

American Black Duck *Anas rubripes* and Mallard *A. platyrhynchos* abundance, occurrence of heterospecific pairing and wetland use between 1976 and 2003 in Northeastern Nova Scotia, Canada

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Abstract

Mallard *Anas platyrhynchos* abundance has increased in eastern North America with a concomitant decline in the number of Black Duck *A. rubripes* in some parts of their range. It has been speculated that introgressive hybridisation or competitive exclusion have been the mechanisms for the opposing population trajectories of these species. In particular, the prevailing view is that heterospecific pairs of male Mallard x female Black Duck are contributing to the hybridisation of the two species, with a combination of Mallard releases and use of urban areas increasing the frequency of these pairings. This paper reports long-term survey data documenting the relative frequency and combination of sexes of mixed pairs from two sites in eastern Canada, and the extent of movement of Mallard into habitat dominated by Black Duck from points of Mallard concentration in Nova Scotia. This study indicates no long-term decline in Black Duck, nor an increase in Mallard, in northeastern Nova Scotia between 1976 and 2003. Heterospecific pairs in Nova Scotia were rare and consisted primarily of male Black Duck x female Mallard; heterospecific pairings were more common in a St. Lawrence River study area and were mainly of the expected male Mallard x female Black Duck combination. Two clines with respect to heterospecific pairing are suggested from these data: (1) an increase in frequency, and (2) a change in male : female composition by species moving from east to west. The occurrence of Mallard appears to be limited to a 1-km to 3-km radius from discrete points of introduction or concentration. Within this radius, Black Duck abundance was low. Outside this area, at a 3-km to 15-km radius, it then increased twofold at Shubenacadie and sevenfold at Goshen. Thus, Mallard releases in this area appear to have only localised effects. This study found no evidence for Mallard or hybrid increases, Black Duck declines, the occurrence of competitive exclusion, or of introgressive hybridisation in Black Duck in northeastern Nova Scotia between 1976 and 2003.

Key words: Black Duck, hybrid, Mallard introduction, population trend, mixed pairing.

Historically, Mallard *Anas platyrhynchos* occurred only occasionally in northeastern North America, the primary range of the Black Duck *A. rubripes* (Stewart 1958; Heusmann 1974). Since the beginning of the 20th century, however, a gradual eastward expansion of Mallard from the central part of the continent into the Black Duck's range has occurred, with Erskine (1992) reporting that by the 1980s the Mallard had become a relatively widely distributed breeder in the Maritime Provinces of Canada. Concurrent with the Mallard range expansion was a reported dramatic decline in the Black Duck populations (Johnsgard 1961; Johnsgard & DiSilvestro 1976; Dennis *et al.* 1984; Heusmann 1991; Conroy *et al.* 2002). This seems to have been most obvious during a period beginning in the 1950s and continuing into the 1970s, particularly in southern Ontario, southern New England, the Mid-Atlantic States, and parts of the American Midwest (Heusmann & Sauer 1997; Conroy *et al.* 2002).

The decline of the Black Duck in the east has been attributed to several causes (Conroy *et al.* 2002). Johnsgard & DiSilvestro (1976) speculated that it was related to hybridisation with the taxonomically similar Mallard, and Johnsgard (1961) warned that the Mallard would swamp Black Duck gene pools, eventually leading to widespread extirpations. Indeed, Heusmann (1974, 1988) suggested that Black Duck have few traits to prevent hybridisation with Mallard, further supporting the contention that the Mallard poses a threat to the Black Duck as a distinct species. Heusmann (1987) further speculated that sites of Mallard release, such as urban parks, could allow these introduced

ducks to become established in Black Duck range, with Mallard possibly expanding its range from these sites. If true, this may be significant, as Mallard have been released in many parts of Black Duck range, with Heusmann (1991) reporting more than 1.8 million having been released in the Atlantic Flyway between 1940 and 1990. Ankney *et al.* (1987) stated that increased Mallard numbers in an area cause declines in Black Duck through introgressive hybridisation and competitive exclusion, claiming that these factors were the main causes of Black Duck decline in parts of Ontario where Mallard now occurs in habitats formerly occupied only by Black Duck. Despite debate over this issue (e.g. Conroy *et al.* 1989), little is known about the frequency of introgressive hybridisation for any wild Black Duck population.

