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INHERITANCE OF BEHAVIORAL CHARACTERS IN F_2 MALLARD x PINTAIL (*ANAS PLATYRHYNCHOS* L. x *ANAS ACUTA* L.) HYBRIDS

by

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(With 3 Figures)
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Although the use of species-typical behavior patterns for taxonomic purposes has now become widespread and rather generally accepted as a useful systematic tool (CULLEN, 1959), its validity relies on the premise that related species exhibit genetically controlled behavioral differences within a larger framework of homologous behavioral patterns that can be recognized and measured. Additionally, the utilization of behavioral traits for taxonomic purposes depends not only on one's abilities to recognize and evaluate such species-typical variations among homologous behavioral phenotypes, but also to choose only those behavioral traits which are largely or entirely free of variation resulting from experience.

Of these criteria, the first is largely subjective, and depends on the experience and, to a degree, the intuition of the biologist (LORENZ, 1951-1953), while the second is at least theoretically subject to objective evaluation by controlled breeding experiments. Although a considerable degree of success in this latter area has been achieved with invertebrates, particularly insects, studies on the genetic basis of behavior in vertebrates have not been as numerous or successful (DILGER, 1962). In particular, it has been found with regard to birds that those species which differ sufficiently in behavior to provide useful contrasting types generally will not hybridize or, at most, produce sterile F_1 hybrids (HINDE, 1956; DILGER, 1962). In most birds,

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fertile F_1 hybrids can be achieved only between such closely related parental stock that behavioral differences between them are at most of a quantitative nature. For reasons still unknown, these restrictions do not apply to the waterfowl family Anatidae, which has been responsible for the largest number and variety of interspecific hybrids of any avian family (GRAY, 1958; JOHNSGARD, 1960). In addition, the behavioral variations in this family are diverse and reasonably well inventoried (LORENZ, 1951-1953; JOHNSGARD, 1965). This is particularly true of the large genus *Anas,* in which a great deal of interspecific variability of sexual displays is present, as well as a remarkable degree of interspecific hybrid fertility. These favorable circumstances have been used by LORENZ (1958) and VON DE WALL (1963) to prove that interspecific *Anas* hybrids exhibit male pair-forming displays which may be intermediate between those of the parental species, may represent new combinations of displays found in one or both parental species, or which may occur in neither parental form but are present in related species. In the examples of hybrid behavior patterns studied by LORENZ and VON DE WALL, a major limitation has been the small number of F_2 individuals available for study, and thus there has been little or no opportunity to evaluate the possibility of segregation and independent assortment of behavioral traits in the hybrids. The present study was undertaken to compare the inheritance of behavioral and morphological features of two closely related species of *Anas,* and to attempt to establish whether any significant degree of behavioral variation occurs in the second generation which could be attributed to these genetic processes.

Two closely related species of *Anas,* the Common Mallard (*A. p. platyrhynchos*) and the Common Pintail (*A. a. acuta*), were selected for study. Both species have been repeatedly hybridized in captivity (GRAY, 1958; PHILLIPS, 1915, 1921), and occasionally hybrids occur in the wild. MAYR (1963) has commented on the fact that these sympatric Holarctic species have complete interspecific hybrid fertility, have a combined world population possibly exceeding 100,000,000 and yet the rate of natural hybridization is probably less than one in several thousand. Thus, isolating mechanisms other than hybrid sterility, which presumably consist primarily of plumage and behavioral differences, are effective in maintaining the two species as distinct entities.

METHODS

The initial F_1 generation was produced in 1961 at the Round Lake Waterfowl Station, Round Lake, Minnesota, when approximately ten male Pintails were placed in a covered pen with the same number of female

Mallards. Most of the resulting eggs proved to be infertile, but several dozen offspring hatched. Many of these died during an outbreak of botulism, but four males and three females were reared. During 1962 and 1963 these birds were bred *inter se,* and 41 F_2 individuals were reared, including 23 males. In 1963 and 1964 a number of third and fourth generation birds were produced but not studied as they were of varied and uncertain origins.

For an evaluation of male morphological phenotype variations, a "hybrid index" system was utilized, similar to that used previously in studies of Mallard x Black Duck (*Anas rubripes*) hybrids (JOHNSGARD, 1961). Feathers were chosen from various areas, which in the nuptial plumages are distinctly different in the two species, to provide the basis for the hybrid index. These areas and patterns are listed below:

Outer Rectrices: Predominately white in Mallard; brownish with narrow white edge on outer vane in Pintail.

