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Paul A. Johnsgard
University of Nebraska-Lincoln, pjohnsgard1@unl.edu

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A QUANTITATIVE STUDY OF SEXUAL BEHAVIOR OF MALLARDS AND BLACK DUCKS

BY PAUL A. JOHNSGARD

IN recent years an increased interest in the use of behavioral characteristics in evolutionary studies has developed, and this is particularly true in the case of waterfowl. The classical studies of Heinroth (1911), who was one of the first to apply knowledge of waterfowl behavior to systematics, have been elaborated on by Lorenz (1941; 1951–1953) in his important contribution toward the understanding of relationships in the Anatinae. These, and other, studies have stressed the qualitative behavioral differences occurring among different species as providing possible isolating mechanisms through their presumed function of conveying species-specific recognition signals. To the present, no extensive quantitative studies of the behavior of very closely related forms of waterfowl have been undertaken, although Dr. D. F. McKinney's still uncompleted studies on the races of the Common Eider (*Somateria mollissima*) will provide an important contribution in this field. By studying the reproductive behavior of such closely related forms the evolution of isolating mechanisms can be fruitfully studied in their early stages and thus provide an insight into the general process of speciation.

As part of a more general study (Johnsgard, 1959) concerning the evolutionary relationships between the Mallard (*Anas platyrhynchos*), the Black Duck (*Anas rubripes*), and other closely related forms, behavorial characteristics were utilized as taxonomic characters. The results of this general study, which will be published later, indicate that the Black Duck is much more closely related to the Mallard than is generally supposed and that the two forms should probably be considered to be only subspecifically distinct. The purpose of the present paper is to summarize the quantitative aspects of the behavioral studies and to discuss their probable significance in terms of (1) the evolution of behavioral isolating mechanisms; (2) the relative importance of display and plumage in species-recognition signals of these birds; and (3) the concepts of response specificity and response thresholds, or "drive."

METHODS AND OBJECTIVES

Observations were made over a two-year period on flocks of Mallards and Black Ducks in the Cayuga Lake region of New York. Mallard observations were carried out in large part at Stewart Park, Ithaca, where a semi-tame flock of approximately 200 birds is present the year around. Wild Black Ducks were observed primarily at the Howland's Island Game Management Area, near Port Byron, New York, where large numbers (1000 to 2000) of

these birds winter with the waterfowl breeding stock of the New York State Department of Conservation. Wild Mallards also winter at Howland's Island, and supplementary observations on this form were made there. Most observations were made with the aid of a 20-power spotting scope, and approximately 1000 feet of 16 mm. motion picture film were exposed and analyzed for critical comparisons between the two forms.

For the use of camera and projection equipment I extend my sincere thanks to Dr. W. C. Dilger. I especially express my deepest appreciation to my graduate committee chairman, Dr. C. G. Sibley. Dr. L. C. Cole suggested certain statistical analyses. The study was financed in part by fellowships from the Cornell University Graduate School and the National Science Foundation.

Although the sexual displays of the Mallard are well known (e.g., Lorenz, 1951–1953; Weidmann, 1956; Ramsay, 1956), very few observations on the corresponding displays of the Black Duck have been published. The few which have been published, such as those of Trautman (1947) and Wright (1954), have dealt for the most part with copulatory behavior or aerial chases. According to Ramsay (1956) and Delacour (1956), Black Ducks differ in their sexual behavior from the Mallard only in that the "Head-up-tail-up" and "Nod-swimming" displays are independent in the former, but are linked in the latter. (Names given displays are those of Lorenz, 1951–1953, and detailed descriptions of them can be found in that paper or in those by Ramsay, 1956, or Delacour, 1956.) Cursory observations of Mallard and Black Duck displays soon made it clearly apparent that courtship patterns of the two forms are extremely similar, and motion picture analysis failed to establish any qualitative differences between them. However, it was believed that possible differences might be present which could take the form of (1) differences in frequencies of the various male displays, (2) differences in seasonal periodicity of displays, or (3) differences in the contextual occurrence of the various displays in the two forms.

With this in mind, it was decided to record the male responses which were usually elicited by unmated females and which could conceivably act as potential isolating mechanisms by providing specific recognition signals. There are three such responses, those called by Lorenz (1951) the "Grunt-whistle," the "Head-up-tail-up" with associated "Nod-swimming," and the "Down-up." Other male responses, such as "Mock Preening" and copulatory behavior, either occur very rarely or are of uniform nature throughout a wide range of species and thus probably could not function effectively in species recognition. The total number of each of the three mentioned male displays observed during each "bout" of display was tallied. A "bout" could range from a single male display to five or more males displaying simultaneously

with the same or different movements toward a single female. The accurate recording of such combined displays involving several drakes has an obvious limit, depending upon the experience of the observer and the limitations of human perceptive powers. This limit, in my case, is approximately five birds. Fortunately, displays involving more than five birds displaying simultaneously were relatively rare. For the present purposes, "simultaneous" means that no noticeable temporal break occurred between the end of the first male display and the beginning of the last display. Each display in a bout involves a different male, since no male was ever observed to perform two displays during a single bout (the Head-up-tail-up and Nod-swimming are considered as a single display unit). A total of over 3000 Mallard and over 1300 Black Duck displays were recorded in this manner from September, 1958 through April, 1959, and form the primary basis for the following results and discussion.

Results

Seasonal Periodicity.—No definite differences in seasonal periodicity of displays were found. Mallards were observed displaying sexually as early as September 13, and Black Duck sexual displays were observed on the first trip to Howland's Island on October 11. The frequency of Black Duck displays observed at that time, however, indicated that they had begun considerably earlier. In Table 1 is presented the frequency of displays observed for Mallards and Black Ducks on a unit-time basis for the period September through April, and some idea of seasonal periodicity can be derived from these data. However, total numbers of birds under observation varied considerably, both between the two forms and at different times for a single form, and this makes close comparisons impossible. In addition, cold temperatures, wind, and disturbance had strong depressing effects on display frequency during any time period, and these factors also complicate the picture. Disturbance was a particularly important factor in the case of Black Ducks, which were a hunted population, and this single factor accounts in large part for the considerably lower overall frequency of courtship activity observed in that form.