Mixed pairing (i.e. heterospecific pairs) is one mechanism by which hybrids might be produced. Although both combinations of heterospecific pairing (male Mallard x female Black Duck and male Black Duck x female Mallard) have been observed in wild populations, Johnsgard (1960) suggested that mixed pairs should be predominantly of male Mallard mated to female Black Duck. Furthermore, Brodsky & Weatherhead (1984) reported an apparent preference for male Mallard by female Black Duck, despite there being an excess of male Black Duck from which to choose in a wintering population in Ontario. Brodsky *et al.* (1998) say that male Mallard dominate male Black Duck. This influences social interactions, such as those leading to pair formation, and can be one factor contributing to hybridisation. However, Hoysak and Ankney

(1996) caution that dominance relationships between these two species are more complex than were originally thought. D'Eon *et al.* (1994) concluded that mixed pairs likely accounted for the 2% hybridisation rate in Black Duck near Sackville, New Brunswick, where one of the highest densities of Mallard in Atlantic Canada occurs. For heterospecific pairing leading to introgressive hybridisation to have a significant effect on a population, the characteristics of that population must change in a consistent manner over generations. However, none of these studies was of sufficient duration to determine long-term population trends. Elliot (1990, 1994) highlighted the importance of long-term studies to understand the ecology of wild populations. Specifically, he maintained that their value is in providing reliable estimates of baseline variation that reveal population trends, while elucidating rare but potentially ecologically important events.

This study reports long-term survey data for wild Black Duck and Mallard populations. The objectives were to determine (1) the relative frequency of occurrence of Black Duck, Mallard and mixed pairs in four locations of eastern Canada, (2) the male : female combination of heterospecific pairings, and (3) the extent of movement of Mallard and mixed pairs into wetlands around two sites where Black Duck were present until Mallard were artificially introduced and have become concentrated. It was predicted that there would be few Black Duck at and close to these release sites.

Methods

Study areas and populations

The results reported here are from four study areas of eastern Canada, three in Nova Scotia and one on the St. Lawrence River near the provincial border of Ontario and Québec (Fig. 1). The principal study area consisted of five contiguous estuaries (Pictou, Merigomish, Antigonish, Pomquet and Tracadie) that drain into the Northumberland Strait in Pictou and Antigonish counties of northeastern Nova Scotia. The senior author has studied Black Duck in the Antigonish estuary and associated watersheds since the 1970s (see Seymour & Titman 1978, 1979; Seymour 1984; Seymour & Jackson 1996; Seymour *et al.* 2002) ensuring consistent, single-observer sampling over the entire study period.

Black Duck establish territories and raise broods in the wetlands of the watersheds associated with the five estuaries (Seymour & Titman 1978). The landscapes of these watersheds are an interspersed of mixed forest and agricultural lands with broadly defined wetland types consisting of rivers, lakes and freshwater marshes. The wetlands themselves are widely dispersed permanent, semi-permanent and annually recurring temporary ponds that range in size from 0.1 ha to 5.5 ha. Mallard or Black Duck broods were fledged in at least some of the years of study at each wetland included in the survey, so all wetlands were considered suitable sites for rearing ducklings (N.R. Seymour, unpubl. data).