Outer Scapulars: Broad and rounded, with vermiculated grayish-brown throughout in Mallard; black centrally, with gray edges and vermiculations in Pintail.

Secondary (Greater) Coverts: With narrow terminal black edge and subterminal white band in Mallard; with broad terminal cinnamon-buff edge in Pintail.

Central Upper Tail Coverts: Glossy, greenish-black in Mallard; ashy-brown with lighter edges in Pintail.

Breast: Chestnut-brown over most of vane in Mallard; unpigmented in Pintail.

A gradient of three intermediate feather conditions was selected from hybrid feathers. Feathers from F_1 males were used to establish mid-points between the parental conditions, and from various F_2 males to provide the rest of the gradient. Hybrid index values given these feathers were 0 for Mallard phenotype, 1 for appearance approaching Mallard phenotype, 2 for intermediate appearance, 3 for appearance approaching Pintail phenotype, and 4 for Pintail phenotype. Other measurements, such as bill and foot colors, culmen and wing lengths, and body weights were also obtained but proved less usable for establishing a hybrid index. The index values obtained for each bird from these five feather areas were then totalled, resulting in a cumulative plumage hybrid index. A maximum cumulative hybrid index of 20 therefore represents a "pure" Pintail phenotype, while a "pure" Mallard phenotype would score 0. A summary of the hybrid index values obtained for the 4 F_1 and 23 F_2 males is presented in Table 1. It may be seen that among the F_2 males there occurred a few individuals which approached but did not quite reach pure parental phenotypes, while the majority of males clustered

TABLE 1

Plumage hybrid indexes obtained for F_1 and F_2 males.

Individuals	Tail	Scapulars	Wing Coverts	Tail Coverts	Breast	Total
F_1 Generation						
B	0	2	4	1	2	9
C	3	2	2	2	2	11
D	2	2	2	2	3	11
A	3	2	2	2	3	12
F_2 Generation						
C	0	0	1	1	0	2
U	2	1	1	0	0	4
F	0	1	1	3	2	6
V	3	1	1	1	1	7
R	0	1	2	2	2	7
Q	1	2	1	3	1	8
O	3	1	1	0	3	8
P	1	1	2	2	3	9
J	3	2	2	0	1	9
I	3	1	2	3	1	10
E	2	2	3	1	2	10
N	3	2	2	1	3	11
G	3	3	3	1	2	12
S	3	3	3	2	2	13
W	3	3	2	3	3	14
T	4	2	2	3	3	14
M	3	3	3	3	2	14
L	3	3	3	3	2	14
D	2	3	3	3	3	14
K	3	2	4	3	3	15
B	3	3	2	3	3	14
H	4	3	4	3	3	17
A	4	3	3	3	4	17
Average:	2.4	2.0	2.2	2.0	2.1	10.7

in the intermediate area. In spite of this central clustering, a definite segregation of Mallard-like and Pintail-like plumage features did appear. PHILLIPS (1921) reported considerably less segregation of parental plumage features in the F_2 generation (16 males) he bred, as well as in a backcross to pure Pintail, than occurred in crosses between Mallards and more closely related forms such as Black Ducks, Florida Ducks (*A. platyrhynchos fulvigula*), and Gray Ducks (*A. superciliosa*). With respect to our data, it appeared that all of the feather patterns exhibit polygenic inheritance, resulting in continuous gradients between the parental types. Furthermore, in feather areas where the parental types differ in two or more characteristics (such

as pigmentation patterns and shape of vane) these characteristics appeared to be inherited independently of one another. Thus, it was sometimes difficult to assign an index value that exactly fit the reference gradient.

From this group of 23 F_2 males, individuals that provided representative Mallard-like and Pintail-like phenotypes as well as intermediate forms were selected for behavioral study. Unfortunately, both the most Mallard-like individual (C) and the most Pintail-like individuals (A & H) died before they were analyzed behaviorally. However, 14 individuals that exhibited plumage hybrid indexes from 4 to 15 were available for study. These 14 males plus 2 female hybrids were placed on a pond that contained a number of other waterfowl, including wild and domestic Mallards and a few Pintails. Observations of sexual activity were made through the winter and spring of 1965, supplemented whenever possible by filming these displays with a 16 mm cine camera. Approximately 800 feet of film were obtained and were the basis for some of the critical behavioral comparisons that were made, in addition to aiding in the subsequent establishment of a behavioral hybrid index.

