Evidence for Mallard *Anas platyrhynchos* and American Black Duck *Anas rubripes* competition in western New Brunswick, Canada

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Abstract

The hypothesis that Mallard *Anas platyrhynchos* and American Black Duck *Anas rubripes* compete during the breeding period has generated considerable debate. To further evaluate this hypothesis, the following predictions were tested for sympatric Mallard and Black Duck breeding in New Brunswick: 1) Mallard and Black Duck do not partition breeding resources in space and/or time, 2) Mallard reduce the amount of breeding habitat available to Black Duck, and 3) production of Mallard and Black Duck is inversely related over time. Study results supported all predictions. Mallard and Black Duck pairs were distributed among wetland classes independent of species, though Black Duck were more likely to be observed alone or without Mallard on wetlands that were surrounded by > 75% upland forest. Mallard and Black Duck hatch dates did not differ, indicating they do not temporally partition breeding resources. Black Duck were more likely to be observed on wetlands where Mallard had been removed than on wetlands where they were not removed. This result supported the prediction that Mallard reduce the availability of breeding habitat for Black Duck through interference competition. To test the prediction that production of Mallard and Black Duck is inversely related over time, brood surveys were conducted from 1990 to 1994 to determine relative and absolute changes in numbers of Mallard and Black Duck broods. The ratio of Black Duck to Mallard broods declined from 0.938 in 1990 to 0.244 in 1994. Total number of Black Duck broods on 59 wetlands surveyed with equal effort in 1990 and 1994 declined from 45 in 1990 to 19 in 1994, while Mallard broods increased from 48 in 1990 to 78 in 1994. These findings support the hypothesis that Mallard and Black Duck compete.

Key words: *Anas platyrhynchos, Anas rubripes,* interspecific competition, niche overlap.

The hypothesis that competition with Mallard *Anas platyrhynchos* has contributed to a decline in Black Duck *Anas rubripes* has generated considerable debate. Several studies suggest that Mallard out-compete Black Duck for the most nutrient rich breeding habitat (Ankney *et al.* 1987; Merendino *et al.* 1993; Dwyer & Baldassare 1994; Merendino & Ankney 1994), yet there is little evidence for differences in reproductive success between the two species (Laperle 1974; Krementz *et al.* 1992; Dwyer & Baldassare 1993; Longcore *et al.* 1998; Petrie *et al.* 2000). Efforts to evaluate behavioural mechanisms have provided mixed results as Mallard were dominant under some study conditions (Brodsky & Weatherhead 1984; Brodsky *et al.* 1988; Seymour 1990), but not others (D'eon *et al.* 1984; Hoysak & Ankney 1996; McAuley *et al.* 1998). Black Duck populations have declined in some areas where Mallard increased (Dennis *et al.* 1989; Petrie 1998), but have remained stable in other areas of Mallard-Black Duck sympatry (Nudds *et al.* 1996). Zimpfer & Conroy (2006) found evidence for density effects of Mallard on Black Duck reproduction rates and suggested that this may be due to Mallard reducing Black Duck carrying capacity. However, others have argued that Mallard are simply filling a niche vacated by Black Duck (Maisonneuve *et al.* 2006).

Mallard and Black Duck defend wetland territories to protect paternity and allow females to forage undisturbed (Anderson & Titman 1992). In addition, the two species treat each other as conspecifics and exclude each other from established breeding territories (Seymour 1992). Black Duck numbers could be limited by this spacing behaviour if the two species fail to partition breeding resources and habitat is limiting. Although Black Duck and Mallard do not differ in bill morphology, foraging behaviour, or prey size selection (Eadie *et al.* 1979; Nudds & Bowlby 1984; Belanger *et al.* 1988), utilisation of different wetland types or differences in reproductive chronology may enable resources to be partitioned in time as opposed to space (Toft *et al.* 1982). Failure to partition macro-habitat may lead to declines in Black Duck if demands for breeding resources exceeds supply and Mallard reduce breeding habitat availability through interference competition. If competition coefficients are asymmetrical in favour of Mallard as suggested by the competition hypothesis (Merendino *et al.* 1993), population trends for the two species should be inversely related over time (Nudds 1992).

To evaluate the hypothesis that Mallard and Black Duck compete for breeding resources, three predictions were tested for Mallard and Black Duck breeding sympatrically in western New Brunswick: 1) Mallard and Black Duck do not partition breeding resources in space and/or time, 2) Mallard reduce the amount of breeding habitat available to Black Duck, and 3) production of Mallard and Black Duck is inversely related over time.

Methods

Study area

The study area was approximately 500 km^2 in the Woodstock-Florenceville area of Carleton County, mid-western New Brunswick, Canada (68°40' N 46°15' W).