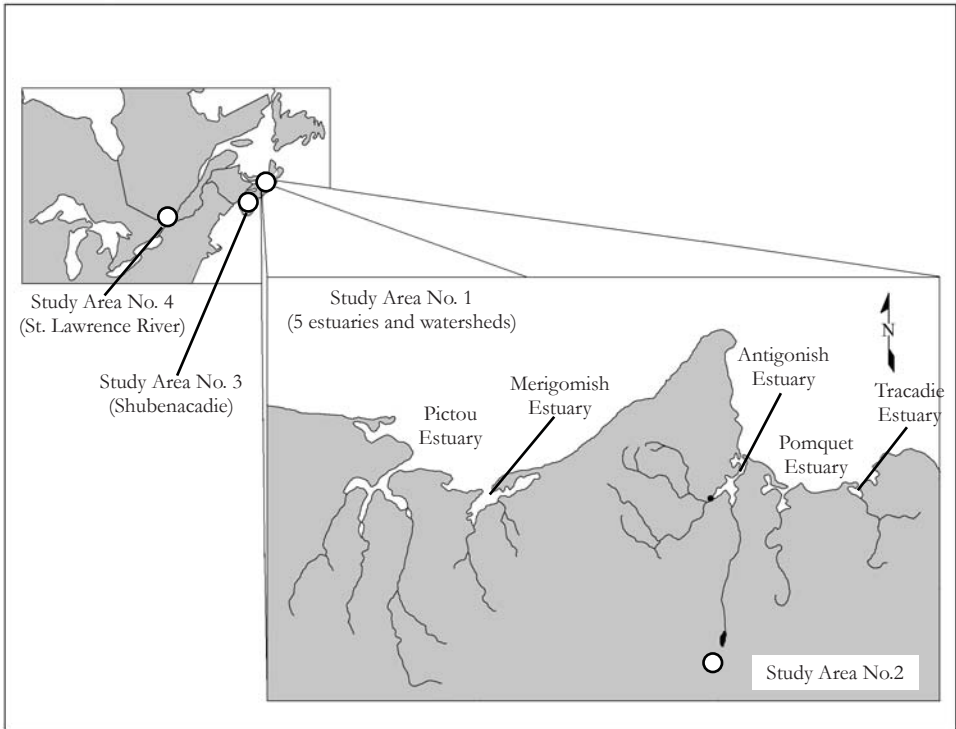


Figure 1. Four areas surveyed during the study: (1) five estuaries in northeastern Nova Scotia, (2) Goshen, (3) Shubenacadie (central Nova Scotia), and (4) St. Lawrence River. Map scale of inset (Study Areas 1 & 2) approximately 1 : 850,000.

Each year the Black Duck winter in the estuaries and, except for Pomquet and Antigonish, there is little movement of ducks between these estuaries, where courtship and pair formation occur in this largely resident population (N.R. Seymour, unpubl. data). Small numbers of Mallard have bred and wintered in the watersheds and estuaries each year since at least 1972, when observations began. Aspects of the breeding behaviour of each species, including interspecific interactions, have been reported by Seymour (1990, 1992).

The second study area included the wetlands around a private wildlife facility

that operated for about 20 years from the mid-1970s until the early 1990s near Goshen, on the divide between the Antigonish and Country Harbour watersheds (Study Area No. 2 in Fig. 1). This facility was a source of an undocumented but significant number of Mallard releases. Order of magnitude estimates are of 200–300 Mallard released over a 5-year to 7-year period from this facility. Despite the curtailing of these releases in the early 1990s, this resident population of Mallard remains at this site (see Results).

The third study area included the wetlands near a wildlife park at Shubenacadie,

Nova Scotia (Study Area No. 3 in Fig. 1), approximately 150 km southwest of the principal study area. The park has been a site of Mallard concentration since at least the 1970s and was once a release site. Winter concentrations of Black Duck also occur at the park, and pairs of both species disperse from there into the surrounding breeding habitat.

Finally, surveys were also conducted on the north shore of the St. Lawrence River between the villages of Summerstown, Ontario, and St. Zotique, Québec (Study Area No. 4 in Fig. 1). The landscape adjacent to the river is an interspersed of agricultural land and stands of hardwood trees. In this area, both Mallard and Black Duck use small creeks and rivers that flow into the main river, as well as widely dispersed permanent, semi-permanent and temporary wetlands.

Surveys

Survey data were collected during a long-term study of behavioural interactions between Black Duck and Mallard to investigate whether Mallard may be having a negative influence on Black Duck in eastern Canada as documented in other areas. The long-term study includes all behavioural interactions (e.g., Seymour & Titman 1978, 1979; Seymour 1984, 1990, 1992; Seymour & Jackson 1996; Seymour *et al.*, 2002) but this study includes only abundance and pair associations. Specifically, the *post hoc* null hypotheses (generated after data collection) were that (1) Mallard abundance is not increasing over time, and (2) Black Duck abundance is not decreasing. Surveys of the five estuaries in northeastern Nova

Scotia were conducted in 21 years between 1976 and 2003 (Table 1) to determine the abundance and sex ratio of Black Duck, Mallard and hybrids. Strategic lookout points enabled observation of most of each estuary. Observations were made exclusively by the senior author, and bird identification could usually be made reliably with binoculars and a spotting scope. The timing of the surveys varied each year, but they were scheduled to coincide with the widespread freezing of inland wetlands, typically between December 10 and 20. At this time there was little open fresh water available for the ducks, and the birds were concentrated on the still unfrozen waters of the estuaries. Each year the entire survey of the five estuaries spanned two days, lasting each day from 08:00 h to 15:00 h (EST). Observation time spent at each estuary was similar, except for the relatively small Tracadie estuary (see title of Table 1 for drainage areas of the estuaries).

