

TIME AND ENERGY CONSTRAINTS ON COURTSHIP IN WINTERING AMERICAN BLACK DUCKS

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ABSTRACT.—Courtship in wintering American Black Ducks (*Anas rubripes*) was studied at three sites that differed substantially in food supply. Courtship started earlier and occupied more of the ducks' time at the site where food was most nutritious. Ducks at the site with intermediate food quality only began courting after temperatures rose sufficiently to reduce their energetic costs of maintenance. Ducks with the least nutritious food began courting latest and spent the least amount of time in this activity. The seasonal sequence of courtship displays used by the courting ducks was similar between sites. This suggests that ducks with the best food (i.e., those starting courtship first) reached the peak of courtship activity earliest and thus should have been best prepared for breeding in the spring. Consequently, the northern limit to winter ranges in species with early pairing may be determined, in part, by the availability of sufficient food for early courtship.

Studies of avian reproductive biology normally focus on events that take place on the breeding grounds. Factors such as the quality and quantity of food available to an individual in the nonbreeding season, however, will affect its physical condition which may influence the timing and extent of its reproductive effort (e.g., Jones and Ward 1976, Ankney and MacInnes 1978). We examined how courtship behavior in American Black Ducks (*Anas rubripes*) is influenced by the quality and availability of food on the wintering grounds.

Courtship and pair formation in American Black Ducks take place during the winter (Johnsgard 1960). Animals must satisfy their maintenance requirements before allocating time and energy to breeding (King 1974). Thus, differences in food available to wintering Black Ducks may affect their fitness without actually affecting individual survival. We tested three hypotheses regarding the manner in which food availability could influence courtship behavior. We postulated that greater food availability would: (1) allow courtship to begin earlier, (2) allow more time for courtship, and (3) allow courtship displays to be more advanced before the breeding season. The third hypothesis refers to the type of courtship display used by Black Ducks. Males of this species have three main courtship displays: the *Grunt-whistle* associated with early courting activity, the *Head-up-tail-up* display seen after courtship begins, and the *Down-up* display associated with the peak of courtship and usually leading to copulation (Johnsgard 1960).

METHODS

We conducted the study at three sites located within 20 km of Ottawa, Ontario, near the

northern limit for wintering Black Ducks (Godfrey 1979). Each site was separated from the others by at least 15 km; owing to the continuous sub-freezing temperatures during the winter of the study, these sites were the only open water occupied by Black Ducks in this area. Stable population sizes at each site and no observed flights from any of the sites indicated that little or no exchange occurred between populations during the study.

Site A, which supported 250 Black Ducks and 350 Mallards (*Anas platyrhynchos*), was on a section of the Rideau River kept open by the outflow from a dam. Ducks fed 3 km away at a feeding station supplied daily with 50 kg of cracked corn scattered on the ground. Site B, which supported 185 Black Ducks, was a shallow bay on the Ottawa River kept open by warmed outflow from a nearby sewage treatment plant. Ducks fed on aquatic vegetation (*Myriophyllum* sp.) by "tipping up," a common foraging technique of dabbling ducks (Bellrose 1976). Site C was on a section of the Rideau River which had an open central channel of deep, fast-flowing water. The 10 Black Ducks that overwintered here fed on aquatic vegetation (principally *Cladophora* sp.) that could be obtained only by diving, a foraging technique infrequently used by dabbling ducks and not one for which they are well-adapted (Bourget and Chapdelaine 1975; Miller 1983; Brodsky and Weatherhead, unpubl.).

To quantify food availability at sites B and C, we cut holes through the ice next to areas used for foraging at 15 randomly selected points per site. We inserted a 0.5 m²-frame into each hole at site B and a 0.01 m²-frame into each hole at site C (which had more irregular substrate), removed all the vegetation within the

frames, and oven-dried the vegetation at 60°C for three days. The dried vegetation was then weighed to obtain a measure of food density in g/m². We estimated the size of the foraging area at sites B and C from maps drawn to scale.

We monitored the ducks at site A from 14 January to 21 March 1982, at site B from 12 January to 28 February 1982, and at site C from 1 January to 21 March 1982. Our observation period at each site ended when the ducks began dispersing; it ceased earlier at site B because shooting began at an adjacent rifle range. To determine whether any differences in courtship activity between sites could be attributed to differences in the availability of mates, we recorded sex ratios at each site. Females were distinguished from males by the color and spotting of the bill (Godfrey 1979).