The area lies in the Saint John River ecodistrict of the Continental Lowlands Ecoregion. Although stands of tolerant hardwood species once dominated the area, these forest types now mostly exist as small woodlots in an agricultural matrix as relatively dense human settlement has fragmented the forest. Major coniferous species include Red Spruce *Picea rubens* and Eastern Hemlock *Tsuga canadensis* that are generally confined to lower slopes and valley bottoms. Most of the ecodistrict is covered by deep non-compact soils derived from Ordovician rocks (Anonymous 1996). Approximately 45% of the land base in the study area had been cleared for agriculture. Potatoes are the primary cash crop, often in rotation with grain and livestock operations. The area contained a variety of wetland types including most classes of palustrine wetlands as well as riverine and lacustrine habitats (Cowardin *et al.* 1979).

Prediction 1: Resource partitioning in space and time

To test the prediction that Mallard and Black Duck do not partition breeding resources by using different habitat types, the distribution of breeding pairs was determined using helicopter surveys. Breeding pair counts from these aerial surveys were used in subsequent analyses of resource partitioning. Mallard and Black Duck pairs were surveyed on 58 wetlands in 1990 that were identified from aerial photographs. The number of wetlands surveyed for breeding pairs was increased to 72 in 1991 and to 80 in 1992 because we discovered wetlands not visible on aerial photographs. Two large rivers in the study area (St. John and Meduxnekeag) were also surveyed in all years.

Surveys were conducted in the first week of May 1990, 1991, and 1992 to minimise the probability of encountering migrant birds (Erskine *et al.* 1990). The same two observers conducted breeding pair surveys in all years. For both Mallard and Black Duck, breeding pairs were defined as a male and female observed together or a male or female observed alone. To reduce the probability that two male Black Duck would be recorded as a pair we distinguished sex of this species using bill colour and the appearance of scapular feathers (Ross & Fillman 1990). When one or more females were observed with two or more males the number of females was assumed to equal the number of breeding pairs. Groups of birds consisting of > 5 individuals, regardless of whether they included females, were assumed to be migrants and were not included in any analysis. In some surveys, groups of ≤ 5 males are considered equal to five breeding pairs (Dzubin 1969). However, groups of ≤ 5 males may consist of birds that have congregated on a wetland while females are laying or incubating (Dzubin 1969). The conservative definition of breeding pair adopted here increased the likelihood that birds were observed on wetlands used during establishment of breeding territories.

All wetlands surveyed for breeding pairs were classified according to Cowardin *et al.* (1979) at the class level. An additional category was created for eutrophic wetlands used in treating livestock waste. Riverine habitat in the St. John and Meduxnekeag rivers was classified to subsystem; however, a section of the St. John River was classified as lacustrine because of the presence of a dam (Cowardin *et al.* 1979). To further evaluate resource partitioning, 11 habitat characteristics were also measured for wetlands surveyed between 1990 and 1992 (Table 1). However, these characteristics were not measured for the St. John and Meduxnekeag rivers because their size precluded meaningful measurements (*e.g.* % upland forest cover varied widely along the length of these rivers).

To determine if Mallard and Black Duck partitioned habitat in time, brood surveys were conducted to compare reproductive chronology between species. Hatch dates for both species were estimated by back-dating duckling age. Mallard and Black Duck lay similar sized clutches and have similar incubation periods (Bellrose 1980). Thus, high overlap in hatch dates would indicate high overlap in reproductive chronology. Brood surveys were conducted once every 10–14 days between the last week of May and mid-July on 100 wetlands in both 1990 and 1991. Eighty of the same wetlands were surveyed in both 1990 and 1991, as were the St. John and Meduxnekeag Rivers. Twenty of the wetlands surveyed in 1990 were not surveyed in 1991 because they no longer existed (*e.g.* beaver dams had broken or been removed) or had proven extremely difficult to access. Twenty wetlands surveyed in 1991, but not 1990, were created by recent beaver activity or had been discovered but not surveyed in 1990. Surveys were conducted from shore areas that provided good visibility or by kayak depending on wetland size and were scheduled during periods of peak brood activity (06:00–09:00 h and 18:00–21:00 h; Parker *et al.* 1992). Information on duckling age (determined by plumage characteristics; Gollup & Marshall 1954) and number was used to identify broods that were observed on previous visits to a wetland, to avoid duplicating counts (Ringelman & Longcore 1982). Finally, a brood survey was conducted by helicopter shortly after completion of ground counts in mid-July in both 1990 and 1991. Helicopter surveys were conducted on all wetlands surveyed from the ground.

To determine if Mallard and Black Duck pairs partitioned macro-habitats, Fisher's exact test was used to examine the association between species and wetland class (SAS Institute Inc. 1990). Log-linear modelling was used to determine whether breeding pair surveys could be pooled across years when examining the association between species and wetland classes. For this analysis, wetland classes that had few observations were combined to meet sample size requirements. Finally, a chi-square test was used to examine the association between species and wetland class when results from all three years were combined (SAS Institute Inc. 1990).

In addition to wetland class, 11 habitat variables were evaluated on their ability to explain patterns of wetland use by Mallard and Black Duck (Table 1). Polytomous logistic regression (Hosmer & Lemeshow 1989) was used to determine which covariates were useful in distinguishing wetlands where both Mallard and Black Duck were present, only Black Duck were present, only Mallard were present, and wetlands where neither species was observed. This approach was used as an alternative to multivariate discriminate

Table 1. Habitat variables used to assess Mallard and Black Duck niche partitioning.