In years with a winter survey, a spring survey of breeding pairs was also conducted at wetlands in the watersheds associated with each estuary (Table 1). This was made along a 143-km route between April 25 and May 5, when females in this population are typically laying eggs and males are defending territories (Seymour & Titman 1978). This is a period when pairs are most sedentary and there is only one pair of either Black Duck or Mallard at a wetland site (Seymour & Titman 1978). The presence and absence of pairs was recorded in all surveys, as were the male : female combinations of heterospecific pairs.

The Goshen survey involved evaluating use of wetlands that surrounded a point of Mallard concentration. Twenty annual visits

Table 1. Years of surveys of wetlands and estuaries for Black Duck and Mallard in three areas of Nova Scotia and one location on the St. Lawrence River. *Areas of drainage per estuary ~ 1,000 km² (Pictou), ~ 800 km² (Antigonish), ~ 325 km² (Merigomish), ~ 160 km² (Pomquet), ~ 125 km² (Tracadie). †The 104 wetlands distributed among the five estuaries were: 12 wetlands in the Pictou watershed, 18 in Merigomish, 53 in Antigonish, 13 in Pomquet and 8 in Tracadie.

Survey years		Number of wetlands
Northeastern Nova Scotia (Study Area No. 1)		
Estuaries* (winter survey)	1976, 1978–1982, 1986, 1988–1992, 1994–1997, 1999–2003	
Wetlands (spring survey)	1976, 1978–1982, 1986, 1988–1992, 1994–1997, 1999–2003	104†
Goshen (Study Area No. 2)		
(spring survey)	1976, 1978–1982, 1986, 1988–1992, 1995–1997, 1999–2003	109
Central Nova Scotia (Study Area No. 3)		
Subenacadie (spring survey)	1974–1975, 1978–1979, 1982, 1986, 1989, 1992, 1995, 1997, 2000	72
St. Lawrence River (Study Area No. 4)		
(spring survey)	1975, 1978, 1982, 1986, 1990, 1995, 1997, 2000, 2001, 2003	22

were made, at regular intervals between 1976 and 2003 inclusive, to all wetlands within a radius of 15 km from the release site (Table 1). These included 109 wetlands where Black Duck and Mallard females fledged broods periodically throughout the study period. These wetlands appeared unchanged throughout the study (i.e. there was no obvious increase in human activity or changes in land use) and therefore it is probable that they remained suitable for brood rearing. To detect the presence or absence of pairs, each wetland was visited at

least three times per week during the general egg-laying and incubation period for the species in this area, typically from April 10 to May 30 (Seymour & Titman 1978).

The Shubenacadie survey also evaluated wetland use at and adjacent to an area with a concentration of Mallard, but it differed from the Goshen study. The former survey did not include the wetlands surrounding the release site, but covered 72 wetlands along a 50-km transect running northeast from Shubenacadie, in the direction of Antigonish. These sites were visited once

each week between April 10 and May 30 of each survey year (Table 1) to determine presence or absence of pairs.

Surveys of breeding pairs on the St. Lawrence River study area were conducted two or three times annually at 22 sites during 10 years between 1975 and 2003. Mallard, Black Duck and hybrid pairs were counted during the period April 5–20 along a route of approximately 30 km.

Statistical analysis

Where means are calculated, the uncertainty associated is presented as standard error. Coefficient of variation, when presented, is ($CV = s.e./\bar{x} \times 100$). Simple linear regression was used to quantitatively describe temporal trends in abundance of Black Duck, Mallard and hybrids.

Results

On average, within a year, Black Duck comprised 96.9% of the total number of Black Duck, Mallard or hybrids counted in the five estuaries of northeastern Nova Scotia during the 21 years between 1976 and 2003 in which December surveys were conducted. Mallard comprised 2.3% and hybrids < 1.0%. The average annual abundance for the five estuaries combined was 411.2 (s.e. = 11.3) Black Duck, 9.6 (s.e. = 0.39) Mallard and 3.2 (s.e. = 0.19) hybrids. Annual numbers recorded over the whole study period increased for Black Duck, while remaining stable for Mallard and hybrids (Fig. 2). Relative variation over the period of record was lowest for Black Duck

($CV = 12.6\%$) and higher for Mallard ($CV = 18.6\%$) and hybrids (27.2%). The average annual Black Duck sex ratio (females : males) across all estuaries was 0.79 (s.e. = 0.013), and ranged from 0.65 (1981) to 0.88 (2003). There were too few Mallard or hybrids in any year to report meaningful sex ratios.

