

THE CONDOR

VOLUME 46

JULY-AUGUST, 1944

NUMBER 4

THE NATURE OF HERITABLE WILDNESS IN TURKEYS

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INTRODUCTION

The field work on which this report is based was conducted in the Ozark region of southern Missouri in the years 1939 to 1943. The objectives of the study have been to determine insofar as possible the fundamental, heritable differences between wild and domestic turkeys, and to compare the ecological relationships and general productivity of existing turkey populations which differ in degree of "wildness." The problem is of practical importance in wild turkey management because the intermixing of the domestic strain with wild populations has had certain adverse effects upon the hardiness of the native turkeys of Missouri. It is of theoretical importance in offering an opportunity better to understand the nature of wildness in a locally adapted, indigenous race of birds.

For encouragement and guidance in this study I am deeply indebted to Dr. Alden H. Miller of the University of California. Grateful acknowledgments also are extended to the Charles Lathrop Pack Forestry Foundation, which financed a preliminary period of study at the University of California, to the Missouri Conservation Commission through whose Federal Aid Program the field investigation was made financially possible, and to the Martens Fund of the Museum of Vertebrate Zoology which supported the final period of study.

THE PROBLEM OF HYBRIDIZED TURKEYS

The Wild Turkey, *Meleagris gallopavo*, is confined to North America. There are five recognized geographic races, each confined to a sector of the total range. The Eastern Wild Turkey, *M. g. silvestris*, is native to the eastern hardwood forests of the United States, from the Atlantic seaboard to the Great Plains, and south to the Gulf of Mexico. The Florida Turkey, *M. g. osceola*, occupies the peninsula of Florida. In the chaparral country of Texas and northeastern Mexico occurs the Rio Grande Turkey, *M. g. intermedia*, and in the southern Rockies the Merriam Turkey, *M. g. merriami*. The Mexican Turkey, *M. g. gallopavo*, occurs on the plateau lands on both sides of the Sierra Madre, from northern Chihuahua and Sonora to Oaxaca and Vera Cruz. A sixth race, *M. g. onusta*, recently has been described by Moore (1938) from northern Sonora, but its validity has not yet been confirmed, and for simplicity here all the turkeys of the Sierra Madre are regarded as *M. g. gallopavo*.

Each local form is presumed to be specifically adapted to its native range. These adaptations are probably far more elaborate than the aspects of external anatomy so far used as taxonomic criteria. There may be fundamental differences, not only in morphology but also in physiology and psychology, which accommodate each local population to its particular environment. The nature and sharpness of these assumed local adaptations in wild turkeys are as yet unknown.

Unlike any other American gallinaceous bird, the wild turkey has a domestic counterpart, which is known to have been derived from the Mexican race, *M. g. gallopavo*. The domestic strain has been subdivided into many varieties, all of which are adapted to existence in a symbiotic relationship with man. In the capacity of a barnyard fowl the tame turkey has been transplanted to most sections of the North American continent, and in fact, over a large part of the world.

Although the great majority of domestic turkeys within the continental United States are unconfined and are allowed to wander at large over farms and woodlands, there are, to my knowledge, no authenticated instances in which they have become permanently established in the wild. Even within the present range of wild turkeys, the domestic strain apparently is unable to thrive on its own without the protective custody of human beings. There are many instances of barnyard turkeys straying to the woods and independently raising one or more generations of young, but sooner or later these incipient free colonies disappear. On the basis of this *prima facie* evidence it seems safe to conclude that the domestic turkey is unable to thrive in a wild state anywhere within the bounds of the United States; at least it has shown very little ability to do so. Something inherent in the bird, derived either from its southern ancestry or more probably from its long tenure in the barnyard, appears to prohibit its establishment as a member of our wild fauna. This condition may be referred to as a state of heritable domesticity, or in a negative sense, lack of "wildness," the latter term connoting in addition to wariness and secretive behavior the ability to exist in free and independent populations.

Hybridization of wild and domestic strains.—The domestic turkey is quite capable of interbreeding with most, and probably all, races of wild turkeys. Accidental intermixing probably has taken place at one time or another in every section of the United States or Mexico that supports wild turkeys. This has been an inevitable result of the widespread distribution of the barnyard bird.

In some parts of the United States hybridization has been brought about more or less deliberately. In an effort to restore diminishing populations of wild turkeys, it has been common practice for some conservation agencies and private shooting clubs to propagate, and to liberate in the woods, semi-wild turkeys that are actually hybrids between wild and domestic strains. Hybrid stocks are resorted to because of the extreme difficulty of raising wild turkeys in captivity. It is intended that the hybrid birds "go wild," and establish themselves in nature, in time giving rise to increased populations of "wild" turkeys. In some states, notably California, this procedure has been followed in an effort to introduce the turkey into new range. No introduction of this sort has yet resulted in the establishment of a permanent turkey population outside the original range of the species, and there has been much controversy over the effectiveness of artificial replenishments within the native range. Of one result, however, there can be no doubt: germinal elements of the domestic lineage have been injected into great segments of the remaining wild stocks. In my opinion modification of racial purity induced by deliberate releases of "semi-wild" birds has been far more prevalent than that resulting from the accidental crossing of stray domestic stock with wild birds.

Of all the native subspecies, *silvestris* probably has been subjected to the greatest amount of hybridization with the domestic strain. This is due partly to the number of barnyard birds existing in its range (roughly proportional to the number of farmsteads); of even greater importance, however, has been the extensive restocking with hybrid birds in the eastern United States.

Since the domestic turkey is apparently unadapted to a wild existence, it is logical

to suspect that the hybrid birds may be less fitted for independent life than a locally adapted native race. Until now this has not been proven.

The practical problem of hybrid turkeys in Missouri.—The original wild turkey of Missouri belonged to the eastern race, *M. g. silvestris*. Here, as elsewhere in the range of *silvestris*, hybridization has occurred. Bennitt and Nagel (1937) accurately appraised the situation as follows: "Biologically, many of the turkeys now inhabiting the Missouri Ozarks represent a mixed strain . . . [Hybridization] has come about in two ways—by natural mixture when tame turkeys stray from the farms or wild turkeys are attracted by domestic birds, and by the release of artificially propagated stock which is mixed to begin with . . . Over 11,000 birds, some of domestic and the rest of mixed stock, have been released in Missouri during the past ten years."

Since the above statement was written, liberations of hybrid turkeys have continued each year in Missouri, although in lessening numbers. Recent additions raise the total releases in the state to approximately 14,000 birds. The turkeys liberated in the past few years have more closely resembled the eastern wild strain than those of earlier releases, but they are hybrids nonetheless. (Liberations of artificially propagated turkeys will cease in Missouri after 1943.)

Not all parts of the Missouri turkey population have been equally affected by the liberations of hybrids. It has been an accepted policy to release birds only on managed and protected areas, which, in Missouri, means principally the state game refuges and certain cooperatively managed areas, chiefly on National Forests. Probably three-quarters of the 14,000 hybrids released to date have been placed on the state refuges. Hence hybridization has to a considerable extent been localized.

The localization of past liberations on the refuges raises a serious practical question: if the hybridized turkey populations are less thrifty than the native populations and less able independently to sustain themselves, then the whole management program has been retarded, and perhaps actually endangered, by the plan of restocking, since hybridization is now most prevalent among the managed segments of the state population of turkeys. From the practical and theoretical standpoints it seems important that a critical investigation of turkey restocking be made in order to evaluate the real gains and losses resulting from the liberation of hybrid birds.

Fortunately, there are some parts of the turkey range in Missouri that have not been restocked and where the turkeys appear to be almost pure *silvestris*. Four of the state refuges fall in this category. This leaves open the possibility of perpetuating the native strain, and perhaps of expanding it by natural spread. It also makes possible a comparative study of the wild and hybrid types of turkey under field conditions, a procedure followed in this study.

The fundamental question of inherent wildness in turkeys.—What is this attribute which we loosely call "wildness" that is present in the native turkey and deficient in the domestic bird? What does it mean in terms of specific behavior patterns of the individual turkey and of survival mechanisms in populations? In short, exactly how is the native race of Missouri turkeys adapted to existence in the Ozark region, and what is lacking in the domestic strain that precludes its success in this environment? To what extent do the hybrid stocks possess "wildness?"

The term wildness commonly is used indiscriminately to denote both inherent and acquired characteristics in an organism. Either or both may conform to the popular notion of wild behavior. Thus, domestic turkeys that stray to the woods and lose their familiarity with man are said to have "gone wild." As used here in reference to turkeys, wildness will refer only to the inherent behavior patterns and other adaptations that

permit the successful existence of free populations. I do not overlook the existence of acquired wild characteristics in turkeys; but their study is a separate problem.

Inherent wildness must be passed in some form from parent to offspring, through the basic physiological and anatomical mechanisms of the individual organism. A native turkey chick must be born wild. Are there criteria by which this attribute may be recognized?

Gerstell and Long (1939) investigated one phase of the problem. Measurements were made in the laboratory of the comparative activity patterns and metabolic rates of two strains of turkey chicks obtained from the Pennsylvania state game farm, one of which was wilder than the other. The wilder juveniles were derived by crossing hybrid game farm hens with wild gobblers. The tamer chicks came from pure game farm stock, that is, from hybrid hens crossed with hybrid gobblers. Both groups of juveniles were hybrid, but the degree of wildness differed because of the two types of sires used. The following differences in the behavior and the metabolism of the juveniles are reported: (1) At the age of 12 hours, body temperature was found to be slightly higher in the wilder chicks, and the respiratory rate also was higher. (2) Measurements of the muscular activity of chicks in darkened cells showed that the wilder birds tended to be the more active, making more frequent and violent movements than were exerted by the game farm hybrids. (3) Measurements of the metabolic rates of juveniles varying from 2 to 48 days in age indicated a slight average difference between the strains, metabolism being more rapid in the wilder birds; their data on this point, however, are far from conclusive.

It is unfortunate that Gerstell and Long did not include in their study some pure wild and some pure domestic birds, so that the total divergence in juvenal activity patterns between the two parent strains could have been measured. Significant differences in metabolic rates might also have been demonstrated. The relative placement of their two hybrid stocks in the span of divergence could then have been determined.

In any event, these studies point toward the existence of inherent, physiological distinctions between turkeys of varying degrees of wildness, which distinctions are undoubtedly associated with the phenomena of wild and tame patterns of behavior.

The present study attempts to extend this concept of the nature of wildness in turkeys by (1) defining the differences in field behavior, productivity and ecological relationships in established populations of turkeys of varying degrees of wildness, and (2) by seeking within the turkeys themselves a more adequate definition of the anatomical and physiological bases of wildness than that supplied by Gerstell and Long.

Difficulties in the study of wildness in turkeys.—A wild turkey in confinement cannot exhibit the normal behavior patterns of a free bird; the relations of the turkey to the Ozark environment can be observed only in natural populations. Since in addition, *silvestris* is an extremely difficult bird to raise and work with in captivity, controlled studies of penned wild and domestic birds were deemed generally impractical; in any event they would tell us little about why the one strain survives in the wild and the other does not.

On the other hand, a direct comparison between wild and tame strains under comparable conditions in the woods is impossible. As previously stated, the domestic turkey does not, and apparently cannot, exist in feral populations. Hybrid turkeys, however, exist in established populations in Missouri, hence they and native birds can be studied under similar circumstances. A field comparison of wild and hybrid populations was selected as the most practical approach to an investigation of wildness in Missouri turkeys.

The use of game farm stocks in the field studies introduces one unknown that reduces the whole comparison of wildness and domesticity to a relative basis; this is the impossibility of defining the genetic make-up of the hybrid birds. There are all degrees of hybridization in turkeys, and the term "hybrid," which has no fixed meaning, may be applied to any of the intermediate types. A later section of this paper includes a history of the game farm stocks in Missouri; it can readily be seen that their genetic background is a hopeless maze. This means, of course, that all measurements given here of behavior phenomena, morphology, and other points of difference, are relative only, as they apply to the basic problem of comparing wildness and domesticity.

In view of these limitations, it is clear that the present study cannot yield quantitative measurements on all points of distinction between a wild and a domestic turkey. I can claim only that various differences in internal and external morphology are shown between wild, domestic and hybrid turkeys. The field studies demonstrate marked differences in behavior and in "survival ability" between *silvestris* and hybrids. Wherever possible, distinctions in behavior are related to the controlling physiological mechanisms in the bird.

METHODS

Field studies.—The comparative field studies were conducted on a selected group of state game refuges, three of which support native turkeys and the other three hybrid populations derived from artificially propagated stocks. Refuge areas were used in these studies because (1) illegal hunting, one of the important factors controlling turkeys in Missouri, could be largely eliminated as a variable, (2) other problems of management, such as the control of fire and grazing, could be handled uniformly, (3) local personnel (refuge patrolmen) were essential in helping to keep records on the several areas, and (4) extensively hybridized turkey stocks exist as established populations only on managed and protected areas.

Work was not conducted with equal intensity on all areas. Most of the detailed life history investigation of the native turkey was carried on at Caney Mountain Refuge in Ozark County, with only supplementary observations made at Wilderness and Drury refuges. Study of the hybrid birds was centered largely on Deer Run and Blue Spring refuges.

Study areas; native turkeys. (1) *Caney Mountain Refuge.*—Purchased by the Conservation Commission (Federal Aid Program) in 1940 as a demonstration turkey management project, Caney Mountain Refuge in three years has become one of the most productive turkey refuges in the state. The population of 10 native turkeys on the refuge area in 1939-40 increased during the study period to 88 birds in the spring of 1943; the increase of turkeys in the zone immediately surrounding the refuge has been nearly as rapid. The area never has been restocked. Irregularities in the plumage color of a few birds indicate some past crossing with the domestic strain, but by and large the turkeys of this refuge, and in fact those of all central Ozark County, are as close to the native type as can be found in the Ozarks.

(2) *Wilderness Refuge.*—Situated in the Irish Wilderness region along the upper reaches of the Eleven Points River, Wilderness is one of the largest state refuges in Missouri. It is operated cooperatively by the Forest Service and the Conservation Commission. This unit was unproductive of turkeys in its early years due to the constant disturbance accompanying a large lumbering operation. In 1941 timber cutting ceased and the residue of native turkeys began to increase. The present turkey population is well above the average for other refuges and is still increasing. Save for the release of 45 hybrid birds in Greenbriar Hollow just south of the refuge in 1937, the native stock has been maintained in relative purity.

(3) *Drury Refuge.*—Drury Refuge is a turkey and deer management project, maintained by the Conservation Commission, but owned privately and operated in part as a livestock ranch. The local turkeys are predominantly native wild stock, although some of the birds show indications of past hybridization with stray domestic stock (light-colored rumps and tails, and traces of albinism).

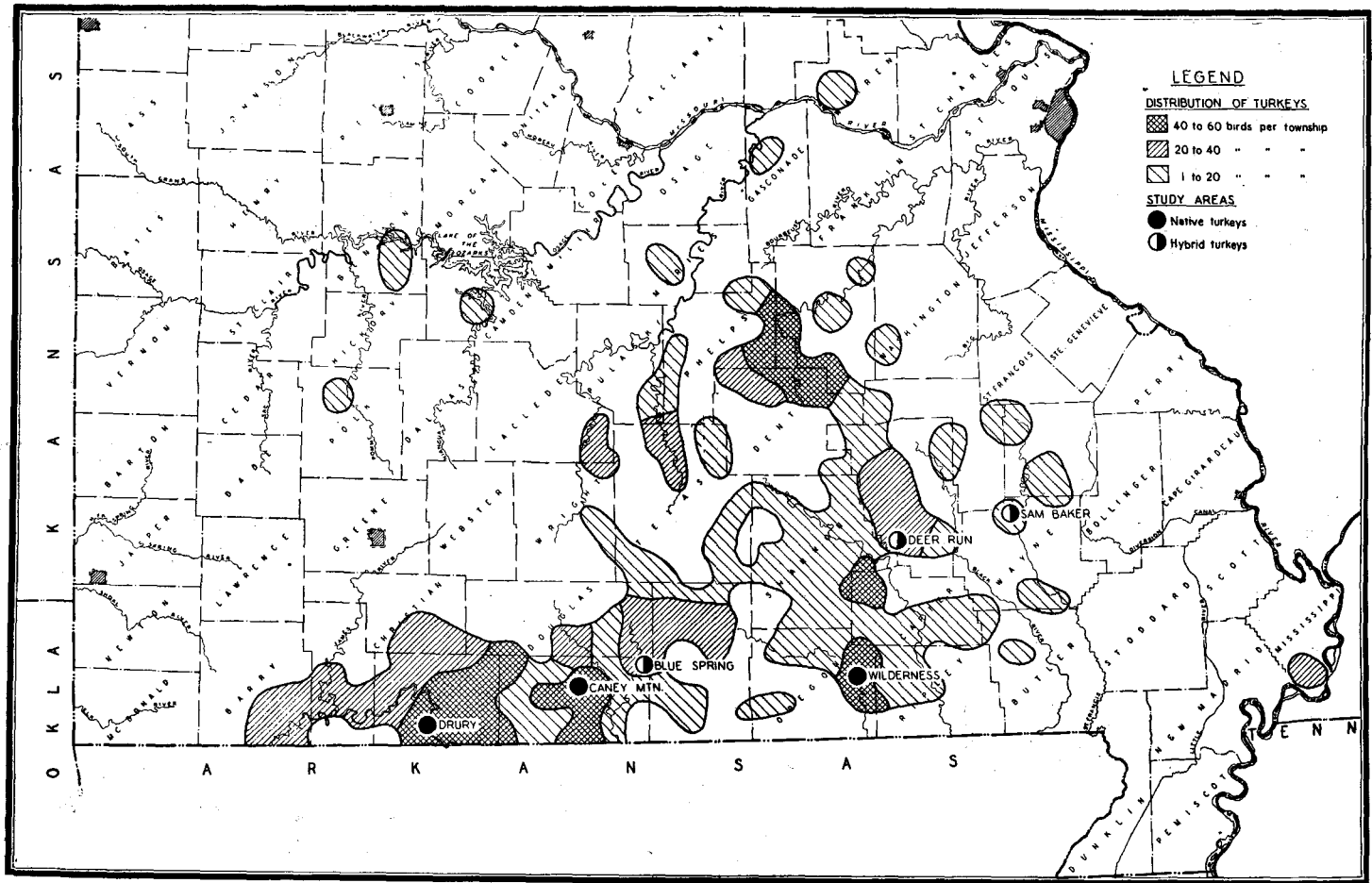


Fig. 19. Occupied turkey range in Missouri in 1942; locations of six study areas.

There are no records of releases on the refuge, but both hybrid and domestic hens have been liberated in a near-by area to the north. In 1942 the neighborhood of Drury Refuge had the highest density of turkeys in the state. This refuge was the site of turkey studies conducted by the Missouri Cooperative Wildlife Research Unit from 1940 to 1942, and some of the data given here were supplied by the Unit through the courtesy of Paul D. Dalke.

Study areas; hybrid turkeys. (4) *Deer Run Refuge.*—Deer Run was one of the first refuges established in southern Missouri; it has been in operation for 19 years. Although there were native turkeys on the area at the time it was made a refuge, repeated liberations of game farm birds have completely hybridized the local stock. This is one of the best examples in the state of an established hybrid population of moderate density, persisting, but not increasing, under favorable conditions of management and protection.

(5) *Blue Spring Refuge.*—Situated in Ozark County within 20 miles of Caney Mountain Refuge, the Blue Spring unit supports a low density population of hybridized turkey stock. The refuge is under Forest Service management, and provides excellent turkey range. The existence of a remnant of native birds just north of the refuge, that apparently overlaps the area occupied by hybrids, makes this an imperfect example of a population derived solely from game farm stock. There is a mixing of native and hybrid birds along that border of the area that results in some natural backcrossing of the hybrid strain to the wild type. In the main, however, the records obtained here relate to the semi-wild birds.

(6) *Sam Baker Refuge.*—From 1933 to 1936 Sam Baker Refuge was the site of the State Turkey Farm. In a battery of pens, hybrid birds were produced in great numbers. Many were released locally (table 1), and hundreds of additional unrecorded birds doubtless escaped from the enclosures. The present dwindling turkey population was derived entirely from the hybrid game farm stock. Only limited records, mostly pertaining to broods, were obtained on this area in the present study.

The study areas in relation to the Ozark turkey range.—The Ozark region is situated in the zone of interspersions of the western prairies and the eastern hardwood forests. The original abundance of wild game, including turkeys, along this border was attested by many early writers. Agricultural development during the past century and a half has eliminated most species of big game, and the turkey has been crowded back into the more rugged parts of the Ozark plateau. Even there, overgrazing, burning and lumbering have greatly altered the range for turkeys, mostly adversely.