Variable	**Description**
WLCLASS[a]	Wetland Classification (Cowardin *et al.* 1979)
ORIGIN[a]	Natural *versus* man-made wetlands
BEAVER[a]	Water levels influenced by current or past beaver activity *versus* water levels not influenced by current or past beaver activity
AREA[b]	Wetland area (ha)
PER[b]	Wetland perimeter (m)
VDP[a]	Visible disturbance present *versus* visible disturbance not present. Visible disturbance is defined as an occupied dwelling or road travelled at least twice a day that was visible from any part of the wetland
DTD[b]	Distance to disturbance (m), where disturbance is defined as an occupied dwelling or road travelled twice a day but is not conditional on being visible from the wetland
UPLAND[b]	Percent of upland that is forested within 500 m of wetland perimeter. Four categories of UPLAND were recognised: 1) 0–25%, 2) 26–50%, 3) 51–75%, 4) 75–100%
VEG[a]	Percent of wetland surface area covered by emergent vegetation. Four categories of VEG were recognised: 1) 0–25%, 2) 26–50%, 3) 51–75%, 4) 75–100%
HERB[a]	Percent of wetland surface area that is herbaceous sp. vegetation. Four categories of HERB were recognised: 1) 0–25%, 2) 26–50%, 3) 51–75%, 4) 75–100%
ERIC[a]	Percent of wetland surface area that is ericaceous sp. vegetation. Four categories of ERIC were recognised: 1) 0–25%, 2) 26–50%, 3) 51–75%, 4) 75–100%
FT[a]	Percent of wetland surface area that is flooded tree sp. vegetation. Four categories of FT were recognised: 1) 0–25%, 2) 26–50%, 3) 51–75%, 4) 75–100%

[a] Determined at wetland.

[b] Determined from aerial photographs.

analysis because it allows interactions between variables of interest to be incorporated, can easily accommodate more than two response levels, and does not require the assumption that predictor variables are normally distributed (Johnson 1998). Variables considered for inclusion in the model included those listed in Table 1, as well as wetland class. Data were combined across all 3 years (1990–1992), for a total of 186 wetland * year observations. Maximum number of wetland * year observations was 210 given that 58 wetlands were surveyed in 1990, 72 wetlands in 1991, and 80 wetlands in 1992. Preliminary descriptive analysis indicated that for some variables the number of classes would have to be reduced. Contingency tables were constructed of occupancy (both species present, Black Duck only, Mallard only, no ducks present) by each predictor variable. If there were empty cells or cells in these tables containing only one wetland, collapsing was necessary as the logistic regression models would fail to converge. The following modifications were made to the predictor variable classes: Wetland Class (WLCLASS) = Lacustrine unconsolidated bottom (L-UB), Palustrine emergent (PEM), Palustrine unconsolidated bottom (PUB) and Others (collapsed wetland classes); % Vegetative cover (VEG) = 0–25%, 26–100%; % Herbaceous cover (HERB) = 0–50%, 51–75%, 76–100%; % Ericaceous cover (ERIC) = 0–25%, 26–75%, 76–100%; % Forested upland (UPLAND) = 0–50%, 51–75%, 76–100%. Percent flooded tree cover (FT) was excluded from modelling as only 10 percent of the wetlands had any flooded trees, of which only one wetland hosted Mallard only.

Missing values were highest for Visible disturbance (VD) and UPLAND (30 wetland * year observations missing for each variable), with VEG, HERB, and ERIC missing 20 observations each. We analysed the complete data from 149 * year observations where the model was simplified via a backwards elimination procedure. A full model with main effects of all predictor variables was initially fitted. The variable yielding the smallest likelihood ratio statistic (least significant) was then eliminated and the model re-fitted until only significant variables remained (Agresti 1990).

To determine if Mallard and Black Duck partitioned habitat in time by relying on differences in reproductive chronology, hatch dates for both species were grouped into discrete 10-day intervals and the association between species and hatch date was evaluated using log-likelihood ratios for 1990 and 1991 (*G*-test: PROC FREQ: SAS Institute Inc. 1990). The start date for the first 10-day interval was the date on which the first Mallard or Black Duck brood was observed in each year. Hatch dates from 1990 and 1991 were used because sample sizes were large for both species during these years. This allowed contingency tables to be constructed with narrow hatch day intervals, while still meeting minimum cell requirements.

