

SALT TOLERANCE IN AMERICAN BLACK DUCKS, MALLARDS, AND THEIR F1-HYBRIDS

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ABSTRACT.—We performed experiments on pure, wild-strain Mallards (*Anas platyrhynchos*), American Black Ducks (*A. rubripes*), and first filial (F1) Mallard-Black Duck hybrids to investigate whether duckling survival and growth varied with salinity, and whether hybrids acquired salt tolerance. Ducklings were assigned to treatments in a 4 × 3 factorial experiment that involved a salinity gradient (0, 0.5, 1.0, 1.5% NaCl) and duckling age (7, 14, 21 days). An additional experiment subjected ducklings to 3% NaCl at 48 h post-hatch. Black Duck ducklings had higher survival and growth rates than did Mallards with salt concentration increasing up to 1.5%. Hybrids were more similar to Black Ducks than to Mallards in that regard. Salinities >2% were uniformly fatal to all 48-h-old ducklings. Salt glands obtained from fully grown individuals from each treatment were heaviest in Black Ducks and hybrids, and glands increased in size with increasing age and salinity. Salt glands hypertrophied to a maximum size at 1% NaCl, which indicates that even Black Duck ducklings possessed salt glands capable of osmoregulation only at low levels of salinity. Interspecific differences with respect to salt tolerance are probably insufficient to serve as a postmating reproductive isolating mechanism between these species in estuarine habitats. Received 24 January 1990, accepted 18 July 1990.

GEOGRAPHIC isolation may once have been the most important pre-mating reproductive isolating mechanism between breeding populations of American Black Ducks (*Anas rubripes*; hereafter Black Ducks) and of Mallards (*A. platyrhynchos*). Historically, land clearing in eastern North America altered habitat and may have contributed to the eastward range expansion by Mallards into areas formerly occupied primarily by Black Ducks (Heusmann 1974, Dennis et al. 1984, Conroy et al. 1989). Concomitantly, Black Ducks declined (Collins 1974, Rogers and Patterson 1984). Because the decline in Ontario (where Mallards have increased) has been particularly marked (Collins 1974, Johnsgard and DiSilvestro 1976, Dennis et al. 1984), introgressive hybridization, competitive exclusion, or both, have been proposed to be major, proximate agents of the decline of Black Ducks (Johnsgard 1967, Brodsky and Weatherhead 1984, Ankney et al. 1987).

The continued eastward expansion of the Mallard may eventually cause the loss of the Black Duck phenotype through introgressive hybridization (Ankney et al. 1987) in much the same way that indigenous species of ducks have lost specific integrity through hybridization with introduced populations of the Mallard elsewhere (Braithwaite and Miller 1975, Hadson 1984, Gillespie 1985).

On the other hand, a stable coexistence between the two species might develop where new reproductive isolating mechanisms can be established. Black Ducks principally occupy brackish, coastal marshes and may have secondarily expanded their breeding range to include wooded freshwater ponds (Heusmann 1974). Black Ducks may continue to decline in freshwater habitats where they are sympatric with Mallards. Ultimately, Black Ducks might reside only in some form of habitat refuge in coastal wetlands isolated from gene introgression with Mallards.

Little information exists about the suitability of brackish habitats for duckling growth and survival and, specifically, about the ability of ducklings to regulate the salt concentration of body fluids (Serie and Swanson 1976, Swanson et al. 1984). Many aquatic birds and reptiles possess nasal salt glands, which constitute an extrarenal excretory pathway for the elimination of excess electrolytes accrued in a saline environment (Schmidt-Nielsen 1960, Bradley and Holmes 1972, Holmes and Phillips 1985, Grigg 1981). These supraorbital glands also exist in nonmarine waterfowl (Scothorne 1959a, b) and secrete fluids containing NaCl at concentrations equal to or greater than that of seawater (Schmidt-Nielsen and Fange 1958, Schmidt-Nielsen 1960). Size and, therefore, functional

capacity of the salt gland depends on both genetic and environmental determinants (Holmes et al. 1961, Cooch 1964, Cornelius 1982).

Mallard ducklings were intolerant of salt (Ellis et al. 1963, Schmidt-Nielsen and Kim 1964, Cooch 1964, Anonymous 1983, Swanson et al. 1984) at concentrations as low as one third of that found in the coastal marshes where Black Ducks breed and winter. Solutions of 1–1.5% NaCl (10–15 ppt) supplied as drinking water to captive Mallard ducklings retarded growth rates and caused some mortality; 2–3% NaCl caused 100% mortality in 2–5 days (Anonymous 1983, Swanson et al. 1984). If wild Mallard ducklings are affected in much the same way, then breeding success of Mallards in brackish environments may be impeded.