Taking all of these factors into account, it was apparent that the largest numbers of birds were displaying sexually during November and December (Fig. 1). Sexual displays tapered off during the cold weather of January, and increased again in February and March. Displays were seen, sporadically, until the end of June, although females began laying early in April. However, the great majority of displays being observed from February onward was accounted for by the relatively small percentage of males not already mated, and the actual major period of sexual display appears to occur in

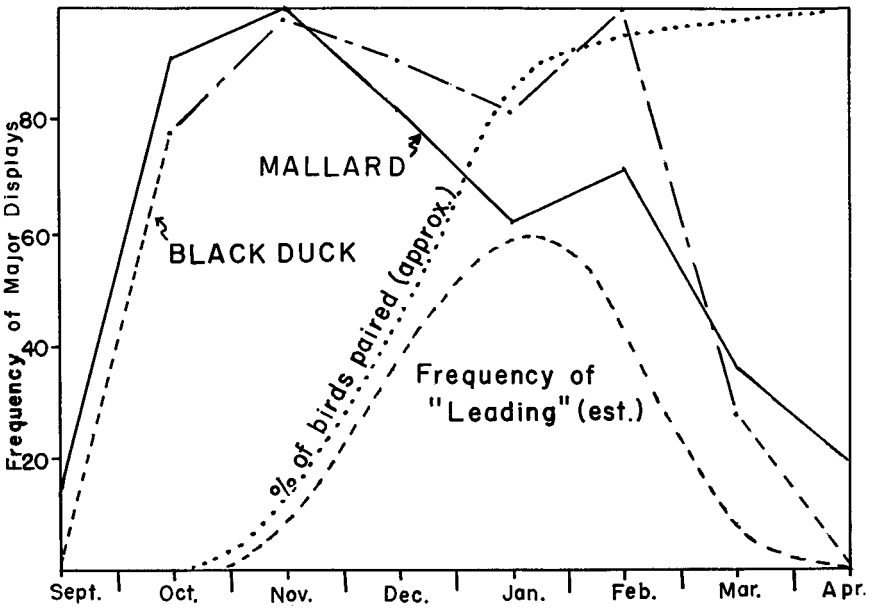

FIG. 1. Relation of approximate period of pair formation in Mallards and Black Ducks to relative frequencies of major male displays and "Leading" display.

November and December in both the Mallard and the Black Duck. These figures agree fairly well with those presented by Ramsay (1956), who found (in Maryland) a peak display frequency in December and January. The period of time required for individual pair formation in both Mallards and Black Ducks is probably much longer than is generally appreciated, and although some evidence of pairing was observed as early as late October, such pairs often appeared to be temporary. The period of pair formation does not seem clearly correlated with either the frequency of copulation (which was highest in October and November) or with the gonad cycle (Höhn, 1947), since the testes do not begin to recrudesce until the lengthening photoperiod provides a mechanism for gonadal stimulation. Stotts (1958) found a gradual increase in the percentage of paired Black Ducks from about 10 per cent in late September to about 60 per cent by April, and then rising sharply to nearly 90 per cent by early May. My own estimates of the period of major pair formation are indicated in Fig. 1, and are rather earlier than Stotts' estimates. I agree with Höhn (1947), who believed that the primary function of sexual display is in the formation of pairs, and that fall and winter copulations may serve to strengthen the bond between incipient pairs. It cannot be doubted, however, that a great many copulations occur between non-mated

birds, and that therefore copulation *per se* appears to be relatively unimportant in pair formation. The apparent means by which pair formation is effected in Mallards has been discussed by Weidmann (1956), and my observations bear out his conclusions. In short, it may be stated that female Mallards (and Black Ducks) actively "select" potential mates by "Inciting" (Lorenz, 1951) them against other birds. The male response to such Inciting may be to attack the indicated individual (usually another male) or, more often in preliminary stages of pair formation at least, to respond with a special display I have termed "Leading" (Johnsgard, 1959). This display involves an orientation of the back of the male's head toward the Inciting female while swimming rapidly ahead of her. Which factors of display and/or plumage result in the selection of a specific drake by a female are still uncertain, but a few observations on this point will be discussed later.

Individual Display Responses.—In Lorenz's studies of the Mallard (1951), he concluded that the three major male displays were "of equal value," and whichever one was performed by a male was largely a "matter of chance." However, Lorenz's student Weidmann (1956) investigated this point and concluded that this is not the case. Weidmann's opinion was that the Grunt-whistle display indicates a low intensity courtship whereas the Down-up and the Head-up-tail-up displays are indicative of high intensity courtship situations. Thus, of a total of 1074 individual male displays of these types he recorded, he found that the Grunt-whistle was usually performed when a single male displayed toward a female. During displays where many males reacted simultaneously, the Head-up-tail-up or Down-up displays were usually performed. As shown in Table 1, my observations support Weidmann's conclusion that the displays are not of random occurrence or of equal probability of elicitation, since there are distinct differences in frequency of the three displays during the same time period, and of individual displays during the course of the entire pair formation period. In both the Mallard and the Black Duck the Grunt-whistle tended to be the most frequent display during the first few months of pair formation, and the Down-up tended to be least frequent. As time progressed, however, the Down-up became more frequent and comprised about half of the total male displays during peak pairing activity. This increase of Down-up displays was achieved primarily by the reduction in frequency of the Grunt-whistle in the Black Duck and the Head-up-tail-up in the Mallard. These figures thus corroborate Weidmann's opinion that the display performed most frequently during low intensity courtship situations early (and very late) in the season is the Grunt-whistle. However, in the present case the data also point to the conclusion that the Head-up-tail-up and Down-up are not equivalent either, but that the Down-up represents

TABLE 1

SEASONAL FREQUENCIES OF MAJOR MALE DISPLAYS

	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	Total
Grunt-whistle									
Mallard	40(42%)	279(45%)	379(46%)	170(38%)	59(35%)	150(35%)	102(42%)	74(41%)	1250
Black Duck	—	66(41%)	148(30%)	34(26%)	62(27%)	43(15%)	5(19%)	—	358
Head-up-tail-up									
Mallard	35(37%)	185(29%)	202(25%)	95(21%)	19(11%)	71(16%)	41(17%)	46(26%)	694
Black Duck	—	64(40%)	200(41%)	36(28%)	81(35%)	108(38%)	8(31%)	—	497
Down-up									
Mallard	20(21%)	163(26%)	239(29%)	187(41%)	90(54%)	212(49%)	101(41%)	49(33%)	1071
Black Duck	—	30(19%)	144(29%)	60(46%)	86(37%)	133(47%)	13(50%)	—	468
Total Displays									
Mallard	95	627	820	452	168	436	244	179	3018
Black Duck	—	160	492	130	229	284	26	—	1321
Total Bouts									
Mallard	52	464	467	303	104	234	151	122	1897
Black Duck	—	76	237	74	132	144	10	—	673
Displays/Bout									
Mallard	1.8	1.3	1.8	1.5	1.6	1.9	1.6	1.4	1.6
Black Duck	—	2.1	2.1	1.8	1.7	2.0	2.6	—	2.0
Frequency of Display*									
Mallard	.13	.91	1.0	.82	.61	.71	.35	.20	—
Black Duck	—	.78	.98	.91	.81	1.0	.27	—	—

*Per unit of time, relative to month having highest frequency.

the highest intensity display since it occurs most frequently during the period of very intensive display.