Each population was watched at least every other day (often more than once a day) using a spotting scope approximately 50 m away from the birds. Using the scan-sampling technique (Altmann 1974), we observed a new individual every 5 s, and recorded the bird's behavior as soon as we focused on it. We began scanning with the duck farthest to the left of the population and proceeded to the closest individual to the right until the entire population had been scanned, at which time we repeated the procedure. Each observation period lasted 1 h, yielding approximately 720 observations. Total hours of observation (175 h—site A, 135 h—B, 190 h—C) were accumulated with an approximately equal distribution from all daylight hours (07:00 to 17:00) at each site.

We calculated the proportion of time spent courting in a particular period by dividing the number of observations involving courtship by the total number of observations. For each observation of courtship, we recorded the display (i.e., Grunt-whistle, Head-up-tail-up, Down-up). We calculated the proportion of courtship spent in a particular display in an observation period as the number of observations of that display divided by the total number of courtship observations.

RESULTS

We calculated the amount of food energy available per duck per day at each site in order to objectively estimate the relative quality of each site for an individual duck. At site A, a daily ration of 50 kg of cracked corn with an energy value of 18.0 kJ/g (Kendeigh and West 1965), corrected for the 15% moisture content of cracked corn (Wiens and Dyer 1975), provided 1,391 kJ per duck per day. At site B, a mean density of 13.1 (\pm SD 4.9) dry g *Myriophyllum* per m² in an area of 62,500 m², with an energy value of 13.4 kJ/dry g (Cummins

and Wuycheck 1971) provided a maximum average of 886 kJ per duck per day based on an estimated period of 67 days of site use. At site C, a mean density of 11.6 (\pm SD 4.2) dry g *Cladophora* per m² in an area of 2,750 m², with an energy value of 8.8 kJ/dry g (Cummins and Wuycheck 1971) provided a maximum average of 540 kJ per duck per day in a 65-day period of occupancy. The above estimates yield a site A:B:C energy ratio of 2.5:1.5:1. This ratio does not account for assimilation efficiencies of the different foods, which would further increase the quality of the food source at site A, relative to that at site B or C, because corn is metabolized more efficiently than either aquatic plant species (Sugden 1973). Furthermore, the relative costs of the foraging techniques at sites A, B, and C (gleaning from the ground, tipping-up, and diving, respectively) would further amplify the differences between sites even when energetic costs of flight at site A are considered (Brodsky and Weatherhead 1984a).

At site A, there were 137 males and 113 females; at site B, there were 108 males and 77 females; and at site C, there were six males and four females, which were later reduced by predation to five males and three females. The similarity of these sex ratios makes it unlikely that any differences in courtship could be attributable to differences in mate availability. We were not concerned that possible differences among populations in the number of birds paired would seriously affect courtship because courtship does not terminate with pairing (L. M. Brodsky, pers. obs.).

The date when courtship began and the percent of time allocated to courtship differed substantially among sites, in a fashion consistent with our hypotheses (Fig. 1). Ducks at site A started courting in January, despite cold temperatures (mean $< -20^\circ\text{C}$). Ducks at site B did not begin courting until mid-February (mean temperature = -10°C); while those at site C did not begin until the end of February (mean temperature = -5°C). For statistical purposes, we paired observations at one site with those made closest in time at another site. After 26 January, courtship was always higher at site A than at site B (25 of 25 times) and higher at A than C (31 of 31 times), both of which are highly significant differences (Wilcoxon matched-pairs signed-ranks test, both P 's $\ll 0.01$; Seigel 1956). Before 15 February we saw no courtship at either site B or site C. In the 11 comparisons between B and C following that date, courtship at site B always exceeded that at site C (Wilcoxon matched-pairs signed-ranks test, $P < 0.01$).

Although both the onset of courtship and

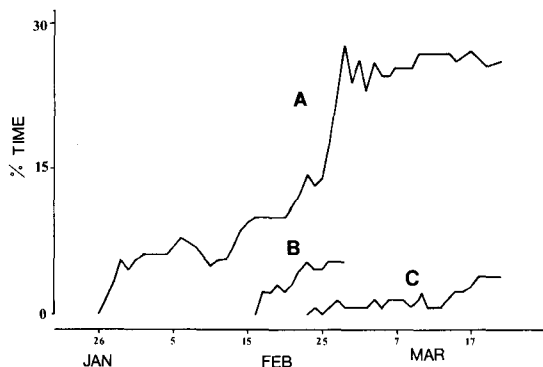


FIGURE 1. Initiation of and percent time spent in courtship by ducks at each site.

the time devoted to courtship differed greatly among sites, once courtship began, the seasonal sequence of behaviors was remarkably similar among sites (Fig. 2). At each site, the Grunt-whistle display predominated initially, with the Head-up-tail-up display rapidly increasing to an equal or greater frequency. For statistical analysis, we divided the study period into 2-day periods. For each site, we defined period 1 as that in which we first observed courtship at that site. This provided seven 2-day periods for which sites could be compared. Friedman two-way analysis of variance (Siegel 1956) for each of the seven periods revealed no significant differences (all P 's > 0.05) among sites in the allocation of courtship time to the different displays.