We conducted tests to determine whether (1) Black Duck ducklings possessed functional salt glands at hatch and (2) introgressive hybridization might lead to the Mallard's acquisition of an efficient extrarenal excretory mechanism. If Mallard ducklings cannot acquire functional salt glands through hybridization with Black Ducks, a new postmating isolating mechanism might be established (through impaired reproductive success of Mallards and hybrids), and Mallards should not have the potential to expand their range to include the coastal regions presently occupied by Black Ducks.

METHODS

In June 1985, 39 eggs from 7 clutches of wild Mallards were collected in central Saskatchewan, approx. 80 km NW of Saskatoon, and 34 eggs from 6 clutches of wild Black Ducks were collected from Prince Edward Island, Nova Scotia, and New Brunswick. Collecting in these regions maximized the probability that eggs obtained were a product of pure strain parents of each species (Johnsgard and DiSilvestro 1976). All ducklings were hatched and reared at an aviary located on the University of Guelph campus. Experiments were conducted under the auspices of the University Animal Care Committee.

Birds used for captive breeding were wing-clipped and were maintained on an *ad libitum* commercial waterfowl maintenance diet during the months of August through March in each of 1985/1986 and 1986/1987. During these months, groups of birds were housed in 15 × 7 × 3 m outdoor flight pens. We used pure Black Ducks (7 female, 7 male), pure Mallards (8 female, 7 male), and Mallard male–Black Duck female (6 female, 7 male). Natural hybridization apparently occurs most frequently between female Black Ducks and male Mallards (Brodsky and Weatherhead

1984). Birds were allowed to pair naturally through the winter months.

In April 1986, pairs were transported to Lake St. Clair National Wildlife Area (NWA). Each pair was placed in a 4 × 3 × 2 m pen isolated visually from the others and supplied with *ad libitum* commercial waterfowl breeding diet (19% protein) and oyster shell, a 44-l tub for bathing, and a nest box. All birds were returned to the aviary for the winter months.

In March 1987, identified pairs remained in five large pens (15 × 7 × 3 m) at the Guelph aviary because the transportation of pairs to Lake St. Clair NWA in the year previous seemed to delay breeding. No more than 4 females and 4 males bred in each pen. Birds were supplied with a 3-m diameter wading pool, nest boxes, and *ad libitum* food and oyster shell.

In both years, all clutches were removed on day 5 of incubation to induce renesting. Ducklings were hatched in incubators at the Research Station, Poultry Division of the Ontario Ministry of Agriculture and Food (OMAF), Arkell, Ontario, according to procedures in Ward and Batt (1973). At hatch, ducklings were sexed and web-tagged.

Experiments.—The first experiment was designed to examine the ability of Black Ducks, Mallards, and their F1-hybrids to maintain water and electrolyte homeostasis when forced to drink water with a salinity of 3% NaCl, 48 h post-hatch. Effects of salinity on growth and survival are known for Mallards and other prairie-nesting species (Cooch 1964, Holmes et al. 1968, Anonymous 1983), but not for Black Ducks.

In 1986, ducklings of the same age were kept in groups of <20 in brooder pens that consisted of a cardboard ring 3 m in diameter and 1 m high. The floor was covered with wood shavings, and ducklings were reared according to procedures outlined in Ward and Batt (1973). Forty-eight hours after hatch, ducklings of each sex were randomly assigned to either fresh water or a 3% NaCl solution as their sole source of drinking water.

We designed a second experiment in 1987 to determine whether more subtle differences exist in the development of the salt gland that may influence the development of a functional salt gland found in adult waterfowl (Scothorne 1959a, Cooch 1964) and that might facilitate habitat segregation in these species. Ducklings were assigned to 1 of 10 treatments involving a salinity gradient (0, 0.5, 1.0, 1.5% NaCl) and duckling age (7, 14, 21 days), subject to the constraint that siblings were distributed across groups. Ducklings were housed in (2 × 1 × 1 m) metal cages and supplied with fresh water before treatment. Room temperature was maintained at 25°C until birds were 14 days old, when the temperature was reduced to 20°C. Pens were cleaned every 2–4 days, and water containers were washed and refilled daily. Ducklings were fed *ad libitum* a commercial starter diet (21% protein) to age 21 days, after which they received a commercial grower diet (19% protein).