It is of interest that the Head-up-tail-up, the most spectacular and complicated of the three displays, is apparently a lower intensity reaction than is the Down-up, which is a relatively simple display. However, it may be significant that, of the three displays, the Down-up has the narrowest range of interspecific occurrence, being restricted as such to the Mallard group and, in rather modified form, to the Gadwall (*Anas strepera*) (Lorenz, 1951–1953). The Grunt-whistle is of much wider distribution, occurring in the Mallard group, the Gadwall, the Green-winged Teal group (*Anas crecca, A. flavirostris,* etc.), the Pintail group (*Anas acuta, A. georgica,* etc.), and others. The Head-up-tail-up display also occurs in most of the species which possess the Grunt-whistle display. Thus the Down-up may be the most important of the three displays from the standpoint of recognition in Mallards, even though it is not the most complex.

To test the hypothesis that the three displays represent a hierarchy of reaction intensities, it must be hypothesized that the lowest intensity display would, since it results from low intensity stimulation, tend to occur most frequently as isolated displays. Conversely, when the female's behavior provides a strong stimulus, it would be expected that larger numbers of males would tend to respond simultaneously with one of the higher intensity displays. By determining the frequency with which a given display is performed by a single male, two males, etc., to the maximum number of males observed to perform a display simultaneously (i.e., during a single bout), this hypothesis can be tested. In Figs. 2 and 3 are presented such data for Mallards and Black Ducks. It will be noted that in both forms the Grunt-whistle occurs more frequently as a single display than does either the Head-up-tail-up or the Down-up. This latter display is more frequently performed simultaneously by several drakes than is either of the other two. These data thus correlate well with the supposition that the Grunt-whistle is the lowest intensity reaction and the Down-up represents the highest intensity reaction, with the Head-up-tail-up being intermediate.

At this point the assumption is that multiple simultaneous displays of a single kind are the result of a specific stimulus from a female and not simply the result of a contagious or mimetic effect resulting from several males "imitating" the display performed by the first male to respond. Although this possibility is almost impossible to test experimentally, it can nevertheless be tested statistically. That is, if the males are reacting completely independently of one another the frequency distribution patterns shown in Figs. 2 and 3 should follow a Poisson distribution, whereas if any contagious effect is present such a distribution will not obtain. A typical Poisson dis-

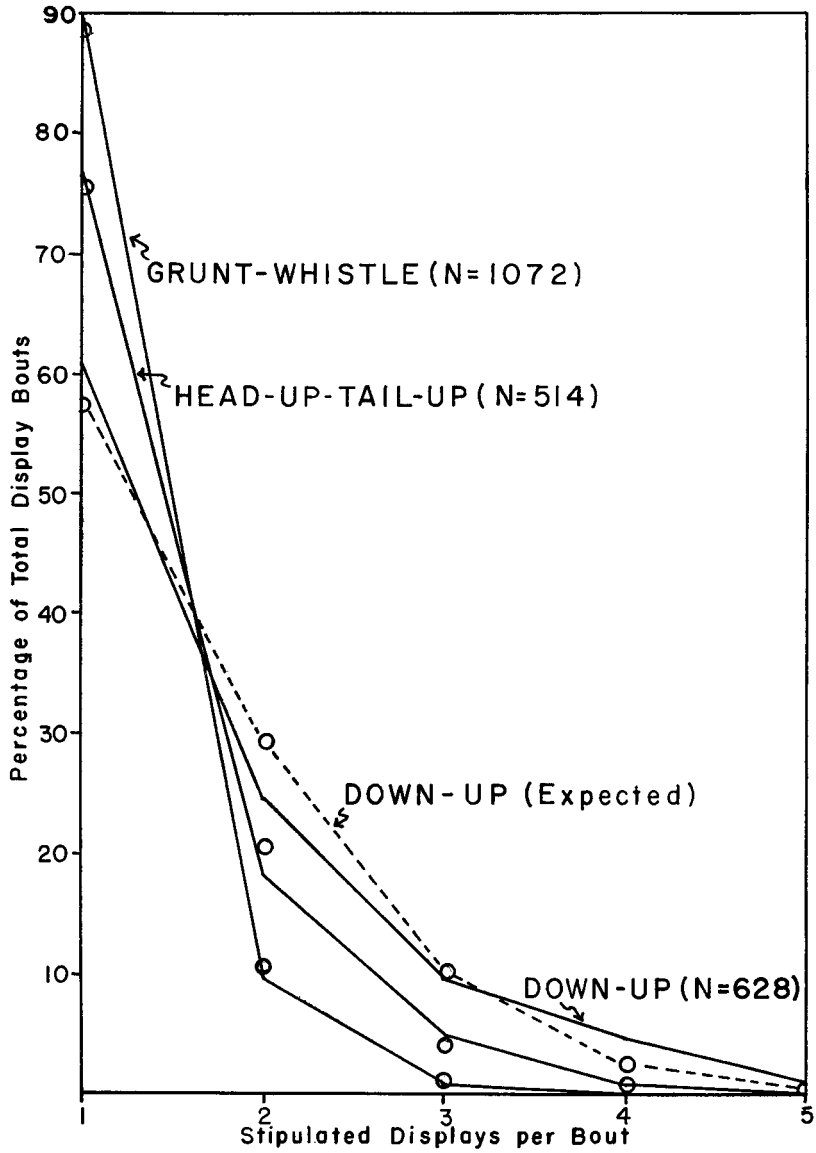

FIG. 2. Frequency distribution patterns of displays per bout observed in male Mallards. Solid lines connect observed frequencies; open circles (connected by dotted line in the case of Down-up) indicate calculated frequencies based in Poisson distributions. "N" equals number of bouts involving each of the indicated displays.