It is not within the scope of this paper to consider the relations of the turkey to the Ozark range as a whole. Our principal concern is the comparison of two strains established on refuges where environmental conditions generally have been improved. Sauer (1920) adequately describes the geography of the region and gives a history of its settlement. Miller and Krusekopf (1929) present a classification of the soils of Missouri. Problems of Ozark forestry are discussed by several authors in a bulletin compiled by Hammar and Westveld (1937). A report on the status of wild turkeys in Missouri in 1942 (Leopold and Dalke, 1943) relates the present distribution of turkeys to soils, topography and land use practices.

Table 1

Refuge	The study areas		Years operated as refuge	Liberations of hybrid turkeys 1925-1942 ¹	Turkey population in 1942
	County	Acres			
Native turkeys					
1. Caney Mountain	Ozark	5,500	3	None	140
2. Wilderness	Oregon	12,800	5	45	134
3. Drury	Taney	4,600	4	None	191
Hybrid turkeys					
4. Deer Run	Reynolds	8,380	19	1316	101
5. Blue Spring	Ozark	5,920	7	219	72
6. Sam Baker	Wayne	5,150	16	904	7

¹The population figures for 1942 show the number of turkeys on standard-sized census areas of 120 square miles, within which each refuge is centered.

The fourteen state refuges in Missouri that support turkeys are all situated in sections of the Ozarks having rough topography; most are heavily wooded, the predominant forest type being an oak-hickory association with scattered groves of short-leaf pine and red cedar on the poorer sites (fig. 20). There are, however, differences between refuges in the degree of control of hunting, grazing, fire and other factors of management that influence the welfare of turkeys, as well as in the inherent quality of the various areas for turkey production. In selecting six refuges for study areas, every effort was made to choose sites of comparable desirability from the standpoint of the turkey. No two of the areas are identical in geography or management; but in the main the three on which hybrid populations were studied present, in my opinion, as good an environment for turkeys as the three sites occupied by native stock.

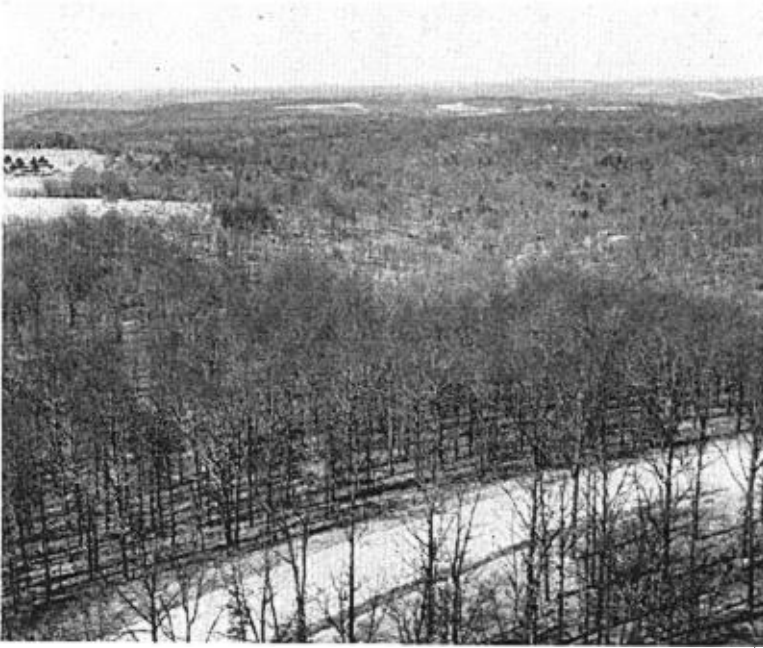


Fig. 20. View north of Siloam Springs fire tower near Blue Spring Refuge. The oak-hickory forest, with scattered short-leaf pines, is characteristic of most of the Ozark turkey range.

In partial substantiation of this claim, table 2 is presented, which compares the six areas on the basis of seven points of management. Examination of this table will disclose that the administrative programs on the six refuges are generally comparable. If there are any advantages in the degree of protection and environmental improvement, they lie with the group of areas stocked with hybrids, all of which have existed as refuges for relatively long periods (table 1).

As regards geographic suitability of these samples of the turkey range, the differences are not great. Drury Refuge is situated in a region of extensive "balds" and open-faced hillsides in the southwestern part of the Ozarks (fig. 21), which is perhaps the best natural turkey range in the state, judging from the distribution of birds in 1942 (Leopold and Dalke, 1943). Sam Baker Refuge is on the extreme eastern edge of the

limestone soils in the Ozarks and borders the region of granitic soils, which is generally inferior as wildlife habitat. The other four areas are situated on the same soil type in the well forested central Ozark region. Because Drury Refuge is admittedly in a superior site and Sam Baker Refuge in an inferior one, some advantage in geographic location may lie with the three areas supporting native birds. Taken as a whole, however, the two sets of study areas are of comparable quality. Differences in the productivity of wild and hybrid populations, which are shown later, could not, I think, be traced back to influences in the environment.

Table 2

A comparison of management practices on the study areas

Refuge	Protection from poaching	Grazing	Recent severe fires	Winter feeding of game	Permanent water supplies	Predator control (approx. take per year)	Human disturbance
Native turkeys							
1. Caney Mt.	Complete	Eliminated in 1941 by fence	None	16 food patches (avge., 1A.)	Moderate	2 wolves 3 foxes	None
2. Wilderness	Some internal poaching up to 1941	Controlled since 1939 by a poor fence; some hogs and cattle gain access	About 3000 acres burned in 1941	None	Adequate	3 wolves 5 foxes 3 bobcats	CCC camp 1936-41; lumbering operation, 1938-41
3. Drury	Complete	Grazed fairly heavily by cattle; few hogs	None	Incidental feeding of corn around deep traps	Moderate	None	Farming and stock handling
Hybrid turkeys							
4. Deer Run	Complete	Eliminated in 1936 by fence	About 2000 acres burned in 1941	4 food patches (avge., 2A.)	Adequate	2 wolves 2 bobcats	CCC camp 1934-42; lumbering operation, 1941-42
5. Blue Spring	Virtually complete	Controlled grazing, under Forest Service permit	None	4 food patches (avge., ½ A.) 1938-40	Adequate	None	CCC camp 1936-39
6. Sam Baker	Complete	Eliminated in 1935(?) by fence	None	6 food patches (avge., 3A.)	Moderate	1 wolf 5 bobcats	CCC camp 1938-39

Assembling of field records.—Caney Mountain Refuge was used as field headquarters. Most of the field records from that area I collected personally, with assistance from the refuge patrolman. However, with simultaneous observations required on a number of refuges, it was necessary to depend for much of the field work on personnel of the Conservation Commission attached to the other study areas.

Three types of data were collected by cooperating observers. (1) Annual winter turkey censuses of the study areas were based largely on the recorded observations of the local refuge patrolmen; I spent from one to five days on each area every winter filling in the gaps in the information handed me by the patrolmen and completing the censuses. (2) Gobbling records were kept by all the field men, who noted at daylight each spring morning the number and vigor of birds gobbling. (3) Summer observations of broods were similarly assembled, each man recording the size and location of broods he might happen upon during the course of other work. Only written records, properly kept in field diaries, were accepted. I visited all the study areas regularly, and assisted in the field work and the checking of records and observations. Acknowledgements are due the refuge field force for the willing assistance given in these tasks.



Fig. 21. Typical "bald" country in eastern Taney County. Drury Refuge, situated in the timbered breaks along the White River, is adjoined by areas of this nature.

All other records, including nesting data, I obtained personally, although most of the nests were originally discovered and pointed out to me by others.

Not all aspects of life history were given equal attention in this study. Emphasis was placed on the particular phases of behavior and population mechanics that might relate to "survival ability" in the two strains, particularly those in which differences between strains were readily apparent. Thus food preferences, roosting and water requirements are treated here only casually, whereas the reproductive cycle is discussed in some detail.

Laboratory studies.—Comparisons of morphological and anatomical features included domestic turkeys as well as the native and hybrid birds. Permission was obtained to handle 28 domestic turkeys on farms near West Plains, Missouri. Measurements and weights of the live birds were taken, and samples of certain feathers were clipped and preserved for color comparisons with other specimens. Photographs of each bird were made.

Similar records were obtained of 74 hybrid birds at Lost Trail Game Farm. An additional 23 hybrids from other sources were handled, including birds trapped on the Robert Gideon ranch in Taney County. The writer's skin collection and that of the Wildlife Research Unit in Columbia jointly include 60 hybrid turkeys from various sources in Missouri.

The whole comparison of turkey morphology was weakened by my inability to obtain an adequate sample of the native *M. g. silvestris* from Missouri. Collecting birds on the refuges was generally inadvisable, and repeated attempts to trap native turkeys, particularly on Caney Mountain Refuge, failed. As an alternative procedure, skins of *silvestris* in several midwestern collections were examined, and morphological data were taken from them for comparison with the domestic and hybrid types. This method had obvious disadvantages in that weights were generally not obtainable, comparative photographs of the live birds could not be had, and the specimens came from all parts of the eastern United States and did not represent the Ozark population. The compensating advantage was that most of the old skins could be assumed to be pure *silvestris*, without trace of hybridization.

In addition to examining grown birds, both alive and as skins, 40 juveniles, representing the wild, hybrid and domestic types, were dissected to obtain gross comparisons of the relative size and development of the brain and certain of the endocrine glands.

Table 3
Number and sources of specimens of turkeys examined

	Number	Totals
Native turkeys		
Skins available in Missouri (collections of the writer and the Research Unit)	4	
Museum of Vertebrate Zoology, Berkeley	2	
Chicago Museum	12	
Kansas Museum, Lawrence	4	
Colorado College Museum, Colorado Springs	1	
Juveniles dissected	4	
	—	27
Hybrid turkeys		
Examined alive, Lost Trail Game Farm	74	
Examined alive, other sources in Missouri	23	
Skins available in Missouri (collections of the writer and the Research Unit)	60	
Juveniles dissected	22	
	—	179
Domestic turkeys		
Examined alive, farms in Howell County	28	
Juveniles dissected	14	
	—	42
		248

WILD AND HYBRID POPULATIONS

PROPAGATION OF HYBRID BIRDS, AND THEIR SURVIVAL AFTER LIBERATION

Sources of liberated stock.—Turkey restocking in Missouri started in 1925. Table 4 summarizes all available records of turkey liberations from 1925 to 1943. Since releases will be discontinued after 1943, this table is a final account of restocking efforts in the state.

In the early years of the restocking program, little attention was paid to the type of turkey released, as witnessed by the following excerpt from the report of the Missouri Game and Fish Department for 1928: "A new method of propagating turkey was inaugurated by the department last spring when it was decided to purchase domesticated hens from farmers whose flocks may have become mixed with wild turkeys. They were released on refuges with the native wild gobblers already on the properties. Some looked upon this in a rather skeptical manner but this method proved unusually successful during 1928. The turkeys crossed readily and the increase was beyond expectations."

This optimistic announcement did not terminate expressions of skepticism: "It is doubtful whether turkey plants of partially domestic strain are effective" (A. Leopold, 1931).

Several years later Blakey (1937) reported: "The immediate failure of these liberations [of domestic hens] brought on a search for the best available wild turkey stock."

In the early 1930's an effort was made to raise on various of the state refuges and parks turkeys that approached the native type. Attempts to produce birds of the pure native strain failed. Accordingly an alternative procedure of "improving" existing hybrid strains was adopted.

The new breeding method was based on the principle of selective breeding toward the wild type, accelerated by annually backcrossing the hens to wild gobblers. Blakey (1937) describes the so-called "wild pen" breeding plan as follows: "Breeding pens of two to four acres each are scattered through the most isolated parts of the native wild

turkey range where native gobblers are available. . . . Gobblers over a wide area about the pens soon become aware of their presence, and, if proper isolation is maintained, will frequent the pens regularly throughout the breeding season. . . . Eggs are collected by pen keepers, . . . and are hatched in electric incubators; the poults are removed to a brooding farm the second day." The juveniles are then raised in rearing fields to an age appropriate for releasing.

Table 4
Total liberations of artificially propagated turkeys in Missouri, from 1925 to 1943 (in part from Bennitt and Nagel, 1937)

Year	Source	Number
1925	Reared at Big Spring State Park (eggs from Florida and North Dakota)	350
1926	"Purchased in the South"	300
1927	"Imported from the South"	263
1928	Some purchased; some raised on state parks	630
1929	Purchased	646
1930	Purchased	352
1931	Purchased	159
1932	Produced on state parks and state game farms	1,628
	Purchased	675
1933	Some purchased; some produced at Sam Baker State Refuge	4,390
1934	Some purchased; some produced at Sam Baker State Refuge; released by U. S. Forest Service	480
1935	Produced at Sam Baker State Refuge (estimated)	500
1936	Produced at Sam Baker State Refuge (estimated)	500
1937	Purchased from Lost Trail Game Farm	496
1938	Same	500
1939	Same	498
1940	Same	494
1941	Same	487
1942	Same	542
1943	Same	232

14,122

This procedure was adopted at about the same time (1932) by a private game breeder, Mr. B. K. Leach (Lost Trail Game Farm, Reynolds County), who soon developed it to a degree of effectiveness not attained on the State Turkey Farm at Sam Baker Refuge. In 1936 the state farm was abandoned, and thenceforth all turkeys liberated in Missouri were purchased from Mr. Leach.

The present turkey populations on Deer Run and Blue Spring refuges were derived principally from the Lost Trail strain. The turkeys on Sam Baker Refuge descended from the State Turkey Farm stock.

The "wild pen" method of breeding.—Wild pen breeding is an accepted practice on the turkey farms of states other than Missouri. Published descriptions of the mechanics of the plan are available from Pennsylvania (Gerstell and Long, 1939) and Virginia (Mosby and Handley, 1943).

In theory, the consistent backcrossing of selected hens to wild gobblers over a period of generations should soon yield a 99 per cent wild turkey. Starting with F_1 hybrids that are 50 per cent wild, successive backcrosses should produce 75, 87.5 and 93.7 per cent wild birds; in the seventh generation the stock will be 99 per cent wild. This simple mathematical concept accounts for the general acceptance of the plan and for the apparently justified claims that birds so derived are "practically pure wild turkeys."

Up to 1942 the Lost Trail stock had passed through ten generations of wild pen backcrosses. Yet the birds liberated in recent years, and their descendents observed in

this study, show unmistakable indications of inherent, semi-wild behavior. There are several reasons why this breeding method fails to attain wildness in the stock produced, the most obvious one of which may be discussed here. The "wild" gobblers attracted to the pens are themselves often hybrids and are genetically no wilder than the hens. For example, at the Lost Trail Farm the breeding pens are not "scattered through the most isolated parts of the native wild turkey range," but have always been situated around the borders of Indian Trail Refuge in Dent County; this area in past years has received liberations of hybrids totalling 1050 birds (Leopold and Dalke, 1943). The present stock on Indian Trail is mixed. Under such circumstances, the probability of attracting hybrid gobblers to the pens is high, since they are much more tolerant of human disturbances than are the native gobblers. Males that are clearly hybrids are known to have frequented some of the pens. When this occurs, the theoretical advantages of wild pen breeding obviously are lost.



Fig. 22. Rearing fields and enclosed roosts on Lost Trail Game Farm, Reynolds County, August 28, 1940. The larger turkeys are twelve weeks old.

Gerstell and Long (1939) report an instance of the same thing in Pennsylvania: "It is believed that the male which bred the females in Area No. 1 (breeding pen) quite probably was a game farm bird released the year before." This assumption is borne out by their physiological data.

A more fundamental limitation of the propagation plan is taken up later.

Liberations of hybrids.—For discussion of the problems associated with liberating turkeys, reference is made to Bennitt and Nagel (1937), Blakey (1937), and Mosby and Handley (1943). The considerations which have governed Missouri liberations in recent years are, briefly:

(1) Releases on unprotected and unmanaged range are usually frustrated by the

same factors of range deterioration and poaching that depleted the original turkey population. Therefore, liberations have been confined to protected areas, where adequate food, water and cover seem to be available.

(2) Birds held in confinement too long develop marked symptoms of *acquired* tameness. On the other hand, juveniles cannot fend for themselves until they are old enough to be independent of parental or artificial care and brooding; initial losses are high among birds released at the age of 10 weeks or younger. From 12 to 14 weeks has been selected as the optimum age for releasing young turkeys. In Missouri this means late August and early September. Mosby and Handley recommend release of 16-week-old birds in Virginia.

(3) Young turkeys have been liberated in flocks of all sizes from 5 to 200, and in varying sex ratios. The most recent practice has been to put out groups of 15 to 35 birds, females predominating two to one; artificial food is supplied for the first week and is then "tapered off."

Behavior of birds after release.—From 1939 through 1941 special studies were made of ten separate liberations of birds from Lost Trail Game Farm (see table 5). The birds were marked with colored as well as aluminum bands to facilitate identification and study.

The behavior of the young turkeys after release followed a rather constant pattern. For the first few days the birds settled down contentedly at the release site, where their customary food (compressed pellets) and water were available. The flocks were gentle, and an observer could approach within 100 feet without disturbing them. At night some individuals chose low limbs for roosting perches, but many roosted on logs or on the ground.

The unwary birds were soon discovered by predators. A night attack by a Great Horned Owl or a fox, coming usually within the first week after the release, would result in the death of one or more turkeys, and in the dispersal of the flock; in no case did the birds reassemble. A period of wandering followed, in which scattered groups of 1 to 10 birds drifted about, apparently aimlessly. Mosby and Handley speak of this period of wandering following liberations in Virginia, and they record instances of birds moving 10 to 15 miles from the site of release. The longest movement observed here was 10 miles (release no. 4 in table 5); the majority of the birds stayed within a radius of two miles.

The period of vagrancy was usually terminated by one or another of the following attachments being made by the homeless birds: (1) association with wild turkeys, where present, usually resulted in the juveniles adopting the range of the wild birds, and becoming established; this is the principal way in which wild populations become hybridized; (2) some groups adopted unoccupied ranges, and established themselves independently; (3) many of the wanderers arrived in farmyards, where they readily took up association with domestic poultry (turkeys or chickens). The latter tendency has been described in almost every report on the releasing of turkeys, although its importance in Virginia is minimized by Mosby and Handley. Observations in Missouri indicate that once birds take up residence around farmyards they rarely can be induced to revert to the woods; in many instances birds driven from one barn lot, or trapped and moved away, would quickly seek out another. From the restocking standpoint, such birds can be considered a total loss.

Survival through the first winter.—The principal causes of mortality among released hybrids are believed to be as follows: (1) predation, apparently by foxes, horned owls,

bobcats and stray dogs; (2) poaching, where birds stray from protected areas; (3) disease, particularly in the instances of flocks frequenting farmyards. This expresses merely my personal opinion, based on general observation; it is not backed by much corroborative evidence.

Table 5

Over-winter survival of 237 turkeys from Lost Trail Game Farm, liberated at the age of 12 weeks

Place of liberation	Liberation date	Number of birds released	Known spring survival	Per cent survival
1. Lake Spring Area, Phelps and Dent counties	Aug. 21, 1939	40	8	20
2. Maries County, Area No. 1	Aug. 21, 1939	20	6	30
3. Maries County, Area No. 2	Aug. 21, 1939	15	5	33
4. Stoner Refuge	Aug. 23, 1939	25	6	24
5. Big Spring Refuge	Aug. 28, 1940	10	2	20
6. Bay Area, Gasconade County	Aug. 28, 1940	37	5	14
7. Blue Spring Refuge	Sept. 4, 1940	25	11	44
8. Big Spring Refuge	Aug. 29, 1941	21	0	0
9. Stoner Refuge	Aug. 29, 1941	15	4	27
10. Blue Spring Refuge	Aug. 21, 1941	29	7	24
		237	54	

A number of apparently authentic reports have been received of released birds appearing to be sick or weak; in two instances farm boys were alleged to have caught some of the birds by hand. Unfortunately, none of these was obtained. No instances of debility were observed in the specific studies of the ten liberations.

Whatever the combination of causes of mortality, survival through the first winter averaged 23 per cent for the 237 birds kept under observation (table 5). This figure is known survival, or the per cent of birds actually accounted for and known to be alive by February or March. The figure may be somewhat lower than actual survival due to failure to locate all surviving birds. In Virginia, Mosby and Handley (1943:201) found a winter survival rate of 47.5 per cent among 440 turkeys liberated in the fall of 1940. The difference may be due in part to the more advanced age of the Virginia birds, which were released at 16 weeks instead of 12 weeks of age.

Assuming an average survival rate of 25 per cent among the Missouri liberations, four birds must be released in the fall to supply one breeding turkey the following spring.

Although initial losses among the young hybrids are high, repeated liberations under favorable conditions may result in establishing hybrid populations. The three study areas for hybrids were stocked repeatedly before the game farm strain became firmly implanted.

PRODUCTIVITY OF WILD AND HYBRID POPULATIONS

Evidence from the 1942 turkey inventory.—Early in 1942 (January to April) a state-wide turkey inventory of Missouri was conducted. The methods and findings of this census have been reported separately (Leopold and Dalke, 1943). Some aspects of the report that bear on our present problem will be reviewed briefly here.

