



Reproductive effort and success of wild female mallards: Does male quality matter?

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ABSTRACT

In accordance with the differential allocation hypothesis, females are expected to increase their reproductive investment when mated to high-quality males. In waterfowl, reproductive investment increased when captive female mallards (*Anas platyrhynchos*) were mated to more attractive males, but information for wild ducks is lacking. Studies of waterfowl mating systems have focused primarily on the importance of plumage coloration of males and female mate choice, whereas investigations of reproductive ecology examine female attributes and virtually ignore the role of males in investment decisions. Here, we used unique data for 253 pairs of wild mallards to test whether females mated to high-quality males would increase reproductive effort and reproduce more successfully. We derived measurements of female and male body size and condition, and indices of male plumage quality, and related these traits to patterns of reproductive effort and performance of females. Consistent with predictions, yearling females nested earlier and had higher nest survival when mated to males with better plumage scores. Furthermore, when paired with larger bodied males, yearling females renested more often, and nest and brood survival increased among older females. Although the strength of male effects varied with breeding stage and female age or experience, this is one of a few studies to demonstrate an additive effect of male quality on investment and success of females, in free-ranging birds.

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1. Introduction

Life-history theory predicts that females adjust reproductive investment to reflect the costs and benefits of a given breeding attempt (Stearns, 1992). Consistent with this theory, the differential allocation hypothesis states that individuals should allocate resources in response to characteristics of their mate and predicts that male attractiveness will influence the reproductive value of a female's breeding attempt (Burley, 1988; Sheldon, 2000). Plumage, ornaments or morphology may reliably signal a male's ability to acquire high-quality habitats or increase parental care (Møller, 1994; Sheldon, 2000; Rowe et al., 2011). For instance, males with better quality plumage may be more aggressive and able to out-compete other males for prime habitat (Germain et al., 2010; Crary

and Rodewald, 2012). Thus, females will trade-off current and future reproduction in response to male attractiveness, such that females will increase their reproductive investment when mated to high-quality males (Burley, 1988; Sheldon, 2000).

Support for differential allocation has been found in birds, insects, amphibians and mammals (Sheldon, 2000). Female birds mated to more attractive males may alter their pre-hatch investment by laying larger clutches (Petrie and Williams, 1993), larger eggs (Osorno et al., 2006; Velando et al., 2006; Loyau et al., 2007; Horváthová et al., 2012), or by differentially depositing concentrations of egg internal compounds (Gil et al., 1999; Loyau et al., 2007). Yet, differential allocation also could be driven by an underlying correlation between male and female quality, especially in studies of wild animals where there may be many alternative explanations for correlations that seem consistent with differential allocation (Sheldon, 2000). For instance, in avian species with biparental care or where pair formation occurs during the breeding season, females may choose a mate based on the quality of the territory as opposed to male ornamentation, and may lay more eggs in response to abundant food resources despite male attractiveness.

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In migratory waterfowl, specifically *Anas* spp., pair dissolution generally occurs during incubation, so male ducks do not participate in brood-rearing nor do they engage in incubation or nest-guarding (Williams, 1983). Furthermore, pair formation occurs during winter, prior to arrival on the breeding grounds (Johnsgard, 1960). In these systems, females do not choose mates based on the males' ability to raise offspring; moreover, the quality of breeding habitat cannot be used as a criterion for selecting a breeding partner (McKinney, 1992). Thus, mate selection is based on morphology, male ornaments or behaviors of males (McKinney, 1992). As such, females may choose males that are more similar to themselves (i.e., mate assortatively; Cooke and Davies, 1983), or possibly select males based on qualities that signal the ability to migrate faster, obtain preferred breeding habitat or sufficiently protect the female from forced copulations (Williams, 1983; Wishart, 1983). Therefore, quality of both males and females must be considered simultaneously so that correlations between male and female quality can be controlled when evaluating differential allocation in natural systems.

Seminal studies of waterfowl mating systems revealed the importance of male plumage coloration as a key predictor of female mate choice, suggesting that females prefer good-looking males, or males with better plumage quality (Klint, 1980; Holmberg et al., 1989; Weidmann, 1990). Specifically, these studies highlight important ornaments of male mallards (*Anas platyrhynchos*) and suggest that preferred males possess an unmolted green head, wide white neck-collar, uniform rusty breast, pale-gray unblotched flanks, two curled-up tail feathers, and black upper and under tail-coverts (Klint, 1980; Holmberg et al., 1989; Weidmann, 1990). Holmberg et al. (1989) also illustrated that females respond positively to male size and display activity, while subsequent research by Omland (1996) found correlations between pairing success and bill and plumage ornaments of male mallards; males with bright yellow-green bills and higher average plumage ornaments had greater pairing success.