COMPARISON OF PARENTAL MALE BEHAVIOR PATTERNS

The pair-forming displays of both parental species are relatively well known as a result of the work of LORENZ (1951-1953), WEIDMANN (1956), JOHNSGARD (1961), and SMITH (1963). A short review of the major male displays which occur during pair formation in the two species may be made, however, to point out the similarities and differences in the two forms.

Grunt-whistle (LORENZ, 1951-1953): The Grunt-whistle is shared by both species, and is performed in a nearly identical manner by each. It basically consists of the male flicking his bill backward and upward through the water, throwing a shower of droplets toward the "courted" bird, then rearing up and back in the water, and finally shaking the tail after settling back to the normal position. In both species a whistle is uttered during the display, followed by a low grunt.

Head-up-tail-up and Nod-swim (LORENZ, 1951-1953): This display sequence is present in both species, but differs considerably in the two. During the Head-up-tail-up, the head is raised while the tail is strongly lifted. The bill is then pointed to a specific female ("bill-pointing"), and a call is uttered. The Mallard performs this pointing while the tail is still raised, whereas the Pintail lowers the tail just prior to pointing. The male Mallard remains in this pointing posture only a short time, but the Pintail

male reorients the body into a straight axis with the head and holds this "Attention" (VON DE WALL, 1961) or "Facing" (JOHNSGARD, 1965) position momentarily. The Mallard normally proceeds from the Head-turning directly into Nod-swimming, although a small percentage of Head-up-tail-ups are not followed by Nod-swimming (JOHNSGARD, 1961). Nod-swimming in the Mallard consists of a rapid, often semi-circular swimming movement with the head and neck held low over the water, and usually terminates in Turning-the-back-of-the-head (LORENZ, 1951-1953) toward the female. In the Pintail Nod-swimming is essentially absent, and at most consists of a few inconspicuous jerky head movements as the bird swims forward.

Down-up (LORENZ, 1951-1953): This display occurs in the Mallard but not the Pintail and is clearly a ritualized form of drinking. In the Mallard, as in 11 other species of *Anas* which are known to perform it (JOHNSGARD, 1960), the Down-up consists of quickly lowering the bill into the water while simultaneously raising the hindquarters. The bird then quickly lifts the head and bill while simultaneously uttering a multisyllable whistle. In Mallards, the Down-up is performed with about the same approximate over-all frequency as the two displays listed above, but appears to represent the strongest behavioral repsonse to female stimuli (JOHNSGARD, 1961).

Burp (LORENZ, 1951-1953): The Burp does not occur as an independent display in the Mallard and is only expressed as an integral part of the Head-up-tail-up. In Pintails it is a very common and independently performed posture and call. The display consists of lifting the head by stretching the neck vertically, tilting the bill downward slightly, and uttering a flute-like call.

Chin-lifting (VON DE WALL, 1963). Chin-lifting, which is distinctly ritualized in the Pintail, is basically an agonistic display between males, but occasionally appears as a greeting display to females. It consists of one or more rapid upward movements of the bill, silently performed. Evidently no homologous movement is present in the Mallard although a slight chin-lifting is associated with Turning-the-back-of-the-head.

Other displays: Bridling (LORENZ, 1951-1953) is the usual post-copulatory display of both species, but in Mallards this is immediately followed by Nodswimming. In neither species does Bridling normally occur during social pair-forming display. Mock-preening (LORENZ, 1951-1953)

behind the wing occurs in the same manner in both species, but is not a commonly performed display. Likewise the Introductory Shaking (LORENZ, 1951-1953) occurs in the same manner in both species. The male Mallard has a double-syllable "conversation", call, or "Raeb-raeb", which is lacking in the Pintail.