According to the compiled census figures, there were 596 flocks of turkeys in the state, totalling 4,340 birds. As a check on the accuracy of the count, one test area of 220 square miles in Howell County was re-censused by thorough and painstaking methods, and 14 per cent more birds were found than were tallied in the original inventory. This indicates that the census was approximately 86 per cent accurate; the total

may be considered conservative. Figure 19 shows the distribution of turkeys in terms of three zones of relative density.

It proved impossible to sort flocks into "natives" and "hybrids"; in too many instances nothing was known of flock origins. Therefore, there is no way to calculate what per cent of the state population is *silvestris* and what per cent hybrid, nor can we compare on a state-wide basis the general thrift of populations of various origins. Some local comparisons can be made.

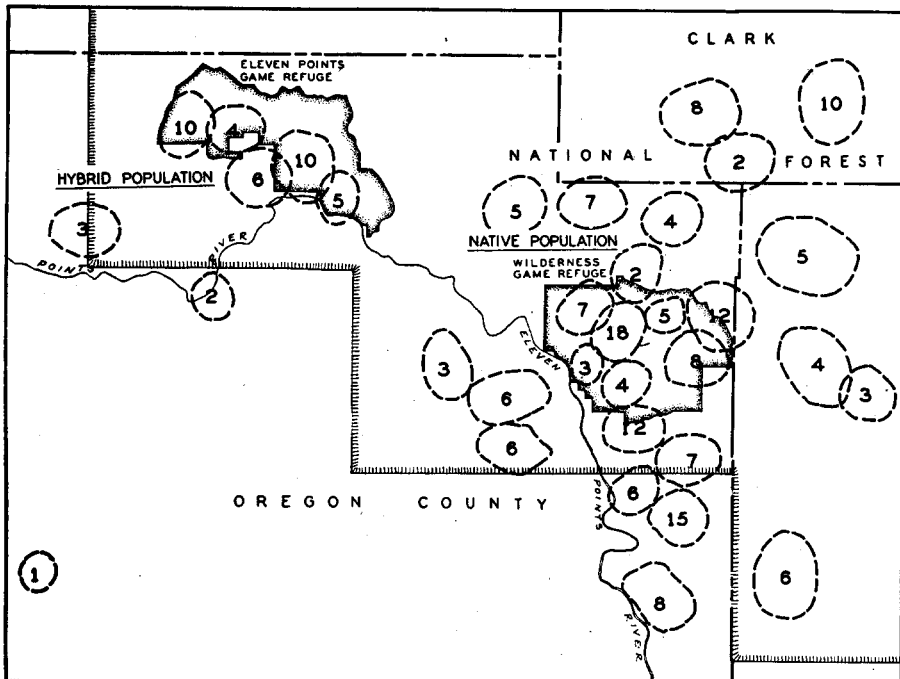


Fig. 23. Comparison of a thrifty native turkey population around Wilderness Refuge with a low-density hybrid population around Eleven Points Refuge in 1942; each circle represents a flock, the size of which is shown by the enclosed number.

There are fifteen state refuges that have been managed for turkeys. Fourteen had turkeys on them in 1942, but of these only five supported densities on and around the refuge areas of 40 turkeys or more per township; above this density, refuges are considered "successful." Of the five successful refuges, four sustain predominantly native turkey populations (Drury, Hercules, Caney Mountain and Wilderness). The fifth, Indian Trail Refuge, supports a mixture of native and hybrid birds, as already mentioned. The other ten refuges, which are under similar programs of management and appear to be equally good turkey areas, had lower densities, many ranging down to levels below 10 birds per township. All support predominantly hybrid stocks. Liberations on these ten areas in past years have totalled 5,215 birds; the aggregate population on and around the same areas in 1942 was 445 turkeys.

Figure 23 compares the status of the native turkeys around Wilderness Refuge with the hybrid stock on near-by Eleven Points Refuge. The two areas are very similar in topography and general aspect, and the management plans are almost identical. The

native population on Wilderness is increasing, and has extended its range in recent years; the hybrids within Eleven Points Refuge remain at a static low level and show no indication of spreading outside the refuge.

On unprotected and unmanaged areas the differences in population levels are even more noticeable. In various parts of the Ozarks remnants of native turkeys persist on overgrazed and burned range, even under severe poaching pressure. Three such remnants gave rise to the populations on Caney Mountain, Drury and Wilderness refuges, all of which are relatively new projects. On the other hand, there are no instances known to me of heavily hybridized turkeys sustaining themselves for long without full protection from hunting. Hybrid populations are quickly eliminated by poachers.

In short, the native birds are more tenacious under adversity and achieve higher populations under protection than the hybrids. The following records from the study areas seem to bear out this conclusion.

Population densities on the study areas.—Annual winter turkey censuses were taken on all study areas except Wilderness, which was censused only in 1942. The tallies were compiled from many individual flock observations and are thought to be accurate within a few per cent. Figure 24 depicts for the period 1940-43 the population levels on the five refuges from which records are available. The figures for Drury Refuge were supplied by the Wildlife Research Unit, Columbia.

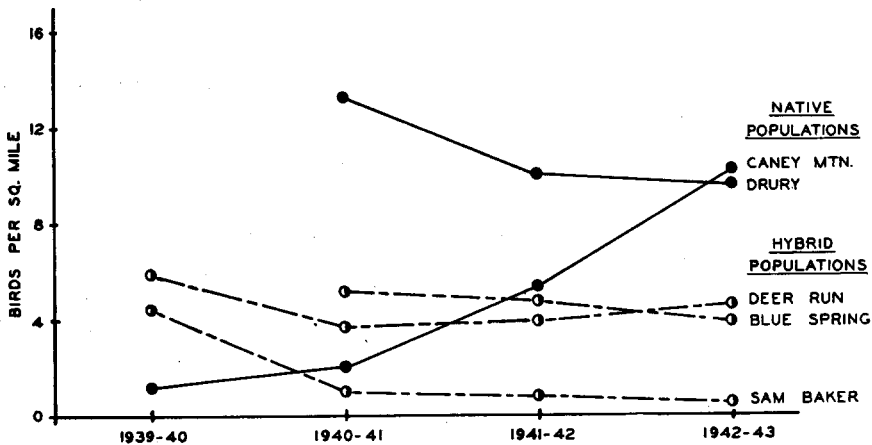


Fig. 24. Relative densities of native and hybrid turkey populations on five of the study areas, based on late winter censuses.

Two methods are used in this report to express the status of turkey populations on refuges:

(1) Table 1 presents the number of birds on *standard-sized census areas* of 120 square miles (76,800 acres), within which each refuge is centered. This gives a measure of the population around as well as on each refuge, and is a true expression of refuge productivity. The figures also may be converted to densities; thus, 40 turkeys per township has been selected as the minimum standard for "successful" refuges. Refuge size is eliminated as a variable.

(2) On the other hand, the densities presented in figure 24 apply to the refuge areas alone (total birds divided by area in square miles). While this procedure does not take cognizance of the "overflow" to surrounding areas, it has the advantage of comparing

populations under similar conditions of management and protection, which vary outside the different refuge units.

Discussion of the individual areas may help to explain the trends of the curves in figure 24.

Native turkeys. Caney Mountain Refuge.—The sharp upward swing during 1941 and 1942 represents the response of a remnant of wild birds to the protection established in 1940. The curve may level off in another year or two, when the number of birds approaches the carrying capacity of the area.

Drury Refuge.—Turkeys have been relatively abundant on the Drury unit for several years, but accurate census figures are available only for the past three winters. No explanation for the drop in 1941 is available, unless it be the disturbance accompanying intensive turkey studies carried on there during 1941-42, which might have caused some birds to move off the refuge. This suggestion came both from D. L. Spencer who made the studies, and from the local refuge patrolman. However, the present density of 9.6 birds per square mile is still high.

Hybrid turkeys. Deer Run and Blue Spring refuges.—The hybrid populations on these two areas persist at low levels, varying from 3.9 to 5.9 birds per square mile. During 1941 and 1942 Blue Spring Refuge received additional releases totalling 54 birds, which, however, failed to increase the local density, even temporarily.

Sam Baker Refuge.—The originally ample number of hybrids on this refuge has decreased steadily, without apparent cause. In 1940 when this study started, there were 39 turkeys on the area; in 1942-43 only 2 birds were left. Sam Baker Refuge is well managed and fully protected from poaching. The only possible explanation for the decline is failure of the game farm birds to sustain their numbers in the face of predation and other natural losses. A moderate population of native turkeys exists without protection on similar range a few miles to the northeast.

The important comparison to be made here is not in the trends on the various areas, which may go up or down with changing local influences, but in the relative densities of the wild and hybrid populations. The two native populations now stand at densities approximating 10 birds per square mile. The hybrids, under equally favorable conditions, exist in densities ranging downward from 5 birds per square mile.

The evidence presented here strongly indicates that *M. g. silvestris* is better able to sustain itself under the various conditions found in the Ozarks than is the hybrid stock. This is interpreted as a reflection of specific adaptation of the native bird to its ancestral environment, which adaptation is presumed to be deficient or absent in the alien strain.

NATURAL HISTORY

FLOCKING HABITS

Flock size.—One of the first differences noticed in the behavior of native and hybrid turkeys lay in winter flocking habits. Hybrid turkeys tend to form large flocks, even at low population levels. The wild turkeys in Missouri normally remain in small flocks, particularly in low density populations, and gather into larger groups only when local populations are high. The significance of this differential flocking behavior is unknown; in itself it may not be important, but it is presumed to relate in some way to wildness.

As a specific illustration, in the expanding native population on the Caney Mountain area (see table 6), flock size generally increased as the density built up, but the average flock still remained small. During the same period the moderately large hybrid population on Deer Run Refuge divided itself each year into flock units consistently larger and fewer than those of Caney Mountain. The density curves of these two populations crossed in 1941-42 (fig. 24); in the February-March census of 1942 the number of birds on the two areas was approximately equal. The 47 native turkeys on Caney Mountain Refuge were divided into flocks of 10, 9, 8, 6, 6, 5 and 3. The 51 hybrids on Deer Run occurred in flocks of 33, 11 and 7.

The compiled flock records from all six study areas for the four-year period, 1940 to 1943, furnish a more conservative measure of the difference in size of flocks. In figure 25, average flock sizes are plotted against population densities for the wild and hybrid populations. In both strains flock size increases as densities go up, as one might expect. But the hybrid curve rises the more sharply. At the moderate density of 5 birds per square mile, for example, the average flock in a wild population will be in the neighborhood of 8 birds, in a hybrid population, 14 birds. The curve for the hybrid strain cannot be projected beyond the low density classes, because high-density local populations do not occur.

Table 6

Flock size in the native turkeys of Caney Mountain Refuge and hybrid turkeys of Deer Run Refuge

Refuge	1940	1941	1942	1943		
Caney Mountain	3	8	10	12		
	3	6	9	12		
	3	3	8	9		
	1		6	8		
			6	8		
			5	7		
			3	6		
				5		
				5		
				5		
				4		
				3		
				2		
				2		
	Total birds		10	17	47	88
	Average flock		2.5	5.7	6.7	6.3
Deer Run	29	16	33	22		
	25	10	11	17		
	15	10	7	11		
	8	8		9		
		6				
	Total birds		77	50	51	59
	Average flock		19.2	10.0	17.0	14.8

Sex and age composition of flocks.—There is a strong tendency toward partial winter segregation of the sexes in the wild strain of turkeys, but not in the hybrid strain. In *silvestris*, the proclivity of most adult gobblers to flock separately from the hens and young is well known, and has been adequately described by Audubon (1831), McIlhenny (1914), Mosby and Handley (1943) and others. I have observed the same segregation in *merriami* in Arizona, and also in *M. g. gallopavo* in northern Chihuahua, Mexico.

In the present study, flocks of adult males were found every year on each of the study areas for native turkeys. A few old gobblers remained solitary; these generally appeared to be the oldest and largest birds. But most of the males gathered in flocks varying from 2 to 10 birds, the larger groups occurring in high density populations. Even in 1940 on Caney Mountain Refuge, when there were only 10 turkeys on the 5,500 acres, one distinct flock of 3 old gobblers was found.

Segregation was never complete. Some mature males always were found attached to groups of hens and young. This differs from the report of Mosby and Handley (1943: 171) who state that in Virginia "old gobblers seldom, if ever, associate for any length of time with hens and their young." Among the various native populations that I have observed, I would estimate that from 10 to 30 per cent of the gobblers failed to segregate, choosing instead to associate with other sex and age groups.

Among the hybrid populations, separate gobbler flocks were not observed. All the adult males on Deer Run, Blue Spring and Sam Baker refuges were consistently found flocking with hens and young birds through the fall and winter seasons. In these mixed flocks the gobblers may display a closer affinity toward each other than toward the other birds. Thus, when a flock is spread out feeding, the gobblers often are grouped together; this has been observed several times in hybrid flocks, and is also true of mixed flocks of *silvestris*. On one occasion on Deer Run Refuge a hybrid flock was observed on the roost; the three gobblers were in the same tree whereas the hens and immature males were grouped in trees 100 feet away. But in no instance did the adult male hybrids flock entirely independently.

I conclude that the tendency toward sexual segregation during the winter is but weakly present in the hybrid strain.

There is considerable variability in both flock size and composition among wild turkeys. Both may be affected by factors other than population density. In regard to flock size, I have observed, and Mosby and Handley also state, that normal flocks may be disrupted and scattered by hunting and other disturbances. On the other hand, on wintering grounds where turkeys are abundant, several flocks may assemble to form large but loosely organized "droves," such as were first described by Audubon (1831). However, the present differences in flock size between wild and hybrid birds, shown in figure 25, are apparently due to inherently different behavior in the two strains, and not to varying external influences. The large groups of hybrids are definitely flock units, and are not droves; the native birds voluntarily remain in smaller flocks. These patterns of behavior are too distinct and too consistent to be accidental.

Similarly, I interpret the differential tendency toward sexual segregation as a distinction in the inherent behavior of the two strains. There is an obvious relationship between sexual segregation and flock size. The willingness of the hybrid males to flock

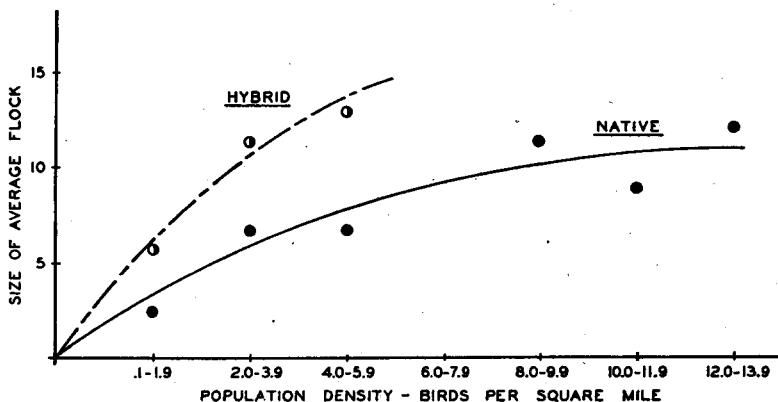


Fig. 25. Relation of flock size to population density in native and hybrid turkey populations; based on 58 native and 37 hybrid flocks tallied in the winter censuses of the study areas over the period 1940 to 1943.

with the hens and young to some extent explains the smaller number of flocks and the correspondingly larger average size of flock in hybrids. In a native population, the occurrence of small gobbler units would in itself materially reduce the average size of flock, thereby accounting, at least in part, for the situation shown in figure 25.

My limited observations of *M. g. gallopavo* in Mexico, from which race the domestic turkey originated, indicate that in flocking behavior the Mexican birds resemble *silvestris*. Sexual segregation is distinct, and flock size approximates that of native Missouri turkeys under similar densities of population. Therefore, the unsegregated flocking habits of the hybrids probably are derived from inherent traits arising in the domestic strain during the course of its acclimatization to the barnyard. It is not illogical that such specific flocking tendencies as sexual segregation might have been broken down in the genetic alteration that accompanied domestication.

MOBILITY OF WINTER FLOCKS; FOOD HABITS

Fall movements among wild turkeys.—There is a definite period of fall movement in wild turkeys during which the flocks select their winter ranges. This seems to be the equivalent of the familiar "fall shuffle" in Bob-white Quail (A. Leopold, 1931). On Caney Mountain Refuge, where this movement was best observed, it occurred each year in November and early December.

Without banding, it was impossible fully to trace the extent of fall movement. But from 1940 to 1942, when the Caney Mountain turkey population was relatively low, I was able to recognize certain individual flocks and to follow some of their shifts of range.

During this period most of the broods were raised on the eastern and southwestern portions of the refuge, in which two localities the old fields and open "bald" hillsides are concentrated. As will be brought out later, turkeys prefer to nest and raise their young near open grassy areas rather than in continuous woods. During the summer and early fall months only gobblers were found in the unbroken timber of the central and northern parts of the refuge.

However, each year in November we would begin to find hens and young all over the refuge, many in sites where no broods were believed to have been raised. On several occasions family flocks were observed only once in a particular locality and were never found there again. Flocks would disappear from localities where they were known to have been early in the fall. These observations indicate some definite shifting of range during November.

I have some indirect evidence that the fall shuffle may involve movements of considerable distance. During the winter of 1941-42 there were more adult males on Caney Mountain Refuge than could possibly be accounted for by natural increase, that is, by maturing of young males of the previous year. Therefore, some of the extra gobblers must have drifted in from the outside, most probably from the southwest where there was a considerable wild population. This presumed movement would have been at least three to four miles.

Winter ranges of wild flocks.—By late December we could begin to identify individual flocks with particular localities. Thus, on December 24, 1941, a mixed group of three old gobblers and six hens was seen for the first time near the refuge headquarters. During the rest of that winter the same flock was identified eight times, never more than a mile from where they were first observed. Their range throughout the winter covered an elliptical area of less than four square miles.

In the same winter, three young gobblers were found a mile west of the refuge headquarters on January 6. These three birds subsequently were seen four times, always on the same ridge, and they were observed gobbling there in early April. The area of their range was about two square miles. No other turkeys wintered on the ridge. Just where these two flocks originated and how far they had moved during the late fall before settling on their respective ranges is unknown. Many similar instances could be cited to exemplify the localization of winter ranges among wild flocks.

Sometimes flock ranges overlap and are not so easily traced as in the two instances mentioned. Due to this tendency to overlap and even to merge, as occurs when "droves" are formed, it is doubtful whether the winter ranges of turkey flocks can be considered such definite entities as the covey territories found in California Quail, Bob-white and some other gallinaceous birds.

The selection and occupation of particular areas appears to be influenced to a considerable extent by the supply and distribution of winter food. For three consecutive years all the turkeys on Caney Mountain Refuge wintered in the southern and eastern parts of the area, where a heavy mast of post oak acorns was available. These acorns were clearly the staple food during those years. The northwest corner is predominantly a white oak woods, and during this period had few acorns and no turkeys. In 1942-43, on the other hand, there was a heavy white oak mast and a very light crop of post oak. By December of that year the concentration of birds had shifted to the white oak region in the northwest corner, and there most of the birds wintered.

Audubon (1831:2) describes this gravitation toward winter food supplies as follows: "Whenever the mast of one portion of the country happens greatly to exceed that of another, the Turkeys are insensibly led toward that spot, by gradually meeting in their haunts more fruit the nearer they advance toward the place where it is most plentiful." This is perhaps as clear a statement of the influence of food on turkey movements in autumn as has been written.

We may conclude that after a period of wandering in late fall, wild turkey flocks tend to settle down on more or less definite winter ranges, the selection of which is influenced by local supplies of winter food. The size and stability of individual flock ranges may be affected by hunting and other disturbances and by the density of the turkey population itself. Rigid territorial bounds between flocks, implying defense of a territory by each flock, are not apparent; the ranges of individual flocks often overlap.

Comparative mobility of hybrids.—My winter observations of hybrid populations are less specific than those just cited for the native turkeys on Caney Mountain Refuge. The large hybrid flocks display definite attachment to a particular segment of the range. I found it easier, in fact, to define flock ranges on Deer Run Refuge than on Caney Mountain. This may have been partly due to the tameness of the hybrids and ease of observation. The ranges of hybrid flocks varied in area from less than two to more than five square miles, which is approximately the same scale of variation found on Caney Mountain; overlapping of ranges also was apparent. However, my limited observations indicate somewhat less of a fall shuffle among the hybrids.

In the summer of 1941, one hen on the east edge of Deer Run Refuge had the distinction of raising a brood of nine young gobblers. This easily recognizable group wintered on the very range where the brood was raised. On the same refuge, one big gobbler lived for four years in the vicinity of the refuge patrolman's house, each winter joining the flock that customarily frequented the near-by barnyard. Another old male stayed near the C.C.C. camp on the north edge of the area, where he could usually be located

at any time of year, in winter accompanied by a mixed flock of other turkeys. On Blue Spring Refuge a hen lived around the C.C.C. camp for three years, leaving each spring to mate with the nearest male and returning to nest (always unsuccessfully) near the buildings. I believe that many of the hybrid birds move very little from one season to the next.

