



Correlates of behavioural dominance in mallards and American black ducks

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Abstract. American black duck, *Anas rubripes*, populations are thought to be in decline largely because of competitive exclusion by mallards, *A. platyrhynchos*, and/or introgressive hybridization. Mallard males reportedly are behaviourally dominant to black duck males, which may allow mallards to acquire black duck females as mates and/or exclude black ducks from high-quality breeding sites. The purpose of this study was to examine the influence of body size, body mass, degree of body symmetry and testosterone levels on dominance interactions between these two species, while controlling for effects of previous experience. Thirty dominance trials were performed in the winter and spring with groups of six males (three mallard and three black duck). Surprisingly, mallards were not generally dominant to black ducks. General linear model analyses revealed that morphological and hormonal variables were not consistently correlated with dominance, but place of origin and home pen dominance were. Pre-trial plasma testosterone concentration and change in testosterone concentration were significant effects in the winter trials, but in the opposite direction to that predicted. Size-adjusted body mass was correlated with dominance between Ontario mallards and wild-source black ducks in the spring. Dominance relationships between these two species are more complex than was originally thought.

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The decline of American black duck, *Anas rubripes*, populations in eastern North America and the simultaneous increase in mallard, *A. platyrhynchos*, abundance have been well documented (Johnsgard & Di Silvestro 1976; Dennis et al. 1984). Several hypotheses for the cause of this phenomenon have been proposed, including habitat changes (Heusmann 1974; Conroy et al. 1989), over-hunting (Conroy et al. 1989), competitive exclusion (Ankney et al. 1987, 1989; Merendino et al. 1993) and introgressive hybridization (Ankney et al. 1987, 1989; Rusch et al. 1989). These hypotheses are not mutually exclusive, but Ankney et al. (1987, 1989), Rusch et al. (1989), Merendino et al. (1993) and Merendino & Ankney (1994) have concluded that hybridization and competition have been the most important factors influencing population dynamics of black ducks and mallards in eastern North America.

Twice a year, interactions between black ducks and mallards have particularly important conse-

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quences for these two species' population dynamics. Both species spend the winter in flocks, and males compete to form pair bonds with females (McKinney 1992). Brodsky & Weatherhead (1984) studied a mixed population of black ducks and mallards wintering in Ontario. They found that once all mallard females were paired, some remaining unpaired mallard males successfully courted black duck females despite the presence of competing black duck males. In a study of captive black ducks and mallards, Brodsky et al. (1988) found that mallard males were nearly always dominant to black duck males, and females of both species primarily associated with dominant males regardless of their preferences in tests with isolated males. These two species are extremely similar genetically (Ankney et al. 1986; Avise et al. 1990), hybrids are fertile (Phillips 1915, cited in Rusch et al. 1989), and there is no reported evidence of direct selection against inter-specific pairing. Thus, as a result of competitive superiority of mallards over black ducks in wintering areas, mallard males may often breed with black duck females, leading to introgressive hybridization.

The breeding season is the second time of year when mallards may have a negative impact on black duck populations. Upon arriving at the breeding grounds in the spring, black ducks and mallards compete for territories (Seymour 1993). Competition between mallards and black ducks for breeding habitat has rarely been directly observed, but Merendino et al. (1993) provided evidence from historical data that mallards have systematically excluded black ducks from high-quality breeding habitat in southern Ontario. Furthermore, Merendino & Ankney (1994) showed that, in central Ontario, mallards now occupy the most productive breeding sites and predominate in more productive geographical areas. D'Eon et al. (1994) found that mallards were more aggressive than black ducks in the period preceding territory formation. Seymour (1993) observed two cases in which black duck pairs were supplanted from their territories by mallards, whereas mallards were never supplanted by black ducks.