TABLE 1. Means (\pm SE) and univariate statistics for male and female differences in growth rates (k) of American Black Ducks, hybrids, and Mallards raised on fresh water.

Group	Sex	n	k	F	P
Black Duck	male	14	1.0214 ± 0.0007	1.67	0.21
	female	12	1.0208 ± 0.0005		
Mallard-Black hybrid	male	11	1.0255 ± 0.0004	2.48	0.14
	female	16	1.0244 ± 0.0007		
Mallard	male	19	1.0253 ± 0.0006	2.22	0.15
	female	13	1.0247 ± 0.0005		

In both experiments, we weighed ducklings at hatch (day 0) and every other day until day 14, after which mass was recorded every 4 days. Mass was measured to the nearest 0.1 g with an electronic balance until ducklings attained 400 g, and thereafter, to the nearest 10 g with a Pesola spring scale until the individual reached an asymptotic body weight. Ducklings were placed in a nylon stocking to restrict movement during weighing, and they were weighed at the same time each day to minimize variability caused by di-

urnal changes in weight (Blake 1956). At the time of death, either as a result of the treatment or euthanasia after attaining asymptotic mass, the salt glands were excised and weighed to the nearest 0.001 g on a digital pan balance. Skull length was measured with calipers to the nearest 0.01 mm.

Statistical analyses.—Increments to body mass of each individual in each of three groups (Black Ducks, Mallards, and hybrids) were plotted and curves fit by eye. To determine whether curves were best described by

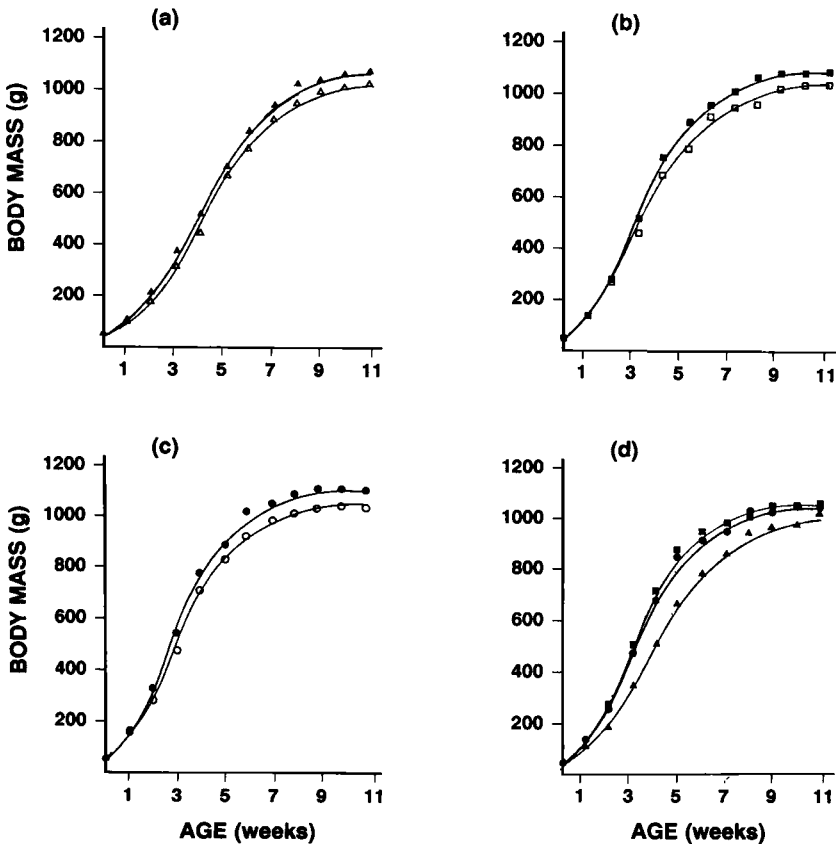


Fig. 1. Growth curves for body mass (g) of Black Ducks (▲), hybrids (■), and Mallards (●) raised on fresh water in 1986: (a-c) Males (solid symbols) and females (open symbols) plotted separately; (d) Males and females combined. Curves were best fit by the Gompertz equation. For clarity, only weekly values are plotted.