These notes are too scant to form the basis for any conclusions regarding differences in mobility. If there is any significant difference, the hybrids are probably less mobile, particularly in autumn, than are the native birds.

Food habits.—Through field observation alone, I was unable to detect any differences in the food preferences of wild and hybrid turkeys; no laboratory studies of food habits were made. Dalke, Clark and Korschgen (1942) have reported on the contents of 3,244 turkey droppings collected from various refuges in Missouri through all months of the year. The sample represented both native turkeys and hybrids. In Missouri both strains depend heavily upon acorns for winter food; dogwood berries (*Cornus*) are taken in quantity; the leaves and seeds of various grasses are important throughout the year. These three foods also were found to be of great importance in the diets of wild turkeys in Virginia (Mosby and Handley, 1943:154); but the reports both from Missouri and Virginia emphasize the wide variety of foods eaten by turkeys.

The utilization of cultivated crops by wild turkeys varies from winter to winter, depending apparently upon the supply of natural foods. On Caney Mountain Refuge I repeatedly have noted that flocks ignore cultivated food patches of cane, soy-beans, and other crops when acorns are to be had. The wide use of oak mast by wild turkeys seems to reflect a definite food preference on the part of the birds and is not due solely to availability. Hybrids show the same high regard for acorns.

WARINESS AND TOLERANCE OF DISTURBANCE

Wariness.—A familiar attribute of the wild turkey is its keenness in detecting and eluding danger. It is this quality, even more than its size and beauty, that makes the wild gobbler a prized trophy of the hunt. Perhaps the most obvious difference between wild and hybrid turkeys is the lack of alertness and wariness in the latter. I speak now of hybrids that have been hatched and raised in the wild, not pen-reared birds that would naturally display some acquired tameness.

Wariness is a difficult quality to define. In four years I have been unable to devise a way of measuring it, and must rely here on general description to illustrate this most important point.

A wild turkey does not always flee at the sight of man or his implements. Both wild and hybrid birds are quick to recognize the sanctity of a refuge. On protected areas, even the wildest gobblers can be approached in a noisy and direct manner, as in a car or with wagon and team, without causing alarm. On Caney Mountain Refuge it is not uncommon to drive within 75 yards of turkeys and have them trot away in a most leisurely fashion. The same is true of hybrids on other refuges.

But attempting to approach a flock in a stealthy manner is a different matter. The native birds display an uncanny ability to "see you first," and their retreat is immediate and complete. Hybrids, on the other hand, often can be approached closely without being frightened. When an intruder is observed, the birds usually withdraw a few hundred yards and then resume normal activity, whereupon they can be stalked again. I have pursued a flock of hybrids for several hours in this manner, without causing the birds any serious unrest. Such tactics are impossible with a wild flock, as any Ozark hunter will attest.

The ease with which hybrid flocks are approached and counted in the winter censuses, and the relative difficulty of tallying the wild flocks, are further manifestations of this difference. Similarly, it proved rather easy to locate and count hybrid broods during the summer months; wild broods were difficult to see and even harder to count. Native hens are much the more secretive with their downy chicks.

Susceptibility to poaching and predation.—It appears that the superior wariness of the native turkey makes it less susceptible than the hybrid strain to hunting losses. The importance of turkey poaching in the Ozarks can scarcely be overemphasized. This has been brought out in all previous reports on Missouri turkeys. Bennitt and Nagel (1937) state: "We believe that the illegal kill is at least equal to the legal kill and is probably much greater." This report was written at a time when there was still a one-month open turkey season. Blakey (1937) wrote more emphatically: "The illegal kill by man is the greatest factor limiting the turkey population in Missouri." In my opinion, this is no overstatement, but at this date is still very close to the truth.

It previously has been mentioned that native turkeys persist under poaching pressures that would quickly eliminate hybrid populations. The ability to elude the hunter is an absolute requisite in turkeys that would exist on the open range in Missouri. Only on refuge areas have the hybrid turkeys been able to establish themselves. Repeated efforts to establish the game farm strain on poorly protected range have failed.

There may well be a similar differential susceptibility to predation in the native and hybrid strains, but this I am unable to demonstrate in adult birds; relative survival of juveniles will be discussed later. Only five instances of predation upon adult turkeys have been observed in this study: two were attributed to dogs, one to a wolf (*Canis niger*) or a dog, and two to foxes. Three of these deaths were among hybrids, two among native turkeys. However, if hybrids are more easily approached by a man, they probably are more readily stalked by a predator.

Tolerance of disturbance.—An indirect expression of differential wariness in turkeys may be observed in their relative tolerance of human disturbance. Logging operations, C.C.C. timber improvement programs, road construction and similar sustained local activities will cause native turkeys temporarily to leave a locality, abandoning their normal winter ranges. This has been observed repeatedly, on the state refuges, including Caney Mountain, Wilderness and Drury, and among other populations of *silvestris*.

Hybrids appear to be oblivious of such disturbances. I have a dozen records of semi-wild turkeys wintering in the immediate vicinity of active C.C.C. camps. During the winter of 1941-42 two flocks on Deer Run Refuge remained on their ranges in the midst of an active logging project. It is not uncommon for established flocks to take up temporary residence in barnyards, especially during snowy weather. In effect, the hybrid birds display little of the aversion to humans which is so characteristic of *silvestris*.

THE PERIOD OF MATING

Dispersal of winter flocks.—Wild and hybrid turkeys are similar in the manner in which the winter flocks break up preparatory to entering the breeding season. They differ in the time at which the dispersal takes place. As will presently be shown, the whole reproductive cycle of the hybrid strain is advanced, each stage occurring several weeks earlier than in *silvestris*.

In both strains the first indication of the impending gobbling season is the separation of the mixed flocks into component sex groups. Adult males that may have wintered

in the company of hens and young part company with the smaller birds. Soon after, the young males drift away from the hens. Also during the early stages the flocks of adult gobblers, which occur in *silvestris* only, separate into units of one to three birds. The flocks of hens break down gradually into smaller groups; even after gobbling has begun, two or three hens may occasionally be seen together during mid-day.

The processes of flock disintegration occupy from two weeks to a month, depending upon the "suddenness" of the arrival of spring. In Missouri, the break-up of wild flocks occurs in late March; in 1941 it extended into early April. Among hybrids the same events take place in late February and early March.

Casual gobbling and strutting may begin even before the flocks have dispersed. On February 9, 1943, a warm sunny morning, I observed a flock of seven adult gobblers crossing a field on Caney Mountain Refuge on their way to water. I quote from my notes: "One bird spread his tail, dropped his wings, and assumed a half-hearted strut, after which he gobbled weakly; the gobble sounded like the 'bark' of a young male. The same bird then lowered his head and pursued one of the others in two complete circles, still maintaining a half-strut in tail and wings." This pecking continued intermittently during the fifteen minutes I was able to observe the flock. It appeared that only one bird, a very large gobbler, was exhibiting this display. Such activity may go on for some time preliminary to the actual severance of flock ties and the commencement of vigorous gobbling.

Hour of gobbling.—Early season gobbling, indicative of the beginning of the breeding cycle, begins on the roost just at daybreak and lasts less than an hour. There is a definite break between the initial gobbles on the roost (normally 1 to 10) and the re-

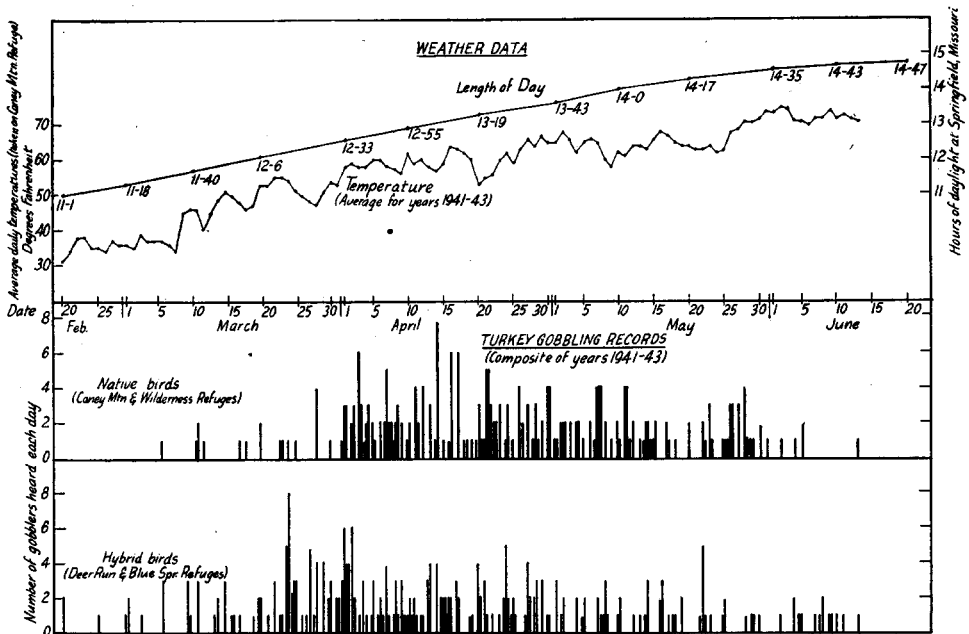


Fig. 26. Gobbling records of native and hybrid turkeys, compiled on four of the study areas over a three-year period; each vertical bar represents for a particular day the number of gobblers heard on one area. Weather data are included to facilitate comparison with gobbling records in other regions.

sumption of gobbling activity on the ground. As the season progresses, gobbling becomes more vigorous and sustained, extending later into the morning. By late April in the hybrid strain and early May in *silvestris* sporadic gobbles may be heard at any time of day, even in the evening. Mosby and Handley (1943:105) observed this same seasonal progression in intensity.

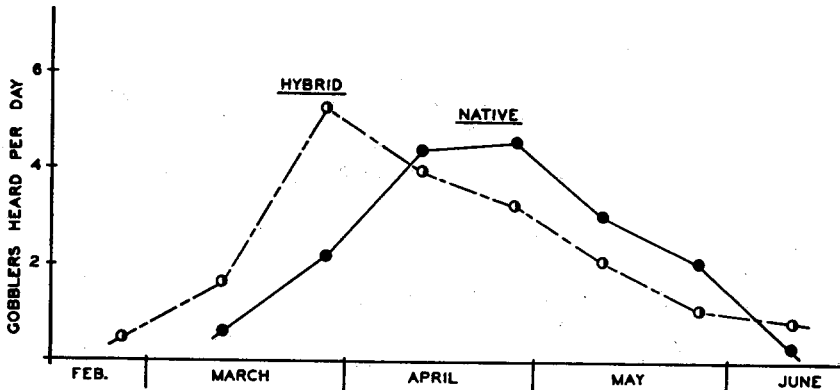


Fig. 27. Summarized records of gobbling in native and hybrid populations derived by averaging the daily records shown in figure 26 by fifteen-day groups.

The gobbling cycles of wild and hybrid turkeys.—Daily gobbling observations were made on Caney Mountain, Wilderness, Deer Run and Blue Spring refuges through three springs (1941 to 1943). Refuge patrolmen and others assisted in keeping records. Figure 26 presents a composite graph for the three years, comparing in the wild and hybrid populations the average periods of gobbling. A summary comparison of these data, plotted by fifteen-day averages, is shown in figure 27. The number of gobbling males heard on each date is the criterion used to measure the extent of display in the two populations. The method is not ideal, since the relative vigor of display in individual birds cannot be shown; one audible gobble by a turkey would suffice to record him as a gobbling bird for that day, while on the same day another male, similarly recorded, might have gobbled vigorously for an hour. Nonetheless, the compilation is useful in comparing the two cycles of gobbling and showing the peak periods when the largest number of males displayed.

Included in figure 26 are 270 observations, each being the record for one area on one morning. As many mornings again were spent in the field, but are not shown here because no gobbling was heard. Also plotted on the graph are (1) average daily temperatures, calculated from hygrothermograph records taken on Caney Mountain Refuge over the three-year period, and (2) a curve showing the increasing length of day through the spring, taken from the World Almanac for 1942. No attempt is made to correlate gobbling with these weather data, but the records may be useful in comparing the incidence of gobbling in turkeys of other regions with events in Missouri. The following phenological notes, taken on Caney Mountain Refuge in 1943 at the beginning of the gobbling season, may be of value for the same purpose.

March 28.—Spice-bush (*Benzoin aestivale*) in full flower.

March 29.—Arrival of Louisiana Water-thrushes and Black-and-white Warblers; first flowers of serviceberry (*Amelanchier canadensis*).

March 30.—Heard first "bob-white" calls, and saw indications of dispersal in two covies; heard first gobbling among the wild turkeys.

March 31.—Saw the first Myrtle Warbler and the last junco of the spring; fragrant sumac (*Rhus aromatica*) in full bloom; first blossoms of bloodroot (*Sanguinaria canadensis*).

April 2.—Flowers of redbud (*Cercis canadensis*) starting to open.

Active gobbling among the native turkeys in Missouri usually starts about the first of April, and lasts approximately two months, tapering off sharply in vigor after the middle of May. The hybrids begin gobbling actively by the middle of March, and some males may still be heard in early June, almost three months later; as in *silvestris*, the vigor of display falls off after mid-May.

Analysis of the records from individual areas for any given year shows local variations not visible in the composite record. Thus, in 1941 gobbling started on Deer Run Refuge a full month earlier than on Caney Mountain. The following year the difference was only two weeks. But in every case, the hybrids preceded the wild birds by an appreciable interval; the average period of disparity between the two cycles is about three weeks.

Comparison with domestic turkeys.—It is an accepted fact, among Ozark farmers that domestic turkeys gobble and begin nesting many weeks earlier than wild turkeys. In 1943 I obtained the following records from a flock of domestic bronze turkeys on the Matt Adams farm near West Plains, Howell County. Vigorous gobbling commenced the last week in January and continued unabated through April, tapering off in May and June. The total period of gobbling was over four months. The first egg was laid on February 18; by March 22 the seven hens in the flock had laid 40 eggs.

Each of these breeding stages comes approximately two months earlier than corresponding stages in the breeding cycle of *silvestris*. It is therefore not surprising that the hybrids commence reproductive activity earlier than the native birds.

Gobbling territories.—In most birds, mating displays by the male are believed to be associated not only with attracting females but with the advertising and the defense of a breeding territory against other males. This concept of the function of bird song, and of activities like gobbling and drumming that are equivalent to song, has gained wide acceptance since it was propounded by Howard (1920). Nice (1937) has shown in great detail the function of territories and of singing in the breeding cycle of the Song Sparrow (*Melospiza melodia*).

In turkeys, gobbling and strutting are clearly the displays by which the male attracts females during the period of mating; but the relation of these activities to territorial behavior is not clear. I am of the opinion that breeding territories among gobblers are ill defined at best and do not play the important part in mating that is characteristic of other birds, even of other gallinaceous forms.

Mosby and Handley (p. 106) cite an instance of a gobbler driving three intruding males from his regular gobbling site. They justly present this as evidence that "weakly defined territorial limits may be established and maintained by gobblers that are successful in attracting a harem."

The following account of happenings on Caney Mountain Refuge may further illuminate the problem.

On April 2, 1942, vigorous gobbling commenced among three adult males and a separate flock of three first-year males that occupied ridges opposite one another across Caney Creek. Six hens that had wintered in the company of the adult males had dispersed by this date, but the two flocks of gobblers remained intact on their winter

ranges. Almost every day from April 2 to 14 these two groups were heard gobbling with great vigor. On two occasions the three young males were "called up" with the aid of a cedar box caller by which the hen's "yelp" may be imitated. Relations within as well as between the two groups appeared to be quite amicable.

It was not until April 16 that dispersal of the gobblers commenced. On that date one of the old males, which we shall designate here as A, left the other two and moved south across the valley to the ridge occupied by the yearlings; there he remained for the duration of the gobbling season. For two days the young gobblers also stayed, but on April 18 they left their accustomed range and moved a full mile and a half north, where they remained together on an otherwise unoccupied ridge well into the summer. The adoption of their original ridge by A, and the subsequent desertion of that area by the young birds, strongly suggests that he had claimed a territory there and had driven out his lesser competitors.

On April 21 the two remaining adult males, B and C, separated; B remained on the winter range; C moved to an adjacent ridge half a mile east. Each presumably then had a territory. These positions were occupied thenceforth until gobbling ceased. During the later stages of gobbling, A was "called up" twice and B once, but it was impossible to observe these birds regularly and to ascertain whether the territories were actually defended.

By good fortune, a nest was discovered within the territory of B, and the hatching date of the eleven eggs was accurately ascertained as May 25. Tracing back the chronology of this nest, it is easily demonstrated that the nest must have been built and the first fertile egg laid not later than April 15. The hen, therefore, must have mated with one or another of the three adult gobblers *before* they dispersed and occupied territories.

If territorial behavior among the breeding males is not even begun until mating is underway, it could not hold the importance in the reproductive affairs of turkeys that it occupies in the Song Sparrow and other species.

Comparable observations were not made among populations of hybrids, and no comparisons can be made.

Non-breeding of first-year native males.—In a normal population of wild turkeys, the year-old males probably do not breed. This fact has been stated by Blakey (1937), Mosby and Handley (1943) and others, and is borne out by my observations. Young hens, however, breed and nest freely.

Among domestic turkeys, first-year gobblers are considered the most vigorous breeders. Marsden and Martin (1939), in their treatise on domestic turkey breeding, state: "A sexually well-matured young male will serve from 14 to 20 (or even more) females. . . . Older males will serve fewer hens, 8 to 14 on the average." It is common practice for turkey raisers to use only young males for breeders. This raises a question of the age of sexual maturity in wild and domestic gobblers and the status of the hybrids in this regard.

It has not been clear whether young wild males are (1) physiologically incapable of breeding, (2) are sexually mature, but are psychologically inhibited, or (3) are simply prevented from breeding by the aggressiveness of old gobblers.

Mosby and Handley discuss this question but arrive at no conclusion other than the practical statement that there are enough old gobblers in Virginia to meet the needs of the hens. However, they offer the following bit of evidence, which I shall quote in full (p. 107): "Observations on yearling native wild gobblers, reared at the Virginia wild turkey propagation unit from eggs obtained from deserted wild nests, have been made over a three-year period to determine if they would breed. When these young toms were

placed in pens with hens, but with no other males present, they showed no interest in mating with the hens. These experiments with yearling wild captive toms have not extended past June 15th but, up until that date, the young males had not strutted or shown any other visible symptoms of breeding." They do not indicate whether these same birds bred in their second or third years.

B. K. Leach has recounted to me his unsuccessful efforts to induce either young or mature native gobblers to breed in captivity. His experiments were made in the early days of Lost Trail Game Farm and preceded development of the wild pen breeding method. Non-breeding of captive males may be due as much to confinement in a pen as to age.

On Caney Mountain Refuge I found that young males failed even to gobble in 1941 and 1943. It is not difficult to differentiate the full rolling gobble of an old male from the short, hoarse "bark" of a young bird. In these two spring seasons only sporadic gobbles of first-year males were heard. But in 1942, as already related, some young gobblers on the area were heard regularly for a period of two weeks in April. I have no explanation of this year-to-year fluctuation in the behavior of yearlings, but the implication is clear that these birds probably take little if any part in breeding.

John Mohr, foreman of Lost Trail Game Farm, told me that in the spring of 1937 or 1938 (exact date uncertain) a young wild gobbler frequented one of the breeding pens near Indian Trail Refuge for about ten days. The bird entered the pen readily, gobbled and strutted vigorously, but did not copulate with any of the hens. An observer was hidden in a near-by blind nearly constantly during this period. Mr. Mohr's interpretation was that having found a company of 20 hens, the inexperienced bird accentuated his display, but "did not know what to do next." On approximately the tenth day an old gobbler entered the pen, drove the young bird out, and the first morning mounted "nearly all" of the hens, proving that the females were fully receptive. The failure of the young male to breed in this instance appeared to be due to a psychological inhibition, reflecting perhaps incomplete physiological preparedness to complete the cycle of events that results in mating.

In 1943 a young gobbler was attracted to an experimental breeding pen on the Peck Ranch in Carter County, an area populated solely with native turkeys. No adult gobbler entered the pen. Copulation between the young male and some of the females was observed, but of all the eggs produced by 20 hens (unfortunately I do not have the number) only 22 hatched. In this instance, the young gobbler mated, but fertility was very low.

In summary, non-breeding of year-old males of *silvestris* may result from any or all of the three reasons postulated, namely, physiological immaturity, psychological inhibition, and aggressiveness of old gobblers. Final solution of this question must await a thorough investigation of breeding physiology among wild gobblers of various ages.

Breeding activities of first-year hybrid males.—Young hybrid males breed freely, both in the wild and in pens. On Lost Trail Game Farm young males gobble and strut with vigor each spring and have proved their ability to produce fertile eggs from the confined hens.