These studies of pair formation and territorial competition suggest that behavioural dominance is an important mechanism driving the population dynamics of mallards and black ducks. In this context, dominance may be defined as competitive superiority of one individual over another such that the dominant individual gets priority of access to a resource (Kaufmann 1983). As important as dominance is in the interactions between black ducks and mallards, and in the behavioural ecology of animals in general (Wilson 1975), it is not well understood in waterfowl and has rarely been studied under controlled conditions. Therefore we do not know why mallards should be dominant to black ducks.

Some correlates of intraspecific dominance have been observed in wild waterfowl populations. For example, males tend to dominate females, older birds tend to dominate younger birds, and paired birds tend to dominate unpaired birds (Paulus 1983; Hepp & Hair 1984; Lamprecht 1986; Alexander 1987; Sorenson & Derrickson 1994). These factors, however, are unlikely to be important in the observed pattern of dominance between black ducks and mallards. Therefore, it is necessary to examine determinants of dominance within a given class of age, sex and pair status to shed light on mallard-black duck interactions.

Intra-class correlates of dominance have not been well studied in waterfowl. In studies of waterfowl and other taxa, factors observed to be

related to dominance status within a class have included body size (Scott 1978, cited in Scott 1980), body mass (Lamprecht 1986), body symmetry (Thornhill 1992) and androgen levels (Wingfield et al. 1987). Success in competitive interactions can also influence an individual's performance in subsequent encounters (Beacham & Newman 1987; Popp 1988), and therefore must be accounted for in tests for correlates of dominance. The purpose of this study was to examine the simultaneous influence of these morphological and hormonal factors on behavioural dominance of males in a captive population of mallards and black ducks, while controlling for effects of previous experience. Multivariate analyses of correlates of dominance are rare, but the approach is promising in that it simultaneously assesses the relative importance of potential determinants of dominance (e.g. Collias 1943).

METHODS

Study Population

A captive population of ducks was established in the summer of 1991 at the St Clair National Wildlife Area near Chatham, Ontario (42°35'N, 82°9'W). The animals were acquired from several sources: mallards came from eight wild clutches in central Ontario (hereafter referred to as OMs) and seven wild clutches in Saskatchewan (SMs); wild-source black ducks (WBs) came from five wild clutches in central Ontario; captive-source black ducks (CBs) came from two aviculturalists in southwestern Ontario (unknown number of clutches). OMs and WBs were acquired as eggs and were hatched in incubators. SMs were acquired as young ducklings (3–30 days old). CBs were acquired as full-grown juveniles (2–3 months old).

We housed newly hatched ducklings indoors until they were 1 week old (grouped by clutch). Thereafter, they were housed outdoors in six visually isolated 'home' pens. Pens measured 7 × 3 × 2 m each and contained open water, dry resting areas and shelter. Ducks were fed ad libitum with a mixture of corn and commercial duck food. Each pen held 18 ducks (10 males and eight females) with two pens containing OMs, one pen containing SMs, one pen containing WBs, one pen containing CBs, and one pen containing half CBs and half WBs. In summer 1992, all ducks

were removed for breeding (male ducks were isolated in individual pens and females were returned to their home pens) during the breeding season.

To facilitate identification of individuals, we fitted all ducks with numbered aluminium bands and nylon nasal markers. The markers were of various shapes and sizes to allow easy visual recognition (Lokemoen & Sharp 1985).

Six ducks died during the course of the study, including three mallards and three black ducks. Dead individuals were not replaced in pens, but in the dominance trials (to avoid using juvenile ducks from a seventh pen) we used substitutes to keep numbers constant in the trials. These replacement ducks were used only in analyses.

Body Measurements

We assessed body size and symmetry of each individual in autumn 1992. The following measurements were made: culmen (most of culmen on forehead to bill tip; 'culmen length' in Cooch 1992), bill width (widest point of bill at nares), left and right tarsus length (tarsus including head of tibiotarsus; 'tarsus length' in Dzubin & Cooch 1992), and left and right wing length (proximal end of metacarpal III to longest primary with wing flat and feathers relaxed; measured wing length to the nearest millimetre with a ruler, and made other measurements to the nearest 0.05 mm with calipers). All measurements were taken three times (on separate days) and averaged them.