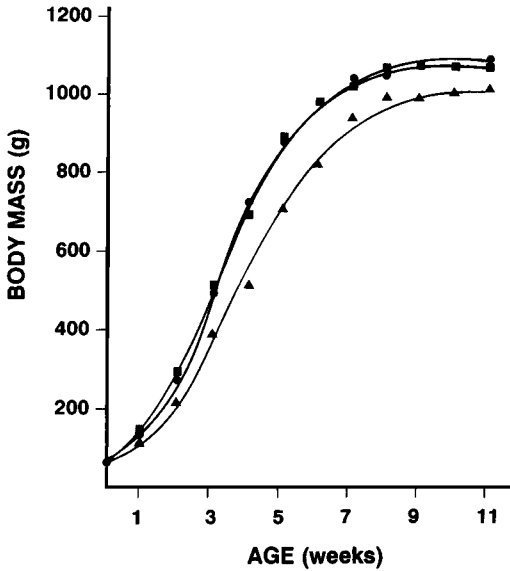


Fig. 2. Growth curves for body mass (g) of Black Ducks (▲), hybrids (■), and Mallards (●) raised on fresh water in 1987. Curves were best fit by the Gompertz equation. For clarity, only weekly values are plotted.

logistic, Gompertz, or Von Bertalanffy equations, each curve was transformed to a straight line following Ricklefs (1967). The slope of the transformed curve is proportional to the overall growth rate. A growth rate constant (k), which takes into account the form of the curve, was calculated from the growth equation (Ricklefs 1967). "Adult" mass was considered to be the asymptote of the juvenile growth curve even though this mass may underestimate true body mass, which includes more fat (Lightbody and Ankney 1984). Because repeated measures were taken on each individual through time, we used the means for single measurements through time to calculate a growth rate for each individual rather than calculate a single growth rate for each species. This allowed for a more conservative test of differences between Mallards, Black Ducks, and hybrids.

For both experiments, contingency analysis was used to test the hypothesis that the probability of survival was the same in all treatments. In 1986, we compared differences in growth rates, salt-gland size, and skull

length among Black Ducks, Mallards, and hybrids by analysis of variance (ANOVA) and, where appropriate, we analyzed differences between means with the least significant difference (LSD) multiple range test (SAS Institute Inc. 1985). Log transformations were used to normalize data (Ostle and Mensing 1975). In 1987, we analyzed growth rates and gland mass by 3-way factorial ANOVA, testing for interaction (Snedecor and Cochran 1980). If ANOVA indicated significant interactions, data were separated by one of the interacting effects and reanalyzed.

RESULTS

In 1986, 62 ducklings were hatched from 9 Black Duck clutches, 54 from 7 hybrid clutches, and 47 from 10 Mallard clutches. Mean duckling mass did not differ among groups at hatch ($F = 1.30$, $P = 0.30$) or at 48 h post-hatch ($F = 2.98$, $P = 0.18$). Mean duckling mass at 48 h was 51 ± 5.3 grams.

There were no differences in growth between males and females in any group (Table 1), so we pooled sexes for all subsequent analyses. On fresh water in 1986, Black Ducks grew slower ($F = 37.62$, $P < 0.0001$) than hybrids and Mallards (Fig. 1). Hybrids and Mallards did not differ in growth. No mortality occurred in ducklings raised on fresh water, but all ducklings given 3% NaCl at 48 h post-hatch died within 50 h. Postmortem examinations were not done, but ducklings exhibited signs associated with salt intoxication. The earliest signs were a dull, listless appearance, followed by progressive muscular weakness characterized by staggering. Eventually, ducklings were too weak to stand and remained close to or directly in their water containers and drank constantly until death. At death, mean mass (29 ± 8.1 g) of all ducklings combined was 43% lower than the body mass of 48-h-old ducklings.

In 1987, 68 ducklings hatched from 6 Black Duck clutches, 72 from 9 hybrid clutches, and 69 from 7 Mallard clutches. Limited numbers of ducklings prevented equal numbers of males

TABLE 2. Univariate statistics and multiple comparisons for differences in growth rates, gland weights, and skull lengths of American Black Ducks (B), Mallards (M), and hybrids (H) raised on fresh water.

Variable	Source	df	F	P	Multiple comparison ^a
Growth rate	species	2	37.62	0.0001	<u>B < H < M</u>
Gland weight	species	2	7.01	0.0001	<u>B > H > M</u>
Skull length	species	2	1.09	0.3393	<u>B < H < M</u>

^a Species underscored by the same line are not significantly different at $P < 0.05$.