Prediction 2: Mallard reduce the amount of breeding habitat available for Black Duck

In 1993, Mallard pairs were removed from selected wetlands to test whether the probability of observing a Black Duck pair is greater on wetlands where Mallard pairs are removed. It was assumed that observing Black Duck at a higher rate on these removal wetlands would support the prediction that Mallard reduce the amount of habitat available to breeding Black Duck. Wetlands that were included in the removal experiment met the following criteria; 1) occupied by a single pair of Mallard over three consecutive days, and 2) less than 1 ha in size. The 1ha size restriction was imposed to minimise the probability of including wetlands that could accommodate more than one pair of breeding birds. Mallard and Black Duck pairs were observed together on larger wetlands in the study area and have been observed using the same wetlands elsewhere (Merendino *et al.* 1993; Merendino & Ankney 1994; McAuley *et al.* 1998; McAuley *et al.* 2004). Although these wetlands may have resources for several breeding pairs, intra and interspecific competition can still take place in these habitats (Merendino & Ankney 1994). However, including large wetlands in a removal experiment could require that multiple pairs be removed or confound bird response. For example, Black Duck pairs that are using the wetland when Mallard are shot might abandon it because of disturbance.

Daily surveys of wetlands meeting the size criterion began on 13 April along a pre-determined route. Prior to this date Mallard and Black Duck had only been observed in riverine habitats that were ice-free. Wetlands were either observed from a vehicle or approached on foot depending on distance from a road. To avoid observing wetlands at the same time each day, we alternated the direction along the survey route as well as the times of day surveys were initiated. Wetlands that met both the size and occupancy criteria were assigned to one of two treatments: 1) maintained free of Mallard, via removals, for the duration of the experiment, 2) Mallard remained undisturbed (control). Wetlands were assigned to one of these two treatment groups on the third consecutive day that a single pair of Mallard was observed on the wetland. Treatment assignments (removal *versus* control) were alternated among wetlands meeting the size and occupancy criteria. Between 16–22 April, seven and five wetlands were assigned to the removal and control treatments, respectively. Ten of these twelve wetlands were assigned a treatment on or before 19 April. A Fisher's Exact test was used to determine if the probability of observing a Black Duck pair on a wetland was independent of whether Mallard had or had not been removed from a wetland (SAS Institute Inc. 1990).

Prediction 3: Production of Mallard and Black Duck is inversely related over time

To test the prediction that Mallard and Black Duck production is inversely related over time, changes in the ratio and absolute number of Mallard and Black Duck broods from 1990 to 1994 were determined. To determine changes in the ratio of Mallard and Black Duck broods, brood surveys were conducted in all years between 1990 and 1994. The number of wetlands, as well as the frequency at which wetlands were surveyed, varied among years. One hundred wetlands were surveyed in 1990 and 1991 at 10–14 day intervals between the last week of

May and mid-July. Analysis of the 1990 and 1991 data indicated that Mallard and Black Duck broods did not differ in their distribution among wetland classes (Petrie 1992, 1998). The number of wetlands surveyed in 1992 and 1993 was reduced because of time constraints imposed by an ongoing study of Mallard and Black Duck reproductive success (Petrie *et al.* 2000). In 1992, 63 wetlands were sampled at two week intervals between 1–30 June, which was the time period in 1990 and 1991 when the majority of broods of both species were observed. Wetlands surveyed in 1992 and 1993 were taken from the pool of 80 wetlands sampled in both 1990 and 1991, and the 20 wetlands sampled in 1991 but not 1990 (see Prediction 1). In 1994, 74 wetlands were surveyed over the same time period and at the same frequency as in 1990 and 1991 with the exception that helicopter surveys were conducted in 1994. Fifty nine of these 74 wetlands had been surveyed in 1990 and 1991. The remaining 15 wetlands had been surveyed in 1991 but not 1990. All wetlands surveyed for Mallard and Black Duck broods between 1990 and 1994 were located in the original study area boundaries established in 1990.

Absolute changes in numbers of Mallard and Black Duck broods were examined to determine the underlying cause of any change in brood ratios. For example, Mallard : Black Duck brood ratios could increase over time solely as a result of increases in Mallard broods. To examine absolute changes in brood numbers, we compared the number of Mallard and Black Duck broods observed on the same 59 wetlands that were surveyed in both 1990 and 1994. These wetlands were ground-sampled with identical effort in 1990 and 1994; however, broods that were located only by helicopter in 1990 were excluded when comparing counts between the two years. Sixty four percent of Mallard and 64% of Black Duck broods in 1990 were observed on these 59 wetlands. In addition, the ratio of Mallard to Black Duck broods on these wetlands in 1990 was identical to that of the study area as whole. As a result, absolute changes in Mallard and Black Duck broods that occurred on these 59 wetlands were assumed to be representative of the study area.

To evaluate changes in the relative abundance of Mallard and Black Duck broods over time, linear regression was used to determine if the slope of the line describing changes in the ratio of Black Duck to Mallard broods between 1990 and 1994 differed significantly from zero (SAS Institute Inc. 1990). Because survey efforts were not constant among years, a least squares regression was conducted with weights proportional to the number of wetlands surveyed within a year (SAS Institute Inc. 1990). To assess changes in Mallard and Black Duck broods that occurred on the same 59 wetlands surveyed with the same effort in 1990 and 1994, we evaluated changes in the ratio of the two species using a *G*-test (SAS Institute Inc. 1990), and also examined changes in the absolute numbers of Mallard and Black Duck broods.