Female mallards reportedly lay larger eggs (Cunningham and Russell, 2000) and increase albumen lysozyme concentrations (Giraudeau et al., 2011) when mated to more attractive males. Remarkably, females also may compensate for predictable deficits in offspring viability when breeding with non-preferred partners by increasing egg mass (Bluhm and Gowaty, 2004). Male attractiveness is often determined based on female choice in captive populations (Cunningham and Russell, 2000; Bluhm and Gowaty, 2004) and ornament quality is seldom evaluated (but see Giraudeau et al., 2011). Female preference for multiple male ornaments, specifically plumage (i.e., Holmberg et al., 1989; Weidmann, 1990, but see Omland, 1996), has been studied extensively, whereas reproductive decisions of females associated with natural variation in male plumage have not been considered.

Mallards are known to mate assortatively by body condition and age (Heitmeyer, 1995), and females can adjust reproductive allocation in response to male quality (Cunningham and Russell, 2000; Giraudeau et al., 2011). Thus, mallards are ideal for evaluating differential allocation in natural systems. First, we evaluated whether mallards mate assortatively by body size and condition by using unique data collected from a large sample of free-ranging male and female mallards. Then, we tested the hypothesis that females mated to high-quality males increase reproductive effort and have higher reproductive success. Specifically, we evaluated the predictions that females mated to high quality males would (i) initiate nests earlier in the breeding season, (ii) reneest faster or more often following nest failure, (iii) lay larger clutches, and (iv) have greater nest and brood survival rates, than females mated to low quality males.

2. Materials and methods

2.1. Study sites

During 1997–1999, data were collected at six, 65 km², study sites in the Canadian Prairie Parkland ecoregion of Alberta, Saskatchewan, and Manitoba (Table 1). Sites were randomly selected as part of a larger study to test the efficacy of habitat management programs designed to increase breeding success of upland-nesting ducks (e.g., Emery et al., 2005).

2.2. Field methods

Mallards were captured from early April to early May, before or concurrent with the earliest recorded nesting attempts, by placing decoy traps (Sharp and Lokemoen, 1987) in wetlands where pairs or lone males had previously been observed. Traps were frequently moved among wetlands throughout the study site to ensure the local mallard population was represented (Brasher et al., 2002). We banded all trapped birds, weighed them with a 1.5 kg Pesola scale (nearest 10 g), and used a ruler to measure wing chord (nearest 1 mm) from the end of the carpo-metacarpus to the tip of the longest primary feather (see Table 1 for sample sizes). With dial calipers, we also measured (1) head length (nearest 0.1 mm; from the back of the head to the tip of the bill), (2) tarsus length (nearest 0.1 mm; length of the tarsometatarsal bone) and, (3) keel length (nearest 0.1 mm, females only; from the tracheal pit to the hind margin of the sternum). We classified female age as either second-year (i.e., yearling) or after-second year (i.e., adult) by visually inspecting the greater secondary covert against a known-age sample, or measuring characteristics of the feather and performing a discriminant function analysis (adapted from Krapu et al., 1979). All females were equipped with a 22 g intra-abdominal radio transmitter (Model IMP/150, Telonics, Mesa, Arizona, Rotella et al., 1993; Paquette et al., 1997), tracked intensively using vehicle-mounted, null-array antenna systems and triangulation (Kenward, 1987) and monitored closely to determine reproductive histories of females (Emery et al., 2005; Devries et al., 2008). We radio-marked males with a 9 g back-mounted radio transmitter (Model 2040, Advanced Telemetry Systems, Isanti, Minnesota; Rotella et al., 1993; Paquette et al., 1997) in 1998 and 1999, as part of an associated study by MGB (Brasher, 2000; Brasher et al., 2002).

Criteria were established a priori to determine pair status based on characteristics of captured birds Table 2 (Brasher et al., 2002). In 1997, we assumed that all birds were assigned correctly as mated pairs. In 1998 and 1999, we radio-tracked a sub-sample ($n = 35$) of assigned pairs to confirm pair status, and validated results obtained for all presumed pairs by repeating analyses using the sub-sample of confirmed pairs when sample sizes were sufficient.

2.3. Plumage characteristics

Male plumage was recorded only in 1997 at 4 sites for males presumed to be paired with a radio-marked female ($n = 223$; criteria in Table 2). We identified important male plumage characteristics (Klint, 1980; Holmberg et al., 1989; Weidmann, 1990; Giraudeau et al., 2011), and recorded the (1) maximum and minimum width of the white neck ring, (2) number of places on the head and chest where feathers were missing or unmolted and, (3) number of curled tail feathers. By modifying methods used by Holmberg et al. (1989) and Weidmann (1990), we ranked each plumage characteristic according to the extent of either naturally-occurring blemishes or deviations from ideal plumage (Table 3), and summed individual characteristics so that smallest rank signified fewest deviations (i.e., better quality plumage).

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