexible home range that overlaps with other pairs (Austin et al. 1998). After pair formation, intrasexual selection continues through FEPCs that are performed primarily by unpaired males (Afton 1985). In Lesser Scaup, FEPCs are present and common. In a field study, almost half of all observed copulations were FEPC attempts, but only 20% of those were deemed successful (based on behavior, not genetic data; Afton 1985). A comparative study of FEPCs in waterfowl classified the frequency of FEPCs in Lesser

Scaup as 3 on a qualitative scale (1: FEPCs absent, 2: FEPCs rare, 3: FEPCs common, 4: FEPCs very common, no pair bond; Coker et al. 2002). The fully developed penis in Lesser Scaup is relatively short (4–8 cm) for their body mass (700–800 g) and its surface is covered with smooth ridges (Coker et al. 2002; Figure 1A, 1B). The species is described as nonaggressive and sociable (Austin et al. 1998), although paired males will defend their female against FEPCs (Afton 1985).

Ruddy Ducks are highly promiscuous and males compete aggressively for access to females throughout the breeding season mid-spring to late summer. Ruddy Ducks have extreme male-biased sex ratios, even among waterfowl (Belrose et al. 1961). On the breeding grounds, courtship parties of 2–15 males assemble on large ponds and attempt to form temporary pair bonds that are very short in duration (a few days) compared to any other duck (Brua 2002). Males do not establish territories but defend an area around the female (Brua 2002). Ruddy Duck males engage in frequent agonistic interactions and are considered the most combative of waterfowl (Brua 2002). Only 25% of males in breeding condition are successful in their copulation attempts (Gray 1980), and therefore they are likely to be under stronger sexual selection than Lesser Scaup where most males can potentially form a pair bond. Copulations in Ruddy Ducks are very aggressive and females do not perform the inciting display observed in other duck species (Brua 2002). Level of FEPCs was classified as 4 on the FEPCs scale of Coker et al. (2002). The fully developed penis in Ruddy Ducks can be very long (20+ cm), despite their small body mass (400–550 g), and the surface of the penis is elaborated with keratinized hooks (Coker et al. 2002 and data shown here) (Figure 1C, 1D).

Experimental Conditions

Captive waterfowl were kept at the Livingston Ripley Waterfowl Conservancy in Litchfield, Connecticut, USA. All ducks were kept in naturalistic outdoor enclosures covered with heavy netting and blocked visually but not acoustically from neighboring enclosures. Enclosures were protected with buried metal screens and external electric fences to deter predators. Individuals were fed ad lib with commercial duck pellets (for breeders); all enclosures had ponds available for swimming and each had one nest box per female. All males were purchased by LRWC as birds of the year, and were in their first breeding season at the beginning of the experiment.

To test the role of social environment on penis morphology, we assigned males randomly to each of 2 treatments in 2 consecutive years: a large/high-density group treatment with a male-biased sex ratio, where 2 or 3 males would be left unpaired (2 replicates each year: G1 and G2, Year 1, 8M:5F, Year 2, 7–8M:5F, each enclosure

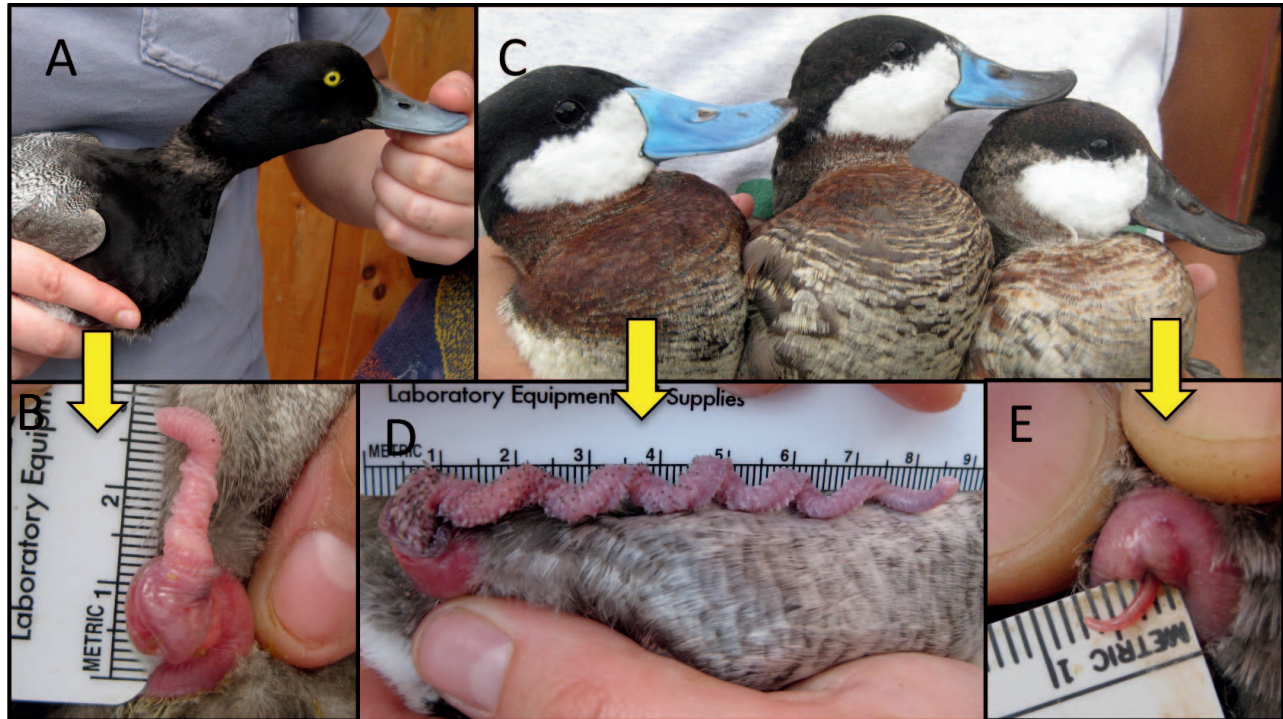


FIGURE 1. Genital morphology and plumage characteristics of males in the study. Arrows connect males with their genital morphology. (A) Male Lesser Scaup experience intermediate intrasexual competition during the breeding season, and (B) their penis is typically short with a smooth surface. (C) Ruddy Duck males experience high competition. On the left a male in breeding condition with ruddy body, blue bill, and a well-developed penis (D). (C) Male in center is beginning to develop breeding plumage, and on the right a male that delayed reproduction with gray body, black bill, and an undeveloped penis (E).

approximately 80 m²), and a no-competition control, in which a male and a female were housed together (1M:1F, Year 1: 10 replicates, Year 2: 8 replicates, each enclosure ~12.5 m²). The number of males was lower in Year 2 because of winter mortality. At the beginning of Year 1, all birds were in their first post-hatching breeding season. Both sexes were assigned randomly to treatments both years. Males were placed in each treatment from late February until mid-November and they were kept together outdoors in large flocks between November and February.