We performed a principal component analysis (PCA) on the correlation matrix of the morphological measurements. This analysis yielded a single principal component (PC1) with positive loadings between all variables that accounted for 61% of the variance in the measurements (eigenvalue = 2.61). We used PC1 scores as a measure of body size.

We assessed morphological asymmetry by comparing right to left wings and right to left tails. Between-individual variation in asymmetry was greater than that expected from measurement error (Swaddle et al. 1995). We measured asymmetry in the following characters (wing: $F_{56,224} = 2.167$, $P = 0.002$; tail: $F_{58,232} = 1.731$, $P = 0.002$). The measurement of asymmetry is the

were removed for breeding (male-female pairs were isolated in individual pens), but they were returned to their home pens following the breeding season.

To facilitate identification of individuals, we fitted all ducks with numbered aluminum leg bands and nylon nasal markers. The nasal markers were of various shapes and colours and allowed easy visual recognition of individuals (Lokemoen & Sharp 1985).

Six ducks died during the course of the study, including three mallards and three black ducks. Dead individuals were not replaced in the home pens, but in the dominance trials (see below) we used juvenile ducks from a seventh home pen as substitutes to keep numbers consistent between trials. These replacement ducks were not used in analyses.

Body Measurements

We assessed body size and symmetry for each individual in autumn 1992. The following measurements were made: culmen (most distal feather on forehead to bill tip; 'culmen 1' in Dzubin & Cooch 1992), bill width (widest point distal to the nares), left and right tarsus length (tarsometatarsus including head of tibiotarsus; 'tarsus bone' in Dzubin & Cooch 1992), and left and right wing length (proximal end of metacarpal to distal tip of longest primary with wing flat and straight). We measured wing length to the nearest millimetre with a ruler, and made other measurements to the nearest 0.05 mm with calipers. We took all measurements three times (on separate days) and averaged them.

We performed a principal components analysis (PCA) on the correlation matrix of the six body measurements. This analysis yielded a first principal component (PC1) with positive covariation between all variables that accounted for 43.5% of the variance in the measurements (eigenvalue=2.61). We used PC1 scores as a measure of body size.

We assessed morphological asymmetry by comparing right to left wings and right to left tarsi. Between-individual variation in asymmetry was greater than that expected from the estimated measurement error (Swaddle et al. 1994) for both characters (wing: $F_{56,224}=2.167$, $P<0.001$; tarsus: $F_{58,232}=1.731$, $P=0.002$). The most widely used measurement of asymmetry is the absolute value

of the right minus the left measurement, with a possible adjustment for character size (Palmer & Strobeck 1986). In this study, however, there was a measurement bias between right and left sides: measurements for both tarsus and wing tended to be larger for the right side (binomial $P<0.005$). We did not have 'left-handed' calipers or rulers, so the measuring technique was slightly different between the two sides. To correct for this bias, we performed regressions of right versus left for both tarsus and wing length and used the residuals from the resulting lines as measures of deviations from symmetry (the measurement bias did not depend on the absolute size of the characters; the slopes of the lines were not significantly different from 1.0; $P>0.05$). The final measures of asymmetry were the absolute values of these residuals divided by the means of the left and right measurements. Both tarsus and wing asymmetry were skewed towards zero, so they were log-transformed for analysis.

Home Pen Observations

We observed interactions between males in the home pens to evaluate the males' competitive ability outside of the dominance trials (described below). We made observations eight times for each pen (approximately every 2 weeks) between late October 1992 and late February 1993. We started observation periods between approximately 1500 and 1600 hours Eastern Standard Time (EST), each lasted about 1 h (preliminary observations suggested that aggression could occur throughout the day). We recorded all male-male interactions. The animals apparently were not affected by the presence of an observer, because we detected no differences in behaviour between these observations and preliminary observations made from a blind. We classified behaviour patterns as follows. (1) Attack. One duck used its bill to grasp feathers on another duck. The attack was either from the front, with the attacker grasping breast feathers, or from behind, with the attacker grasping feathers on the wing, back, or tail of its opponent. (2) Peck. The aggressor thrust its head forward, using its bill to jab another duck. (3) Threat. Same motion as pecking but without contact. (4) Displace. The aggressor moved towards another duck and supplanted it without any obvious physical gestures.