COMPARISON OF HYBRID MALE BEHAVIOR PATTERNS

Grunt-whistle: This display (Fig. 1) was exhibited by all the F_2 individuals studied (Table 2). No differences were noted in the form of the display as performed by the hybrids from that of the parentals. It has been found previously (JOHNSGARD, 1961) that in Mallards the Grunt-whistle is the most commonly performed of the major male pair-forming displays (41 percent of 3,018 observed major displays) and that it is especially typical of "low intensity" displays which presumably result from minimal stimuli. In the hybrids it was found (Table 2) that the Grunt-whistle ranged from 56 percent to 82 percent of the total major displays observed in each individual, and averaged 68.5 percent. This high frequency of Grunt-whistles is probably a reflection of the generally reduced sexual display activity of the hybrids.

TABLE 2

Summary of Major Displays Recorded for 14 F_2 Males

Individual	Total No. Displays	Grunt-whistle	Head-up-tail-up	Grunt-whistle, Head-up-tail-up Sequence	Down-up
U	49	34 (69%)	7 (14%)	6	8 (16%)
F	11	8 (73%)	3 (27%)	1	–
V	44	28 (64%)	14 (32%)	10	2 (4%)
O	5	3 (60%)	2 (40%)	1	–
R	36	23 (64%)	7 (19%)	4	6 (17%)
P	7	5 (72%)	2 (28%)	–	–
J	15	10 (66%)	5 (34%)	2	–
E	13	9 (69%)	4 (31%)	–	–
S	47	32 (68%)	15 (32%)	10	–
W	9	5 (56%)	4 (44%)	2	–
T	11	9 (82%)	2 (18%)	2	–
L	9	7 (78%)	2 (22%)	1	–
D	8	6 (75%)	2 (25%)	–	–
K	19	15 (79%)	4 (21%)	1	–
Total:	283	194	73	40	16
Average:		68.5%	25.8%		5.7%
Range:		56%–82%	14%–44%		0–17%

Head-up-tail-up—Facing—Nod-swim: The first phase of this display is identical in both species and in the hybrids (Fig. 2). The subsequent phases, however, varied considerably in the hybrids. The tail-lowering and bill-pointing component was either Pintail-like (eight individuals) or Mallard-like (three individuals) in 11 hybrids. Nine of the eleven performed Facing in a typical Pintail fashion, while the other two were Mallard-like. The performance of Nod-swimming was more variable, with three individuals judged Pintail-like (no obvious Nod-swim), three performed a rudimentary Nod-swim, four performed an intermediate Nod-swim, and one performed a normal Mallard-like Nod-swim. Although the Head-up-tail-up—Facing—Nod-swim was observed in the other three males studied, no films were obtained; therefore, these individuals could not be evaluated critically for these differences. Although each individual normally performed these various phases of this display sequence without variation, two aberrant instances were noted. One F_2 male (individual U) once performed the bill-pointing, Facing and Nod-swim sequence without the preliminary Head-up-tail-up. An F_3 male performed a normal Head-up-tail-up, then proceeded into a Bridling display. We have also recorded on film a single instance of this irregular display sequence performed by a pure Pintail drake. This situation is similar to that mentioned by LORENZ (1958), in which an F_2 Bahama Pintail × South American Pintail (*Anas bahamensis* × *Anas georgica spinicauda*) began a Bridling display and then performed a Head-up-tail-up. Such abnormal "linkage" of displays or display components may be a result of abnormal arrangement of the genetic controlling factors for these displays.

In several species of *Anas* the Grunt-whistle and Head-up-tail-up are associated as a display sequence, in which the latter display follows the Grunt-whistle after an interval of a few seconds. Such species include most of the "green-winged" teal and the "austral" teal (JOHNSGARD, 1965), but neither in the Mallard nor the Pintail is this "linkage" strongly evident. In the Pintail a significant proportion (SMITH, *in litt.*, reports 6.9 percent) of Grunt-whistles are followed shortly by Head-up-tail-ups. This sequence occurs occasionally in Mallards, but a definite "linkage" is not evident. However, no quantitative data on this are available. As shown in Table 2, a substantial percentage of Grunt-whistles in the hybrids were followed by Head-up-tail-ups, ranging from apparently none in three males (although sample size for these is small) to as many as 40 percent in individual W, and averaging 20.6 percent for all 14 males. This apparently increased tendency toward sequential "linkage" of the two displays cannot be readily

Fig. 1. Early (right) and late (left) phases of Grunt-whistle display as performed by hybrids. The nearer individual ("U") has a plumage hybrid index of 4.