Spring surveys of breeding pairs at the 104 wetlands in the watersheds associated with the estuaries during the 20 years between 1976 and 2003 in which observations were made showed that Black Duck pairs occurred at, on average, 74.7% (s.e. = 1.01) of the wetlands each year (Fig. 3). Mallard and hybrid pairs used only 3.03% (0.28) and 1.97% (0.27) of these wetlands, respectively. This meant that an average 20.3% (1.05) of the available wetlands were not used in any given year.

Heterospecific pairing was observed on only 41 occasions at the 104 wetlands (Table 2); these accounted for < 2.5% of 1,617 Black Duck and Mallard pairs observed over 20 years. The male Black Duck x female Mallard combination was most common (61.0%). The remaining combinations were never seen more than three times in each of the watersheds of the four larger estuaries, and mixed pairs were never observed in the Tracadie watershed. In contrast, there were four times as many heterospecific pairs at 22 wetland sites on the St. Lawrence River during the 10 years of surveys between 1975 and 2003 (Table 2). The most common (~72%) pairing was male Mallard with either a female Black Duck or hybrid. Male Black Duck were paired with female Mallard only ~16% of the time (26 of 161 observations, Table 2).

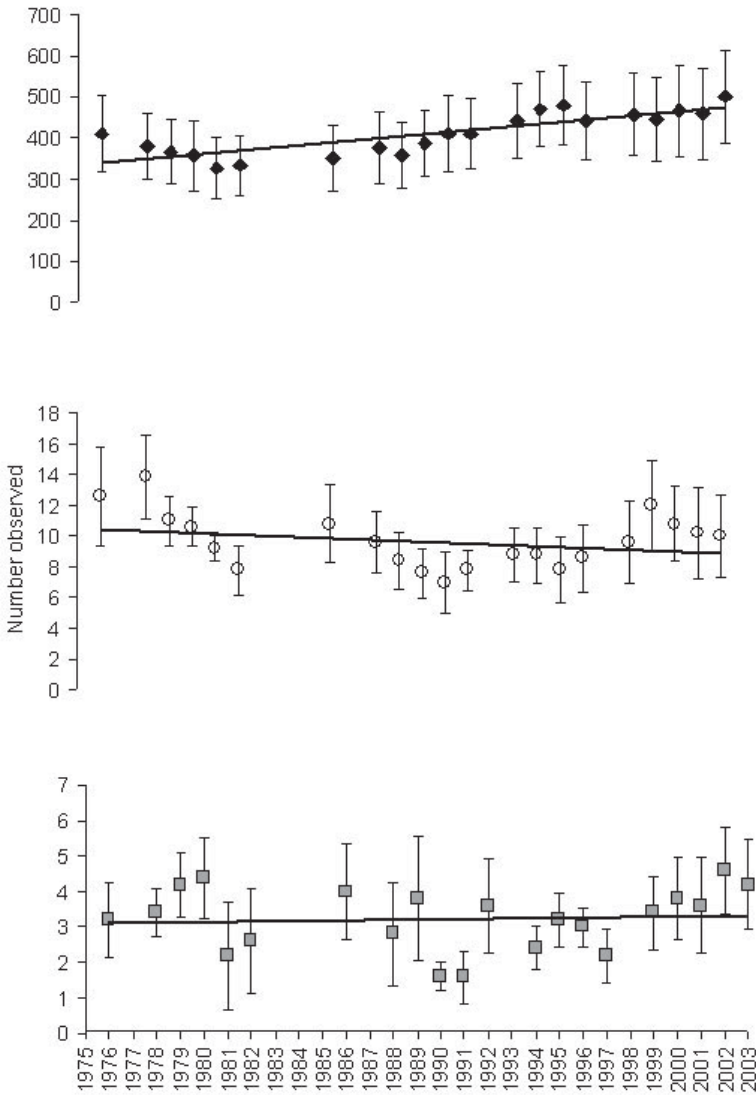


Figure 2. Mean annual numbers of Black Duck (upper panel), Mallard (middle panel), and hybrids (lower panel) observed on five northeastern Nova Scotia estuaries during December, for 21 years between 1976 and 2003. Error bars are s.e. Regression equations are: Black Duck = $4.95 (\pm \text{s.e.} = 0.79) \cdot X + 334.7 (\pm 13.90)$ ($F_{1,19} = 39.15, r^2 = 0.673, P < 0.0001$); Mallard = $-0.06 (\pm 0.04) \cdot X + 10.6 (\pm 0.80)$ ($F_{1,19} = 1.63, r^2 = 0.079, P = 0.22, \text{n.s.}$); Hybrids = $0.01 (\pm 0.02) \cdot X + 3.1 (\pm 0.41)$ ($F_{1,19} = 0.19, r^2 = 0.01, P = 0.67, \text{n.s.}$). Regression equations are based on years numbered 1 to 28 rather than calendar years.