Results

Prediction 1

Distribution of breeding pairs among wetland classes (Table 2) was independent

Table 2. Distribution of Mallard (MAL) and Black Duck (BD) breeding pairs across wetland classes 1990–1992.

Wetland subsystem / class	1990 BD		1990 MAL		1991 BD		1991 MAL		1992 BD		1992 MAL	
	%	*n*	%	*n*	%	*N*	%	*n*	%	*n*	%	*n*
Riverine lower perennial	27.1	(19)	29.6	(16)	34.1	(30)	43.5	(27)	37.5	(30)	34.8	(24)
Lacustrine limnetic	25.7	(18)	27.8	(15)	25.0	(22)	25.8	(16)	17.5	(14)	28.9	(20)
Palustrine emergent	15.7	(11)	20.3	(11)	17.0	(15)	14.5	(9)	15.0	(12)	13.0	(9)
Palustrine unconsolidated bottom	27.1	(19)	13.0	(7)	12.5	(11)	8.1	(5)	15.0	(12)	11.6	(8)
Palustrine scrub shrub	2.9	(2)	0.0	(0)	2.3	(2)	0.0	(0)	1.3	(1)	0.0	(0)
Palustrine forested	0.0	(0)	1.9	(1)	4.6	(4)	3.2	(2)	7.5	(6)	1.4	(1)
Palustrine aquatic bed	0.0	(0)	1.9	(1)	2.3	(2)	1.6	(1)	1.3	(1)	2.9	(2)
Eutrophic	1.4	(1)	5.6	(3)	2.3	(2)	3.2	(2)	5.0	(4)	7.2	(5)
TOTAL		70		54		88		62		80		69

of species in 1990 ($P = 0.22$, n.s.), 1991 ($P = 0.90$, n.s.), and 1992 ($P = 0.41$, n.s.). Comparison of log linear models to test for conditional independence of year with species and combined wetland classes, indicated that information on breeding pair distribution could be pooled across years (likelihood ratio: $\chi^2_{18} = 17.21$, $P = 0.51$, n.s.). Using this conditional independence model as a basis and contrasting it with a model characterised by further independence of species and combined wetland class, we found that Mallard and Black Duck distribution across wetland classes did not differ when surveys were combined across years (likelihood ratio: $\chi^2_4 = 4.75$, $P = 0.31$, n.s.). Four variables (WLCLASS, ORIGIN, PER, UPLAND) were retained in the model associating habitat characteristics with observations of Black Duck only, Mallard only, both species present, and no ducks present (Table 3). Mallard, alone or with Black Duck, were observed in greater proportion

Table 3. Variables retained in a model associating habitat characteristics with the presence of Mallard and Black Duck. L-UB = Lacustrine unconsolidated bottom; P-EM = Palustrine emergent; P-UB = Palustrine unconsolidated bottom; Other = Palustrine scrub shrub, Palustrine forested, Palustrine aquatic bed and Eutrophic.

Variable	**Wetlands with Mallard and Black Duck**		**Wetlands with Black Duck only**		**Wetlands with Mallard only**		**Wetlands with neither Mallard nor Black Duck**	
	%	(*n*)	%	(*n*)	%	(*n*)	%	(*n*)
L-UB[a]	7.1	(2)	32.2	(9)	7.1	(2)	53.6	(15)
P-EM[a]	17.3	(9)	21.2	(11)	11.5	(6)	50.0	(26)
P-UB[a]	7.0	(3)	23.3	(10)	20.9	(9)	48.8	(21)
Other[a]	23.1	(6)	34.6	(9)	15.4	(4)	26.9	(7)
Natural[b]	8.3	(11)	28.6	(38)	15.0	(20)	48.1	(64)
Man-made[b]	56.2	(9)	6.3	(1)	6.3	(1)	31.2	(5)
< 50% Forest[c]	16.2	(6)	13.5	(5)	21.6	(8)	48.7	(18)
50–75% Forest[c]	13.3	(8)	26.7	(16)	8.3	(5)	51.7	(31)
> 75% Forest[c]	11.5	(6)	34.6	(18)	15.4	(8)	38.5	(20)

[a]WLCLASS; [b]ORIGIN; [c]UPLAND

on Palustrine Unconsolidated *vs*. Lacustrine Unconsolidated wetlands, and were more likely to be observed on wetlands with shorter perimeters. Black Duck only or with Mallards were likely to be observed in greater proportion on Other wetlands than on Palustrine Unconsolidated wetlands. Both species together were more likely to be observed on man-made *versus* natural wetlands: however, few man-made wetlands were present in the study area (16 of 149 wetland-years used in modelling). Of the four variables retained in the model, only UPLAND was associated with the presence of one species. Black Duck only were more likely to be present on wetlands that had > 75% upland forest cover than wetlands that had < 50% upland forest cover (Table 4).

Hatch dates determined for Mallard and Black Duck broods in 1990 and 1991 (Fig. 1) showed that the two species failed to partition breeding resources in either time or space. Hatch dates were independent of species in both 1990 ($G^2_4 = 4.72$, $P = 0.32$) and 1991($G^2_3 = 1.70$, $P = 0.64$).