Fig. 2. First phase of Head-up-tail-up, performed by F2 individual "M", with plumage hybrid index of 14.

explained, but presumably is genetically regulated and thus subject to alteration through hybridization.

Down-up: The Down-up was performed by only three of 14 males, all of which executed the display in typical Mallard form. None of the other males were observed to perform even a rudimentary version of the Down-up, suggesting genetic control of this display by a relatively few genes. The relative frequency of occurrence of the Down-up display in these three individuals was considerably less than the 36 percent reported earlier for Mallards (JOHNSGARD, 1961). The maximum hybrid incidence was observed in individual R, in which the Down-up comprised 17 percent of the total of the three major male displays. The most likely explanation for this low incidence was the lack of adequate stimulus, since this is a "high intensity" display which is often performed by several males almost simultaneously (JOHNSGARD, 1961).

Burp: The Burp was observed in only two individuals (K and W). In both, the form of the display was somewhat aberrant, and no call was heard during the neck-stretching. Unlike the typical Pintail Burp, the head was lifted up and back in a manner slightly resembling preflight neck-jerking. In these two males this display was observed a number of times (more than ten in each), but it was relatively inconspicuous and possibly occurred in even more rudimentary form in other hybrid males. Considering that this is the most frequent display of the male Pintail, its infrequence in the hybrids is surprising, although an independent Burp is lacking in Mallards.

Chin-lifting: This display was exhibited by five individuals (D, E, K, P and W) and was performed in typical Pintail fashion. As in that species, it usually occurred in agonistic situations. Like the Down-up, this display appeared in "all or none" form and thus is probably also regulated by only a few genes.

Other displays: Bridling was not observed in any F_2 males. Introductory Shaking was present in unmodified form, but Mock-preening was not observed. The "Raeb-raeb" call of Mallards was probably present in all individuals, but the male hybrids had greatly reduced vocalizations (a common situation in interspecific duck hybrids), and this point was not established with certainty.

General Activity: Perhaps because of the small number of hybrid females present (14 males to 2 females), considerable homosexual behavior was exhibited by the males. Mutual precopulatory Head-pumping (JOHNS-

GARD, 1965) was frequently observed between males, and certain males were closely associated with other individuals. These "pairs" tended to rest, feed, and display together. In many instances the pair-forming displays observed in the F_2 males appeared to be directed toward other males.

No copulations were observed in the hybrids, and in general a distinctly reduced incidence of display in the hybrids was apparent. Although both Mallards and Pintails on the same pond were active in sexual display throughout the winter and spring, the hybrids displayed only sporadically. They did not enter into the social display groups of either species, nor did they actively "court" female Mallards or Pintails, but rather displayed among themselves. Of the 14 males, four (R, S, U, and V) were fairly active, but these, too, largely displayed to one another. It is possible that the absence of a large number of hybrid females was a partial cause of this general inactivity, or perhaps because of their composite genetic stimulus-response systems the available female stimuli were not "correct". LORENZ also has found a reduction in sexual activity in the interspecific hybrids he has studied (DAGMAR KALTENHAUSER, pers. comm.), and believes that this was caused by generally poor health in the hybrids. Likewise, PHILLIPS(1915, 1921) found that the Mallard x Pintail hybrids that he bred had low vitality. The hybrids used in the present study, however, appeared to be in good physical condition. Such a reduced sexual activity of the hybrids would probably preclude the possibility of their obtaining wild mates of either species in a free-choice situation, and thus might contribute toward maintaining isolating mechanisms in spite of apparently complete hybrid fertility.

Behavioral Hybrid Index: Variability in the displays of the F_2 males allowed for the estabishment of a behavioral hybrid index similar to that used for plumage characters. A four-point scale was likewise adopted, with values of 0 and 3 respectively representing Mallard-like and Pintail-like extremes for each character used, according to the following criteria:

Head-up-tail-up, Nod-swim complex:

A. Position of tail during bill-pointing Mallard-like, with tail raised (0), or Pintail-like, with tail lowered (3).

B. Degree of body turn toward female Mallard-like, with partial turn (0), or Pintail-like, with complete turn (3).

C. Degree of Nod-swimming Mallard-like, with fully developed Nod-swim (0), intermediate (1), rudimentary (2), or lacking, as in Pintail (3).