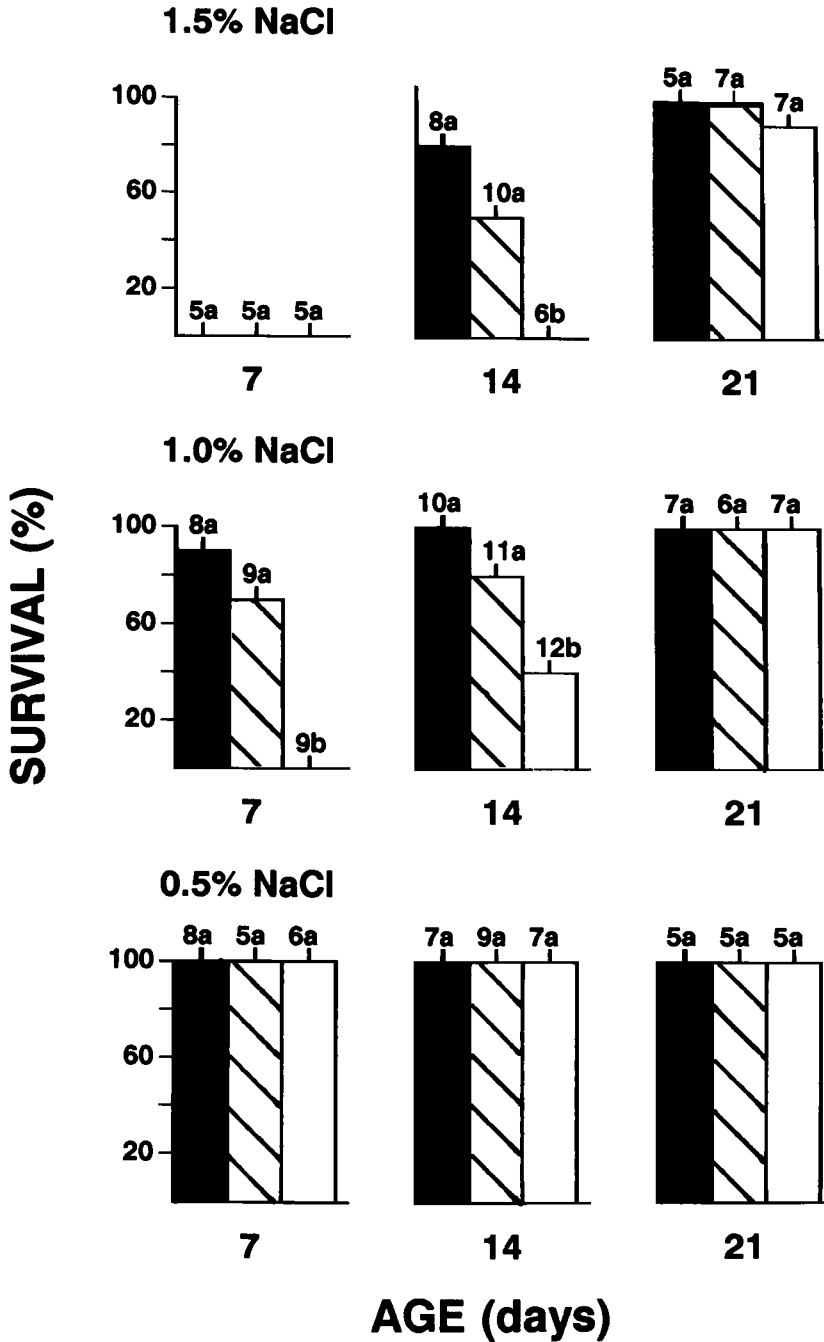


Fig. 3. Proportions of Black Ducks (solid bars), hybrids (cross-hatched bars), and Mallards (open bars) that attained adult body mass in each age-salinity treatment. Groups sharing similar lower-case letters do not differ ($P < 0.05$) by contingency analysis. Numbers above histograms are sample sizes.

and females in each treatment, and therefore data could not be analyzed by sex. As in 1986, Black Ducks on fresh water grew slower ($P < 0.05$) than hybrids and Mallards (Fig. 2, Table

2). Although skull length did not differ among groups, Black Ducks and hybrids on fresh water had heavier salt glands than Mallards (Table 2). Survivorship, measured as the proportion of