We marked the birds with numbered metal bands; we caught them one at a time using a hand net. One assistant held each male on its back with the cloaca exposed, while the same observer (PLRB) manually everted, photographed, and measured the penis of each male every 16–20 days between March and November (in Year 1) and every 2 weeks between March and November (in Year 2) and weighed males to the nearest 10 g using a 1,000 g Pesola scale (Pesola AG, Schindellegi, Switzerland). Males grew accustomed to this manipulation and penis eversion was achieved quickly once the birds were in hand. All penises were everted until the ostium (tip of the penis) became visible and stretched to their maximum extension each time.

Statistical Analyses

Rejecting the null hypothesis. The first step in our analysis was to assess whether we could reject the null hypothesis that the size of a duck penis is independent of its environment. In light of the small sample size, we did this by performing a nonparametric permutation test on the maximum penis size attained by the ducks. Under the null hypothesis, the distribution of the maximum penis size in the 2 environments should be the same, which implies that shuffling the environment assignments of each duck should not affect the overall distributions. Thus, by shuffling the labels (10,000 times), we calculated the null distribution of the difference in the mean values of the maximum phallus size from the 2 environments. A *P* value was calculated by comparing our observed difference value to the null distribution.

Average penis length during the breeding season. We analyzed the effect of treatment on penis length of males during 9 mo of the year, using repeated measures analysis of variance. We used mixed procedure in SAS, where the dependent variable was penis length, the random effect (subject) was individual ID, the fixed effect was treatment (G1, G2, and Pairs), and the estimation method was restricted maximum likelihood (REML), including body mass as a covariate. Repeated measures analysis does not

assume that a subject's measurements across time are uncorrelated. We used an autoregressive covariance method because we assume that each measurement is most likely to covary more with the point immediately prior to it, rather than covary equally with all measurements, because penis growth is seasonal.

All analyses were performed separately for Year 1 and Year 2 of the study for 2 reasons. First, the experimental design was unbalanced between years as males were assigned to treatments at random and some males remained in their original treatment while others switched treatments and there were more males in the groups than in the pairs. Second, we did not collect data for 3 mo between years (Dec–Jan–Feb), therefore the assumption that data points are equally spaced (one assumption of repeated measures analyses) would have been violated if we had analyzed both years together. The assumption that there are no missing data points was fulfilled, as we collected data for all males each time. The results of the repeated measures analysis for each year reported are treatment effect, time effect, the interaction between the two (treatment*time), and the effect of body mass (weight). To determine whether treatment in Year 1 (Y1) influenced the outcome of treatment in Year 2 (Y2), we included Y1 treatment as a covariate in the analyses of Y2. Using the same method we tested differences between G1 and G2 to see whether the high competition groups differed from each other each year. We could not include cage ID as a random factor in these models because pair cages (Pair1–Pair10), had only one male per cage and hence no degrees of freedom to assess cage effect separate from individual effect.

Maximum penis length. We log transformed the data and ran multiple regression (lm function in R) on maximum penis length in Years 1 and 2 for both species using base length of the penis at the beginning of the experiment, average body mass, and treatment (G1, G2, and Pair) as predictor variables. In Y2 we added maximum penis length attained in Y1 as another predictor.

Reproductive tenure. Determining the exact point at which the penis became and stopped being functional was not possible during its seasonal changes. Consequently, to estimate how long ducks remained in reproductive condition we measured the full width/duration at half maximum (FWHM) of the individual penis length increase and decrease curves as a proxy for reproductive tenure. FWHM is given by the distance between points on a curve at which the function reaches half of its maximum value; it is a standard mathematical method used to obtain an estimate of the width or span of a curve (the independent variable, in this case time) (Weisstein 2012). We divided the maximum peak penis measurement for each male in two, and then measured the span of time that the penis was maintained at that length or greater. We used lm to

determine whether this measure of length of breeding tenure (FWHM) was predicted by treatment and/or average body mass.

We performed an ad hoc test on growth rate of the penis in Ruddy Ducks in Year 2 because we noted the slope of the growth curves was different in different males. Beginning with the second penis length measurement, we subtracted the prior measurement (e.g., Time 2 minus Time 1, Time 3 minus Time 2), and then compared the maximum increase (positive values) and maximum decrease (negative values) in penis size, and divided each by the number of days elapsed between measurements to obtain daily rate (cm day⁻¹) of penis length increase or decrease. We used ANOVA to compare these values between males that remained reproductive during the entire season (early-growth EG males) vs. those that did not (variable-growth VG males). We used R for MacOS 1.4, R for MacOS 3.3.1, and SAS v. 9.0 to conduct all the analyses.

RESULTS

Effect of Social Environment

Our results allow us to reject the null hypothesis that there is no phenotypic plasticity in penis size in Lesser Scaup, as we found significant differences in the 2 social environments in which they were kept. The *P* values corresponding to the nonparametric permutation test are 0.0053 (Y1) and 0.0016 (Y2) for Lesser Scaup. However, we could not reject the null in Ruddy Ducks (*P* values 0.3579 [Y1] and 0.4608 [Y2]).