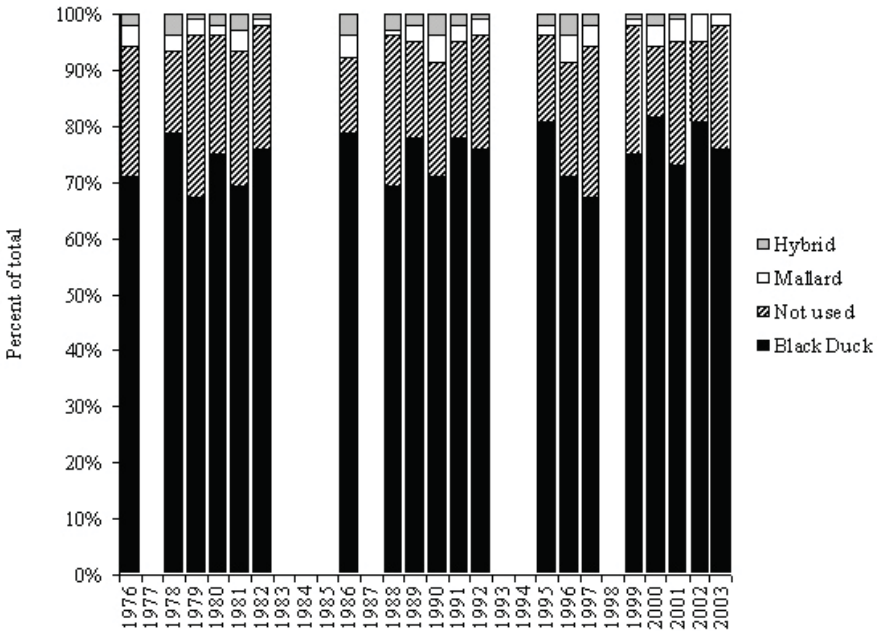


Figure 3. Percentage of the 104 wetlands associated with five northeastern Nova Scotia estuaries at which Black Duck, Mallard or hybrid pairs were present during April through early May each year for 20 years between 1976 and 2003.

Twenty years of breeding-pair surveys between 1976 and 2003 at a site of Mallard release (Goshen) and at the 109 wetlands within the circular area 15 km out from this nucleus showed that Mallard only occasionally occurred beyond the nucleus and at the 17 wetlands within 3 km of it (i.e. mean cumulative number of Mallard within 3 km = 10.95, s.e. = 0.48) (Fig. 4a). Black Duck, however, occurred only on three occasions at the nucleus and were uncommon at the other wetlands within a 3-km radius (mean = 7.5 Black Duck, s.e. = 0.50 at 3 km). Each year Mallard occupied most (7–15) of the 17 available wetlands within 3 km of the nucleus. Beyond this 3-km radius, the cumulative abundance of Black Duck increased steadily, with pairs occupying most

of the remaining 92 wetlands. However, each year 14–36 (15.2%–39.1%) of these 92 sites beyond 3 km were unused by either Black Duck or Mallard, despite the fact that females periodically fledged broods at each of these wetlands during the 20-year study.

Surveys of breeding pairs at another Mallard release site (Shubenacadie) and at 72 wetlands 50 km out from this nucleus showed a trend during 11 years similar to that in Goshen (Fig. 4b; transect shown only out to 15 km in order to be comparable with Goshen data). In addition to the data shown in Fig. 4b, at the 17 wetlands in the 15-km to 30-km range, and at seven wetlands between 30 km and 50 km, cumulative Black Duck numbers increased to 31.1 (s.e. = 2.36) and 36.2 (s.e. = 2.44) respectively. No Mallard or

Table 2. Number, and male : female combination, of heterospecific pairs at 96 wetlands in watersheds associated with four estuaries in northeastern Nova Scotia and 22 wetlands on the St. Lawrence River, Canada. The eight wetlands in the Tracadie estuary showed no heterospecific pairing over the period of study and so are excluded here. Observations made during 21 years on the former study area and 10 years on the latter, between 1976 and 2003 (see Table 1). Percentage of total observed mixed pairs is given in brackets.