Down-up: Present, as in Mallard (0), or absent, as in Pintail (3).

Burp: Absent, as in Mallard (0), or present, as in Pintail (3).

Chin-lifting was not used as an index character. Although this display was observed on a few occasions in five of the Pintail-like hybrids, it was inconspicuous and readily overlooked, thus may also have been present in other hybrid individuals as well. A cumulative behavioral hybrid index ranging from 0 (or completely Mallard-like) to 15 (or completely Pintail-like) was thus possible (Table 3).

TABLE 3

Behavioral Hybrid Indexes of 11 F_2 Males

Individual	Head-up-tail-up Complex			Down-up	Burp	Total
	Bill-pointing	Turning	Nod-swimming			Behavioral Index
R	0	3	0	0	0	3
V	3	0	1	0	0	4
F	0	0	2	3	0	5
U	3	3	1	0	0	7
J	0	3	3	3	0	9
O	3	3	1	3	0	10
S	3	3	1	3	0	10
D	3	3	2	3	0	11
L	3	3	2	3	0	11
W	3	3	3	3	3	15
K	3	3	3	3	3	15
Average:	2.2	2.5	1.7	2.2	0.5	9.1

Of the F_2 males studied, sufficient data were obtained on 11 to allow for establishment of a behavioral hybrid index for these individuals. Two of these individuals exhibited the maximum Pintail hybrid index of 15, while one approximated the Mallard extreme with a cumulative index of 3. The other eight males fell between these extremes, and an over-all average hybrid index value of 9.1 was achieved. This is slightly to the Pintail side of the expected mean (7.5) and may indicate a biased sampling or weaknesses in the original hybrid index values chosen. In any case, a considerable degree of individual variation is evident, presumably resulting from segregation and independent assortment of genes regulating behavioral traits. Individual U, for example, exhibited a Mallard-like Down-up, but also executed the bill-pointing and Facing components of the Head-up-tail-up complex in Pintail-like fashion. Finally, its Nod-swimming was done in a nearly Mallard-like manner. The only explanation for such a mixture of these highly stereotyped display components in this individual is that they were inherited in varying degrees from both parental species.

In general, individuals which inherited a majority of plumage characteristics approaching one parental extreme also exhibited behavioral characters

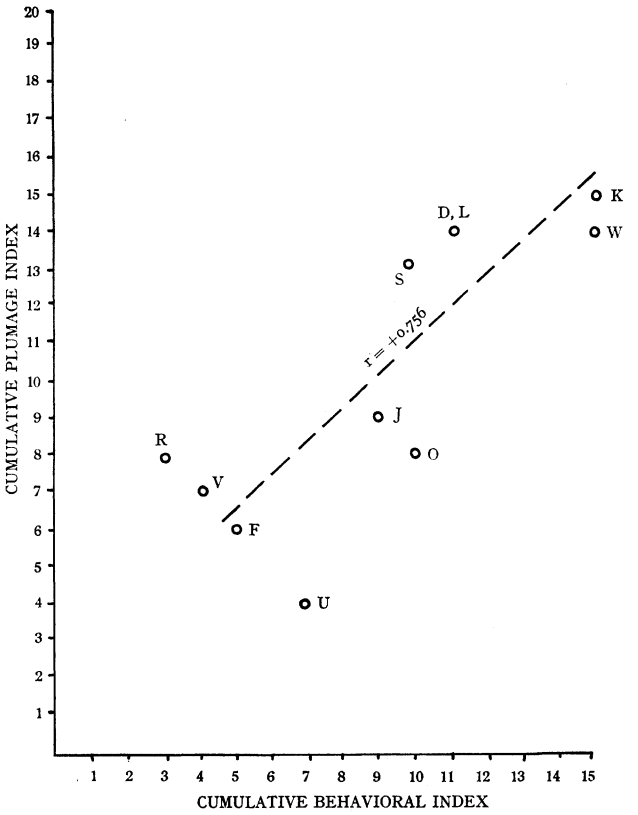

Fig. 3. Correlation between plumage and behavioral hybrid indexes obtained for eleven F_2 males.