Lesser Scaup. As we predicted, the average penis length of Lesser Scaup males was longer in high-competition social groups than in males in no-competition controls, when controlling for the potential effect of body mass (Table 1 Treatment effect; Figure 2A, 2B). In Year 1, the average penis length was not significantly different between G1 and G2, but in Year 2, average penis length in G1 was greater than in G2, but also greater in both G1 and G2 than in the pairs (Figure 2B). Penis growth is highly seasonal, therefore the effect of time was also significant as penis length increases in mid-spring and it starts shrinking in midsummer, following the typically late breeding season of the species (Table 1 Time effect; Figure 2A, 2B). The time*treatment interaction was also significant as males in group treatments continue to grow their penis for a longer period of time than males in pairs (Table 1; Figure 2A, 2B). Treatment in Y1 had no effect on penis length in Y2 (Table 1), showing that phenotypic plasticity is flexible during an individual's lifetime. Regardless of the social environment, the individual penis length increase and decrease curves of all males appeared to be highly synchronized (Figure 3A, 3B). Males remained reproductive for the same period of time regardless of treatment, as the full-width half max (FWHM) measurement was not significantly different

TABLE 1. Results of repeated measures ANOVA, showing whether treatment (Group 1, Group 2, or Pairs), time (day of the year), or their interaction had significant effects on penis length. Weight (g) and Treatment in Year 1 were added as covariates.

	Num DF	Den DF	F	P
(A) Lesser Scaup				
YEAR 1				
Treatment	2	23	3.94	0.03
Time	10	229	73.54	<0.0001
Treatment*Time	20	229	3.40	<0.0001
Weight	1	229	5.45	0.02
G1 vs. G2	1	14	0.36	0.56
YEAR 2				
Treatment	2	20	13.25	0.0002
Time	15	299	32.15	<0.0001
Treatment*Time	30	299	1.70	0.01
Weight	1	299	0.53	0.46
Year 1 treatment	1	18	0.78	0.38
G1 vs. G2	1	13	5.99	0.02
(B) Ruddy Duck				
YEAR 1				
Treatment	2	23	1.90	0.17
Time	11	252	2.64	0.003
Treatment*Time	22	252	1.03	0.42
Weight	1	252	6.73	0.01
G1 vs. G2	1	14	0.37	0.55
YEAR 2				
Treatment	2	20	3.53	0.04
Time	15	299	23.22	<0.0001
Treatment*Time	30	299	2.8	<0.0001
Weight	1	299	9.34	0.002
Year 1 treatment	1	17	0.99	0.33
G1 vs. G2	1	13	0.11	0.73

between treatments (ANOVA Y1: Group: 142.3 ± 8.2 days, Pairs: 155 ± 10.3 days, $F_{1,24} = 1.01$, $P = 0.32$; Y2: Group: 166.6 ± 10.8 days, Pairs: 187.8 ± 14.7 days, $F_{1,22} = 1.34$, $P = 0.25$). Maximum penis length of males was significantly affected by treatment in both years, but not by average body mass (Table 2). However in Y1 (but not Y2) initial penis length at the beginning of the experiment significantly influenced maximum penis length. Neither maximum penis length in Y1 (Table 2) or treatment in Y1 (not shown) were significant predictors of maximum penis length in Y2.

Ruddy Ducks. Ruddy Ducks did not show a significant difference between the treatments in our permutation tests, but this was due to previously unreported delayed reproductive maturation in this species (*sensu* Hawkins et al. 2012). In Y1, there was no significant difference in penis length between the treatment groups or between time* treatment interaction (Table 1). However, body mass covaried significantly with penis length. Most males in Y1 regardless of treatment ($n = 19$ of 26) showed delayed plumage and penis maturation (delayed reproductive maturation, DRM). DRM males retained substantial aspects of the female-like plumage coloration (mottled

gray belly and breast plumage, black bill, and little or no ruddy color in the body), and their genitalia did not grow at all (Figure 1C, 1E). Only 7 first-year males developed a mature penis and molted into definitive male alternate (breeding) plumage (white cheeks, black cap, ruddy body coloration, and bright blue bill; Figure 1), some in the paired control (4 of 10) and some in the groups (3 of 16). In all cases, males in breeding plumage developed their genitalia and males in nonbreeding plumage did not, suggesting primary and secondary sexual traits are coupled in this species. Breeding plumage males also produced ejaculates during penis eversion whereas DRM males did not, suggesting that the latter were incapable of reproducing. The seasonal pattern of penis variation was evident as the time effect was significant (Table 1 Time effect; Figure 2C). Maximum penis length of males in Y1 was also not correlated with treatment, but was significantly influenced by average body mass and penis length at the beginning of the experiment (Table 2).

In Y2 all male Ruddy Ducks entered reproductive condition including both molt into alternate breeding plumage and penis development. There was a significant effect of treatment on average penis length (Table 1 Treatment effect; Figure 2D) with males in the pair treatment having a longer penis, when controlling for body mass. However this difference was likely due to the different time trajectory of penis length increase and decrease in the different treatments (Table 1 significant time*treatment effect; Figures 2D and 4). There were no differences in average penis length when comparing only the high-competition groups either year (G1 vs. G2, Table 1), and treatment in Y1 had no effect on average penis length in Y2 (Table 1). Maximum penis length was not predicted by either average body mass, treatment, maximum length attained in Y1, or penis length at the beginning of the year (Table 2).

However, in Y2, most males in the groups grew their penis out of synchrony with one another and day length (Figure 3C, 3D), remained in reproductive condition for a shorter period of time (Figure 3C, 3D; FWHM in Table 3), and grew their penis faster than males in the pairs (Figure 4 and Table 3). We call these males variable-growth (VG) males, and distinguish them from early-growth (EG) males that grew their penis early in synchrony with the light cycle (Figure 3C, 3D), remained reproductive for the entire breeding season, much longer than VG males (Table 3), and grew their penis more slowly than VG males (Table 3 and Figure 4). All males in the pair treatments and a few of the group males were early growth (EG) males, whereas the great majority of males in groups ($n = 11$ of 15) were variable growth (VG) males. In the breeding pairs, penis length increase and decrease were synchronous even though males were in social isolation from each other (Figure 3C). There was no significant difference in the