	Northeastern Nova Scotia					St. Lawrence
	Watershed					
	Pictou	Antigonish	Merigomish	Pomquet	Combined	
Number of wetlands	12	53	18	13	96	22
Male : Female						
Black Duck : Mallard	3 (50)	15 (65.2)	6 (60)	1 (50)	25 (61.0)	26 (16.1)
Mallard : Black Duck	1 (16.7)	3 (13)	1 (10)	0 (0)	5 (12.2)	65 (40.4)
Hybrid : Black Duck	0 (0)	2 (8.7)	1 (10)	0 (0)	3 (7.3)	--
Hybrid : Mallard	2 (33.3)	3 (13.7)	2 (20)	1 (50)	8 (19.5)	--
Black Duck : Hybrid	--	--	--	--		19 (11.8)
Mallard : Hybrid	--	--	--	--		51 (31.7)
Total mixed pairs observed	6	23	10	2	41	161

hybrids were detected between 15 km and 50 km from the nucleus. Mallard numbers increased up to 1 km from the release site. They then remained stable until 10 km out, when there was a further small increase. Thereafter, Mallard pairs did not occur. Black Duck were rare at or near the nucleus (mean < 2 Black Duck out to 1 km) but cumulative abundance increased steadily beyond 1 km, out to the end of the 50-km transect. Only Black Duck occurred in areas

that were remote from human concentration or activity.

Discussion

The power of this study is in its long-term nature, and in a lack of other comparable studies of Black Duck ecology in which a single population has been monitored using a consistent methodology over such a long

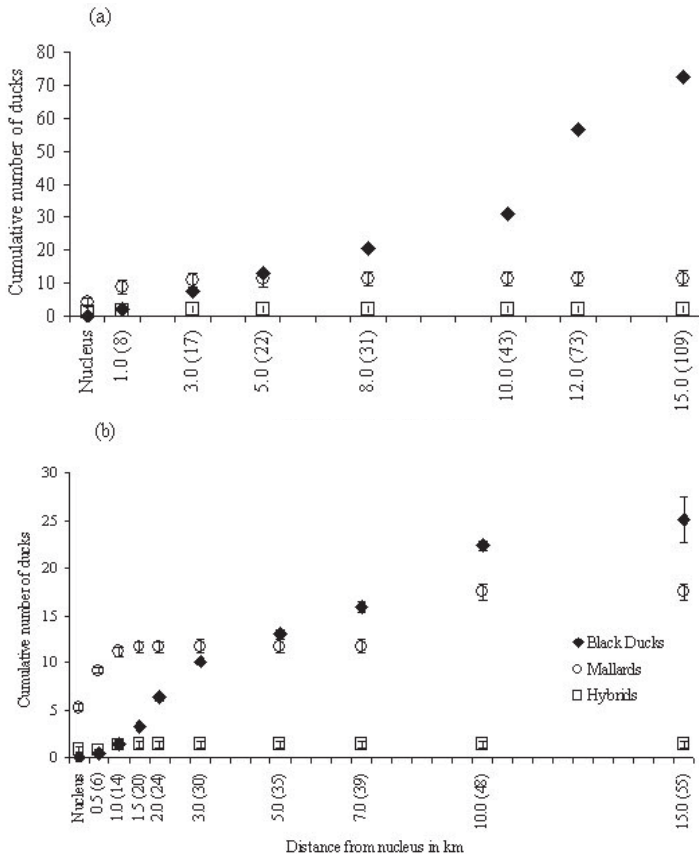


Figure 4. Mean cumulative number of Black Duck, Mallard and hybrid pairs at varying distances from a site of Mallard concentration (nucleus) during (a) 20 years at 109 wetlands near Goshen in northeastern Nova Scotia, and (b) 11 years at 55 wetlands near Shubenacadie in central Nova Scotia. Cumulative number of wetlands, *n*, given as values in parentheses on the x-axis. Error bars are s.e.

period. This allows the drawing of strong inferences about population characteristics. There is no evidence that Mallard or Mallard–Black Duck hybrids were increasing in northeastern Nova Scotia between 1976 and 2003, and they were only ever a small component of the Black Duck/Mallard association. These results are consistent with D'Eon *et al.* (1995), who reported

“relatively low” Mallard increases in the Maritime Provinces between 1965 and 1992. McCorquodale & Knapton (2003) found that Mallard numbers had not increased, nor Black Duck decreased, in three city parks of northern Nova Scotia between 1992 and 2002, and concluded that there was no evidence that Mallard were replacing Black Duck in these park environments. Despite

concern by Johnsgard & DiSilvestro (1976), declines of Black Duck as a result of an eastward range expansion by Mallard are not apparent in this northeastern Nova Scotia study area.