Implicit in these behaviour patterns are clear distinctions between winners and losers.

are arranged to maximize the number of non-zero cells above the diagonal. In a perfectly linear hierarchy with no reversals (interactions in which a subordinate wins over a dominant), all cells above the diagonal are non-zero and all cells below the diagonal are zero. In the home pens, we ranked individuals from 1 to 10; in the dominance trials, we ranked individuals from 1 to 6.

Dominance ranks give an index of an individual's performance within a group; however, they are not necessarily comparable between different groups. We therefore incorporated behavioural components into dominance using principal components analysis (PCA). For the home pen observations, variables used in the PCA were dominance rank, average number of wins per observation period, average number of losses per observation period and number of individuals that were dominated (dominance hierarchies in home pens were not perfectly linear, as described below, so number of subordinates did not necessarily match dominance rank). This analysis yielded a PC1 with a high negative loading on dominance rank and high positive loadings on average number of wins per observation period and number of subordinates. PC1 accounted for 53.8% of the variance in the data (eigenvalue=2.15) and was used as a dominance score for home pen observations.

We did a similar PCA for the dominance trials. We included all individuals in all trials (except the first trial, in which behaviour patterns were not recorded) in the analysis (thus we included most individuals three times). The variables in the analysis were dominance rank, number of wins and number of losses (hierarchies in the dominance trials were strongly linear, see below, so number of subordinates was not included in this PCA). The analysis yielded a PC1 with high negative loadings on dominance rank and number of losses and a high positive loading on number of wins. PC1 accounted for 72.5% of the variance in the data (eigenvalue=2.17) and was used as a dominance score for the dominance trials.

Testosterone Assays

Blood samples were centrifuged for 10 min at 1300 g immediately following collection. The plasma portion was collected and stored at -20°C until the hormone extractions were performed.

We extracted testosterone with ether from 200 μl of plasma from each blood sample and dissolved it in 200 μl methanol. Two 90- μl aliquots of this were dried down and re-dissolved in 100 μl buffer each. Radioimmunoassays were performed on these duplicate samples using ^3H -testosterone and a testosterone antibody generated against 3-[0-carboxy methyl] oxime gamma globulin. Dihydrotestosterone cross-reacts with this antibody at about 50% of the testosterone level (Wiebe & Barr 1984). Analysis of the assay data was done with the Beckman Immunofit EIA/RIA software package (version 2.0, Beckman Instruments, Fullerton, California).

It was not feasible to include all samples in one assay, so we evaluated samples from the first 20 trials in one assay and samples from the last 10 trials in a second assay. Because of inconsistent results for some of the samples (large coefficients of variation for 41 out of 237 samples in the first assay and nine out of 118 samples in the second assay), we performed two further assays to achieve reliable measurements for all samples.

Mean \pm SD extraction efficiency was $92 \pm 5.7\%$. The mean intra-assay coefficient of variation was 2.8% and the mean inter-assay coefficient of variation was 31%. Concentration of testosterone in the samples ranged from 0.06 to 12.38 ng/ml.

We considered two measures of testosterone level for each individual in each trial: (1) plasma testosterone level before the trial started (T_{init}) and (2) change in testosterone level through the trial (T_{diff}). T_{init} was skewed towards zero, so it was log-transformed for analysis. It was also dependent upon time of day at which the blood sample was taken ($r = -0.255$, $N = 168$, $P = 0.001$). Therefore, we corrected values of T_{init} by using the residuals from the regression of T_{init} versus time of day.