In nearly every instance in Missouri where immature birds of both sexes have been released on unpopulated range, some young have been produced the following spring if enough birds lived through the winter to constitute a breeding stock. Similarly, Mosby and Handley (p. 107) recount successful breeding of young game farm birds in Virginia the year after release. There is little question about the ability of year-old hybrid males to breed.

On Deer Run, Blue Spring and Sam Baker refuges, young hybrid toms have been heard and observed gobbling vigorously each spring, but there is no way to estimate the extent to which they are actually permitted to breed by the old males.

Summary of the differences in gobbling and mating.—Adult males of *silvestris* start gobbling the first of April in Missouri, gobble with vigor for a month and a half, and then taper off sharply, virtually ceasing to gobble by the end of May. Young males may or not may gobble, but in any event probably do little if any breeding.

Domestic males, young and old, start gobbling two months earlier than native turkeys and continue mating behavior for a much longer period, usually well into June. Young gobblers are acknowledged to be more vigorous breeders than old males.

Hybrid males, young and old, commence gobbling by mid-March, some weeks after the domestic birds, but two to four weeks earlier than *silvestris*. Their period of active gobbling is slightly longer than in *silvestris*. Young males are capable breeders, but their potency in relation to the old toms is unknown.

NESTING

Nest records.—Mosby and Handley (p. 123) give an excellent account of turkey nesting in Virginia based on a study of 40 nests. Of these, 27 were nests of wild turkeys, probably as nearly pure *silvestris* as Missouri stock; 13 were nests of "captive-reared" (game farm) birds, probably equivalent to Lost Trail hybrids. My nesting data are more limited, including only 15 nests, of which 8 are of *silvestris* and 7 of hybrids. In all essential respects, my findings regarding turkey nesting conform closely with those from Virginia. All 15 nests were found accidentally by refuge patrolmen or cooperating farmers and were pointed out to me. I made no effort to search for nests because of the danger of causing desertions, particularly by native hens.

Nesting sites.—Most turkey nests, of both wild and hybrid birds, are situated along edges of fields, trails, roads or other openings. Not one of the 15 nests listed in table 7 was in unbroken timber. All were close to water; only two were more than 200 yards from a suitable drinking place for the hen. Mosby and Handley note the preference for locating nests near openings, but do not mention near-by water as a requisite for nesting ground.

In one respect only did I find that the sites chosen by native and hybrid hens differed. Native turkeys always place their nests in clumps of ground cover sufficient to form a concealing shelter; four of the eight nests of *silvestris* were in clumps of coral-berry (*Symphoricarpos vulgaris*); the others were under leafy oak sprouts or clumps of grass, in one case Johnson grass. Some of the hybrid hens, on the other hand, selected open locations where concealment was impossible. One hybrid nest (no. 10) was on an old sawdust pile; three (9, 12 and 14) were at the bases of trees, with little or no ground cover. Three hybrid nests were adequately concealed.

A single hybrid hen may utilize quite different types of sites in different nesting attempts. In two consecutive years the same female on Blue Spring Refuge built nest no. 13, which was completely concealed under a blackberry tangle, and nest no. 10, on the bare sawdust pile.

Interestingly enough, Mosby and Handley (p. 111) noticed the difference in nest sites: "Restocked wild turkeys show a tendency to locate their nests in more exposed situations than do native wild hens." The poorly concealed nests may suffer higher predation losses than are suffered by *silvestris*.

Table 7

Records of native and hybrid turkey nests in Missouri

Date found	Locality	Eggs	Hatch	Date of hatch	Notes
			Native		
1. May 7, 1942	Caney Mountain Refuge	11	(4) ¹	May 25	Eggs taken; hatched in incubator
2. May 15, 1941	Pomona, Howell County	13	June 11 ²	Deserted
3. June 1, 1943	Pomona, Howell County	11	June 25 ²	Deserted
4. June 9, 1941	Protem, Taney County	12	(10) ¹	June 27	Nest mowed over; eggs hatched under hen
5. June 13, 1943	Pomona, Howell County	10	(10) ¹	June 27	Eggs taken; hatched under hen
6. June 15, 1941	Pomona, Howell County	11	(8) ¹	July 6	Eggs taken; hatched under hen
7. June 24, 1941	Caney Mountain Refuge	8	?	Deserted
8. July 9, 1940	Aylorville, [*] Douglas County	8	Aug. 2-7 ²	Deserted? Predation?
			Hybrid		
9. April 10, 1940	Blue Spring Refuge	15(?)	Apr. 20-30 ²	Broken up by turkey vultures
10. April 10, 1941	Blue Spring Refuge	13	May 1 ²	Broken up by hog
11. May 1, 1939	Deer Run Refuge	15	15(?)	?	All (?) hatched
12. May 1, 1939	Deer Run Refuge	11	?	?	Not revisited
13. May 6, 1940	Blue Spring Refuge	18	16	May 6	Hatched 16; 2 infertile
14. May 15, 1940	Deer Run Refuge	10	?	Broken up by unknown predator
15. July 18, 1940	Blue Spring Refuge	8	7	June 6 ²	Hatched 7; brood seen June 13

¹ Eggs hatched artificially, in incubator or under hen.

² Estimated hatching date.

Number of eggs; fertility.—No significant differences were found either in clutch size or in egg fertility between the wild and hybrid turkeys. The following table compares clutch sizes, utilizing data from both Missouri and Virginia:

Strain	Source of data	Number of nests	Average clutch
Native	Shown in table 7	8	10.5
	Mosby and Handley	27	11.3
Hybrid	Shown in table 7	7	12.9
	Mosby and Handley	13	10.7

The slight differences are considered accidental results of sampling.

The Virginia report does not compare egg fertility in the two strains, and my records are too meagre to permit a valid comparison. In four egg clutches of *silvestris* that were taken from nests and hatched artificially, 12 eggs out of 44 failed to hatch, but this was due largely to chilling of partly incubated eggs and tells nothing of fertility. In three hybrid nests that were incubated naturally by hens 38 eggs out of 41 hatched. It appears that hybrid hens lay fully as many eggs as wild hens, and these are probably of equally high fertility.

Desertion, and other nest losses.—Desertion of nests which have been discovered by humans is more prevalent in *silvestris* than in hybrid turkeys. This differential behavior is probably directly related to wildness. Of the eight nests of *silvestris*, three were deserted by the hen upon discovery (see table 7); another (no. 8) was probably deserted, although an unknown predator robbed the nest soon after discovery, and there is a possibility that the predator, rather than desertion, was the primary cause of loss. The other four clutches were taken by the discoverers, in one instance (no. 1) by myself to hatch out chicks for dissection, in the remainder by well-meaning farmers who made unsuccessful attempts to raise the juveniles. In the three or four instances in which the hen had an opportunity to return to the nest she failed to do so.

Of the seven hybrid nests, three hatched, three were broken up by predators, and the last one was not revisited. There were no cases of desertion. In the first instance of predation (no. 9) the eggs were eaten by turkey vultures, in fact seeing the vultures on the ground led us to discover the nest. In the second instance (no. 10), a range hog not only ate the eggs but injured the hen, presumably while she attempted to defend her nest; strong circumstantial evidence indicated that the hen died as a result of the injuries. The predator that robbed the third nest (no. 14) was not identified.

Mosby and Handley (p. 124) had similar results in Virginia: "Of the 27 native wild turkey nests studied 18, or 67 per cent, were failures, primarily from desertion, while of the 13 captivity-reared free-range turkeys only 3, or 23 per cent, were lost, principally by predation."

Neither the Virginia data nor mine give a true picture of normal nesting relationships in turkeys. When a nest is discovered, the disturbance to the hen immediately creates an abnormal situation. The only conclusions that can be drawn from the above nesting records are that (1) desertion of nests after discovery is common in *silvestris*, and rarely occurs among the semi-wild birds; and (2) under the normal conditions of nests unvisited by humans, predation may be heavier among the hybrid nests due to the placement of some of these nests in exposed situations.

Hatching dates.—Since hybrid turkeys begin gobbling earlier than *silvestris*, it is not surprising that the period of hatching of the broods is also earlier. Figure 28 compares the hatching dates of 11 native and 22 hybrid broods. The graph combines data taken from nests (observed hatching dates or calculated dates based on the stage of egg incubation), and from young broods. Hatching dates were calculated only from broods ten days or less of age. Since the records are compiled by ten-day groups, small errors in estimating ages of embryos or chicks become negligible.

In both the wild and the hybrid strains there appears to be a period of approximately 50 days during which the early nests (first nestings) hatch. In each there is a second period of hatching later in the summer, which doubtless represents the second nesting efforts of hens whose first nests were broken up. In *silvestris*, 80 per cent of the first nests (8 out of 10) hatched during the month of June. In the hybrid strain 79 per cent (15 out of 19) came off in May. The difference between the peak hatching periods in the two strains is a full month. Second nesting attempts, while represented by only a few nests, are similarly staggered.

The difference in the time of hatching is somewhat greater than the average difference in the timing of the gobbling periods, in which the hybrids preceeded *silvestris* by not more than three weeks (fig. 27). It would seem that the two stages in the reproductive cycle should be equally staggered. I have no explanation for the discrepancy. It is small enough to have arisen from irregularities and limitations in my data, but on the other hand it may have some significance. In any event, it is clear that the whole

reproductive cycle in the hybrid strain is advanced, each stage coming three to four weeks earlier than in *silvestris*.

The significance of timing of the breeding cycle.—One notable characteristic of most wild birds, at least in the temperate zones, is the remarkable regularity of the breeding periods of individual species and even of geographic races. This periodicity has interested naturalists for several centuries (see Rowan, 1938) and has been the subject of much research since 1925. The basic facts of breeding physiology in birds have been known for some time. Breeding behavior is accompanied by a marked increase in the size of the testis and ovary and increased production by these organs of the sex hormones. The development of the gonads is in turn regulated by the gonadotropic hormones of the anterior lobe of the pituitary. The pituitary can therefore be considered the seat of control of the whole breeding process. On these points there is general agreement.

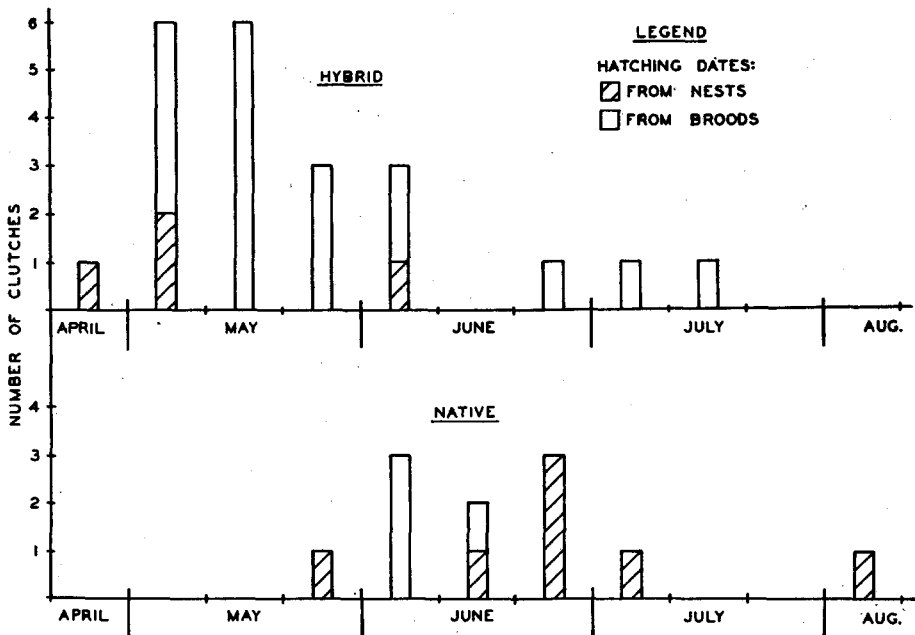


Fig. 28. Comparison of dates of hatching of 11 native and 22 hybrid nests.

What controls the production or release of gonadotropic hormones in the pituitary is still a controversial question. Length of daylight is clearly a factor (Benoit, 1937; Bissonnette, 1937); the relative length of daily periods of wakefulness and sleep may also be a factor (Rowan, 1938; Wolfson, 1941) independent of light as such; and there are unquestionably psychical or exteroceptive influences which affect pituitary activity through stimuli transmitted by the central nervous system (Darling, 1938; Marshall, 1942).

We are not so concerned here with the fundamental mechanism of reproductive periodicity in all birds as with the minor differences in the timing of the breeding cycle in closely related populations of one species. The researches of Blanchard (1941) on the White-crowned Sparrow (*Zonotrichia leucophrys*) and of Wolfson (1942) on the

Oregon Junco (*Junco oreganus*) established certain points which may be useful in understanding the situation in turkeys.

Blanchard studied the differences in gonad cycles and their behavioristic manifestations in two races of White-crowned Sparrows, only one of which migrates; both races winter in central California, which is the range of the resident race. She found differences in the dates and rates of recrudescence of the gonads and other contrasts in the physiological cycle as evidenced by molt and the assumption and loss of fat; the migration of the one race in itself constitutes a difference in behavior. The two forms differ only slightly in morphological characters. She states: "The obvious anomaly in the comparison of these populations is the combination of such deep-seated differences in behavior and physiology with such vague and incipient differences in morphology." Blanchard concludes that there exist in each of the populations inherent breeding rhythms, not initiated by day length yet controlled by the anterior pituitary and that these rhythms and associated behaviorisms are far more fundamental in differentiating the two races than are the minor differences in morphology.

Wolfson's investigations concerned the migratory habits of several Pacific coast races of *Junco oreganus* and the associated effects on breeding cycles. As in the case of *Zonotrichia*, resident and migrant races were found to differ in their gonad cycles, although they flocked together in winter and were subjected to the same environmental conditions. Wolfson thinks that the physiological difference between the resident and the migratory races of the junco lies in a differential response of the pituitary to changing day lengths in the winter. This disagrees with Blanchard's concept only in attributing the basic timing mechanism to external factors in the environment (changing length of day, inducing increased periods of wakefulness) rather than to a fixed internal pituitary rhythm.

Whatever the timing mechanism may be, the studies of *Zonotrichia* and *Junco* jointly establish these points: (1) In closely related races or strains within a species, the gonad cycles and the timing of breeding may differ greatly under identical environmental conditions. (2) The differences are inherent and are associated with the complex endocrine functions which center in the anterior lobe of the pituitary.

In regard to turkeys, I think we can safely conclude that the wild, hybrid and domestic strains are physiologically distinct in their response to the environmental conditions of southern Missouri, as evidenced by time of breeding, and that these distinctions are attributable to inherent differences in the endocrine controls of behavior.

REPRODUCTIVE SUCCESS

Records of broods.—Throughout this study information was collected on the relative survival of juvenal wild and hybrid turkeys. Observations of broods were recorded by the refuge patrolmen on the study areas as well as by myself. Figure 29 presents a compilation of brood records, assembled on five of the study areas (all except Drury Refuge) through the summers 1940 to 1942, inclusive. A total of 98 observations are shown, 34 of broods of *silvestris* and 64 of hybrids.

The observations included here are only those in which the brood counts were felt to be accurate. On many occasions it was impossible accurately to enumerate all the chicks in a brood; partial counts and estimates have been omitted. Furthermore, when a single brood was observed several times, it was counted in this compilation only once during any given month.

As summer progresses it becomes increasingly difficult to recognize individual turkey broods. Family units tend to combine; hens that have been unsuccessful in raising

broods join company with other family flocks. In both wild and hybrid populations it is common in late summer to see flocks made up of two or three hens and a group of juveniles which may be a single brood or two or more broods combined. In figure 29 I have attempted to include only counts of individual broods. Where combination broods have been counted, as evidenced by two sizes of juveniles, each is plotted separately. When doubt existed as to the relationships in a group of young, the record was omitted. For these various reasons, our total of several hundred observations of broods has been reduced to 98 in the present compilation. The impossibility of segregating broods after September has prevented carrying the record farther into the fall months.

Brood size.—A line drawn through the monthly averages of broods (see fig. 29) constitutes for each strain of turkey a regression curve of brood size. Comparison of the curves for *silvestris* and the hybrids shows that in both strains brood size falls off from month to month, but throughout the whole summer the broods of native turkeys are larger than those of hybrids. Of greatest significance is the comparison in September; at the onset of autumn, the average brood of *silvestris* was found to be 7.7 birds, which is approximately 50 per cent larger than the average hybrid brood of 5.2 juveniles.

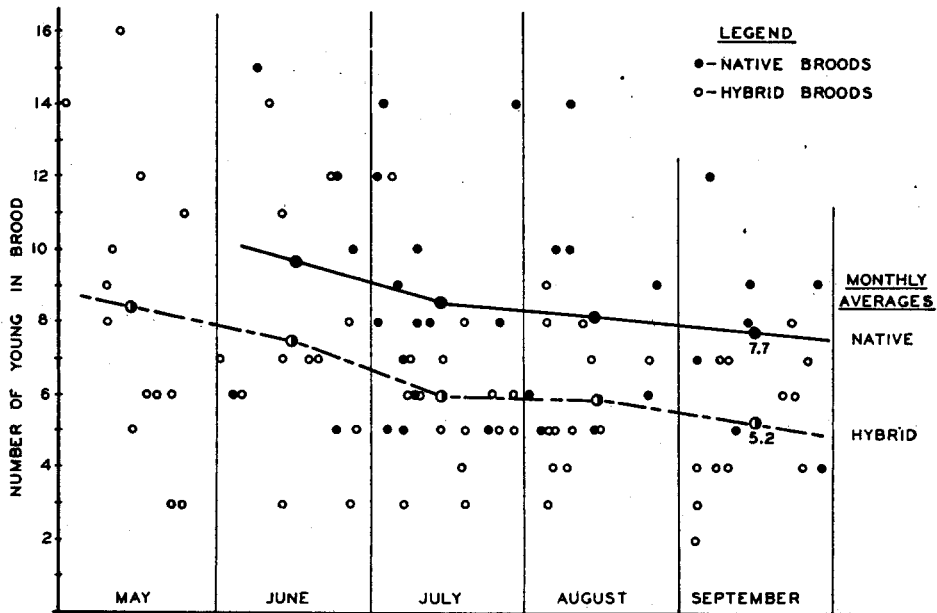


Fig. 29. Comparison of the size of broods in native and hybrid populations; the records were obtained on five of the study areas over the period from 1940 to 1942.

There is considerable variability in the two sets of data, as one might expect. In July for example, wild broods range in size from 5 to 14 birds, while the hybrids vary from 3 to 12 birds. Although the averages show a consistent difference, the wild broods being larger each month, it was necessary to apply statistical analyses to these data in order to establish the significance of the differences between the two curves. Two analyses of variance were performed on the data in accordance with methods presented by Snedecor (1940:179).

Analyses were confined to the records falling in the four-month period June to September, inclusive. Figure 29 shows that 13 hybrid broods were recorded in May but

no wild broods; a comparison could not be made in that month. This further reflects the earlier nesting period of the hybrids.

Table 8

Two analyses of variance of the data on brood size in wild and hybrid populations				
Data treated as two units, without differentiation by months				
Variation	Degrees of freedom	Sum of squares	Mean squares	F
Between wild and hybrid	1	111.06	111.06	14.77 ¹
Within wild and hybrid	83	623.93	7.52	
Totals	84	734.99		
Data divided, and compared by months				
Variation	Degrees of freedom	Sum of squares	Mean squares	F
Between wild and hybrid (four monthly averages)	4	119.67	29.92	3.99 ¹
June	1	15.56	15.56	2.08
July	1	50.22	50.22	6.70 ²
August	1	25.20	25.20	3.36
September	1	28.69	28.69	3.83
Between months	3	38.24	12.75	1.70
Within wild and hybrid	77	577.08	7.40	
Totals	84	734.99		

¹ Difference significant at 1 per cent level.

² Difference significant at 5 per cent level.

In the first analysis (table 8) the sets of data for wild and hybrid broods, from June 1 to September 30, were compared as units; no differentiation was made by months. In this comparison the difference in the size of broods between the two strains was found to be significant at the 1 per cent level. The coefficient "F" is over twice as large as the minimum necessary to establish this degree of significance ($F=14.77$; the minimum value of F necessary to establish significance at the 1 per cent level = 6.87). Stated simply, if there were no real differences except those due to chance variation alone, a difference as large as that found would be expected at the most one time in a hundred.

The second analysis was more detailed (table 8). Dividing the data by months, it was found that: (1) in June, there is no significant difference between the size of broods in wild and hybrid populations at either the 5 per cent or the 1 per cent levels; (2) in July, the difference is significant at the 5 per cent level and almost at the 1 per cent level; (3) in August and September, the differences are not significant, but are close to significance at the 5 per cent level; (4) comparing the four monthly records as two series (wild and hybrid), the difference is for all practical purposes significant at the 1 per cent level ($F = 3.99$; minimum = 4.02).