Prediction 2

Black Duck were more likely to be observed on wetlands where Mallard had been

Table 4. Polytomous logistic regression results of modelling Mallard and/or Black Duck presence as a function of 10 habitat variables, wetland class, and year.

Variable	Likelihood ratio (χ^2)	d.f.	*P* value
HERB[a]	4.53	9	0.87
VEG[a]	1.65	3	0.65
VD[a]	1.92	3	0.59
DTD[a]	2.04	3	0.56
YEAR[a]	6.59	6	0.36
AREA[a]	3.06	3	0.38
ERIC[a]	10.84	6	0.09
BEAVER[a]	4.41	3	0.22
WLCLASS[b]	16.78	9	0.05
ORIGIN[b]	8.80	3	0.03
PER[b]	14.33	3	0.01
UPLAND[b]	12.14	6	0.05

[a] Variables not retained in model based on sequential backwards elimination procedure
[b] Variables remaining in final model

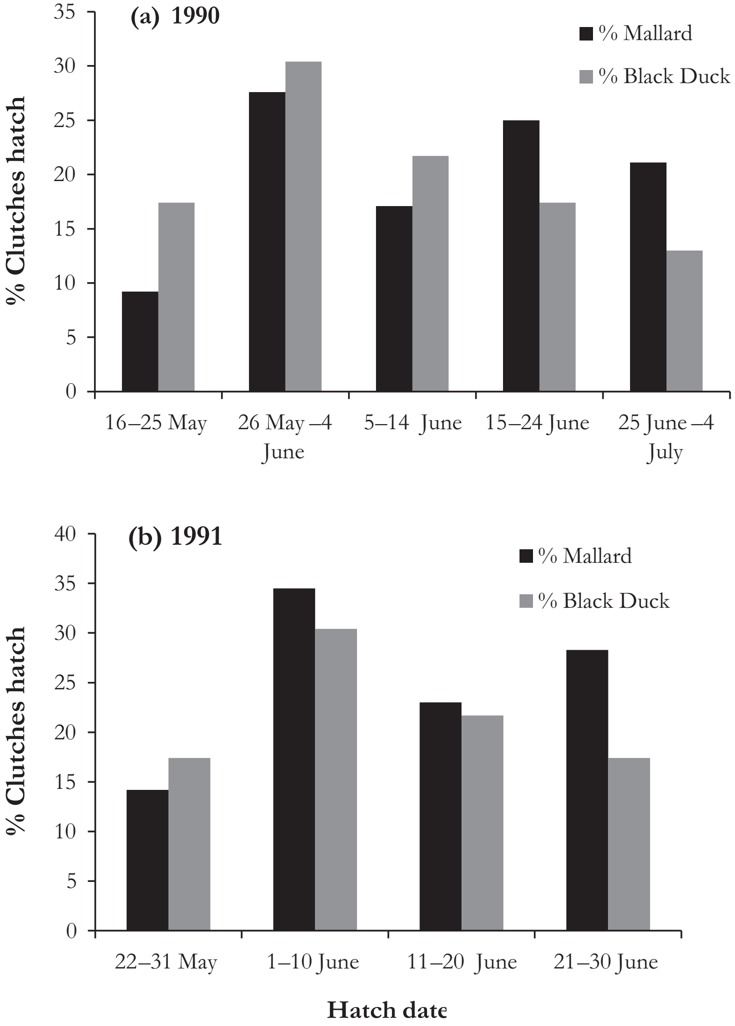

Figure 1. Timing of Mallard and Black Duck hatch dates over 10-day intervals in: (a) 1990 (n = 76 Mallard and n = 69 Black Duck clutches seen to hatch), and (b) 1991 (n = 113 and n = 77 for Mallard and Black Duck, respectively). The start date for the first 10-day interval was the date on which the first Mallard or Black Duck brood was observed in each year.

removed than on control wetlands where Mallard were not removed (P = 0.03). Black Duck pairs were observed on five of seven removal wetlands. On all five of these wetlands a Black Duck pair was observed within a day of removing Mallard (Table 5a). No Black Duck were observed on any of the five control wetlands for the duration of the experiment (Table 5b).

Table 5. Daily observations of wildfowl on: (a) removal wetlands (where Mallard were removed), and (b) control wetlands (where Mallard were not removed). MP = Mallard pair; MP-COL = Mallard pair collected; MP-NC = Mallard pair observed but failed to collect; NWO = no wildfowl observed; MM = Mallard male; MBD = male Black Duck; BDP = Black Duck pair.