RESULTS

Home Pen Dominance

In the home pens, dominance relationships between males were stable over the 4 months of observations. In 71% of dyads in which there were at least two interactions over the eight observation periods ($N = 178$), one individual won every time. In dyads where both birds won interactions, one individual won an average of 82% of interactions. Thus, there was a strong tendency for dominance

We pooled data for dominance relationships in the home pens over the eight observation periods to establish dominance relationships. Four of the six home pens had significantly linear dominance hierarchies ($h=0.44-0.83$).

We performed multiple regression for each home pen to test for morphological correlates of dominance score (independent variables were body size, tarsus asymmetry, wing asymmetry, corrected fall body mass and corrected winter body mass). There were no consistent correlates of dominance in the home pens. Only one pen (containing OMs) had a significant multiple regression ($r^2=0.897$, $P=0.042$), in which body size tended to be greater in more dominant individuals and wings tended to be less symmetrical in more dominant birds ($P<0.05$).

Dominance Trials

Dominance relationships in the trials were unambiguous and perfectly linear in 28 of 30 trials (two trials contained circular relationships). Of 435 dyads in 29 trials, only 12 (2.8%) were ambiguous (i.e. the birds did not interact) and all but 28 (6.4%) were completely one-sided. The protocol for performing dominance trials was not ideal, because blood samples were taken sequentially from the six birds in each trial rather than all at once. However, this did not affect dominance rankings. The mean correlation coefficient between dominance rank and sampling order for 30 trials was 0.114 ($P=0.561$; r s were transformed to $z=0.5 \ln(1+r/1-r)$ to calculate the mean and 95% confidence limits: Steel & Torric 1980).

Contrary to expectations, mallards were not generally dominant to black ducks (Fig. 1). There apparently was as much variation in dominance ranks within each species as there was between them. The most consistent results appear to be that CBs usually were low-ranked, and OMs rarely were low-ranked.

Time of year did not obviously affect dominance relationships between black ducks and mallards (Fig. 1). Also, dominance scores for a given individual were positively correlated between its different trials (trial 1 versus 2: $r=0.507$, $N=53$, $P<0.001$; trial 2 versus 3: $r=0.433$, $N=54$, $P=0.001$, trial 1 versus 3: $r=0.232$, $N=50$, $P=0.105$).

To test for correlates of dominance, data from the first two sets of trials (performed in the winter)

Table 1. Results of GLM analysis to test for correlates of mean dominance score in the winter trials

Source	Coefficient	F	P
Species		2.623	0.113
Origin		7.125	0.002
Body size	0.040	0.122	0.729
Tarsus asymmetry	-0.256	3.646	0.063
Wing asymmetry	0.154	2.218	0.144
Home pen dominance	0.322	8.386	0.006
T_{init}	-0.403	5.178	0.028
T_{diff}	-0.134	4.083	0.050
Corrected body mass	0.001	0.665	0.420

were combined. We calculated mean dominance score, body mass, T_{init} and T_{diff} for each individual for whom data were complete in the first two sets of trials (nine SMs, 17 OMs, 11 WBs and 14 CBs). Thus, we did not include individuals more than once in the analysis. We included origin of the ducks and home pen dominance scores in the analysis to control for differences in experience. A general linear model (GLM) analysis (MGLH with type III SS, SYSTAT version 5.1, 1991) revealed that the strongest correlates of dominance score were place of origin and dominance score in the home pen (Table 1). Initial testosterone level and change in testosterone level were also significant effects. Contrary to expectations, however, both measures of hormone concentration were negatively correlated with dominance score. Body size, corrected body mass, and tarsus and wing asymmetry were not correlated with dominance score. Even when controlling for morphological, physiological and social (previous experience) variables, mallards and black ducks did not differ in dominance scores.