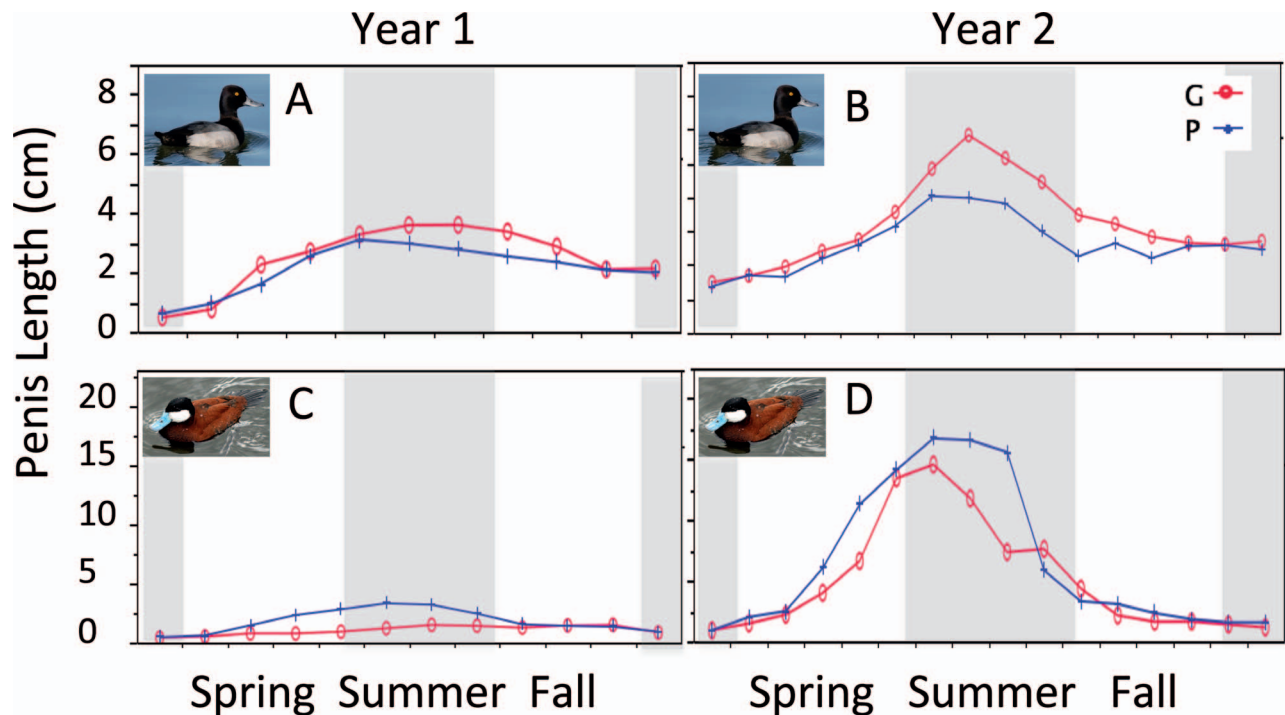


FIGURE 2. Penis morphology exhibited significant phenotypic plasticity in response to social environment. Penis length in cm is the y axis and day of the year is the x axis. Data were collected between the first week of March and the second week of November each year. (A, B) The penis of Lesser Scaup in the high-competition groups (G1 and G2) grew longer than in males in the no-competition treatment in both years (Pairs). (C), In Ruddy Ducks there was no effect of treatment on penis length in Year 1, but in Year 2 (D), males in the control pair treatment had longer penises and remained reproductive for a longer period of time than males in the high-competition treatments (see text).

body mass or rate of penis length decrease of EG and VG males (Table 3). Length of reproductive tenure (FWHM) was significantly affected by both treatment and body mass (Table 2), with the entirely EG males in the pair treatment remaining reproductive much longer than the (mostly VG) males within groups. In summary, Ruddy Duck groups appear to develop a dominance hierarchy in which 2 EG males sexually develop first and maintain their development throughout the season, whereas the majority of VG males sexually develop briefly (albeit more rapidly) and temporally out of phase with one another.

DISCUSSION

Socially Induced Phenotypic Plasticity

We can reject the null hypothesis that there is no phenotypic plasticity in penis length in waterfowl. Our experiments show Lesser Scaup exhibit significant social phenotypic plasticity in penis morphology during adulthood, while Ruddy Ducks show delayed reproductive maturation that is affected primarily by body size in Year 1 and by body size and social environment in Year 2. Determining the exact cause of this phenotypically plastic response however is not possible with our experimental

design, as individuals in groups were exposed to both different sex ratios and densities at the same time. However, the different responses in penis length in the 2 species we examined here strongly suggest that the phenotypic plasticity we encountered is likely adaptive to the relevant ecology of each species. Our results, therefore, should be considered as suggestive evidence that should be further examined with larger experiments that can disentangle sex ratio and density in the future.

Examining the patterns of variation in the plasticity we encountered gives us an insight into biologically relevant processes that may influence this plastic response. The species responses to a male-biased social environment were very different. In Lesser Scaup, penis length increased significantly in groups regardless of age and body size, perhaps as an adaptive response to increased risk of copulatory and post-copulatory competition, consistent with reproductive adjustment to maximize fertilization opportunities (e.g., Wedell et al. 2002).

However, in Ruddy Ducks, where competition is naturally more intense and the penis is already very long (Coker et al. 2002, Brennan et al. 2007), average penis length and length of breeding tenure were longer in the absence of competition in the pairs during Year 2 when all