(a) Removal wetland number

Observation day	1	2	3	4	5	6	7
1	MP	MP	MP	MP	MP	MP	MP
2	MP	MP	MP	MP	MP	MP	MP
3	MP-COL	MP-COL	MP-COL	MP-COL	MP-COL	MP-COL	MP-COL
4	NWO	BDP	BDP	NWO	BDP, MBD	BDP	BDP
5	MP-NC	MP-NC	BDP	NWO	MBD	NWO	MM
6	NWO	MP-NC	BDP	MM	BDP, MBM	MP-NC	NWO
7	MP-NC	MP-COL	MP-NC	MM	MBD, 2MM	NWO	BDP
8	MP-COL	MP-NC	MP-NC	NWO	MBD	MM	MBD
9	MBD	MP-COL	NWO	NWO	MM	NWO	BDP
10	NWO	BDP	MP-NC	MM	BDP, MBD	NWO	NWO
11	NWO	BDP	NWO	NWO	BDP, MM	NWO	2MM
12	NWO	NWO	MP-COL	MM	MBD, 2MM	NWO	NWO
13	NWO	3MM, MBD	NWO	NWO	NWO	NWO	
14	NWO	NWO	NWO	MM		NWO	
15	NWO						
16	NWO						
17	NWO						
18	NWO						

(b) Control wetland number

	1	2	3	4	5
1	MP	MP	MP	MP	MP
2	MP	MP	MP	MP	MP
3	MP	MP	MP	MP	MP
4	MP	MP	MP	NWO	MP
5	MP	NWO	NWO	NWO	MP
6	MP	MM	MP	MM	MP
7	MP	MM	MP	NWO	MP
8	MP	MM	MM	MP	NWO
9	MP	MM	MM	MM	NWO
10	MM	MM	MM	MM	NWO
11	MM	MM	MM	MM	NWO
12	MM	MM	MM	NWO	
13	MM	MM			
14					

Removal wetlands varied in numbers of times Black Duck were observed. On none of the wetlands were Black Duck pairs observed for the duration of the experiment. Black Duck were intermittently observed on removal wetlands, or a Mallard pair was observed at the site after observing Black Duck the previous day. Additional Mallard pairs were shot on three removal wetlands after the initial pair had been removed, as dictated by the treatment. We failed to collect Mallard pairs that were observed on some removal wetlands after the initial pair had been shot (Table 5a). On control wetlands, Mallard pairs or a single male Mallard were consistently observed throughout the experiment (Table 5b).

Prediction 3

The ratio of Black Duck to Mallard broods decreased significantly from 0.92 in 1990 to 0.22 in 1994 ($F_{1,3}$ = 24.74, r^2 = 0.89, P = 0.02), with decreases being most apparent after 1991 (Table 6). The ratio of Black Duck to Mallard broods also declined significantly over this five-year period when ratios were weighted by the number of wetlands sampled in a year ($F_{1,3}$ = 27.26, r^2 = 0.87, P = 0.01). Black Duck to Mallard brood ratios also declined significantly for 59 wetlands that were surveyed with equal effort in 1990 and 1994, from 0.94 to 0.24 (G^2_1 = 18.0, $P < 0.01$). The number of Black Duck broods observed on these 59 wetlands declined from 45 in 1990 to 19 in 1994, whereas the number of Mallard broods increased from 48 in 1990 to 78 in 1994. Total broods of both species increased by < 5%, from 93 in 1990 to 97 in 1994.

Discussion

Increasing Mallard populations in eastern North America have been accompanied by major declines in Black Duck abundance (Collins 1974; Dennis *et al.* 1989; Merendino *et al.* 1993). Consequently, some authors have attributed the decline of Black Duck to competition and/or hybridisation with Mallard (Ankney *et al.* 1987; Dennis *et al.* 1989; Merendino *et al.* 1993). Results of our study supported the hypothesis that Mallard and Black Duck compete for breeding resources.

Table 6. Changes in the ratio of Black Duck to Mallard broods in 1990–1994.

Year	No. of wetlands surveyed (*n*)	No. Black Duck broods	No. Mallard broods	Black Duck/ Mallard ratio
1990	100	70	76	0.921
1991	100	77	116	0.664
1992	63	29	83	0.349
1993	42	17	53	0.321
1994	74	23	106	0.217

Past attempts to document niche partitioning among sympatric species of waterfowl have usually revealed differences in macro-habitat use, diet, or morphological adaptations associated with foraging and micro-habitat use (Nudds 1992). Although resource partitioning appears to be widespread in the waterfowl community (Nudds 1992), we detected no interspecific differences in the distribution of breeding Mallard and Black Duck among wetland classes for any year. We also found no evidence that Mallard and Black Duck partitioned breeding habitat through differences in reproductive chronology.

Earlier studies also failed to find evidence of resource partitioning by Mallard and Black Duck. Mallard and Black Duck breeding in the western Adirondack Mountains of New York did not differ in proportional use of four wetland habitat types (Dwyer & Baldassare 1994). Merendino & Ankney (1994) found that Mallard and Black Duck breeding in central Ontario preferred wetlands of similar size, shape, fertility, and open water, and concluded that competition for breeding habitat was likely. Although these studies generally focused on macro-habitat characteristics, the two species also fail to partition habitat through differences in micro-habitat use or foraging ecology (Eadie *et al.* 1979; Nudds & Bowlby 1984; Tremblay & Couture 1986; Belanger *et al.* 1988).