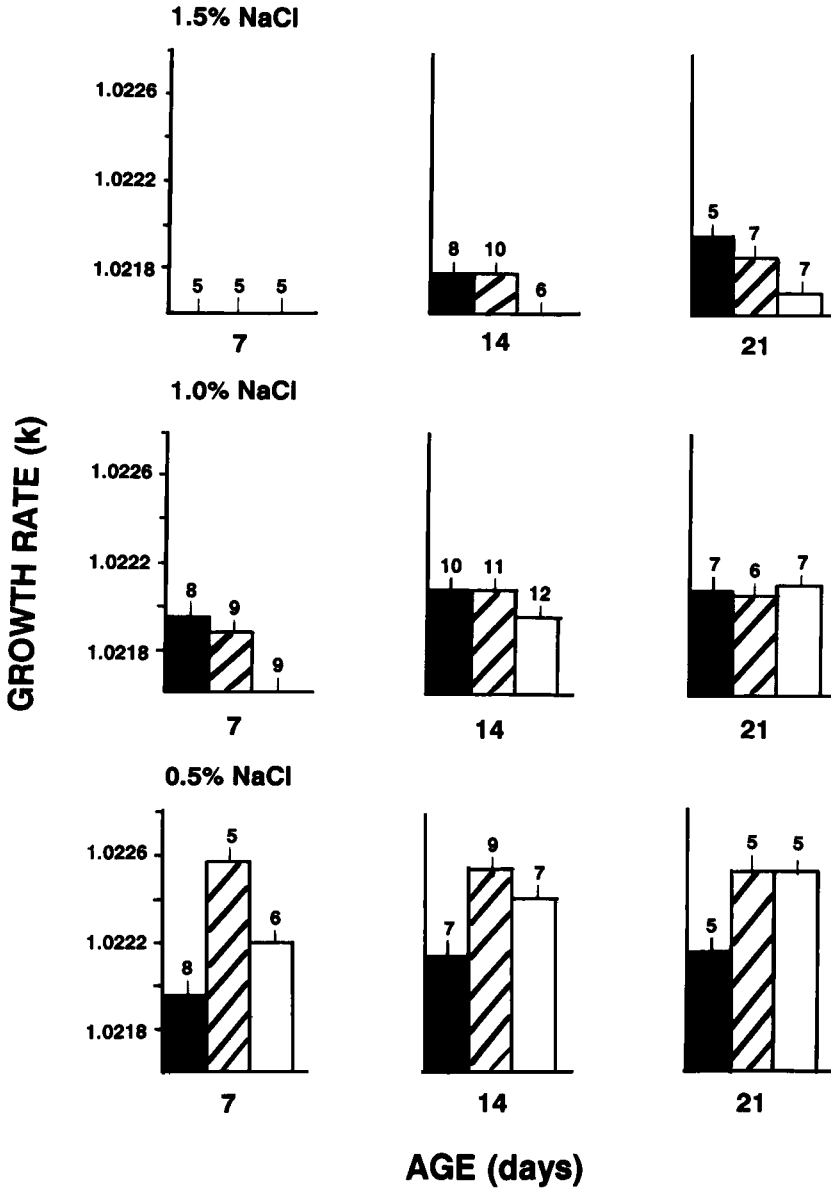


Fig. 4. Mean growth rate (k) for Black Ducks (solid bars), hybrids (cross-hatched bars), and Mallards (open bars) attaining adult body mass in each age-salinity treatment. Numbers above histograms are sample sizes.

individuals that attained adult body mass in each age-salinity treatment, increased with age and decreased salinities for all groups (Fig. 3). No mortality occurred in ducklings raised on 0.5% NaCl, but 1.5% NaCl was fatal to all 7-day-old ducklings (Fig. 3). In general, Mallard ducklings were less tolerant of salt than Black Ducks and hybrids when ducklings <21 days were administered salinities >0.5% NaCl (Fig. 3).

Ducklings that received salt concentrations >0.5% NaCl regularly had nasal fluid coming from their nostrils, indicating a functioning salt gland.

Generally, growth was more retarded the greater the salt concentration in drinking water and the younger the age at which ducklings were administered the treatment (Fig. 4). We found significant interactions among group, sa-

TABLE 3. Effects of group (Mallards, Black Ducks, and hybrids) and salinity on growth rate (k) by age (A), and the effects of species and age on growth rate (k) by salinity (B).