typical of that species. A correlation coefficient of + 0.756 was calculated between the behavioral hybrid index and the plumage hybrid index values obtained from the 11 F_2 males for which data were complete (Fig. 3). The correlation is not a perfect one, but some of the deviations may have resulted from errors of estimation, and a tendency toward the common inheritance of both plumage and behavioral characteristics is strongly indicated. This is ample evidence for believing that the species-typical plumage and display traits of Mallards and Pintails have a very similar genetic basis. With regard to both the behavioral and plumage features studied, the considerable segregation and independent assortment observed would suggest fairly simple genetic control of each of these characters, probably involving relatively few genes. This might be expected, considering that all these traits are of probable significance as species-specific isolating mechanisms,

and thus must be sensitive to relatively rapid modification and divergence under pressures of natural selection as speciation progresses. This should provide further reason for seriously questioning the use of male plumage patterns or male pair-forming displays as primary taxonomic criteria in establishing generic or other major taxonomic categories.

SUMMARY

Through controlled breeding in captivity, 23 F_2 male hybrids between Mallards and Pintails were produced. Breeding plumages in these males were analyzed by the hybrid index method and were found to exhibit considerable variation in a manner suggesting polygenic control.

The pair-forming displays of 14 F_2 males were studied, and sufficient data on 11 of these were obtained to permit the establishment of a behavioral hybrid index. It was found that all the hybrids performed individual displays or display components almost identical with those of the parental species where such displays are very similar in both species (Grunt-whistle), or performed intermediate displays of varying combinations where the homologous displays are present but differ somewhat in the parental species (Head-up-tail-up—Nod-swim sequence). With regard to displays that are present in only one of the parental species, the individual hybrids either performed these in an "all or none" fashion (Down-up, Chin-lifting) or rudimentary or aberrant versions of them (Burp, Raeb-raeb call). No displays occurred in the F_2 hybrids that were not typical of one or both parental species, although an F_3 male performed one display out of context, in that a post-copulatory display (Bridling) occurred during social display and was sequentially "linked" to a typical pair-forming display (Head-up-tail-up).

A significant positive correlation ($r = +0.756$) between the inheritance of behavioral and plumage characteristics in the F_2 generation was found, based on comparison of hybrid index scores determined for 11 individual males. It is concluded that both groups of features are under genetic control, and in most cases probably involve relatively few genes. Such relatively simple genetic control has both evolutionary and taxonomic implications.

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ZUSAMMENFASSUNG

Durch passende Aufzucht in Gefangenschaft wurden 23 F_2-Bastarderpel zwischen Stock- und Spiessenten gewonnen. Ihre Brutkleider fielen, wie die Bastardindexmethode zeigte, so verschieden aus, wie bei polymerer Vererbung zu erwarten.

Die Balzspiele von 14 F_2-♂♂ wurden untersucht, und 11 von ihnen lieferten genug Daten, um einen Bastardindex des Verhaltens aufzustellen. In Verhaltensweisen, die bei beiden Elternarten einander sehr ähneln, wie der Grunzpfiff, stimmten auch alle Bastarde untereinander fast völlig überein; etwas stärker voneinander abweichende Handlungen wie Kurzhochwerden und folgendes Nickschwimmen zeigten die Bastarde in intermediären, individuell verschiedenen Kombinationen. Handlungen endlich, die nur eine der beiden Elterarten hat, zeigten die einzelnen Bastarde entweder ganz oder gar nicht, so das Ab-Auf und Kinnheben, oder rückgebildet oder sonst abweichend, so das Aufstossen und räb-räb-Rufen. Die F_2-Bastarde zeigten keine einzige Handlung, die nicht mindestens einer der beiden Elterarten eignet; aber ein F_3-♂ tat es, indem er im Gesellschaftsspiel das normalerweise nur nach der Begattung bekannte Aufreissen dem Kurzhochwerden unmittelbar folgen liess.

Auf Grund von Vergleichen der beiderlei Bastardindices bei 11 ♂♂ ergab sich zwischen der Erblichkeit der Verhaltens- und Gefiedermerkmale ein statistisch sicherer Korrelationskoeffizient von + 0,756, woraus folgt, dass beiderlei Merkmale genetisch kontrolliert sind und zwar vorwiegend von vergleichsweise wenig zahlreichen Genpaaren. Solch eine schwachpolymere Vererbungsweise hat sowohl stammesgeschichtlich wie systematisch bedeutsame Folgen.