As surprising as the lack of effect of species on dominance was the strong effect of place of origin. A multiple comparison of dominance score versus place of origin showed that CBs had significantly lower dominance scores than both OMs and WBs (Fig. 2; Tukey's HSD test: $P<0.05$). The four groups did not differ in asymmetry or body size (ANOVA: $P_s>0.10$), but mallards had significantly lower corrected body mass than did black ducks (two-way ANOVA: $P=0.001$). The groups also did not differ in T_{init} or T_{diff} (ANOVA: $P>0.40$).

Because the most relevant comparison in terms of the population dynamics of mallards and black

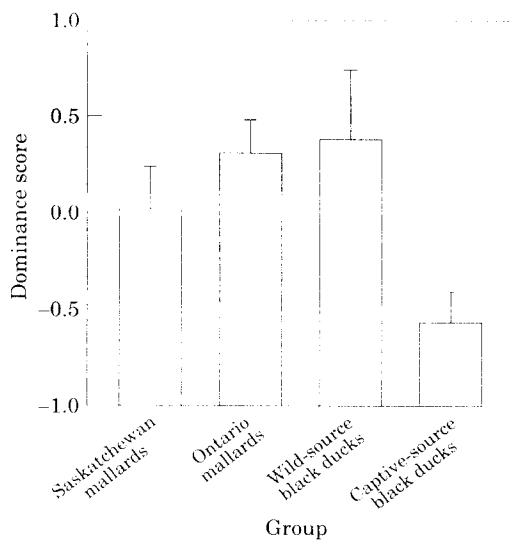


Figure 2. Mean (+SE) dominance score versus place of origin for ducks in the winter trials.

Table II. GLM analysis to test for correlates of dominance score in the winter trials including only Ontario mallards and wild-source black ducks

Source	Coefficient	F	P
Species		0.285	0.600
Body size	0.201	1.204	0.286
Tarsus asymmetry	-0.433	3.150	0.092
Wing asymmetry	0.152	1.152	0.297
Home pen dominance	0.426	9.016	0.007
T_{int}	-0.416	1.680	0.210
T_{diff}	-0.144	2.749	0.114
Corrected body mass	0.002	1.581	0.224

ducks in the wild is between OMs and WBs (these groups came directly from populations that interact in the wild, both on wintering and breeding grounds), we performed a second GLM analysis including only these two groups. This analysis also eliminates the potential for a rearing effect because both groups were reared in the same way. Again, the species did not differ in dominance scores but there was a significant effect of home pen dominance (Table II).

We also did a GLM analysis on the data for the third set of dominance trials (performed in the spring; $N=8$ SMs, 19 OMs, 13 WBs and 14 CBs). As in the winter trials, place of origin was a significant factor but species was not (Table III).

Table III. GLM to test for correlates of dominance score in the spring trials

Source	Coefficient	F	P
Species		0.777	0.777
Origin		3.859	0.029
Body size	0.032	0.048	0.828
Tarsus asymmetry	0.128	0.851	0.361
Wing asymmetry	-0.114	0.898	0.349
Home pen dominance	0.230	3.319	0.075
T_{int}	-0.071	0.204	0.653
T_{diff}	0.033	0.139	0.711
Corrected body mass	0.003	1.543	0.221

Table IV. GLM analysis to test for correlates of dominance score in the spring trials including only Ontario mallards and wild-source black ducks

Source	Coefficient	F	P
Species		0.529	0.474
Body size	0.019	0.009	0.924
Tarsus asymmetry	0.144	0.633	0.434
Wing asymmetry	-0.126	0.848	0.367
Home pen dominance	0.263	3.191	0.087
T_{int}	0.252	1.371	0.254
T_{diff}	0.255	4.035	0.056
Corrected body mass	0.006	5.099	0.034

When we included only OMs and WBs in the analysis, corrected body mass was the only significant effect (Table IV).

The mean dominance scores for ducks of different origin showed the same relative distribution in the spring trials as in the winter trials. WBs had the highest mean scores, followed by OMs, SMs and CBs (as in Fig. 1). A one-way ANOVA on dominance score in the spring trials versus place of origin failed to detect a difference between the four groups ($P=0.080$).