		(A) Age (days)					
		7		14		21	
Source	df	F	P	F	P	F	P
Species	2	999.99	0.0001	999.99	0.0001	2.90	0.0670
Salinity	2	999.99	0.0001	999.99	0.0001	123.39	0.0001
Species × salinity	4	999.99	0.0001	999.99	0.0001	14.66	0.0001
		(B) Salinity (% NaCl)					
		0.5		1.0		1.5	
		F	P	F	P	F	P
Species	2	25.23	0.0001	999.99	0.0001	999.99	0.0001
Age	2	2.15	0.1307	999.99	0.0001	999.99	0.0001
Species × age	4	1.18	0.1353	999.99	0.0001	999.99	0.0001

linity, and age. When growth rates were reanalyzed by age, effects of species and salinity decreased with age (Table 3). When data were reanalyzed by salinity, effect of species and age increased with increasing salinities (Table 3). Although group differences were apparent at low salinities, they were similar to differences found for the freshwater controls (Fig. 2). Black Ducks and hybrids were less affected by changes in salt concentrations than were Mallards.

Mass of salt glands from ducklings that attained adult body mass differed among groups and was affected by age and salinity (Fig. 5, Table 4). Salt glands were heavier in Black Ducks and hybrids than in Mallards and generally increased in mass faster than in Mallards as age and salinity increased. Salt glands of Black Ducks and hybrids reached a maximum size when 1% NaCl was administered at 14 days of age, but not until 1.5% NaCl and 21 days of age for Mallards (Fig. 5). Group differences tended to decrease with age and increase with increasing salinity (Table 4).

DISCUSSION

Few studies have documented the reproductive output of Black Ducks breeding in estuarine or coastal environments (Gross 1945, Wright 1954, Bartlett 1963, Reed and Moisan 1971, Reed 1975). Thus, it is unknown if Black Duck broods inhabit these areas regularly. Black Duck nests have been found on coastal islands in Maine, many of which lacked obvious sources of fresh water (Gross 1945), but brood survival in these habitats is unknown. In our experiments, newly

hatched Black Duck ducklings died after drinking water containing >1% NaCl.

Identification of salt intoxication in wild ducklings is difficult, and this may be why salt

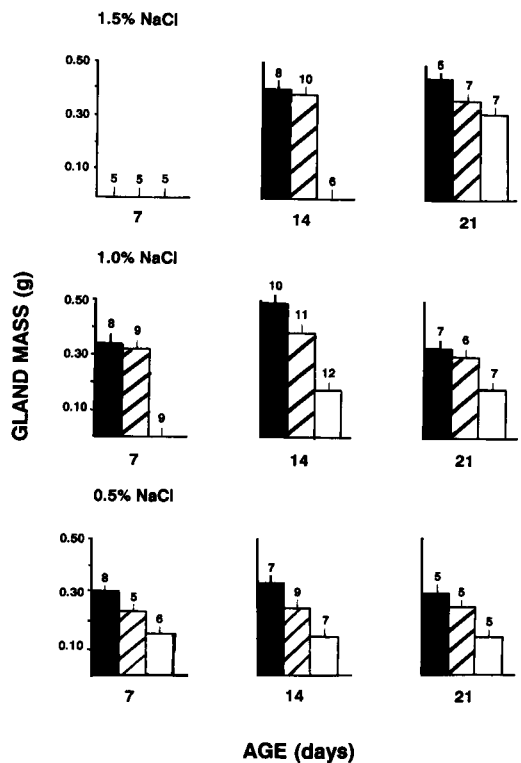


Fig. 5. Mean salt-gland mass (g) for Black Ducks (closed bars), hybrids (cross-hatched), and Mallards (open bars) that attained adult body mass in each age-salinity treatment. Numbers above histograms are sample sizes.

TABLE 4. Effects of group (Mallards, Black Ducks, and hybrids) and salinity on salt gland mass by age (A), and the effects of species and age on salt gland mass by salinity (B).