DISCUSSION

Before discussing our overall results, we must evaluate our observations on the small population of ducks at site C. Given the similarity of the sex ratio between this site and the others, and because in larger populations courtship parties of only one female and 2–5 males are regularly seen (Brodsky and Weatherhead 1984b), we believe it is unlikely that population size was responsible for courtship differences between sites. We also think it unlikely that the ducks at site C were abnormal (e.g., sick, crippled, lead-poisoned). This site was in the center of the city at least 10 km from the nearest place where hunting could occur. Eight of the 10 ducks survived an extremely cold winter, relying entirely on an energetically expensive foraging method for which they are not well-adapted (Bourget and Chapdelaine 1975). We observed these ducks making short flights and they appeared to disperse when the ice broke up in the spring at the same time as ducks at site A. For these reasons, and because site C is the only natural site of the three we studied, we believe our observations there make a valid contribution to our study. We

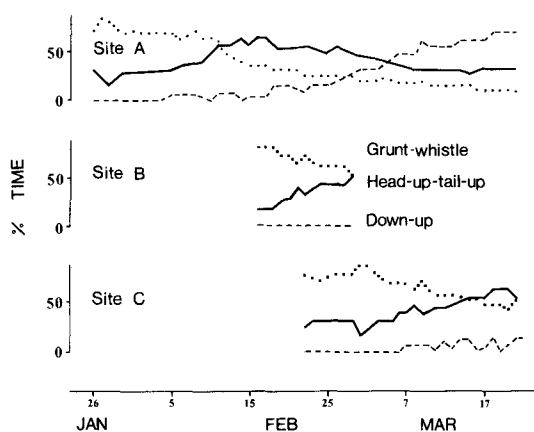


FIGURE 2. Percent time spent by drakes in three courtship displays at each site.

recognize, however, that additional observations of Black Ducks overwintering at natural sites are required before the generality of our observations will be known.

The differences among sites in available energy and the time required by the ducks to acquire that energy appear sufficient to explain differences in courtship. At site A, the daily ration of cracked corn provided abundant energy and required only several hours of foraging (20% of daytime activity, Brodsky and Weatherhead 1984a) to be eaten. Therefore, the ducks at this site had the least constraints on both time and energy available for courtship. In a parallel study of the overall time-energy budgets of the ducks at the three sites (Brodsky and Weatherhead, in press), we found that ducks at site B responded to extreme cold by increasing foraging time (from 45% of daytime activity at 0°C to 65% at -20°C), which would necessarily reduce the time available for courtship. The intermediate level of courtship at site B therefore appears to have resulted from limitations on both time and energy. Ducks at site C responded to extreme cold by ceasing to forage and by spending most of their time (>80%) resting, presumably owing to the high energetic costs of foraging (Brodsky and Weatherhead, in press). The low level of courtship we observed at this site appears to have been entirely due to energy constraints, since the birds had ample time.

The observed patterns of courtship showed both flexibility and rigidity in response to the time and energy constraints. The onset of courtship and the total time devoted to courtship varied among sites, whereas the sequence of displays was fixed, regardless of either the date when courtship began or the total time devoted to courtship. This finding has interesting implications for the subsequent reproductive performance of the ducks from each

site. Given the inflexible sequence of courtship behaviors and the fact that pair formation occurs at the peak of courtship activity (Johnsgard 1960), ducks from energy-rich wintering sites should be better prepared for breeding in the spring. If the ducks can begin breeding earlier, (the advantages of which were outlined by Saylor and Afton [1981]), then the fitness consequences of wintering on an energy-rich or -poor site may be pronounced, even if survival does not differ markedly at the wintering sites.

Considering the implications of our results in the broader context of overwintering habits in migratory waterfowl, there appear to be two conflicting demands which need to be satisfied. Ducks that winter close to their breeding grounds suffer fewer of the risks generally associated with long-distance migration than those which winter farther away, and should reach their breeding grounds earlier in the spring. Since site C was the only natural site we studied, and Ottawa is near the northern limit of the winter range of the American Black Duck (Godfrey 1979), substantial energetic costs may be associated with wintering too far north. Early arrival on the breeding ground is of little value if the birds are not physiologically ready for breeding. This argument suggests that for migratory species with extensive courtship preceding reproduction, the northern limit to winter ranges may be determined not by the ability to survive at that latitude, but rather by the ability to survive with enough time and energy to allow early initiation of courtship.

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