As in the winter trials, the four groups did not differ in body size, tarsus asymmetry, wing asymmetry (ANOVA: $P_s > 0.10$), T_{int} or T_{diff} (ANOVA: $P_s > 0.20$). Unlike the winter trials, however, the groups did not differ in corrected body mass (ANOVA: $P=0.129$). A repeated-measures ANOVA on body mass versus origin and time (first two sets of trials versus third set of trials) showed a significant difference in change in corrected body mass for the four groups between the two times of year ($P < 0.001$). This was not the case for dominance score ($P=0.909$), T_{int} ($P=0.605$), or T_{diff} ($P=0.107$).

The lack of a species effect on dominance in this study is consistent with Brodsky et al.'s (1988) findings, which mallards showed a significant superiority over black ducks. Brodsky used a similar protocol to ours at the same study sites and in the same enclosures. First, Brodsky (1988) compared Manitoba and black ducks from Ontario and New Brunswick. Second, hybridization between Ontario mallards and black ducks increases in an east-to-west gradient (Brodsky 1967). 'black ducks' (Ontario) may have a higher dominance score whereas black ducks from New Brunswick are more likely to have been pure mallards. Ontario mallards are not pure mallards but have more duck genes than are MB mallards. The two 'species' used in our study are more distinct than those in Brodsky's study, resulting in a reduction in dominance score.

Another possible phenomenon in mallard ducks is that, with population expansion in this province is occurring, that can best compete with other species. Only Ontario birds, which were inadvertently selected for high competitive ability.

The relatively poor performance of wild-source black ducks may be due to both of the above phenomena. The geographical origin of the captive mallards and captive breeding may have a significant effect for individuals of different origin (although the converse is also possible).

Finally, early experience may have effects on social behaviour (Brodsky 1993). The ducks in this study were reared in the same way as those in our study (i.e. eggs were collected in the wild, artificially incubated in the laboratory, and our study that were acclimated to the same and CBs) may have a significant effect because of a lack of early social experience or because of differences in facilities or because of differences in the environment of displacement from their natural habitats. Variables may account for the differences in origin in our study, but the lack of difference in dominance score is consistent with the lack of difference in dominance score in the winter trials.

DISCUSSION

The lack of a species difference in behavioural dominance in this study was surprising in light of Brodsky et al.'s (1988) similar investigation in which mallards showed overwhelming competitive superiority over black ducks. Although their study used a similar protocol to ours and was performed at the same study site, there were several differences. First, Brodsky et al. used mallards from Manitoba and black ducks from Ontario, Quebec and New Brunswick. Because the frequency of hybridization between mallards and black ducks increases in an east-to-west gradient (Johnsgard 1967), 'black ducks' in our study (all from Ontario) may have possessed mallard genes, whereas black ducks in Brodsky et al.'s study were more likely to have been genetically 'pure'. Also, Ontario mallards are more likely to possess black duck genes than are Manitoba mallards. Thus the two 'species' used in our study may have been less distinct than those in the previous study, with a resulting reduction in disparity of competitive ability.

Another possible phenomenon in Ontario black ducks is that, with populations in decline, breeding in this province is limited to those individuals that can best compete with mallards. By using only Ontario birds, we may therefore have inadvertently selected for black ducks with strong competitive ability.

The relatively poor performance of captive-source black ducks may be a reflection of either or both of the above phenomena, but the geographical origin of the captive stock is unknown. Also, captive breeding may have resulted in selection for individuals of inferior competitive ability (although the converse seems equally plausible).