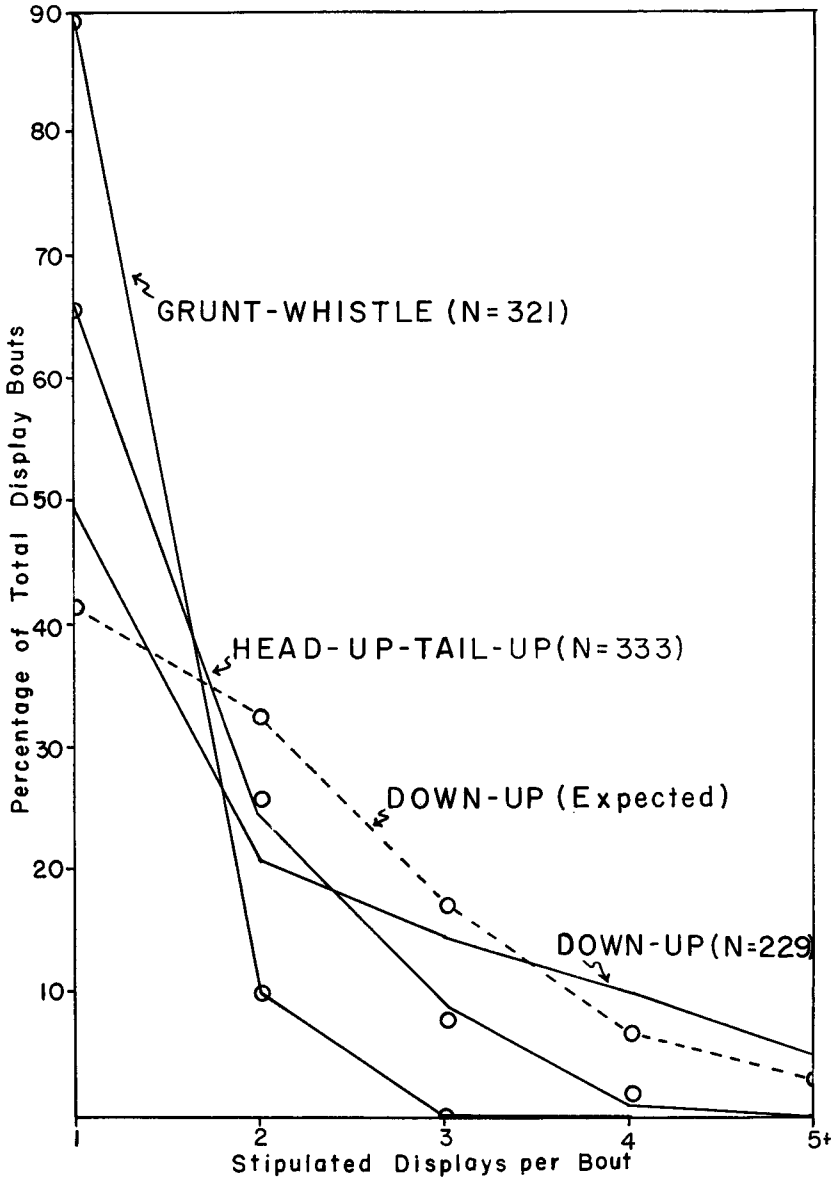

FIG. 3. Frequency distribution patterns of displays per bout observed in male Black Ducks. See Fig. 2 for explanation of symbols.

tribution contains a "O" frequency category, which in the present instance is unmeasurable since one obviously cannot tally the number of times no males displayed toward a female. However, this unmeasureable category can be accounted for (van Rest, 1937), and a mean Poisson value obtained by the general formula: $\bar{X} = \frac{m}{1 - e^{-m}}$. In this case $\bar{X}$ equals the observed, and m the actual, mean. After obtaining this value, the distribution in question can be tested to determine if it can be described by a Poisson distribution having the same mean as the calculated mean. This tended to be the case (see Figs. 2 and 3), for in both the Mallard and the Black Duck the Grunt-whistle and the Head-up-tail-up distributions could be explained ($p=.05$) by Poisson distributions having various means. For the Mallard these means were 0.23 and 0.54 for the Grunt-whistle and Head-up-tail-up, respectively, and for the Black Duck the corresponding values were 0.23 and 0.79 displays per bout. In the case of the Down-up, the observed distributions deviated sufficiently from the calculated ones to be rejected at the 5 per cent level, mainly because of too many observations in the categories of four displays or more per bout. The calculated mean Poisson figures for the Down-up were 1.03 and 1.59 displays per bout for the Mallard and Black Duck respectively. In the case of both the Head-up-tail-up and the Down-up, the Black Duck had a significantly higher ($p=.01$) number of displays per bout. Thus it may be said that the Black Duck has a lower threshold to perform the Head-up-tail-up and the Down-up than has the Mallard, as indicated by the larger average number of males performing these displays simultaneously. This may also be concluded from Table 1, in which it may be seen that the average number of total males displaying per bout is significantly higher ($p=.01$) in the Black Duck (2.0) than in the Mallard (1.6). If the relative frequency of total male displays per bout is plotted graphically (Fig. 4), this difference becomes even more apparent, and it will at once be seen that in the Black Duck multiple simultaneous displays are considerably more frequent than in the Mallard (difference significant at .01 level). The possible biological significance of these differences will be discussed later in the paper.

Finally, it may be said on the basis of the fit obtained using the Poisson distribution that males tend to react independently of one another when displaying (except possibly in the case of the Down-up), and thus presumably are reacting to a mutual specific stimulus (the female).

Combined Display Responses.—Simultaneous displays involving two or more males are frequently "mixed," rather than "pure," and may at times involve all three of the male display patterns. This is indicated in Figs. 5 and 6, in which the percentage composition of the three displays is indicated for all display bouts recorded involving from one to five or more males.