		(A) Age (days)					
Source	df	7		14		21	
		F	P	F	P	F	P
Species	2	108.85	0.0001	151.27	0.0001	33.57	0.0670
Salinity	2	126.84	0.0001	18.89	0.0001	39.01	0.0001
Species × salinity	4	24.85	0.0001	11.22	0.0001	00.50	0.7390
		(B) Salinity (% NaCl)					
Source	df	0.5		1.0		1.5	
		F	P	F	P	F	P
Species	2	39.43	0.001	147.98	0.0001	165.75	0.0001
Age	2	1.38	0.1307	35.27	0.0001	540.84	0.0001
Species × age	4	0.82	0.5203	8.54	0.0001	72.19	0.0001

tolerance in precocial hatchlings has been largely assumed. For example, Reed (1975) reported that Black Ducks on the St. Lawrence estuary nested on mainland areas and on islands 5.6 km offshore. Broods were reared in tidal marshes along the mainland. Of 47 broods hatched on the islands, only 42% migrated successfully to the tidal marshes, and only 36% of these survived. Intensive observations revealed that avian predators caused a small fraction of the observed mortality; the remainder was thought to be due to chilling and exhaustion. However, duck broods routinely travel long distances (Ringleman and Longcore 1982), so exhaustion may be an unsatisfactory explanation for the high mortality. Reed (1975) reported that ducklings that arrived at the tidal marsh did not "display the typical vigor of ducklings of that age when feeding and following the hen" (p. 252), and they often died within 2 days. Perhaps these ducklings were salt intoxicated.

There are at least two ways that precocial young that lack functional salt glands at hatch (like Black Ducks) can fledge in brackish habitats. First, enough "metabolic water" may be produced from digestion. Second, ducklings may respond behaviorally to a salinity gradient in an age-dependent fashion (Bartlett 1963, Reed 1975). For instance, newly hatched Black Duck broods in the St. Lawrence estuary restricted their use of tidal marshes to areas close to shore where salinity levels were typically lower (Reed and Moisan 1971). With increased age, however, broods extended their range "seaward"

(Reed and Moisan 1971). We demonstrated that duckling mortality decreased with age and decreased salinity, and salt-gland weights increased with age and salinity, consistent with Reed and Moisan's (1971) observations that acclimation to salt water is age-dependent. In an east-coast river, distance upstream was negatively related to ages of Black Duck broods, but not broods of Blue-winged Teal (*A. discors*), a typically freshwater breeder whose broods remained upstream regardless of age (Barnes and Martin unpubl. data).

Black Duck ducklings appear to survive and grow slightly better than Mallard ducklings in brackish environments, but the interspecific differences appear insufficient to affect establishment of a postmating reproduction isolating mechanism between Black Ducks and Mallards for two reasons. First, salinities at which we found differences in survival and growth between Mallard and Black Duck ducklings were low and similar to salinities along tidal river systems. Black Ducks appear unable to maintain water and electrolyte homeostasis in their body fluids at salinity levels great enough to facilitate habitat segregation through reduced survival of hybrids and Mallards on coastal breeding areas. Second, the functional capacity of the salt gland was partially dependent upon a genetic component and, although Mallard ducklings were less tolerant of salt than were Black Ducks, hybrid ducklings apparently inherited salt tolerance more similar to Black Ducks. Our data are inconsistent with the "habitat refugia" hypothesis, so it appears that hybrids have the

potential to inhabit coastal regions presently occupied by Black Ducks, and to further back-cross with either Black Ducks or Mallards. Mallards may continue, in the absence of any significant counterselection, to expand their range into estuarine habitats where the Black Duck is the dominant species.

ACKNOWLEDGMENTS

We wish to thank the Canadian Wildlife Service (CWS) for their financial and logistical support throughout this study. In particular, we thank J. Carreiro, G. McCullough, and D. Dennis, whose help in the initial stages made this study possible. We also thank R. Dibblee, E. Pace, A. Smith, L. Beattie, P. Madore, D. Gow, M. Kasserra, and J. Hanselman for their help in various aspects of this research. G. Hurnik permitted use of facilities at the Research Station, Poultry Division of the Ontario Ministry of Agriculture and Food, Arkell, Ontario, and F. Black at the Lab Animal Building, University of Guelph. Special thanks to K. Barnes and C. Earley for help in raising the ducklings and for all aspects of data collection. A. Middleton, V. Thomas, J. Ball, and R. Bethke, G. Hepp, T. Quinney, and an anonymous reviewer provided valuable comments on earlier drafts of this manuscript. This research was supported by grants and contracts from the Natural Sciences and Engineering Research Council (NSERC; Grant No. A7757), the CWS (Ontario Region), and the University Research Support Fund of CWS to Nudds, and scholarships from the Ontario Federation of Anglers and Hunters and NSERC to Barnes.

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