Finally, early experience may have profound effects on social behaviour patterns (e.g. Gottlieb 1993). The ducks in Brodsky et al.'s study were reared in the same way as OMs and WBs in our study (i.e. eggs were collected from wild nests and artificially incubated in captivity). The ducks in our study that were acquired after hatching (SMs and CBs) may have been at a disadvantage because of a lack of early experience in the rearing facilities or because of factors related to the stress of displacement from their natal sites. These variables may account for the strong effect of place of origin in our study, but they do not explain the lack of difference in dominance between the two

species. We controlled for the effect of origin both statistically (Tables I and III) and by including only individuals with similar rearing (OMs and WBs; Table II and IV), and still did not detect dominance differences between mallards and black ducks.

Dominance score in the home pen was a strong correlate of trial dominance, which was to be expected for two reasons. First, if dominance is determined by inherent traits, then those characteristics that make an individual dominant in one situation are likely to make it dominant elsewhere. Second, in some species, winning dominance encounters can greatly increase the probability of winning future encounters, even if inherent determinants of dominance such as hormone levels are experimentally altered (Archawaranon et al. 1991).

The relationship between dominance score and size-corrected body mass varied with the time of year. Inconsistency in the effect of body mass is perhaps not surprising, because its effect in other species is also inconsistent. In some species, body mass is positively correlated with dominance (e.g. bar-headed goose, *Anser indicus*; Lamprecht 1986), but in other species dominant birds tend to be lighter than subordinates (dark-eyed junco, *Junco hyemalis*; Cristol 1992; willow tit, *Parus montanus*; Ekman & Lilliendahl 1993). The change in relationship between body mass and dominance in our study may be a result of loss in body mass between the winter and spring trials. A late winter decrease in body mass is often seen in ducks (Hepp 1986), and the energy reserves left in the spring may either directly affect competitive interactions or indicate general health and ability, which would not necessarily be the case in the winter when all individuals are near their maximum mass.

Morphological asymmetry is often associated with a genetically based lack of resilience to developmental stress (Leary & Allendorf 1989). The relationship between asymmetry and dominance has not been examined in vertebrates, but Thornhill (1992) found that dominant scorpion flies, *Panopa japonica*, had more symmetrical forewings than did subordinates. A correlation between asymmetry and dominance would have been somewhat surprising in our study because the degree of asymmetry in the population was small, probably because of the relatively benign environment in which the ducks were reared (mean relative tarsus asymmetry was 0.33%

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and mean relative wing asymmetry was 0.19%; for comparison, the mean relative asymmetry of Japanese scorpionfly forewings was 1.7% (Thornhill 1992).

Testosterone undoubtedly affects aggressive behaviour in birds, but the exact nature of the relationship is complex (Wingfield & Hahn 1994). Formation of dominance hierarchies in birds is usually accompanied by high levels of aggression and increased plasma testosterone concentration (Wingfield et al. 1987). Once dominance relationships are established, aggression and testosterone levels return to basal levels. The time required for this process varies, but in previous studies, testosterone levels were elevated for 1 day to 1 week after groups were formed (Ramenofsky 1984; Hegner & Wingfield 1986). In our study, testosterone levels actually tended to decrease over the 1-h period of hierarchy formation. Although aggression levels were high at the onset of most trials, they inevitably decreased as the trial proceeded. Therefore, blood samples may have been taken too late to detect aggression-related increases in testosterone levels. Such an effect may have been compounded by the normal diurnal testosterone cycle, in which levels peak early in the morning (Balthazart 1976). Capture and handling of birds can cause stress-related reductions in testosterone levels (Wingfield et al. 1982), but this was not a factor in our study (for log-transformed androgen level versus time between end of trial and blood sample, $r_s = -0.097$, $N = 168$, $P = 0.212$). Although hormone levels in our study may have been influenced by methodology, the negative effect of initial testosterone level and change in testosterone level in the first of our analysis contradicts previous findings. The cause of this result is not clear.

Dominance relationships between male mallards and black ducks are more complex than originally proposed. Further experiments are required to resolve the observed effect of place of origin and lack of effect of species on dominance. This study emphasizes the need for caution when experimenting with animals in captive populations that arose from multiple sources and the potential importance of early experience in social interactions later in life.

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