If the Black Duck declines reported by Johnsgard (1961), Johnsgard & DiSilvestro (1976), Dennis *et al.* (1984), Huesmann (1991) and Conroy *et al.* (2002) elsewhere in their range can be attributed to Mallard, either via competitive exclusion or introgressive hybridisation, this may reflect a regional or habitat-related phenomenon not currently evident in northeastern Nova Scotia. As McAuley *et al.* (2004) found in Maine, there is no evidence that at current densities and availability of habitat competitive exclusion of Black Duck by Mallard is limiting Black Duck populations in northeastern Nova Scotia.

D'Eon *et al.* (1994) reported that Mallard were not extending their range outward from a release site near Sackville, New Brunswick. Similarly, there was no evidence that Mallard were expanding their range from the two sites of release at Goshen or Shubenacadie. The fact that Mallard did not increase beyond 3 km from the nucleus supports the contention that released Mallard remain highly localised, even after several years of successful reproduction. It is known that Mallard may disperse widely from points of introduction (Heusmann 1987, 1988), and the results presented here are not intended to imply that all of the Goshen Mallard remained localised without some dispersal. However, comprehensive helicopter surveys of breeding pairs in two watersheds (Antigonish and Pomquet in 12 years (1973, 1978, 1979, 1981, 1983, 1986,

1987, 1989, 1990, 1991, 1997 and 1998) showed only 0–8 Mallard pairs within these catchments in any one year (N.R. Seymour, unpubl. data). It is therefore speculated that the introduced Mallard either remain very near to the point of introduction, or disperse widely (i.e. outside watersheds). Nor was there evidence that Mallard were excluding Black Duck from the wetlands at or near the more comprehensively surveyed Goshen release site (N.R. Seymour, unpubl. data). Anecdotal evidence suggests that Black Duck are more wary and less tolerant of human activity than are Mallard (e.g. Kortright 1943). If this is so, it may be that Black Duck avoid locations of human activity rather than avoiding Mallard or being excluded by them. Perhaps the absence of Black Duck near Goshen was a case of passive dispersal of Black Duck associated with avoidance of human activity and not active dispersal by Mallard territorial behaviour (cf. Seymour 1992).

Longcore *et al.* (1987) reported a low frequency of mixed pairs in Maine between 1957 and 1986. Mixed pairing, while still relatively low, was more frequent in this Nova Scotia study. However, there was no evidence that it was resulting in significant introgressive hybridisation (cf. Johnsgard & DiSilvestro 1976; Ankney *et al.* 1987; Merindino *et al.* 1993), because the number of hybrids did not increase over time. Certainly there was no evidence for the swamping of the Black Duck gene pool that concerned Johnsgard (1961).

In addition, the data reported here suggest two east to west clines in heterospecific pairing. During the same time period there were four times as many mixed

pairs on the St. Lawrence study area than there were in Nova Scotia, despite there being fewer wetlands surveyed in the former than the latter study area. This indicates an increasing trend in the frequency of occurrence of mixed pairs from east to west, and this is consistent with the increasing trend in number of hybrids from east to west reported by Johnsgard (1967). The second cline is in the male : female combination of heterospecific pairs. The majority in Nova Scotia was male Black Duck x female Mallard but this was reversed on the St. Lawrence study area. These Nova Scotia results are at odds with those predicted by the general literature and specifically by Brodsky & Weatherhead (1984) and Brodsky *et al.* (1988), who hypothesised that male Mallard would out-compete male Black Duck for both Mallard and Black Duck females.

These long-term results over five watersheds confirm that the Black Duck decline is not occurring throughout its range. This conclusion suggests that a particular mechanism hypothesised to be causing a decline in one region may not be applicable across large geographic areas. The results presented here provide insight into an important issue of Black Duck and Mallard hybridisation and expansion, and are significant in that they are long-term, high-resolution and, in contrast to most studies on these ducks, represent a healthy population of Black Duck in the presence of Mallard.

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