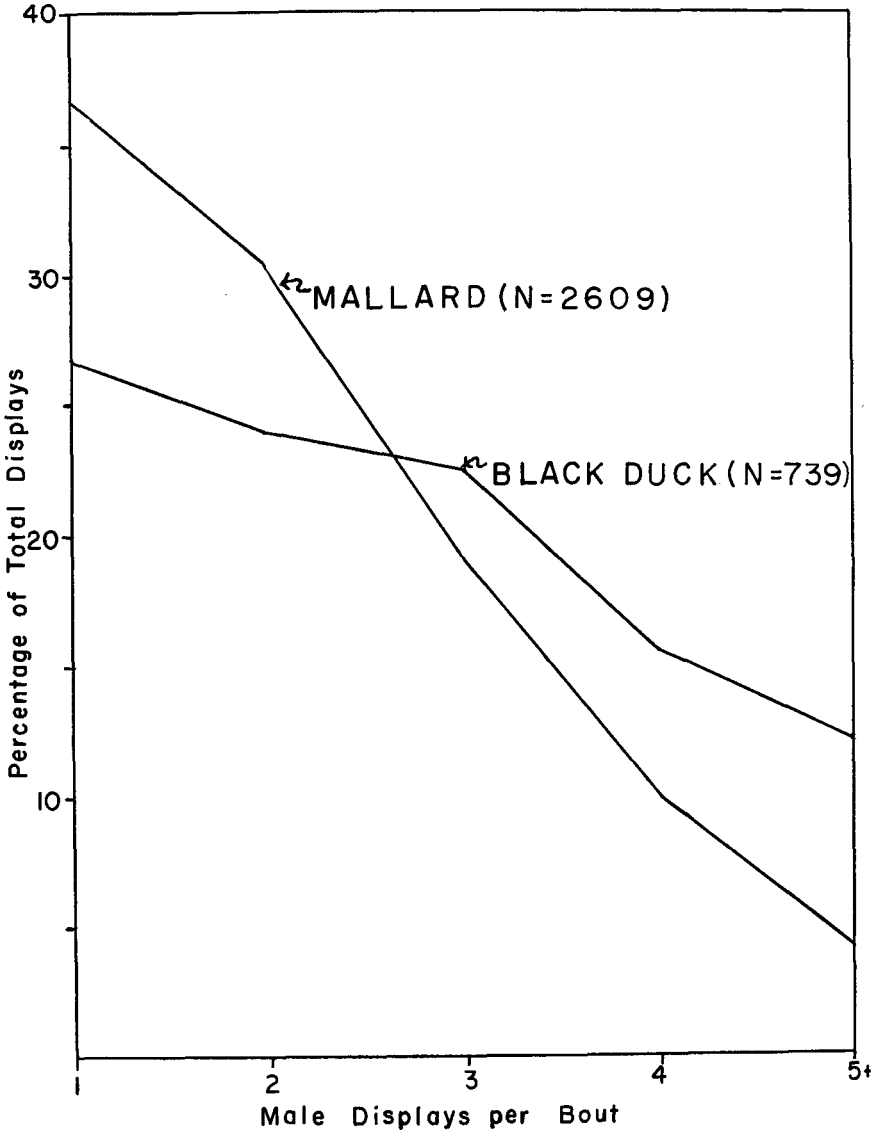

FIG. 4. Total male displays per bout observed for male Mallards and Black Ducks. "N" equals total number of displays included in sample.

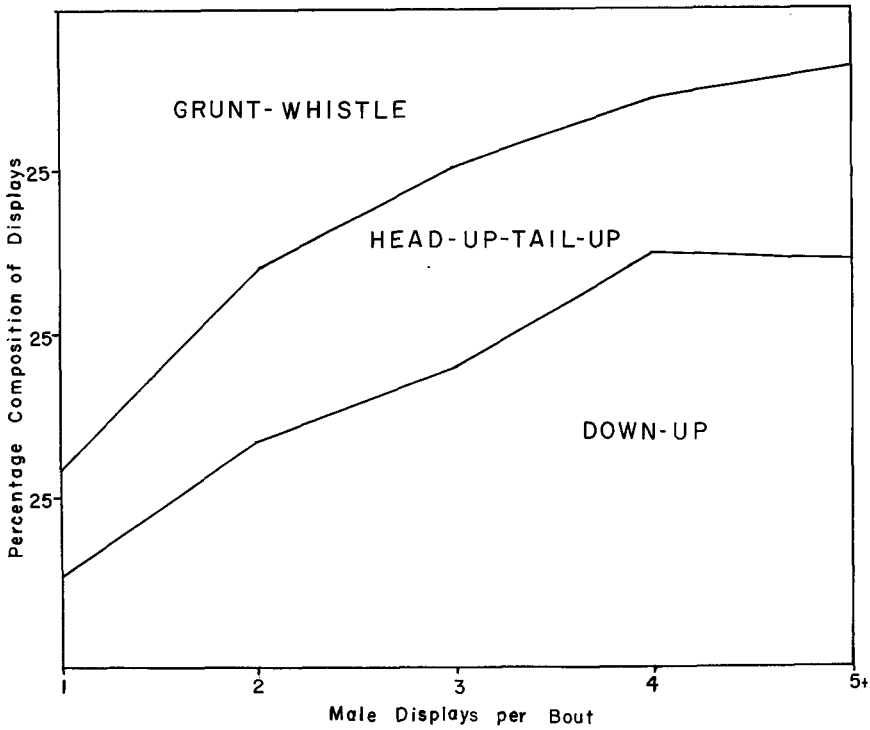

FIG. 5. Percentage composition of major Mallard displays relative to the number of total male displays per bout. Based on 2609 total male displays.

These graphs clearly point out the fact that Grunt-whistles predominate when a single male displays, that Down-ups predominate in bouts where four or more males display, and that Head-up-tail-ups tend to occur most frequently in intermediate situations involving two or three birds. Thus, of all the Grunt-whistles recorded, 58.0 per cent of the total occurred as lone displays in the Mallard and 45.6 per cent as such in the Black Duck. Of all Head-up-tail-ups, 60.3 per cent in the Mallard and 65.2 per cent in the Black Duck were performed when two or three birds displayed simultaneously. Finally, of all the Down-ups recorded, 26.4 per cent in the Mallard and 56.8 per cent in the Black Duck occurred when four or more birds displayed simultaneously. This relatively low per cent of Down-ups in the case of the Mallard suggests that Mallard males are less specific in their response to strong stimulation than are Black Duck males. More will be said of this later.

Field observations indicated that these three displays actually tend to represent graded responses to three increasing strengths of female stimuli.