In summary, the difference in the size of wild and hybrid broods is highly significant when considered either as a whole over the summer period or on the basis of the four monthly averages which determine the curves in figure 29. Only when the data are broken down and considered one month at a time do they lose significance. We can positively say, therefore, that wild hens are successful in raising larger broods than the hybrid hens.

Factors other than brood size that bear on productivity.—Unfortunately, measurements of brood size are not in themselves an accurate measure of population productivity, for they do not take into consideration the percentage of hens in the population

that do not raise broods. A certain number of both wild and hybrid hens fail for one reason or another to raise any young. The number of young per hen in September will therefore be lower than the average broods shown in figure 29. Despite repeated effort, I was unable to measure what proportion of either the wild or hybrid populations of hens was successful in raising young to September. However, some scattered evidence is available.

On May 13, 1940, a hybrid hen on Blue Spring Refuge was observed leading a brood of 16 newly hatched chicks from the nest. On May 17 this family group was seen at a watering place 200 yards from the nest, and at that time the brood had dropped to 12 chicks. On May 31 I located the hen without any young, nor were they seen thereafter. Within a month the female was back in her winter haunts, which happened to be near a C.C.C. camp; there she settled down, apparently content with her reproductive efforts for that season. The whole brood was lost between May 13 and 31, from unknown causes. At least some of the hens that are seen without broods in late summer may have had successful nests but later lost the young.

During the last week in July, 1941, a census was made of the breeding turkeys on the ranch of Judge Robert Gideon, Taney County. The turkeys here are hybrids derived largely from Sam Baker Turkey Farm stock. Nineteen hens were located out of an estimated 24 that were thought to be breeding on the property. Of these, 13 had no broods, and the 6 broods of the remaining hens totalled only 22 juveniles, for an average of 3.6 per brood. The local caretaker stated, however, that earlier in the summer there had been many large broods. Taking into consideration the whole population, there were only 1.1 chicks per hen at the end of July. This is an extreme example of low productivity in a hybrid population. The records were not included in figure 29, because they were not taken on the study areas, and there were factors in the environment of the Gideon property, such as severe grazing, that may adversely have influenced reproductive success in the turkey population.

During the months of June to September in 1940, 6 out of 18 wild hens observed on Caney Mountain Refuge, or one-third of the total, were without broods. During the same period in 1941 on Deer Run Refuge a total of 52 hybrid hens was seen, and of these 27 or about half were unaccompanied by broods. These observations do not prove anything, but they suggest that there may be more unsuccessful hens in the hybrid populations than in *silvestris*. This is distinctly my impression, but proof must await more exact field work.

Comparison of winter populations on the study areas has already led to the conclusion that native turkey stocks are more productive than hybrids. The explanation may lie very largely in the comparative rates of reproductive success. The data on brood size indicate that by that criterion alone productivity should be 50 per cent higher in the populations of *silvestris* than among hybrids; if, in addition, a larger percentage of wild hens successfully raises broods, the difference in productivity would be proportionally greater.

Behavior of hens and their broods; effects on survival of juveniles.—The nesting records showed that clutch size and egg fertility were equally good in the two strains. Nest predation may be slightly higher among the hybrids, but on the other hand nest desertion is more prevalent in *silvestris*. In my opinion the number of young hatched per hen is approximately equal in the two strains; the difference in productivity probably lies in the superior survival of wild juveniles. Comparison of the behavior of wild and hybrid hens and their broods lends credence to this hypothesis.

Mosby and Handley (p. 121) describe the care with which a wild hen attempts to

conceal her brood and the obedience with which the chicks remain hidden after being given the danger signal by the mother hen. My observations bear out these statements in every respect. Until the chicks are a month old and can fly readily from danger, the hen will squat at the approach of a man, and the chicks crouch in the ground cover; the reaction is one of hiding rather than fleeing. Only when one approaches closely will the hen leave, and then the immobile chicks are extremely difficult to find. When the juveniles are older, the flock may fly, crouch, or slip away from danger afoot, depending upon the cover, the proximity of the observer, and other circumstances.

The behavior of hybrid broods is often quite different. I have approached family groups on Deer Run and Blue Spring refuges and have noticed that the hen would "putt" and scold, noisily herding her charges away even before I was close enough to see the chicks. On two occasions I have been led to broods by this display on the part of the hen. Her clucking and fluffed plumage are reminiscent of a broody chicken chaperoning her young across a barnyard. The actions of the young are equally different from *silvestris*. Some chicks in a hybrid brood usually follow the hen instead of hiding, even when she is running about in obvious distress. Others hide temporarily, and then in the excitement of the moment leave their places of concealment and attempt to flee or to join the hen. Usually a few will remain immobile. When pursued, the chicks will try to escape by running, but the hiding reaction is not developed as it is in wild chicks. It readily can be imagined how disastrous this promiscuous behavior might be if the encroacher were a fox rather than a subjectively interested biologist. Even broods that I have watched without attempting to catch become scattered, and chicks may be lost and perish. In short, the lack of secretiveness on the part of hybrid hens may lead to the exposure of the location of broods; the lack among all the chicks of a complete hiding response to the danger signal from the hen results in the scattering of broods and the potential exposure of many chicks to predation. The differences in behavior between wild and hybrid family groups may well contribute to differential losses among the two types, thereby accounting in part for the higher survival of juveniles in *silvestris*.

Farmers that raise domestic turkeys in the Ozark region complain that when hens "steal" nests outside the farmyard, very few young are raised; the blame is customarily placed on foxes. Domestic turkey hens and their broods act very much like the hybrids described above, except that the chicks rarely if ever stay hidden when the hen is driven away; the young will display a definite fright reaction at the sight of a wheeling hawk or when pursued by a man or a dog, but the response is expressed in fleeing rather than in crouching. Indeed, it may be foxes and other common predators that account for wandering broods of poults whose behavior fits them so poorly for escaping such attacks.

The "freezing" of wild chicks in response to a vocal stimulus from the female must have definite survival value; it is a common pattern of behavior among ground nesting birds whose young are precocial, such as sandpipers, plovers, lapwings, and most gallinaceous birds in addition to wild turkeys. Freezing in juveniles must also be an innate or instinctive action. So complete is the response of young just out of the shell that it scarcely could be the result of learning. Lorenz (1937) has called such instinctive reactions which are of survival value "innate perceptory patterns"; the warning call of the hen is the "releaser" of the hiding response. I find Lorenz's concept entirely applicable here.

Young hybrid and domestic turkeys also respond to warning notes of the hen and to certain optical stimuli such as the approach of a predator; the response, however, is of a different character. Tinbergen (1939) describes how juvenal domestic turkeys, as well as downy mallards, will display "intensive flight reactions" when a cardboard sil-

houette of a hawk is drawn overhead on a cable. I have already stated that the tendency to flee is retained in hybrid and domestic turkey chicks. The difference between the wild and domestic strains, therefore, is not in the ability to perceive danger (the hawk) or to receive warning signal of the hen, but rather it lies in the nature of the response, that is, in the *innate pattern of behavior which is released* by these stimuli. If we assume that the hiding response was present in the wild progenitors of the domestic turkey, then it has been lost secondarily; it is a reasonable speculation that the loss may have resulted from the reduction in survival value, hence in selective value, of the hiding reaction when the birds became barnyard fowls; the fleeing reaction, however, has been retained. This presumed alteration of the inherent physiological equipment of young turkeys may therefore have constituted one important aspect of the process which we have called domestication. The hybrid young display a mixed pattern of behavior in conformance with their heterozygous genetic constitution.

The behavior of the hens might be similarly analyzed. As a rule, wild turkey hens during the winter flee at the approach of a man; the same is true of hybrid hens, but the reaction is less violent. Adult domestic hens have acquired a "secondary tameness" through personal familiarity with man, but they definitely show a mild escape reaction in the presence of a strange dog. When accompanied by broods, however, the wild hen crouches or freezes with the brood, whereas the domestic hens, and the majority of the hybrids, scold and give evidence of alarm in the presence of a danger stimulus but attempt to flee with their broods rather than to hide. The differential behavior of adult hens might be merely another manifestation of the physiological divergence indicated in juveniles by my observations on hiding reactions and by the laboratory experiments of Gerstell and Long on general metabolism and activity. While the discussion here has been speculative, the actual differences in the behavior of hens and broods remain as facts, and I am convinced that they have a bearing on the relative survival of juveniles.

One other factor should be mentioned which may affect the fate of young turkeys; this concerns their hardiness to spring weather. Domestic turkey chicks are notoriously susceptible to chilling by cold rains or even dew. Whether wild chicks are better able to withstand weather, or whether the wild hens are more careful than domestic hens in protecting the young from wetting, I do not know. As regards the effects of weather on young turkeys, it will be remembered that most hybrid broods hatch a full month earlier than native broods, and the chicks are exposed to much lower temperatures than are the young of *silvestris*; domestic broods hatch even earlier. Natural supplies of food for the young (primarily insects) might also be critically low. The early date of hatching may therefore be decidedly disadvantageous to the survival of domestic and hybrid juveniles.

To conclude, there is good evidence that native turkeys raise larger broods of young than hybrids; a larger proportion of wild than hybrid hens may be successful in raising broods. The difference in reproductive success cannot be accounted for in clutch size, egg fertility or hatching success. It must stem from differential survival among the juveniles, which could be the result of (1) differences in the behavior of hens in concealing their young, (2) unequal development in the chicks of the instinct to hide and to remain hidden from predators, and (3) exposure of the hybrid chicks to more inclement spring weather and to conditions of food scarcity owing to the early date of their hatching.

ANATOMICAL AND PHYSIOLOGICAL DIFFERENCES

PLUMAGE COLOR

The eastern wild turkey is endowed with a particular set of physical characteristics, which vary only within narrow limits. The color of the plumage and some aspects of size are, in fact, the criteria used in setting apart this geographic race from other turkeys. The introduced domestic bronze turkey differs physically from *silvestris* in several respects. It is a rounder, plumper bird than the "gangly" wild turkey; there are differences in the color of the head and in the development of wattles and caruncles, as well as in the slenderness and color of the tarsi. The most noticeable difference, however, is in the color of the plumage. The tips of the tail coverts and rectrices, which in *silvestris* are cinnamon brown, are white in the barnyard turkey; the whole plumage of the wild bird is darker and more richly iridescent. We are here concerned with the question of relating plumage color to wildness.

On most game farms in the eastern United States, plumage color is the principal criterion used in the selection of turkey breeding stocks. On Lost Trail Farm in Missouri, for example, the breeders are hand picked to resemble the native *silvestris* as closely as possible. Through such selective breeding, which may or may not be accompanied by the "wild pen" system of mating, strains of hybrid turkeys have been derived that appear in most respects like the native bird. Because of this superficial resemblance, these turkeys are tacitly assumed to be "wild." Such an assumption presupposes that there is a direct connection, a genetic linkage or common factorial basis, for morphology and behavior in turkeys. The following discussion will attempt to show that there is no sound basis for this supposition and that at least plumage color and behavior are independently segregated, in short, that plumage color is not a reliable index of wildness.

Comparison of plumage colors.—The plumage of *M. g. silvestris* has been adequately described by Sibley (1940) and others, and no formal description will be presented here. The plumage of the domestic bronze turkey is equally well depicted in Marsden and Martin (1939). As previously mentioned, these two strains differ most obviously in the color of the tail coverts and rectrix tips; the metallic iridescence in the body plumage of *silvestris* is not duplicated in the tame turkey. Hybrids show all stages of intermediacy in the richness of iridescence as well as in rump and tail color. For the purposes of this study it seemed desirable to seek a simple index of plumage color, which could be measured readily and would reflect in a general way the characteristics of the whole plumage. The color of the rectrix tips was finally selected as the simplest and most practical basis of comparison of plumage color.

A sample rectrix was removed from each live bird as it was handled and was preserved in an envelope along with the record of measurements and head photograph of that bird. A clean rectrix was selected from the side of the tail; usually this was no. 6 on the right side, or the fourth feather in from the edge. The central pair in the tail (no. 1 feathers) and the outside pairs (no. 8 and 9) never were taken, because these tend to fade and wear more rapidly than the less exposed feathers. After some 75 samples had been accumulated, representing the native, domestic and hybrid types, a series of seven feathers was selected which illustrated the dark brown color typical of *silvestris*, the white domestic type, and five intergrading stages. This series was mounted on a white cardboard and thenceforth was used to classify all other specimens as to color type. Each of the seven feathers in the series was matched with a sample in Ridgway's "Color standards and color nomenclature" (1912).

Wear, fading and soiling were considered in using the chart. In birds that were molting, I found the year-old feathers to be a full shade lighter than the fresh feathers, due to weathering. Soiled rectrices, particularly on old mounted specimens, may be slightly darker than they were originally. I attempted to allow for these variables and to place each specimen in the color class in which it would have fallen had the plumage been fresh.

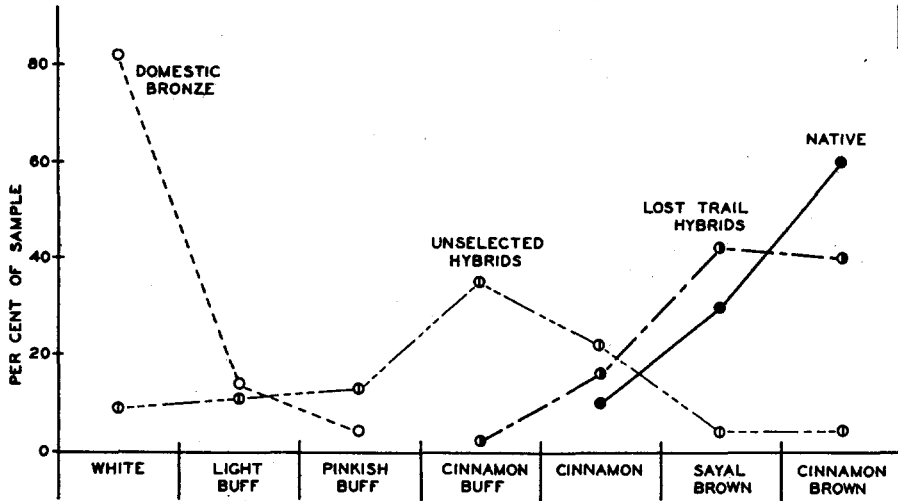


Fig. 30. Comparison of plumage colors, as reflected by the shades of tips of rectrices, in native, domestic, and two strains of hybrid turkeys.

In a previous report on turkey molts (Leopold, 1943) it was shown that some elements of the plumage, including the central parts of the tail, undergo three molts before a stable winter dress is assumed. On immature specimens, the color determination always was made on a winter rectrix (grown in the third molt), since the postjuvenile rectrices are appreciably lighter in color, and are not comparable to adult feathers. For museum skins or mounted specimens, the chart was used in the same manner as with the clipped feather samples. The results of these color measurements are summarized in table 9 and are also presented in graphic form in figure 30. A total of 115 birds is represented, all being individuals eight months of age or older.

Throughout this report it has generally been impractical to divide the hybrid birds into separate strains; the treatment in the present instance will be an exception. The hybrids of Lost Trail Game Farm have been subjected to rigid color selection over a period of ten generations and distinctly resemble *silvestris* in plumage, which is not true of hybrids from other sources. The unselected hybrid stocks, principally from the Sam Baker Turkey Farm strain, are considered separately here.

Examination of table 9 shows that in the Lost Trail strain particularly, and to a lesser extent in *silvestris*, male specimens average approximately one shade darker in color than females. This does not appear to be true in the domestic strain, and not enough males are represented in the unselected hybrid group to judge of this. To simplify figure 30, the sexes have been combined, each curve representing the summarized data for all specimens of a given strain. The sexual differentiation in color, combined with unequal sampling of the sexes in the various groups, may have resulted in slight errors in the relative placement of the various curves.

Table 9

Comparison of plumage colors in four strains of turkeys based on the color of the rectrix tips.

Type of turkey	Color classes						
	White	Light Buff	Pinkish Buff	Cinnamon Buff	Cinnamon	Sayal Brown	Cinnamon Brown
<i>M. g. silvestris</i>							
Males						3	8
Females					2	3	5
					—	—	—
					2	6	13
Lost Trail Game Farm hybrids							
Males				1		3	14
Females					7	15	3
				—	—	—	—
				1	7	18	17
Unselected hybrid stocks							
Males				1	1		1
Females	2	3	3	7	4	1	
	—	—	—	—	—	—	—
	2	3	3	8	5	1	1
Domestic bronze							
Males	8	1	1				
Females	15	3					
	—	—	—				
	23	4	1				

Even allowing for some error, the curves in figure 30 indicate some definite trends. The rectrix tips of *silvestris* vary from Cinnamon to Cinnamon Brown, a majority of specimens falling in the darker shade. Domestic turkeys are clustered around the other end of the scale, most birds possessing white rectrix tips. Unselected hybrids vary from one extreme to the other, but the curve centers in the middle class, Cinnamon Buff. The Lost Trail hybrids, on the other hand, average only a scant shade lighter than *silvestris*, attesting to the efficacy of systematic selection for color in the heterozygous game farm population.

Evidence presented up to now has shown that in nearly all aspects of individual and population behavior the Lost Trail strain is intermediate between the wild and domestic turkeys. I have been unable to detect any significant differences in behavior between the Lost Trail and Sam Baker hybrid stocks, and for that reason the two are considered together throughout this report. But in regard to plumage color, selective breeding in the Lost Trail strain has produced a type of bird superficially resembling *silvestris*, without, however, bringing about a parallel alteration of the hybrid behavior pattern. This situation strongly suggests that there is no genetic connection between color and wild behavior. The two groups of characters are apparently independently segregated.

The mode of inheritance of plumage color.—Plumage color and various other physical characteristics of turkeys probably are governed by multiple genetic factors; in hybrids the differing characters tend to intergrade. As regards plumage color, there are among some strains of domestic turkeys single genes which dictate whole color patterns and which show simple Mendelian inheritance. Robertson has described five major pairs of such allelomorphs, and Asmundson (1939, 1940) and Hutt and Mueller (1942) have added others. But Robertson, Bohren and Warren (1943) speak as follows of the relationship between the color patterns of the domestic bronze and wild turkeys: "Of the domestic varieties of turkeys, the Bronze most nearly approaches the wild type in color pattern. In fact, Robertson's data show definitely that the genetic composition of the two is identical with respect to major color factors." The differences which we ob-

serve between the plumages of *silvestris* and the bronze strain are minor genetic differences, effected apparently by the summation of the slight influences of many genes.

The F_1 generation resulting from a *silvestris* \times bronze cross is intermediate in color between the two parent strains. I have observed several grown broods derived from such crosses. The tail coverts and rectrix tips are Cinnamon Buff, and the degree of metallic iridescence is intermediate as well. In the F_2 and subsequent generations, segregation occurs, and there emerge various intergrading shades of plumage between the two parent types. This is illustrated in the curve for unselected hybrids in figure 30. Among the crossbreeds may be found some birds that resemble the domestic strain and others that look very much like *silvestris*, but the majority are still intermediate in color.

Tendencies of behavior in turkeys seem to be similarly inherited. Hybrids display considerable variability in their behavior patterns, always centering, however, in intermediate classes between the parent domestic and wild strains. But there is no apparent interdependence between the genetic factors governing behavior and those which govern plumage color. Artificial selection may influence the appearance of plumages without exerting any apparent influence on behavior. Plumage color can therefore not be considered a dependable criterion of wildness.

Yerkes' (1913) experiments on the inheritance of wildness in rats, and the results obtained by Coburn (1922) and Dawson (1932) in similar studies of mice, all show that wildness and tameness are heritable characters in these laboratory mammals, transmitted through several genetic factors, but that there is no apparent linkage between these behaviorisms and color or other morphological characters. Specifically, Dawson states that in mice wildness is probably independently segregated from sex, albinism, pink eye, agouti, brown and short ear. Unlike turkeys, mice and rats display wildness as a partially dominant character in the F_1 cross, but subsequent recombinations of genes result in the majority of the F_2 and later hybrids falling in intermediate classes.

The domestic bronze turkey derives its color pattern from the wild turkey of Mexico, *M. g. gallopavo*, which in my experience has proved to be fully as wild as *silvestris*. The dark hue of *silvestris* is therefore not only no guarantee of wildness in turkeys, but is in no way an essential adjunct of it.

MOLTS

Differences in the extent of molts in young turkeys.—The molts of turkeys have been described in a previous paper (Leopold, 1943). Certain differences in the molting procedures of wild, hybrid and domestic birds, which were reported in that paper, are reviewed here; some additional data have been added but complete discussion of the subject is not repeated.

Unlike most gallinaceous birds, young turkeys undergo three molts before acquiring a stable winter plumage; these are the postnatal and postjuvenile molts, common to the Galli, and a "first winter" molt. Only the postnatal molt is complete. Some juvenile and some postjuvenile feathers are retained through the first winter molt. The late winter plumage of a young turkey, after molting has ceased, is therefore a composite of feathers derived from three distinct molts. The differences in molt found between strains concern the extent of postjuvenile and first winter replacement, that is, the relative number of juvenile and postjuvenile feathers that are retained through the winter.