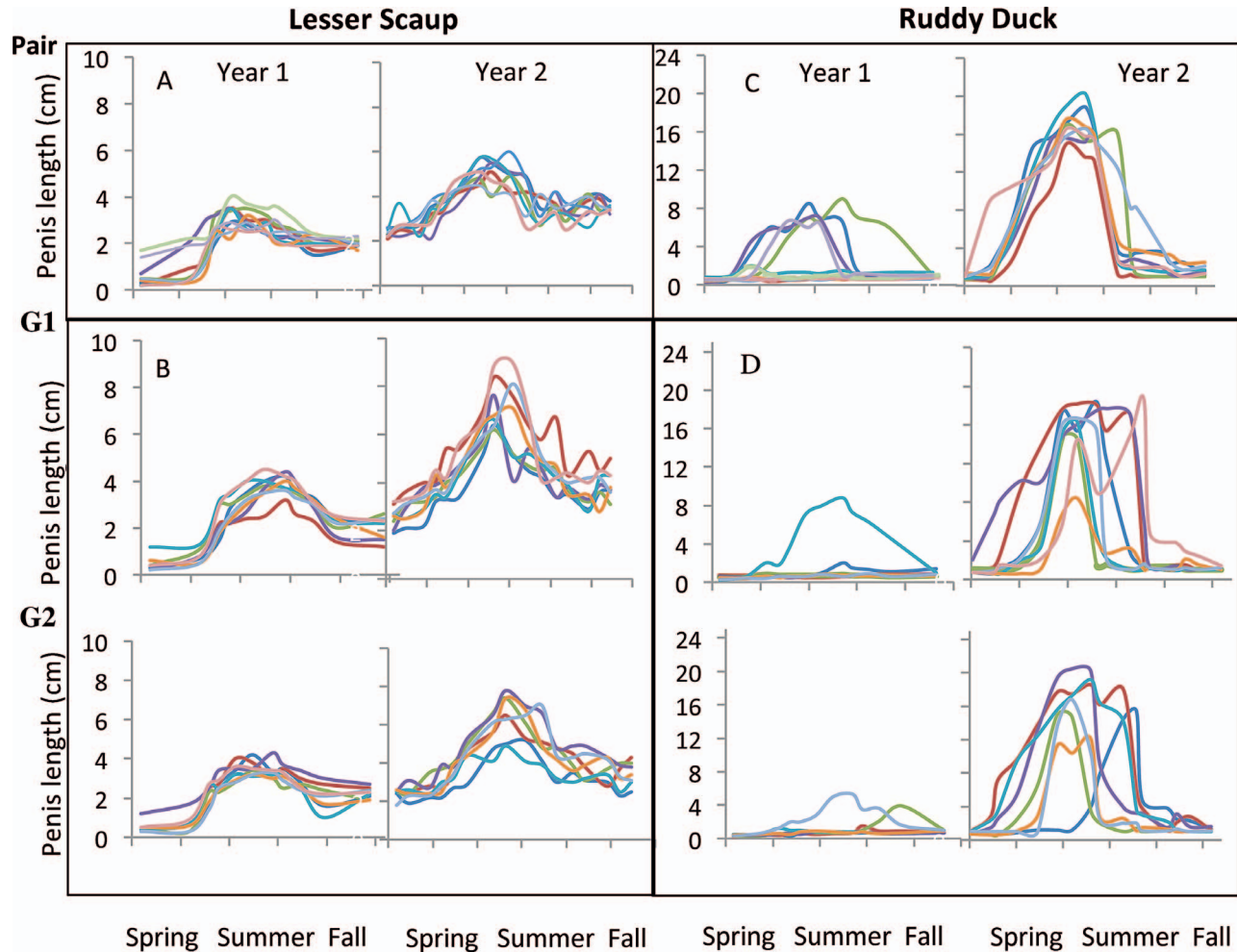


FIGURE 3. Seasonal penis length increase and decrease curves of individual males in the experimental treatments. **(A)** Lesser Scaup in no-competition pair treatments in Y1 and Y2, and **(B)** in two high-competition group treatments (G1 and G2), had seasonal growth curves that were synchronized to external environmental cues. All males grew their penis early and kept it long for the entire breeding season. **(C)** Ruddy Ducks in pair treatments in Y1 and Y2, and **(D)** in 2 group treatments (G1 and G2). Few males in Y1 entered reproductive condition. In Y2, all males entered reproductive condition. In the absence of competitors (Pairs), all males grew a longer penis following the seasonal cycle, but in competitive groups (G1 and G2) only the heaviest males did so, while the smaller males varied the timing and rate of penis length increase and decrease (see text).

males were sexually mature. However, maximum penis length did not differ between treatments. Rather the penis of most males in the groups grew much faster than males in the pairs but was also maintained for a shorter period. In Ruddy Duck, competition appears to have resulted in increased phenotypic variation through plastic responses to the social environment. Either competition among Ruddy Duck males limits the males' ability to maintain a well-developed penis for the entire breeding season or males strategically delay maturation and shorten reproductive tenure (while speeding up penis growth rate) to reduce the direct costs of male–male aggression, the so-called “signal of subordination” hypothesis of Hawkins et al. (2012). The evolutionary history of intense, aggressive sexual competition has apparently led to the evolution of

delayed reproductive maturation, in plumage and coloration, as well as changes in timing and speed of penis development. Surprisingly, the onset of penis development in most Ruddy Duck males in the groups in Year 2 was not triggered by changes in photoperiod as is the case with most seasonal reproductive traits in birds (e.g., Follett 1984, Dawson 2008), but rather as a response to the changing social environment, because second-year males delayed reproductive maturity only in the groups. Delayed reproductive maturation in response to the social environment is known to occur in some birds (Hawkins et al. 2012) but has only previously been reported in one other species of waterfowl, the Mute Swan (*Cygnus olor*) (Conover et al. 2000). In our case, the males were all the same age, so we can show that it is body size, rather than

TABLE 2. Linear models with maximum penis length (MPL) and reproductive tenure (FWHM; see text) as the dependent variables, and average body mass, treatment (G1, G2, Pair), and penis length at the beginning of the experiment (base penis length) as independent variables. In Year 2 we added maximum penis length in Year 1 as an independent variable. LS: Lesser Scaup, RD: Ruddy Duck.

		LS Y1	LS Y2	RD Y1	RD Y2	RD Y2
		MPL	MPL	MPL	MPL	FWHM
Intercept	T	-0.69	0.18	-3.57	0.13	-2.59
	P	0.49	0.85	0.002	0.89	0.017
Average mass	T	1.41	0.15	3.49	0.39	2.69
	P	0.17	0.87	0.002	0.69	0.014
Treatment G2	T	-1.23	-0.82	0.09	0.51	0.11
	P	0.22	0.42	0.92	0.61	0.90
Pair	T	-3.00	-4.01	0.68	1.12	3.07
	P	0.006	0.0008	0.50	0.27	0.006
Base penis length	T	1.83	0.24	0.80	-2.78	0.13
	P	0.008		0.012	0.89	
MPL Y1	T		1.66		0.81	-
	P		0.11		0.42	
Adjusted R^2		0.35	0.55	0.49	-0.10	0.30
	DF	4:21	5:17	4:18	5:17	3:19
	F	4.47	6.55	6.39	0.58	4.27
	P	0.008	0.001	0.002	0.71	0.018

experience/age, that determines which males become dominant in the groups.