Although distribution of Mallard and Black Duck among wetland classes was independent of species, log linear modelling revealed that wetlands surrounded by greater than 75% upland forest cover were more likely to be occupied by Black Duck only than by Mallard only or by both species together. However, Mallard do breed within heavily forested regions of the Black Duck's range (Porter 1993; Dwyer & Baldassare 1994; Merendino & Ankney 1994; Maisonneuve *et al.* 2006), so intact forests do not function as an indefinite isolating mechanism for Black Duck (Dwyer & Baldassare 1994; Nudds *et al.* 1996). While these results suggest that Black Duck prefer more heavily forested landscapes than do Mallard, Mallard were also documented breeding in these landscapes (*i.e.* 26.9% of all Mallard pairs were observed in wetlands surrounded by > 75% upland forest cover).

Failure to partition breeding resources should not affect Black Duck if Mallard do not prevent Black Duck from using these resources, or if breeding habitat is not limited. However, Black Duck were observed at a significantly higher rate on wetlands where Mallard were removed. Although sample sizes were small, no Black Duck were observed at any time on control wetlands where Mallard were not collected. The presence of Mallard on control wetlands appeared to limit the use of these wetlands by Black Duck and supports the prediction that Mallard reduce the amount of breeding habitat available to Black Duck. These results also support Seymour's (1992) conclusion that the two species treat each other as conspecifics when defending breeding territories.

Although Mallard and Black Duck were never observed together on either treatment or control wetlands, the two species can occur together on the same wetland. For example, McAuley *et al.* (2004) observed Mallard and

Black Duck pairs using the same wetlands in northeast Maine. The average size of wetlands in their study was much larger than wetlands included in our removal experiment (all < 1 ha), however, and included wetlands up to 113 ha in size. Larger wetlands are more likely to offer visual obstructions, which can allow pairs to isolate themselves from conspecifics. We purposely chose small treatment and control wetlands to avoid this possibility. However, breeding pair densities on larger wetlands must eventually be limited by spacing behaviour regardless of the greater opportunity to achieve visual isolation in these habitats. It seems that Mallard occupying the same wetlands as Black Duck may ultimately reduce the potential of those wetlands to support Black Duck because the two species treat each other as conspecifics (Seymour 1992). Even if competition coefficients for the two species are symmetrical, Mallard would represent an additional source of intraspecific density dependence for Black Duck.

Recent efforts to model production rates of Black Duck populations have found evidence of intraspecific density dependence on the breeding grounds (Zimpfer & Conroy 2006). The authors suggested that evidence for density dependence in Black Duck reproduction could mean that Black Duck are near habitat carrying capacity and that Mallard could further reduce carrying capacity. Competition between Mallard and Black Duck is conditional on breeding habitat limitation. If Black Duck populations are near carrying capacity, then the likelihood for competition seems high given the failure of these two species to partition resources in time or space.

Inverse changes in population sizes over time are consistent with the hypothesis that waterfowl species compete (Pöysä 1984; Nudds 1992). Within our study area there was evidence that production of Mallard and Black Duck was inversely related. Ratios of Black Duck to Mallard broods declined steadily between 1990 and 1994, and surveys on the same 59 wetlands in 1990 and 1994 documented large declines in numbers of Black Duck broods. This decline was entirely offset by increases in Mallard broods. There were no interspecific differences in distribution of Mallard and Black Duck broods among wetland classes (Petrie 1998). Thus, even if changes in relative abundance of wetland types occurred between years (and there was no evidence that they did), we would expect Mallard and Black Duck broods to respond similarly. Moreover, our conclusions are not dependent on the assumption that all broods are observed, or that Mallard and Black Duck broods are observed with equal probability. We only assume that the probability of observing Mallard and Black Duck broods did not change over time. Changes in relative mortality rates of Mallards and Black Duck young between 1990 and 1994 could have produced changes in brood ratios, especially if these mortality changes occurred shortly after hatch. However, work on the study area between 1992 and 1994 indicated no differences in duckling survival between the two species (Petrie *et al.* 2000).

Inverse changes in Mallard and Black Duck populations have been documented elsewhere. Mallard increased by 600% in southern Ontario between 1951 and 1971, while Black Duck increased by 50% (Collins 1974; Merendino *et al.* 1993). From 1971 to 1985, Mallard increased by another 51%, while Black Duck decreased by 38% (Ankney *et al.* 1987; Merendino *et al.* 1993). However, we concur with Nudds *et al.* (1996) that Mallard are not certain to cause declines in Black Duck. Black Duck populations remained stable in northwest Ontario over a 40-year period despite large numbers of Mallard breeding in the region (Nudds *et al.* 1996). Perhaps breeding habitat in northwest Ontario is sufficient to meet the needs of both species and Black Duck have experienced no population effects as a result of competition with Mallard. We conclude that Mallard and Black Duck will compete where breeding resources are limiting, and concur with Zimpfer and Conroy (2006) that efforts to manage Black Duck using an adaptive management framework should include the possible effects of Mallard.

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