In all races of wild turkeys the two distal juvenile primaries are retained until the bird is approximately a year old (Petrides, 1942); I found this to hold true for all specimens of *silvestris* which I examined. Domestic turkeys, on the other hand, retain only one distal primary, no. 10, replacing no. 9 in the postjuvenile molt; there were

Table 10

Differences in extent of postjuvencal and first winter molts in wild, domestic and hybrid turkeys.

	Native	Hybrid	Domestic
1. Retention of distal, juvenal primaries through first winter			
Retained primaries 9 and 10	9	15	—
Retained only primary 10	—	17	19
2. Replacement of postjuvencal greater upper secondary coverts in first winter molt			
No replacement	9	5	—
Replaced 1 to 3 coverts	—	4	—
Replaced 4 to 6 coverts	—	3	8
Replaced 7 or more coverts	—	—	11
3. Replacement of rectrices in first winter molt			
Replaced 2 central pairs	5	4	—
Replaced 3 to 5 pairs	4	18	7
Replaced 6 to 9 pairs	—	1	12

likewise no exceptions to this rule in my material. Approximately half of the hybrid birds examined on Lost Trail Game Farm fell in each category. The data are summarized in table 10.

The other two differences in molt concern the extent of the first winter molt. In *silvestris*, the postjuvencal greater upper secondary coverts are retained throughout the winter, along with the secondaries. But in the domestic birds, part or all this series of coverts is replaced in the first winter molt with adult feathers; in the majority of individuals, the whole series is renewed. Hybrids are variable in this regard. Of 12 birds examined, five had retained all postjuvencal coverts, four had replaced from one to three coverts on each wing, and three had replaced from four to six coverts.

Similarly, in the first winter molt of the rectrices, only two to four of the central pairs customarily are replaced in *silvestris*, whereas from four to nine pairs (whole tail) of new winter feathers are grown in the domestic turkey. The hybrids are again intermediate, the majority replacing three to five pairs. Thus in three feather tracts, the molts of young domestic turkeys are more extensive than in *silvestris*, and in each tract the extent of replacement among hybrid birds is intermediate.

Experimental evidence has demonstrated that feather replacement is controlled by thyroid hormones; the literature on the subject is summarized by Salomonsen (1939: 388). As with breeding periodicity, however, conflicting views have been presented regarding the nature of the timing mechanism that initiates periodic molting. The most recent evidence seems to indicate that changing length of day is the environmental stimulus which induces molt (Host, 1942), although external temperature may have stimulating or inhibiting effects on both the rate and the extent of replacement. The light stimulus probably activates the production of thyrotropic hormones in the hypophysis, thereby indirectly governing the activity of the thyroid (Bissonnette, 1935).

The points of similarity between this process and the regulation of periodic breeding and migration in birds are striking. In each, the normal environmental control is changing length of daylight, acting, in ways still to be fully determined, upon the pituitary. Specific hypophyseal hormones then induce changes in the activity of the dependent glands or organs (thyroid, gonads). We are inclined to accept as commonplace the fact that birds migrate, breed and molt at appropriate seasons of the year and in accordance with changes in food supply, weather and events in the life history of each local population; yet all these processes are timed by the delicately adjusted reactions of a single gland, the pituitary. Considering this centralized control, it should not be surprising to find that closely related populations of birds that differ in breeding and migratory habits

may also differ in some aspects of molting. It has been mentioned, for example, that Blanchard (1941) found distinctions in the molts of two races of western White-crowned Sparrows, which differed also in migratory habit and in the timing of the gonad cycles; the migratory form undergoes less extensive molting than the resident race. Wolfson (unpublished data) has found similar differences in the extent of molt in migratory and resident juncos. Miller (1931) describes the variable extent of the postjuvinal primary molt in several races of Loggerhead Shrikes, the migratory forms again showing the least replacement. He suggests the existence of "inherent average tendencies in some subspecies to undergo a more complete primary molt than that occurring in other races." Variations in molting tendencies and in migratory habit may have a common physiological origin.

Since the three strains of turkeys which we are considering here are all resident in the same locality and are exposed to identical environmental conditions of light and temperature, the differences in molting procedure must be inherent in the various strains; I can find no explanation for them in environmental influences. Furthermore, these distinct tendencies in molting habit may well be associated physiologically with other differences in development and behavior, such as time of breeding and age of attaining sexual maturity. All are controlled in the individual bird through the endocrine system, and in each the pituitary plays a major role.

Because of this common endocrine relationship, I suspect that differences in plumage replacement, like differential breeding habits, may be directly associated with the phenomena of wildness and domesticity, even though differences in plumage color are not.

WEIGHTS AND MEASUREMENTS

Sources of data.—Table 11 presents a comparison of certain physical characteristics of native, hybrid and domestic bronze turkeys other than plumage color. In this table all hybrid birds are considered together and are not divided into individual strains;

Table 11
Comparison of average measurements (mm.) and weights of wild, domestic and hybrid turkeys

Type	Number of specimens	Wing	Tail	Tarsal length	Greatest tarsal diameter	Least tarsal diameter	Bill from nostril	Beard	Spur	Weight in lbs.
Adult males										
<i>silvestris</i>	24	535	375	167	19.1	11.0	28.6	261	24	17.7
Hybrid	5	536	390	162 ¹	21.0	13.5	28.0	210	26	18.3
Domestic	1	509	380	169	23.0	13.5	29.0	205	25	25.3
First-year males										
<i>silvestris</i>	8	475	346 ¹	158	17.0	10.5	26.5	33 ¹	3 ¹	10.5
Hybrid	17	495	365	158	20.0	12.8	27.5	91	13	13.6
Domestic	9	485	349	156	21.5	13.5	28.0	33	5.5	18.2
Adult females										
<i>silvestris</i>	14	448	305	130	15.5	9.0	25.0	65 ²	—	8.9
Hybrid	18	429	323	125	17.1	10.5	23.3	—	—	8.9
Domestic	6	443 ¹	321 ¹	126	18.0	11.5 ²	26.0	57 ²	—	14.2
First-year females										
<i>silvestris</i>	8	436	330 ¹	128	15.0	9.0	23.0	—	—	7.7
Hybrid	26	412	312	124	16.8	10.3	23.4	—	—	7.9
Domestic	12	425	316	125	18.7	11.0	25.3	—	—	12.8

¹Number of specimens appreciably less than indicated in column 1.

²One specimen only.

in most respects the differences between strains were negligible. Because turkeys of both sexes continue to grow in their second year, and in males perhaps into the third year (Mosby and Handley, p. 101), it was necessary to divide each sex class into two age groups. "First-year" specimens are those from 8 to 15 months of age; all older birds are classed as adults.

In addition to my own measurements of 115 specimens, there are included in table 11 data on some Virginia birds. Mosby and Handley (1943: appendix) give original measurements and weights of 33 specimens of *silvestris*. Most of the 21 wild birds that I examined were museum specimens from various parts of the eastern United States, some in fact from Virginia. Comparison of the measurements of these two samples of *silvestris* showed a close similarity in averages and dispersion, so it seemed advisable to combine the two sets of figures wherever possible to obtain a larger sample of the wild type. The figures for *silvestris* given in the table include for the following measurements both the Virginia data and my own: wing, length of tarsus, beard, spur and weight. Tail measurements were not combined, since the two sets of figures were dissimilar and it was apparent that the measurements were taken differently. All other figures included in table 11 are original data from Missouri.

Descriptions of individual measurements.—Most of the measurements were taken according to the standard procedures recommended by Baldwin, Oberholser and Worley (1931). They are as follows:

Wing.—From anterior edge of wrist joint to tip of longest primary.

Tail.—From coccygeal insertion of two central feathers to tip of longest rectrix.

Length of tarsus.—From mid-point of the joint between tibia and metatarsus behind, to junction of metatarsus with base of middle toe in front.

Large diameter of tarsus.—Anteroposterior diameter of tarsus at middle point.

Small diameter of tarsus.—Lateral diameter of tarsus at middle point.

Bill from nostril.—From anterior edge of nostril to tip of maxilla.

Beard.—From point of insertion in skin to tip of brush.

Spur.—From junction of spur with tarsus on inside edge, to tip of spur.

Evaluation of data.—Statistical analyses were applied wherever the samples were large enough to warrant such treatment (table 12). Taken as a whole, the coefficients of variability are high. This may be due in large part to the inadequate samples, but I am inclined to believe that they reflect also a high degree of variability in turkeys as a group. The domestic bronze strain is represented in these analyses by only 12 first-year females, but this sample, drawn from several different flocks, shows more constancy than either *silvestris* or the hybrids.

The least constant measurements are beard and spur (in adult males only), and body weight. The lengths of beard and spur are often supposed to be good indices of approximate age in wild turkeys. Within certain limits this may be true, but characters that show as much variability as my sample indicates are probably very unreliable age criteria. Mosby and Handley (p. 95) previously have reached this conclusion. Body weight is highly variable within each group, although again it is most constant in the domestic strain.

Even the most careful scrutiny of the data in these two tables fails to bring out many marked differences in the physical properties of wild, hybrid and domestic turkeys. By and large these three strains are morphologically quite similar. Length of wing, tail, tarsus, bill, beard and spur show no constant differences. Body weight and slenderness of the tarsi are exceptions.

Table 12

Statistical evaluation of measurements for which sufficient data were available

Measurement	Type of bird	Number of specimens	Mean with standard error	Standard deviation	Coeff. of variability
Wing	<i>silvestris</i> , adult males	24	535±5	27.84	5.20
	<i>silvestris</i> , adult females	12	448±7	23.91	5.34
	hybrid, adult females	17	429±5	19.20	4.47
	hybrid, 1st-year males	17	495±7	29.52	5.96
	hybrid, 1st-year females	18	412±3	12.00	2.91
	domestic, 1st-year females	12	425±2	7.75	1.82
Tail	<i>silvestris</i> , adult males	9	375±9	29.40	7.86
	<i>silvestris</i> , adult females	5	305±8	17.80	5.83
	hybrid, adult females	17	323±4	17.05	5.28
	hybrid, 1st-year males	15	365±3	14.25	3.90
	hybrid, 1st-year females	18	312±3	14.03	4.50
	domestic, 1st-year females	12	316±5	16.06	5.08
Length of tarsus	<i>silvestris</i> , adult males	24	167±2	8.40	5.03
	<i>silvestris</i> , adult females	14	130±4	13.35	10.27
	hybrid, adult females	18	125±2	6.35	5.08
	hybrid, 1st-year males	17	158±2	7.65	4.84
	hybrid, 1st-year females	26	124±2	7.45	6.01
	domestic, 1st-year females	12	125±1	2.56	2.04
Large diameter of tarsus	<i>silvestris</i> , adult males	9	19.1±.3	.92	4.71
	hybrid, adult females	18	17.1±.2	.82	4.82
	hybrid, 1st-year males	17	20.0±.4	1.81	9.05
	hybrid, 1st-year females	25	16.8±.2	1.00	5.97
	domestic, 1st-year females	12	18.7±.2	.68	3.68
Small diameter of tarsus	<i>silvestris</i> , adult males	9	11.0±.3	.86	7.82
	hybrid, adult females	18	10.5±.1	.55	5.26
	hybrid, 1st-year males	17	12.8±.2	.76	5.97
	hybrid, 1st-year females	19	10.3±.1	.66	6.46
	domestic, 1st-year females	12	11.0±.2	.53	4.85
Bill from nostril	<i>silvestris</i> , adult males	9	28.6±.2	.69	2.43
	hybrid, adult females	15	23.3±.3	1.04	4.46
	hybrid, 1st-year males	14	27.5±.2	1.30	4.72
	hybrid, 1st-year females	22	23.4±.3	1.27	5.43
	domestic, 1st-year females	12	25.3±.3	1.09	4.32
Beard	<i>silvestris</i> , adult males	20	261±6	29.00	11.12
Spur	<i>silvestris</i> , adult males	20	24±2	7.30	30.54
Weight in pounds	<i>silvestris</i> , adult males	14	17.7±.5	1.87	10.57
	<i>silvestris</i> , adult females	9	8.9±.2	.62	6.99
	hybrid, adult females	17	8.9±.3	1.03	11.57
	hybrid, 1st-year males	17	13.6±.5	2.04	15.00
	hybrid, 1st-year females	22	7.9±.2	.77	9.79
	domestic, 1st-year females	12	12.8±.2	.72	5.62

Body weight.—In each sex and age class the domestic birds are appreciably heavier than either hybrids or native turkeys. Despite the fact that weights are highly variable within each class, the gradient between the domestic and wild types is so marked that the difference is undoubtedly significant. Thus, while domestic and wild turkeys show similar measurements of wing, tail and length of tarsus, these appendages are attached on the one hand to a plump, well rounded body, "adapted" through generations of artificial selection to "table use," and on the other to a slender, fusiform body better fitted for an active wild bird that must run and fly for its life.

The weights of the hybrid birds are distinctly closer to *silvestris* than to the domestic strain. As previously mentioned, the Lost Trail hybrids have been selected for small body size as well as dark plumage color, and birds of this strain compose the majority of the hybrids included in the sample. Selective breeding for body size has generally succeeded in simulating the wild type, as in the case of plumage color, still without affecting the degree of wildness of the strain.

Length, slenderness and color of tarsus.—It is commonly stated that wild turkeys have longer legs than domestic birds (Mosby and Handley, p. 90; and others). The measurements of the tarsi given here do not bear this out. But the tarsi of wild birds are appreciably more slender, which makes them appear longer. In both diameters of the tarsus there is a gradation in each sex and age class from the stout bones of the domestic bird through the hybrids down to the slender wild type (table 11). The repetition of this pattern and the magnitude of the differences between the means seems to establish the significance of this gradation, despite some variability within classes. Other bones of the leg were not measured, and it is possible that the long-limbed appearance of *silvestris* may be traceable to the femur or tibia, although I think the slenderness of the tarsi is largely responsible.

The tarsi of *silvestris* are normally some shade of coral red. Wear and weather fade the color and add a grayish tinge. When the tarsal scales become loosened, prior to shedding, they appear silvery gray and obscure the underlying pigment (Pirnie, 1935; Petrides, 1942; Mosby and Handley, 1943). The tarsi of domestic turkeys are black, purplish black or some shade of dusky gray. As in *silvestris*, the color is obscured by wear and is partly concealed when the scales are loosened. Hybrids may show all stages of intergradation in tarsal pigmentation between coral and black. By and large, the Lost Trail birds resemble *silvestris* in tarsal color, which again is due to the influence of selection; tarsal color is one of the minor morphological criteria used in culling the breeding stock.

To summarize, of the various body measurements presented here, only slenderness of tarsi and body weight appear to be significantly different in wild and domestic turkeys. There is also a difference in tarsal color. The Lost Trail hybrids resemble *silvestris* in weight and in tarsal color, but are intermediate in tarsal diameter, which, as far as I know, was not used as a criterion of selection.

SECONDARY SEX CHARACTERS OF THE HEAD

Wattles, caruncles and skin pigmentation.—The fleshy wattles and caruncles on the head and neck of male turkeys are the most obvious of the secondary sex characters in this species. Wild and domestic birds differ in the degree of development of these appurtenances and in the age at which full development occurs. Hybrids are intermediate in both respects.

There are seasonal variations in the color and size of the head wattles in an individual gobbler. During and following the breeding season the appearance of the head is quite different from that during the winter. Furthermore, as the bird struts and gobbles in spring the contractile wattles change rapidly in size, shape and color. Because of these seasonal and momentary changes in the appearance of the individual gobbler, Mosby and Handley (p. 58) adopt the attitude that differences in the color and wattling of the heads of wild and domestic birds are not significant. I think that the differences are of considerable significance.

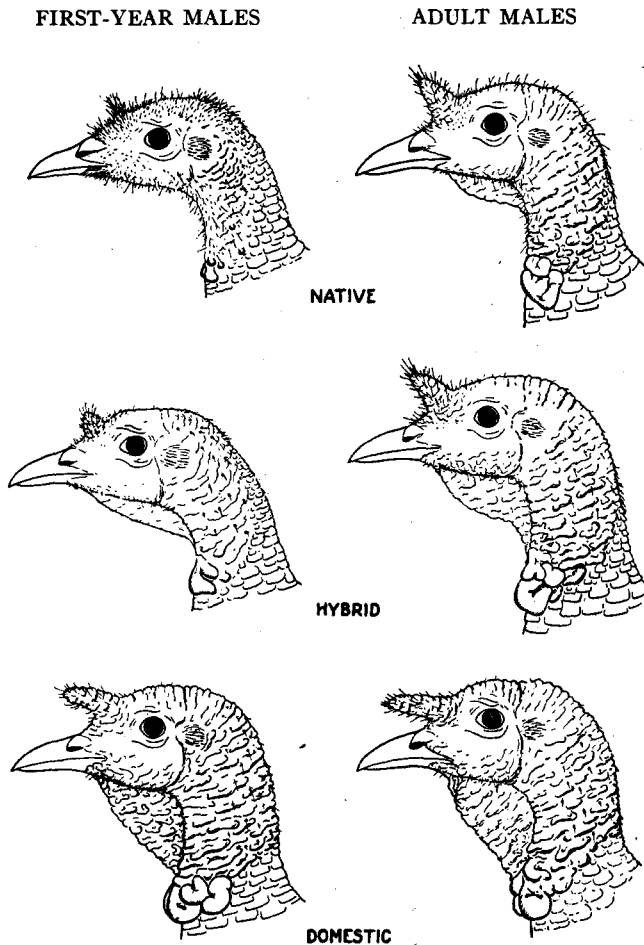


Fig. 31. Comparative development of secondary sexual characters on heads of male native, hybrid and domestic turkeys. These sketches, taken from photographs, depict heads in winter condition.

Comparisons are best made in mid-winter; at that season the color and appearance of the wattles, caruncles and areas of bare skin are quite stable in an individual bird (see figure 31):

M. g. silvestris. Adult males.—Frontal wattle conical, blue; throat wattle small or absent, blue when present; smooth skin of head and neck blue; small red warts and carunculated ridges present on sides and back of neck; large caruncles of lower throat bright red; scattered tufts of hirsute feathers on dorsal surface of neck and on chin and upper throat; frontal wattle heavily tufted with pubescent feathers.

First-year males.—Frontal wattle small, wart-like; throat wattle small or absent, blue when present; smooth skin of head and neck blue; scattered red warts present on sides and back of neck; small red caruncles on lower throat; dusky pubescence (postjuvenile feathers) over whole head except region around eye.

Females.—Frontal wattle wart-like; throat wattle absent in first-year birds, small or absent in adults, blue when present; head and neck blue; scattered red warts on neck and lower throat may

appear in adults; a band of dusky brown feathers extends up back of neck and over head to frontal wattle; dusky pubescence of head and neck denser in first-year females than in males; pubescence sparse in adult females.

Lost Trail hybrids. Adult males.—Frontal wattle larger than in *silvestris*, conical, usually red; throat wattle moderately large, usually red but may be partly blue (anteriorly, under chin); skin of face and crown red; smooth skin of back of head and neck blue; red warts and carunculated ridges abundant on sides and back of neck; large caruncles of lower throat bright red; scattered tufts of hirsute feathers distributed as in *silvestris*, but sparser.

First-year males.—Similar to adult males, but wattles and caruncles are smaller, particularly the caruncles of the lower throat; head more pubescent than in adults, particularly in frontal region and on back of neck, but plumage much sparser than in *silvestris*.

Females.—Frontal wattle small; throat wattle usually present, variable in size; color of head and neck may be all blue, with red only on throat and throat wattle, or predominantly red with blue confined to back of head and neck; plumage of head less abundant in both young and adult birds than in *silvestris*; head plumage usually buffy rather than black.

Domestic bronze. Adult males.—Frontal wattle large, often falling forward instead of standing erect; throat wattle massive, carunculated and bright red; head all red except strips of blue skin between heavy carunculated ridges of sides and back of neck; carunculation of frontal and facial regions common, though not universal; massive red caruncles on lower throat; few hirsute feathers on back of neck and on frontal wattle.

First-year males.—Practically identical with adult males.

Females.—Frontal wattle small, though larger than in *silvestris*; throat wattle large, red, often sparsely covered with buffy feathers; head all red except for blue strips between carunculated ridges on neck; throat caruncles present but small; head plumage sparser than in *silvestris*, buffy in color; first-year females similar to adults, but with smaller wattles.

The essential differences between strains may be summarized as follows. The wattles and caruncles of domestic turkeys are much larger and more highly developed than in *silvestris*. Young domestic males, still less than a year of age, have these secondary sex characters fully developed, whereas first-year wild males can scarcely be differentiated from hens of the same age. The heads of wild turkeys during the winter are predominantly blue, those of domestic birds predominantly red. The head plumage of wild turkeys, particularly of first-year specimens, is much more abundant than that found on domestic turkeys. Hybrids are highly variable, but in general are intermediate between *silvestris* and the domestic strain in the degree of development of wattles, caruncles, head pubescence and pigmentation, and in the rate of growth of the head appurtenances in males.