Our experimental results can only be considered preliminary because we used individuals in the experimental groups (G1 and G2) as the experimental units, rather than the groups. Our rationale for doing so is that we assigned individuals randomly to the experimental treatments each year and, as such, individuals were independent from one another. This differs from studies of naturally occurring groups, where pseudoreplication may be more problematic (e.g., Hurlbert 1984). However, because individuals were living together, the observations themselves may not have been independent once the experiment began. The only way to deal with this difficulty would have been to create more treatment groups and use groups as the unit of analysis; the fact that we only have 2 groups is a limiting aspect of our experiment. If all experimental units (individual males) remain equally different after treatment as they were before treatment except insofar as the treatment effect per se, then nonindependence would be less problematic. This is the case for Lesser Scaup both years and Ruddy Ducks in their first year. However in Year 2, Ruddy Ducks in the groups appeared to form a dominance hierarchy where 2 EG males in each group behaved differently from all the other VG males. In this case some experimental units did not remain equally different from one another. Dominance hierarchies and delayed plumage maturation in Ruddy Ducks were unknown prior to this study, so there was no

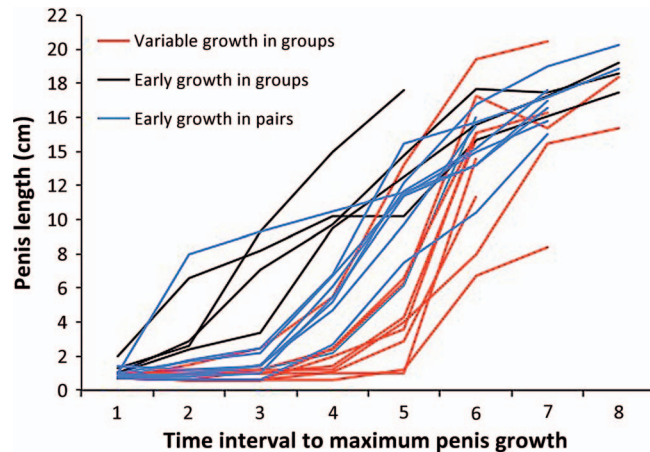


FIGURE 4. Penis length increase in the Ruddy Duck (y axis) in the second year of the experiment from the beginning of the season until reaching peak penis length (x axis). Penis growth in early growth (EG) males in groups is shown in black, and variable growth (VG) males in groups is shown in red. Males in pairs were classified as EG, as their penis grew slowly over a longer period of time (light blue), than VG males.

way we could have anticipated this complication. Despite our experimental limitations, we document a real biological phenomenon of phenotypic plasticity in patterns of genital growth in waterfowl, which occur under different social environments, and find that these patterns are different for each species.

Penis Length and Body Mass

Males may have evolved mechanisms to adjust investment in reproduction in order to maximize fertilization opportunities while minimizing the potential trade-offs between reproduction and other life-history traits (Wedell et al. 2002). Males that are in better body condition may be better able to afford such investment and it is therefore surprising that we found that body mass did not correlate either positively or negatively with average or maximum penis length in Lesser Scaup, where changes in penis length were very significant. If there are any trade-offs of genital growth, they do not appear to affect body mass in Lesser Scaup. In Ruddy Ducks, body mass covaried significantly and positively with penis length in both years of the study, likely because only the largest males became reproductive in Year 1 and only the largest males grew their penis early in the season.

Does Plasticity Enhance Fitness?

We do not know whether males with a longer penis or those who maintain a long penis for a longer period of time achieve higher fertilization success, but the macro-evolutionary correlation between high levels of FEPCs and long penis size in ducks (Coker et al. 2002, Brennan et al.

TABLE 3. Genital plasticity in Ruddy Ducks in Year 2. All males in the pairs grew their penis early in the breeding season and remained reproductive for the whole season (EG, early growth), whereas males in the group treatments (G1 and G2), could be divided into EG and variable growth (VG) males that grew their penis at various times during the season for a shorter time. These VG males showed plasticity in the timing when they became reproductive and in the growth rate of their penis.

	Pairs		Groups		F	P
	Early growth (n = 8)	Early growth (n = 4)	Variable growth (n = 11)			
FWHM ^a (days)	108.8 ± 5.6	127.5 ± 7.9	52.72 ± 4.78		46.0	<0.0001
Maximum penis growth rate (cm day ⁻¹)		0.4 ± 0.03	0.65 ± 0.03		21.9	0.0001
Maximum reduction (cm day ⁻¹)		-0.84 ± 0.06	-0.79 ± 0.06		0.30	0.58

^aFWHM (full width half max is an estimate of days of reproductive tenure).

2007) suggests that longer penises have an advantage when levels of post-copulatory competition resulting from sexual coerced copulations are high. Some studies have reported a fitness effect of intromittent organ length and shape (e.g., Wenninger and Averill 2006, Rowe and Arnqvist 2011, Stockley et al. 2013) and we predict that penis length may also affect fitness in waterfowl. We hypothesize that increased male penis length evolves by male–male competition or intrasexual selection that favors males that can deposit their sperm farther inside the female tract when forced copulations take place (Brennan and Prum 2012), but a longer penis may also permit males to succeed in overcoming coevolved vaginal obstacles during forced intromission and result in a sexually antagonistic coevolutionary process with females (Brennan et al. 2010). Males that remain reproductive longer will likely have increased chances at fertilizing multiple females during the breeding season because female ducks in some species can renest if clutches are lost to predation (e.g., Swanson et al. 1986).

In Ruddy Ducks, larger males that enter breeding condition first can dominate smaller males with physical aggression. Smaller males may either forgo reproduction entirely (exhibit delayed reproductive maturation [DRM] as in Year 1) or may develop mature plumage and genital morphology for a reduced period of the breeding season (as in Year 2), thereby reducing the total physical costs of aggression. DRM is an adaptive strategy by small/younger males to avoid direct competition with older well-established males (e.g., Lyon and Montgomerie 1986, Senar 2006, Hawkins et al. 2012). Further, temporal asynchrony in plumage and genital development among the smaller Ruddy Duck males in the groups appears to be further evidence of strategic phenotypic plasticity. By developing their plumage and genitalia at different times during the breeding season (i.e. out of phase temporally with one another), the cohort of smaller males may maximize their individual sexual opportunities by avoiding additional competition with each other. Thus, smaller males may be following a “best-of-a-bad-job” strategy (John 1993) and entering reproductive condition only for a

short period of time to limit total competition with dominant males and to minimize competition with each other.