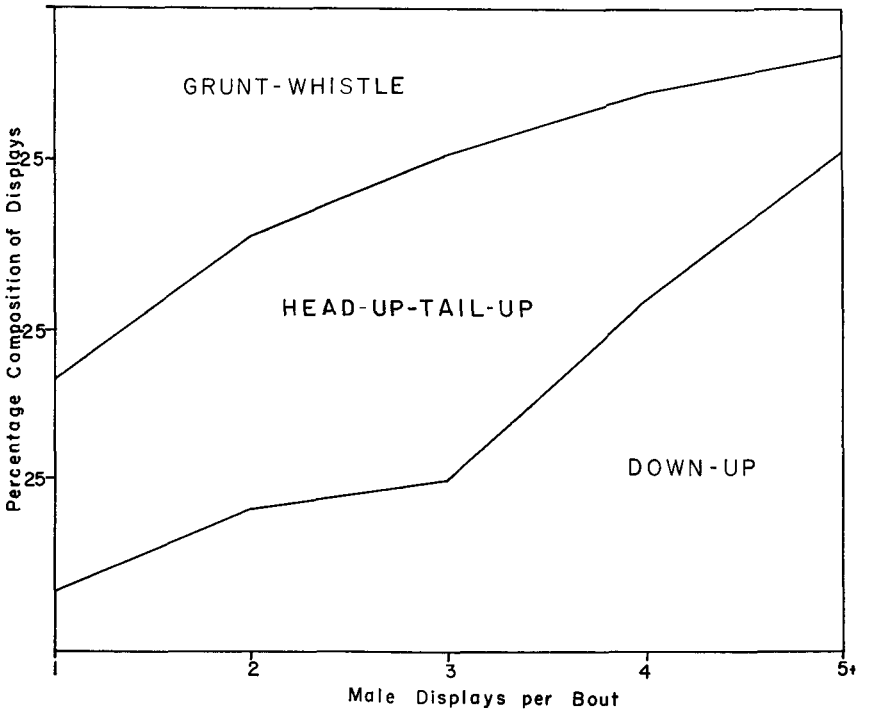

FIG. 6. Percentage composition of major Black Duck displays relative to the number of total male displays per bout. Based on 739 total male displays.

Thus, an Inciting female corresponds roughly in stimulus valence to a male Grunt-whistle response, Nod-swimming parallel to or away from a male corresponds approximately to the Head-up-tail-up response, and Nod-swimming toward a male (the strongest female stimulus) almost always results in the Down-up response. However, an unvarying one-to-one stimulus-response (or "sign stimulus"-"fixed action pattern" in ethological terms) cannot be supported by these data, since the percentage of Down-up displays varied greatly as the season progressed, but the number of male displays per bout remained relatively constant (see Table 1). Thus, a female stimulus which is sufficient to elicit a Down-up response later in the season would, in September or October, for example, most likely result in a Grunt-whistle or Head-up-tail-up. Nod-swimming by females tends to decrease later in the season (Ramsay, 1956), although it was observed as late as April in both forms. Inciting is much more common during this later period, and the male responses tend to shift

from the three major swim displays to the Leading display described earlier, with several males often competing for the Leading position in front of the Inciting female. This Leading display may thus be thought of as possibly representing the highest intensity male response, and it seems very likely that it may have the greatest importance in mate selection of all the male displays. With the beginning of the male Leading displays in late October, courting groups became much more mobile and animated, and male competition became very evident. In their attempts to attain the Leading position, trailing males often made short flights (probably equivalent to the "Jump Flights" of Lebret, 1957) and landed a short distance in front of the Inciting female. Leading was most evident during December and January (when it was usually observed 20 to 30 times per hour) and tapered off in late February and March, and thus was most frequent during the period of apparent formation of pairs. It was, however, observed until the end of April in greatly reduced intensity.

This variable intensity of male displays, associated with constant or even decreasing female stimuli, seems explainable by hypothesizing a varying male response threshold to sexual stimuli. This may be the result of sex hormone level changes associated with testis growth, but no data on seasonal changes in Mallard androgen levels are available for testing this possibility. However, merely saying that the males have an increased sexual "drive" or "tendency" seems to avoid the basic question and does not contribute to its solution.

A crude measurement of this seasonal change in male response thresholds can be obtained by comparing the monthly percentage frequencies of the Down-up display, the highest intensity response of the three displays. These data suggest that the lowest male Mallard display thresholds occur in January and February. Data for the Black Duck, which are much less reliable, indicate low thresholds from December through March. Therefore, this period of low response thresholds does not fit well with the gonad cycle, since the testes do not begin to recrudesce until day-length begins to increase, and males remain sterile until mid-February (Höhn, 1947). In addition, display intensity tapers off in April, although gonad size is at a maximum during this time. Presumably, male hormone levels are closely related to gonad volume or size, which varies immensely in these birds, and this casts doubt on a close connection between male response thresholds and male hormone levels.

Specificity of Response.—Weidmann (1956) believed that simultaneous group displays involving Down-ups and Head-up-tail-ups tended to show a higher frequency of "pure" displays than one would expect to result from chance which, since mimesis is apparently not important, implies that the males tend to respond specifically to female stimuli. Weidmann's conclusions

appeared, judging from his tabular data, to be based on 78 bouts of display. This conclusion seemed important enough to warrant further investigation, so the frequencies of all recorded combinations of these two displays have been determined for the Mallard (927 bouts) and Black Duck (456 bouts), and are presented in Tables 2 and 3. Inclusion of Grunt-whistles, which would have necessitated the construction of a three dimensional table, did not seem justified because they form a very minor component of multiple displays (see Figs. 2 and 3).

As a measure of the randomness of response, the expected frequencies of each of the possible combinations of these two displays can be calculated for each sample of bouts involving a given total number of males perfoming the two displays. That is, if the male responses are random in nature, they should "segregate" according to the random probability frequencies for each combination class. Such expected frequencies have been calculated, and are placed in parentheses below the observed frequencies of each combination class. An index to the relative "purity" of male response is obtained by comparing the number of observed "mixed" display bouts to the expected number. Thus in the Mallard 141 bouts of "mixed" displays were observed, whereas 224 would have been expected on the basis of random response (62.9 per cent of the expected). In the Black Duck 90 out of a calculated 158 expected bouts were recorded, or 57.0 per cent of the expected. In both cases the differences are highly significant (p less than .01), and it may be concluded that male Mallards and Black Ducks do tend to respond specifically to female stimuli. That such a response specificity exists should not be surprising, and the above technique seems to provide a useful measure of the degree of response specificity.

Individual Variation in Response.—Sources of individual variation are presumably of two types, namely variations in intensity of performance of the various displays by a single individual as a result of variations in its internal state or the strength of the external stimulus and, secondly, genetic variation among different individuals in the population. Since only unmarked birds were studied it was not possible to completely separate these two variables, but some pertinent observations might be mentioned here.