Other Considerations

The opportunity for sexual conflict and female choice to operate in our group treatments could have influenced our results. Sexual conflict would be more intense in groups than in pairs because of the increased opportunity for FEPCs to occur. If female genitalia respond to the differential risks of forced copulations by increasing in morphological complexity in the group treatments, it is possible that a phenotypically plastic response to female anatomy could also lead to increased penis length, as coevolution between males and females is generally expected because of their close mechanical interaction (Brennan and Prum 2015). Female genitalia like male genitalia are seasonally plastic (Gilbert 1979) and therefore possibly capable of responding to social environment. We could not test this hypothesis without sacrificing females in the middle of the reproductive season, but this factor deserves to be studied further.

Another possibility is that longer penises may be directly selected by female choice (e.g., mosquito fish (*Gambusia affinis*): Kahn et al. 2010; humans (*Homo sapiens*): Mautz et al. 2013), so that in male-biased groups competition among males to be selected by females could have resulted in a longer penis as we found in Lesser Scaup, but not in Ruddy Ducks. However we think that female choice is unlikely to be the main driving force behind the change in penis length in Lesser Scaup for 2 reasons: First, pair bonding in scaup occurs very early in the spring prior to penis growth, so females cannot be directly selecting for longer penises. Second, we opportunistically measured the genitalia of 3 bachelor male Lesser Scaup that were housed together without females, and their penis size was similar to males in the groups and greater than the paired males on the same peak reproductive day (June 16; group average: 3.5 ± 0.5 cm, paired average: 2.7 ± 0.3 cm, bachelor males: 3.2, 3.5, and 3.8 cm). This suggests that

males are responding to the presence of other males, rather than to female presence and/or anatomy, but again more data would be needed to formally test this possibility.

Similar to the acorn barnacle, the penis of waterfowl grows during the breeding season and regresses to a fraction of its mature size during the nonbreeding season (Hohn 1960, Gilbert 1979, this study). The evolution of seasonal regeneration of the penis in both waterfowl and acorn barnacles has likely facilitated the evolution of social phenotypic plasticity in penis size in these organisms because there is a preexisting mechanism of seasonal change that responds to environmental changes. It is therefore possible that social plasticity in reproductive traits is more likely to be found when such traits exhibit significant seasonal plasticity.

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Author contributions: PLRB designed the study, collected and analyzed the data, and wrote the paper. IG and MG helped collect the data and care for the animals in captivity. DF helped analyze the data, ROP supervised the study, and provided resources to conduct the study. All authors gave feedback on the paper.

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LITERATURE CITED

- Afton, A. (1985). Forced copulation as a reproductive strategy of male Lesser Scaup: A field test of some predictions. *Behaviour* 92:146–164.
- Adler, M. (2010). Sexual conflict in waterfowl: Why do females resist extra-pair copulations? *Behavioral Ecology* 21:182–192.
- Arnqvist, G., and L. Rowe (2005). *Sexual Conflict*. Princeton University Press, Princeton, NJ, USA.
- Austin, J. E., C. M. Custer, and A. D. Afton (1998). Lesser Scaup (*Aythya affinis*). In *The Birds of North America Online* (A. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY. <http://bna.birds.cornell.edu/bna/species/338>
- Belrose, F. C., T. G. Scott, A. S. Hawkins, and J. B. Low (1961). Sex ratios and age ratios in North American ducks. *Illinois Natural History Survey Bulletin* 27:391–474.
- Brennan, P. L. R., and E. Atkins-Regan (2014). Endocrine regulation and sexual differentiation of avian copulatory sexually selected characters. *Neuroscience and Biobehavioral Reviews* 46:557–566.
- Brennan, P. L. R., and R. O. Prum (2011). The erection mechanism of the ratite penis. *Journal of Zoology* 286:140–144.
- Brennan, P. L. R., and R. O. Prum (2012). The limits of sexual conflict in the narrow sense: New lessons from waterfowl. *Philosophical Transactions of the Royal Society* 367:2324–2338.
- Brennan, P. L. R., and R. O. Prum (2015). Mechanisms and evidence of genital coevolution: The roles of natural selection, mate choice and sexual conflict. In *Sexual Conflict* (W. Rice and S. Gavrilets, Editors). Cold Spring Harbor Laboratory Press, Cold Spring Harbor, NY, USA. pp. 385–405.
- Brennan, P. L. R., T. Birkhead, K. Zyskowski, J. Van der Waag, and R. O. Prum (2008). Independent evolutionary reductions of the phallus in basal birds. *Journal of Avian Biology* 39:487–492.
- Brennan, P. L. R., C. Clark, and R. O. Prum (2010). Explosive eversion and functional morphology of the duck penis supports sexual conflict in waterfowl genitalia. *Proceedings of the Royal Society B* 277:1309–1314.
- Brennan, P. L. R., R. O. Prum, K. G. McCracken, M. D. Sorenson, R. E. Wilson, and T. R. Birkhead (2007). Coevolution of male and female genital morphology in waterfowl. *PLOS One* 2(5):e418.
- Briskie, J. V., and R. Montgomerie (1997). Sexual selection and the intromittent organ of birds. *Journal of Avian Biology* 28: 73–86.
- Brown, C. R., and M. B. Brown (2003). Testis size increases with colony size in Cliff Swallows. *Behavioral Ecology* 14:569–575.
- Brua, R. B. (2002). Ruddy Duck (*Oxyura jamaicensis*). In *The Birds of North America Online* (A. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY. <http://bna.birds.cornell.edu/bna/species/696>
- Coker, C. R., F. McKinney, H. Hays, S. Briggs, and K. Cheng (2002). Intromittent organ morphology and testis size in relation to mating system in waterfowl. *The Auk* 119:403–413.
- Conover, M. R., J. G. Reese, and A. D. Brown (2000). Costs and benefits of subadult plumage in Mute Swans: Testing hypotheses for the evolution of delayed plumage maturation. *The American Naturalist* 156:193–200.
- Cornwallis, C. K., and T. R. Birkhead (2008). Plasticity in reproductive phenotypes reveals status-specific correlations between behavioral, morphological and physiological sexual traits. *Evolution* 62:1149–1161.
- Cornwallis, C. K., and T. R. Birkhead (2007). Changes in sperm quality and numbers in response to experimental manipulation of male social status and female attractiveness. *The American Naturalist* 170:758–770.
- Dawson, A. (2008). Control of annual cycle in birds: Endocrine constraints and plasticity in response to ecological variability. *Philosophical Transactions of the Royal Society* 363:1621–1633.
- Dunn, P. O., A. D. Afton, M. L. Gloutney, and R. T. Alisauskas (1999). Forced copulation results in few extrapair fertilizations in Ross and Lesser Snow Geese. *Animal Behavior* 57:1071–1081.
- Eberhard, W. G. (1985). *Sexual Selection and Animal Genitalia*. Harvard University Press, Cambridge, MA, USA.

- Evarts, S. (1990). Male reproductive strategies in a wild population of Mallards (*Anas platyrhynchos*). Ph.D. dissertation. University of Minnesota. Minneapolis, MN, USA.
- Follett, B. K. (1984). Birds. In Marshall's Physiology of Reproduction, Volume 1 (G. E. Lamming, Editor). Churchill Livingstone, Edinburgh, Scotland. pp. 283–350.
- Gilbert, A. B. (1979). Female genital organs. In Form and Function in Birds (A. S. King and J. McLelland, Editors). Academic Press, New York, NY, USA. pp. 237–360.
- Gray, B. J. (1980). Reproduction, energetic and social structure of the Ruddy Duck. Ph.D. dissertation. University of California, Davis, CA, USA.
- Hawkins, G. L., G. E. Hill, and A. Mercadante (2012). Delayed plumage maturation and delayed reproductive investment in birds. *Biological Reviews* 87:257–274.
- Hoch, J. M. (2008). Variation in penis morphology and mating ability in the acorn barnacle, *Semibalanus balanoides*. *Journal of Experimental Marine Biology and Ecology* 359:126–130.
- Hohn, E. O. (1960). Seasonal changes in the Mallard's penis and their hormonal control. *Proceedings of the Zoological Society of London* 134:547–555.
- Hosken, D., and P. Stockley (2004). Sexual selection and genital evolution. *Trends in Ecology & Evolution* 19:87–93.
- Hurlbert, S. H. (1984). Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54:187–211.
- Immler, S., S. R. Pryke, T. Birkhead, and S. C. Griffith (2009). Pronounced within individual plasticity in sperm morphology across social environments. *Evolution* 64:1634–1643.
- John, L. K. (1993). Alternative reproductive tactic in eastern gray squirrels: "Making the best of a bad job." *Behavioral Ecology* 4:165–171.
- Kahn, A. T., B. Mautz, and M. D. Jennions (2010). Females prefer to associate with males with longer intromittent organs in mosquitofish. *Biology Letters* 6:55–58.
- Lyon, B. E., and R. D. Montgomerie (1986). Delayed plumage maturation in passerine birds: Reliable signaling by subordinate males? *Evolution* 40:605–615.
- Mautz, B. S., B. B. Wong, R. A. Peters, and M. D. Jennions (2013). Penis size interacts with body shape and height to influence male attractiveness. *Proceedings of the National Academy of Sciences USA* 110:6925–6930.
- McCracken, K. G., R. E. Wilson, P. J. McCracken, and K. Johnson (2001). Sexual selection: Are ducks impressed by drakes' display? *Nature* 413:128.
- McKinney, F. (1985). Primary and secondary male reproductive strategies in dabbling ducks. In *Avian Monogamy* (P. A. Gowaty and D. W. Mock, Editors). *Ornithological Monographs* 37:68–82.
- McKinney, F., and S. Evarts (1998). Sexual coercion in waterfowl and other birds. In *Avian Reproductive Tactics: Female and Male Perspectives* (P. G. Parker and N. Tyler Burley, Editors). *Ornithological Monographs* 49:163–195.
- McKinney, F., S. R. Derrickson, and P. Mineau (1983). Forced copulation in waterfowl. *Behavior* 86:250–294.
- Peters, J. L., G. L. Brewer, and L. M. Bove (2003). Extrapair paternity and breeding synchrony in Gadwalls (*Anas strepera*) in North Dakota. *The Auk* 120:883–888.
- Pfennig, D. W., M. A. Wund, E. C. Snell-Rood, T. Cruickshank, C. D. Schlichting, and A. P. Moczek (2010). Phenotypic plasticity's impact on diversification and speciation. *Trends in Ecology & Evolution* 25:459–467.
- Pigliucci, M. (2005). Evolution of phenotypic plasticity: Where are we going now? *Trends in Ecology & Evolution* 20:481–486.
- Rowe, L., and G. Arnqvist (2011). Sexual selection and the evolution of genital shape and complexity in waterstriders. *Evolution* 66:40–54.
- Scheiner, S. M. (1993). Genetics and evolution of phenotypic plasticity. *Annual Review of Ecology and Systematics* 24:35–68.
- Senar, J. C. (2006). Color displays as intrasexual signals of aggression and dominance. In *Bird Coloration: Function and Evolution* (G. E. Hill and K. J. McGraw, Editors). Harvard University Press, London. pp. 86–136.
- Stockley, P., S. A. Ramm, A. L. Sherborne, M. D. Thom, S. Paterson, and J. L. Hurst (2013). Baculum morphology predicts reproductive success of male house mice under sexual selection. *BMC Biology* 11:66.
- Swanson, G. A., T. L. Shaffer, J. F. Wolf, and F. B. Lee (1986). Resting characteristics of captive Mallards on experimental ponds. *Journal of Wildlife Management* 50:32–38.
- van Lieshout, E., and M. A. Elgar. (2011). Longer exaggerated male genitalia confer defensive sperm-competitive benefits in an earwig. *Evolutionary Ecology* 25:351–362.
- Wedell, N., M. J. G. Gage, and G. A. Parker (2002). Sperm competition, male prudence and sperm-limited females. *Trends in Ecology & Evolution* 17:313–320.
- Weninger, E. J., and A. L. Averill (2006). Influence of body and genital morphology on relative male fertilization success in oriental beetles. *Behavioral Ecology* 17:656–663.
- Weisstein, E. W. (2012). Gaussian function. *MathWorld—A Wolfram Web Resource*. <http://mathworld.wolfram.com/GaussianFunction.html>
- West-Eberhard, M. J. (2003). *Developmental Plasticity and Evolution*. Oxford University Press. Oxford, UK.