According to Delacour (1956) and Ramsay (1956), Mallards differ from Black Ducks in that the Head-up-tail-up display is linked to the subsequent Nod-swimming in the Mallard, whereas in the Black Duck the two displays are independent. Of 665 Mallard Head-up-tail-up displays I recorded, 625 (94.3 per cent) were followed by Nod-swimming, whereas in the Black Duck 479 out of 490 (97.7 per cent) were followed by Nod-swimming. Thus the two displays are actually strongly linked in both forms, and the statements of Delacour and Ramsay to the opposite effect are not supported by my

TABLE 2

RECORDED BOUTS OF MALLARD DISPLAY COMBINATIONS

		Males Performing Head-up-tail-up Display					
		0	1	2	3	4	5
Males Performing Down-up Display	0		258 / (258)	65 / (60)	17 / (15)	1 / (2)	1 / (0)
	1	258 / (258)	70 / (120)	16 / (30)	4 / (9)	2 / (2)	
	2	104 / (60)	30 / (30)	5 / (14)	2 / (4)		
	3	57 / (15)	8 / (9)	2 / (4)			
	4	20 / (2)	2 / (2)				
	5	5 / (0)					

data. In the small percentage of cases where Nod-swimming did not follow the Head-up-tail-up the apparent reasons were that (1) the male was unfavorably orientated with respect to the "courted" female (e.g., she was swimming away from him), (2) the male was still partially in juvenal or "eclipse" plumage and thus probably had a high response threshold, or rarely, (3) the male was physically prevented from Nod-swimming by the presence of several other birds directly in front of him.

Variations in display intensity were evident in all of the displays. For example, low intensity performances of all three major displays often lacked the whistle that normally is associated with all of them. This was particularly true during the first few weeks of display when many birds were still molting into nuptial plumage and also during the last weeks of display in April. Of the three major displays, the Down-up appears to be the most variable in intensity, judging from inspection of motion picture film. That is, the "Down" phase varied from only a very slight downward body inclination to one in which the whole forepart of the body was submerged. Variations in the length of time required to complete a display did not appear to be great, with the notable exception of Nod-swimming, in which the female's orientation had a profound effect on this display's length.

All of the above examples of variation seem explainable by quantitative

TABLE 3

RECORDED BOUTS OF BLACK DUCK DISPLAY COMBINATIONS

		Males Performing Head-up-tail-up Display					
		0	1	2	3	4	5
Males Performing Down-up Display	0		152 (107)	59 (30)	23 (8)	1 (2)	1 (0)
	1	61 (107)	35 (60)	10 (24)	4 (9)	1 (3)	
	2	27 (30)	14 (24)	5 (14)	0 (6)		
	2	17 (8)	11 (9)	5 (6)			
	4	17 (12)	5 (3)				
	5	8 (0)					

variations in stimuli strength and response thresholds of individual birds. Evidence for genetic variation within the total population was possibly indicated by the small percentage of abnormal displays seen. For example, although the display which Lorenz (1951) termed "Bridling" normally occurs in the male Mallard only after copulation, it was observed to be intercalated between the Head-up-tail-up and Nod-swimming on three occasions out of the total 625 Head-up-tail-up and Nod-swimming combinations recorded. In the Black Duck this variation was recorded twice out of the 479 such combinations. In addition, an independent Bridling followed by Nod-swimming was observed twice in the Mallard and not once in the Black Duck. Finally, an isolated Bridling movement was observed once in the Mallard. It is of interest that Bridling normally occurs in these same display combinations in a few closely related species such as *Anas castanea* (Lorenz, 1951–1953), which suggests that this might be an ancestral mallard condition which is occasionally expressed in certain genetic recombinations or mutant individuals.

Hybrid Behavior and Mallard-Black Duck Interaction.—Wild hybrids between Mallards and Black Ducks are relatively common in the Ithaca area, and repeated counts of wild Black Duck flocks suggest that roughly 3 per cent of the males exhibit rather obvious hybrid ancestry. Hybrid incidence is considerably higher toward the western edge of the Black Duck's range (Johns-

gard, 1959), but they occurred in sufficient numbers in the area of study to allow certain observations of behavior.

Since no qualitative differences were observed in the behavior of the parental forms, it is not surprising that hybrids exhibited no noticeable deviations in their sexual displays. Hybrids also exhibited no greater or lesser frequency of display, although I do not have sufficient data to demonstrate this statistically. In short, hybrids displayed among courting groups of both parental forms, but those which showed a predominance of Mallard or Black Duck characteristics usually were to be found displaying with that form. All of the male displays observed in Mallards and Black Ducks were seen in hybrids and under the same conditions.

Display interaction between Mallards and Black Ducks is an important consideration when trying to determine the degree to which speciation has progressed and isolating mechanisms have evolved. Such interaction did occasionally occur in wild flocks, although courting groups were usually composed entirely of one form or the other. A few observations of Black Duck males displaying with Mallards were obtained, and since they have a bearing on the question of whether male Mallards and Black Ducks are responding to the same female stimuli when they perform the same displays, they will be mentioned here. For example, in the four instances where Black Duck males were observed to perform Down-ups simultaneously with male Mallard displays, these Mallard displays included two Grunt-whistles, three Head-up-tail-ups, and four Down-ups. Although the records are admittedly scanty they do suggest that male Mallards and Black Ducks are responding to the same stimuli when they perform the same displays, and that a female Mallard provides no less of a stimulus than does a female Black Duck under the same conditions, since the Black Duck displays were of equal or higher intensity than the male Mallard displays which were performed simultaneously.

Relationship of Plumage Pattern to Mating Success.—If Darwin's ideas concerning the importance of sexual selection in mating success are correct, it follows that the sexually dimorphic plumage of the male Mallard must be related to its chances of obtaining a mate. It should also be true that males with abnormal or subdued coloration would have less chance of obtaining a mate. Thus, hybrids or Black Duck males presumably would be selected against in a competition for female Mallard mates. Although no information relative to this possibility was obtained on wild birds, some observations bearing on this problem were obtained on the semi-tame ducks at Stewart Park. Here, in addition to the approximately 100 normally plumaged drakes, there were five birds which deviated markedly from the typical male Mallard plumage pattern. These deviations are rather commonly found mutations in domesti-

cated Mallard flocks, such as birds lacking the chestnut breast, having reddish flanks, etc. To test the possibility that such males are less likely to obtain mates because of these aberrations in their plumage signal characters, records were kept on the frequency with which these males displayed relative to the normal "wild type" males. These observations were begun in February, after most birds were already paired and the remaining unattached males were competing for the relatively few unpaired females. The results of these counts are presented in Table 4. It will be seen that the small percentage of drakes possessing abnormal coloration contributed a relatively large percentage of the total male displays recorded during the period of observation, and that they, therefore, were being forced to compete more strongly for mates than were the wild type males. This was most marked during February and March, before mated pairs had begun to break away from the main flock to begin nesting activities. However, by April most pairs had dispersed, leaving only the excess males and a very few females. During that month the aberrant males contributed approximately the expected percentage of displays, since nearly all the other remaining males were also still unpaired. So far as

TABLE 4

FREQUENCY OF DISPLAYS IN WILD-TYPE AND ABERRANT MALE MALLARDS

	Feb.	Mar.	Apr.	Total
Grunt-whistles				
by wild-type males	69	79	60	208
by aberrant males	17	23	14	54
Total displays	86	102	74	262
Head-up-tail-ups				
by wild-type males	40	31	33	104
by aberrant males	6	10	13	29
Total displays	46	41	46	133
Down-ups				
by wild-type males	117	82	50	249
by aberrant males	21	19	9	49
Total displays	138	101	59	298
Combined displays				
by wild-type males	226	192	143	561
by aberrant males	44	52	36	132
Total displays	270	244	179	693
Per cent by aberrant males	16.3	21.3	20.0	19.0
Total wild-type males present	95	76	22	64 (Ave.)
Total aberrant males present	5	5	5	5
Per cent of males aberrant	5.0	6.2	18.5	7.2
Per cent excess aberrant male displays	11.3*	15.1*	1.5	12.8*

*Significant at .01 level.

could be determined, none of these abnormally plumaged males obtained mates. It may be concluded therefore that females are indeed "selecting" normal plumaged birds in preference to these mutants, and that selection for the typical Mallard-type male plumage pattern is probably in operation.

Discussion

The data presented above have pointed out two distinct differences in the displays of the Mallard and the Black Duck. These are (1) the markedly lower male response threshold in Black Ducks in comparison with Mallards, as indicated by the mean number of males responding simultaneously (see Table 1 and Fig. 4), and (2) the somewhat more specific responses of male Black Ducks over Mallards during simultaneous, multiple male displays, especially in those involving five or more birds (see Figs. 5 and 6).

Although these differences are not nearly so great as one might expect to find in two distinct species, they are nevertheless significant from both a statistical and an evolutionary standpoint. It seems entirely reasonable to assume that the Black Duck has been forced to evolve a more specific and sensitive species-recognition system in the form of displays than has the Mallard, as a result of the former's lack of special male plumage characters. Such male plumage patterns as are found in the Mallard would presumably render less necessary a precise behavioral species-recognition system, since these distinctive patterns would probably carry the major burden of signal specificity. In areas where selection for species recognition is reduced (as on oceanic islands where only a single species of *Anas* occurs), male plumage dimorphism is rapidly lost, since selection for concealing coloration is apparently greater than are any pressures for retaining male dimorphism through sexual selection alone. No detailed behavioral studies of any of these isolated populations such as the Hawaiian Mallard (*Anas platyrhynchos wyvilliana*) or the Laysan Mallard (*A. p. laysanensis*) have yet been undertaken, but it would be most interesting to determine whether the behavioral specificity of these forms has undergone a deterioration similar to that of the male plumage patterns because of the absence of a need for a precise species-recognition system.*

In theory, assuming a mixed population of male Mallards and Black Ducks competing for a limited number of female mates, sexual selection would seem to favor the Mallard because of the strong visual stimulus provided by its elaborate plumage, which might possibly provide a kind of "super-normal stimulus" to female Black Ducks. However, this advantage might be counteracted by the male Black Duck's lower, and apparently more specific display threshold, which would provide a potentially more sensitive and effective

* Recent observations at the Wildfowl Trust on these and other island races indicate that this supposition is true.

signal system to females. Such a mechanism might explain the occurrence of male Black Ducks found paired with female Mallards in the wild (Johnsgard, 1959). I have recorded or have been informed of only six such pairs and only three pairs of the male Mallard and female Black Duck type. Additional comments on the possible importance of male plumage patterns, male displays, and female "Releasing Mechanisms" in species-recognition systems are presented by Dilger and Johnsgard (1959).

The behavioral differences encountered between the Mallard and the Black Duck might also be of significance in the general question of the evolution of behavioral isolating mechanisms. It seems to be a general truth that, in the genus *Anas* at least, behavioral differences among distinct but closely related species tend to be relatively minor although male plumage patterns may vary markedly. This also appears to be true in other avian groups (Hinde, 1959). Thus, although several species of *Anas* possess the Grunt-whistle, the optical and auditory stimuli produced by its performance vary greatly in different species as a result of differences imposed by plumage patterns, vocalizations, and variations in body size and form. In addition, variations undoubtedly also occur in the relative frequency of performance of this display and the female stimulus required to elicit it. It might be possible that one of the first stages in speciation is the evolution of threshold differences (or "tendency" differences, see Hinde, 1959) determining the performance of different male displays in isolated populations. Concommitant with these male variations, the females must simultaneously evolve variations in stimulus thresholds so that the male and female stimulus-response systems remain in synchrony (Dilger and Johnsgard, 1959). Conceivably, two such isolated populations might have gradually evolved such quantitative (or even qualitative) differences in these stimulus-response systems that by the time they acheive secondary contact the differences in the two systems are of such a magnitude that a stimulus presented by the females (or males) of one form invariably results in the incorrect response by individuals of the opposite sex in the other form. In such a way behavioral isolating mechanisms might be evolved, which could be strengthened by the evolution of male plumage differences or other morphological (and ecological) variations through selection of random mutations or by reinforcement of morphological, behavioral, and other differences through selection against disadvantageous hybridization (Sibley, 1957).

Conclusions

1. Male Mallards and Black Ducks tend to react independently and rather specifically to female stimuli.

2. Thresholds of male Mallard and Black Duck display responses vary seasonally, as apparently also do female stimulus thresholds.

3. The three major male sexual displays studied have the same hierarchy of reaction intensities in both the Mallard and the Black Duck.

4. No qualitative differences between male Mallard and male Black Duck displays were found.

5. Male Black Ducks have a distinctly lower threshold of display response, and apparently a somewhat more specific response, than do male Mallards.

6. These last two quantitative differences in two forms are believed to be related to the lack of male plumage dimorphism in the Black Duck, which probably must be compensated for by a more sensitive and specific sexual- and species-recognition mechanism than is needed by the Mallard, where male plumage characteristics alone can effect sexual and species recognition.

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