There is also an apparent difference in head shape. The heads of domestic turkeys, particularly of males, appear to be more rounded than the slender, angular heads of wild birds, due perhaps to the thickened, carunculated tissues that cover the skull.

Sexual development in young males.—There is an obvious relationship between the age of breeding and the development of secondary sex characters in male turkeys of the different strains. Young domestic gobblers are capable breeders before they are a year old; and their head wattles are fully developed in the course of the first winter. First-year wild gobblers are inactive breeders and show very little development of the secondary sex characters. Laboratory experiments with the domestic fowl have demonstrated that breeding behavior and the development of male secondary sex characters, such as the comb on a rooster, result from the production of sex hormones in the testes. The initial development of the testes, however, is induced by gonadotropic hormones released from the pituitary. The slow sexual development of young male wild turkeys is therefore probably attributable to lack of secretion of the gonadotropic hormone in the hypophysis and subsequent lack of growth and secretion of the testes. Young do-

mestic males, on the other hand, are mature in every sense of the word before their first spring, which suggests earlier hypophyseal secretion and earlier testicular development. This presumed differential endocrine activity should be checked in the laboratory; I was unable to do so, primarily because of a lack of specimens.

Seasonal and momentary changes in head color.—Both pigments and circulating blood contribute to head color in turkeys. The bright turquoise blue is clearly a pigment. The red color is caused by visible blood circulating near the skin. After death, the red wattles and throat caruncles fade immediately to whitish blue, indicating a draining away of blood.

During the spring gobbling season, the wattles of males (all types) expand in size. The heads of adult wild gobblers also develop more red and may be entirely red by May. Even young wild gobblers show a small wattle and some red on the throat. These alterations correspond in point of time with the period of recrudescence of the gonads and with the consequent increased secretion of testicular hormones; they are doubtless caused directly by the sex hormones. Similar changes occur in the facial "roses" of the Rock Ptarmigan (*Lagopus mutus*) (Salomonsen, 1939) and in the "eyebrows" of the Hungarian Partridge (*Perdix perdix*) and the Prairie Chicken (*Tympanuchus cupido*) during the mating season.

When a male turkey is strutting, the color of the pate and frontal region of the head, and the shape of the frontal wattle may be altered apparently at will. A red crown may change to whitish blue in a few seconds during the strut and then revert to red again. This is undoubtedly accomplished by the pinching off of the arterial blood supply during the contortions of strutting. Similarly, the frontal wattle may be changed from the turgid, red, conical structure to the pendant blue form by an altered blood flow.

The return of the wattles and the head coloring to winter condition occurs slowly in the male turkey. An adult wild gobbler's head may remain predominantly red until September. The red color and characteristic flabbiness of the wattles in summer are commonly ascribed by Ozark hunters to the heat. The gradual regression of the testes and the slowly diminishing supply of sex hormones may be another contributing cause of this condition.

These fluctuations in the appearance of the head of an individual bird in no way invalidate the distinct differences between the various strains.

RELATIVE SIZE OF BRAIN AND CERTAIN ENDOCRINE GLANDS

The work of Crile.—The relative development of the brain, heart and endocrine glands in animals of widely different habit was made the subject of exhaustive study by Dr. George Crile (1941). As a basis of comparison, Crile used the ratio, organ weight/body weight, confining his direct comparisons, however, to forms that were reasonably similar in body size. There are obvious dangers in deducing the functional performance of organs from gross weight alone; nevertheless, so great were the differences found between various animals that many of his correlations are undoubtedly sound.

Some of Crile's conclusions are as follows. Animals that depend upon endurance in pursuit or escape, such as the wolf and the caribou, have relatively large thyroid glands. Through a high output of thyroxin these well developed glands permit a high, constant rate of metabolism and hence a high expenditure of energy over a period of time. Structural features and dependent physiological processes are adjusted to this type of activity. On the other hand, animals which depend upon a rushing attack, or conversely upon

a sudden dash to escape, such as the cat and the mouse, have relatively large adrenal glands, whose output of adrenalin permits the expenditure of "outburst energy" (see Cannon, 1932). Neither the cat nor the mouse has endurance; in both, the thyroids are small relative to adrenal size. In a bird like an accipitrine hawk, the whole brain-heart-thyroid-adrenal-sympathetic system is better developed than in a vulture. Although I find some of Crile's theories of "intelligence, power and personality" in animals hard to accept, particularly those concerning "intelligence" in bird behavior, the basic relationships which he points out between relative organ development and activity seem to be well founded.

Of particular interest here are Crile's findings on the effect of captivity and domestication on brain and endocrine development in animals. Domestic birds and mammals as a group are docile, slow moving, and of tranquil temperament, relative to similar forms in the wild; as a group they are possessed of appreciably smaller brains, thyroids and adrenal glands than are the wild forms. Speaking of the domestication of the barnyard chicken, he says: "When man desires a greater number of eggs from a hen, . . . he breeds for tranquility rather than temperament. To produce tranquility, he [unwittingly] breeds toward a smaller brain and a smaller adrenal-sympathetic system." His weight ratios for domestic chickens show smaller brains and adrenals than were found in any wild birds from passerines to ostriches.

Dissection of turkey chicks.—Following Crile's idea, I made a series of dissections of wild, hybrid and domestic turkeys, to determine the relative development of the energy controlling organs in the three strains, between which we have already noted many differences in behavior. For a number of reasons it seemed best to study the organ ratios in juveniles rather than in adults. Foremost among these was the fact that differences found in newly hatched young could without qualification be considered inherent, whereas differences in adrenal development, for example, between adult wild and domestic turkeys might be partly the result of unequal physical exertion or other environmental influences. My dissections were performed on 40 juvenal turkeys between the ages of 5 and 13 days. Of these, 4 were native turkeys obtained by hatching eggs taken from a nest on Caney Mountain Refuge, 22 were hybrids from Lost Trail Game Farm, and 14 were pedigreed domestic bronze poultz purchased from a commercial dealer. In addition, I dissected four, year-old male specimens of the hybrid strain, but comparable wild and domestic specimens were not available, and the data are not used here.

Through the courtesy of the University of Missouri Poultry Department I was permitted to keep the 40 chicks in a brooder on their experimental farm. They were fed starting mash and cared for along with newly hatched chickens in the same building. All were toe-punched to identify the various strains. The four wild chicks were dissected first, since they were a week older than the hybrid or domestic birds. Dissection of the 36 remaining birds occupied nine days.

The chicks were killed by pressing the thoracic region between thumb and forefinger. Immediately following death, body weights were taken. Dissection proceeded as follows: The abdominal cavity was opened and the viscera were removed. The adrenal glands, visible behind the gonads, were dissected out, placed on a dry watch glass, and cleaned of accessory tissue; a binocular microscope was used during the cleaning process. Contact of the glands with the dry watch glass removed the excess fluids. The two adrenals were then placed in a glass-stoppered bottle and weighed to the hundredth of a milligram on a Traumnner analytical balance sensitive to .02 milligrams. The weights are given here (table 13) to the tenth of a milligram. The glands were preserved in Bouin's fixative solution.

The ribs were then cut so that the sternum could be raised to a vertical position, exposing the thoracic cavity. The two segments of the thyroid were removed, cleaned, weighed and preserved as

were the adrenals. I found the thyroid dissections extremely difficult, because of the attachment of the glands to the parathyroids and the thymus. Part of the thyroid weights, including those of the four wild specimens, had to be discarded because of poor dissection.

The brain was removed by peeling away the skull, starting at the eye sockets. A pair of heavy, blunt-pointed forceps was found to be the most useful tool. When the brain was exposed from above and from all sides, it was severed from the spinal cord at the posterior extremity of the dorsal groove on the roof of the medulla. After the optic and other cranial nerves were clipped, the brain could be removed and weighed. The pituitary gland was then easily removed. After weighing, the brain and pituitary also were preserved in Bouin's fluid. Histologic studies of these structures are contemplated at a later date.

Comparison of brain and gland weights.—Table 13 lists the 40 birds dissected and the weights of the body, brain, adrenals, thyroids and pituitary glands of each. Figures 32, 33 and 34 show for the brain, and for the adrenal and pituitary glands, the individual weights expressed as per cent of body weight and plotted against age; the thyroid weights are not shown in the graphs, because of the incompleteness of my data. Simply plotting the gland weight against body weight was a satisfactory method of comparing the relative sizes of adrenals in the three strains; but in the brain, and to a lesser extent in the pituitary, proportionate size in relation to body weight falls off rapidly as a chick gets older, and for accuracy it was necessary to consider age as a variable. Therefore, to maintain uniformity of treatment, all three series of weights are shown in the figures as percentage of body weight, plotted on age. The sexes are not separated in these compilations. Although Juhn and Mitchell (1929) found slight sexual differences in the size of brain and thyroids in adult chickens, I could detect no such differences in the juvenal turkeys.

(1) Body weight.—Wild turkey eggs are smaller than those of the domestic turkey, and the chicks likewise are smaller (Gerstell and Long, 1939). The body weights shown in table 14 bring out the difference; in this sample, the domestic chicks average 27 per cent heavier than the juveniles of *silvestris*; the hybrids are intermediate in body weight. In interpreting these weights, the variable ages of the chicks must again be considered. The four wild birds were 10 and 11 days old, whereas the hybrid and domestic specimens ranged from 5 to 13 days of age, many of them being in the younger age classes. When only the body weights of birds approximating 11 days of age are considered (see table 13), the difference between the wild and domestic strains is even greater than indicated in table 14.

(2) Brain.—Crile was not the first to detect the reduction in brain size among domesticated animals. Darwin (1876:134), in his indefatigable investigations of variation in animals, found that the brain capacity of a domestic rabbit's skull was 21 per cent less than that of a wild rabbit of similar weight. As between several domestic varieties, he reported that the Angora breed, "which is said to differ from other breeds in being quieter and more social," had the smallest brain in proportion to its body size. Darwin explained the reduction in brain size in the tame strains on the basis of his familiar theory of use and disuse.

Donaldson (1915) gives the average weight of the brain of a 400-gram male wild Norway rat as 2.40 grams. Comparable specimens of the laboratory albino rat were found to have a brain weighing on the average 2.05 grams. The difference here is 17 per cent.

Examination of figure 32 discloses a definite difference in the relative size of brain in wild and domestic turkey chicks. The brain is consistently larger in the wild birds when measured as per cent of body weight, and there is no overlapping in this regard. Even when actual brain weights are compared, without allowing for the 27 per cent

Table 13

Specimen number	Sex	Age in days	Weights of body, brain and certain endocrine glands				
			Body	Brain	Weights in grams		Pituitary
			Wild turkeys from Caney Mountain Refuge, Ozark County, Missouri		Adrenals	Thyroids	
132	F	10	50.9	1.706	.0160	—	.0018
133	F	11	59.9	1.818	.0172	—	.0020
134	M	11	59.4	1.910	.0171	—	.0013
135	M	11	52.2	1.773	.0204	—	.0016
Hybrid turkeys from Lost Trail Game Farm							
137	F	5	48.8	1.543	.0131	—	.0011
138	M	5	65.5	1.794	.0110	—	—
141	F	6	56.1	1.716	.0101	—	.0014
142	F	6	55.3	1.667	.0078	—	.0012
147	F	7	49.4	1.813	.0135	.0052	.0015
149	F	7	46.0	1.687	.0140	.0063	.0011
150	M	7	49.5	1.867	.0148	.0047	.0014
151	F	8	74.1	1.803	.0132	.0064	.0014
152	M	8	67.3	1.936	.0128	.0045	.0017
153	M	8	53.9	1.911	.0157	.0044	.0014
156	F	8	56.6	1.804	.0118	.0055	.0013
157	F	8	62.2	1.799	.0147	.0054	.0014
158	M	10	63.4	1.948	.0144	.0039	.0015
159	F	10	66.1	1.945	.0143	.0038	.0015
162	M	11	87.1	2.011	.0153	.0057	.0019
163	F	11	61.0	1.937	.0138	.0040	.0016
164	M	11	71.6	2.021	.0168	.0044	.0017
167	M	11	73.0	1.976	.0124	.0048	.0013
168	F	11	71.9	1.988	.0133	.0048	.0017
169	F	12	62.3	2.005	.0143	.0030	.0016
170	F	12	78.0	1.913	.0132	.0057	.0017
171	F	12	70.1	1.960	.0163	.0043	.0018
Domestic bronze turkeys							
136	F	5	63.9	1.525	.0070	—	.0016
139	F	6	60.7	1.560	.0089	—	.0015
140	F	7	68.2	1.530	.0099	—	.0014
143	M	7	69.2	1.626	.0100	—	.0011
144	M	7	60.4	1.606	.0096	—	.0010
145	F	8	67.1	1.488	.0116	.0052	.0011
146	M	8	64.8	1.744	.0112	.0043	.0011
148	M	8	70.8	1.804	.0111	.0048	.0014
154	F	9	59.9	1.618	.0098	.0044	.0013
160	M	11	90.3	1.787	.0143	.0061	.0018
161	F	11	82.0	1.741	.0118	.0041	.0014
165	F	12	75.5	1.773	.0100	.0056	.0019
166	M	12	74.7	1.881	.0134	.0040	.0020
172	M	13	81.5	1.935	.0135	.0048	—

difference in body size, the brain of the average wild chick is larger (table 14, part 1). The hybrids are much more irregular in their distribution than the comparable sample of domestic specimens. The majority are intermediate in brain size, but the extremes overlap the averages of the two parent types.

(3) Adrenals.—Figure 15 shows the adrenal/body weight ratios. In the domestic strain, adrenal size is very constant at about 0.015 per cent of body weight. The adrenals of the four wild birds average 0.032 per cent of body weight; proportionately, they are twice the size of the glands in domestic chicks. As in the case of the brain, the actual

adrenal weights of *silvestris* exceed those of the domestic birds, even when no allowance is made for body size. The hybrids are variable but intermediate in adrenal size.

(4) Thyroids.—The thyroid weights of 18 hybrid and 9 domestic chicks are summarized in table 14. I find no significant difference between these samples, but owing to the inadequacy of my data, no conclusion can be reached. Further dissections will have to be made to ascertain the comparative development of this gland.

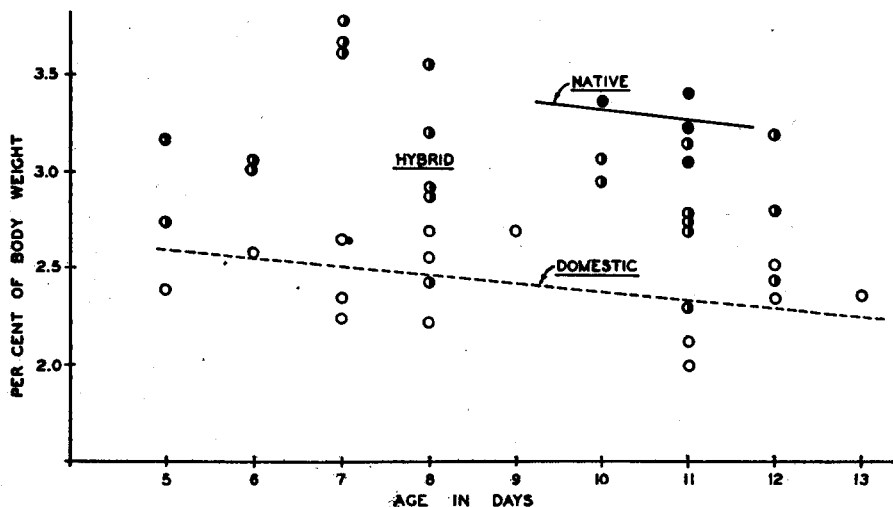


Fig. 32. Brain weights, expressed as per cent of body weight, in native, hybrid and domestic turkeys.

(5) Pituitary.—Figure 34 compares the pituitary/body weight ratios. Because the pituitary is so small, variability in weights within a homogeneous sample, as for example in the 14 domestic birds, may be due more to mechanical difficulties in weighing than to actual differences in size. The differences between pituitary weights are measured in ten-thousandths of a gram, and minute errors in the use of the scales appear large. Despite variability within the samples, there is a significant difference in the proportionate size of the gland in the three strains, the largest glands again occurring in *silvestris*.

Subject to the inaccuracies inherent in averaging samples of different size and of different age distribution, the following simplified figures are given which summarize the extent of divergence in brain and endocrine development. In terms of per cent of body weight, *silvestris* exceeds the domestic turkey by 35 per cent in brain size, by 101 per cent in adrenal size, and by 50 per cent in the size of the pituitary. In each instance, the hybrid chicks are intermediate.

Table 14

Strain	Number of specimens	Body weight	Brain	Adrenals	Thyroids (incomplete data)	Pituitary
1. Average weights in grams						
Native	4	55.6	1.802	.0177	—	.0017
Hybrid	22	63.2	1.866	.0135	.0048	.0015
Domestic	14	70.7	1.688	.0109	.0048	.0014
2. Weights expressed as per cent of body weight						
Native	4	100	3.25	.0320	—	.0030
Hybrid	22	100	3.01	.0224	.0076	.0023
Domestic	14	100	2.41	.0154	.0066	.0020

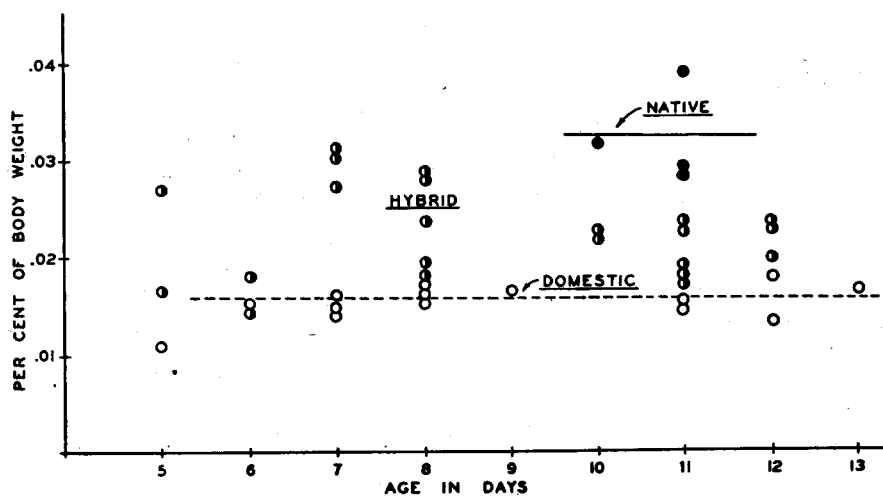


Fig. 33. Adrenal weights, expressed as per cent of body weight, in native, hybrid and domestic turkeys.

Correlation between weights of adrenals and brain.—Very little is known of the relationships between the brain and the adrenal glands during the period of body growth. Hoskins (1933) discusses the possible developmental interdependence of these organs in a human embryo. He states: "There is a rare fetal anomaly in which, when the infant is born, it is found to be without a brain. For some reason, not at all understood, the adrenal cortex . . . also is lacking or very small." The medulla of each adrenal is derived embryologically from nervous tissue, namely from a modified sympathetic ganglion.

An apparent correlation found here between the weights of the brain and the adrenals in individual domestic turkey chicks may be of some significance (figure 35). There

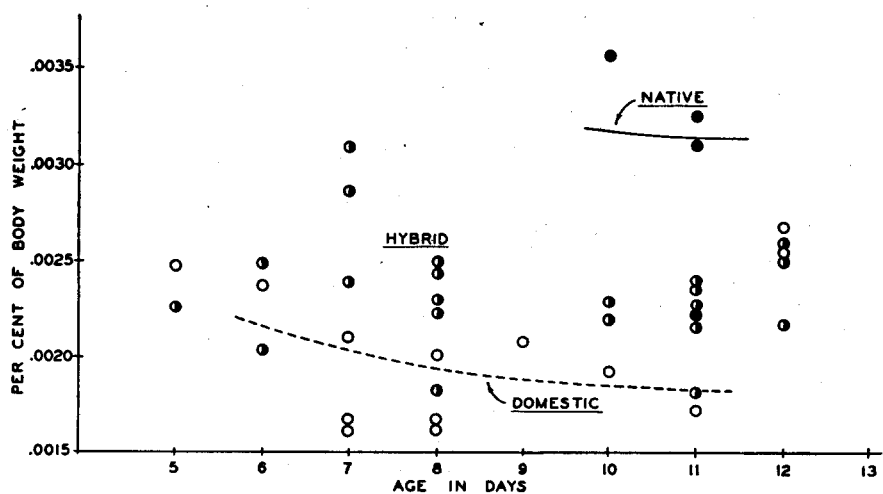


Fig. 34. Pituitary weights expressed as per cent of body weight, in native, hybrid and domestic turkeys.

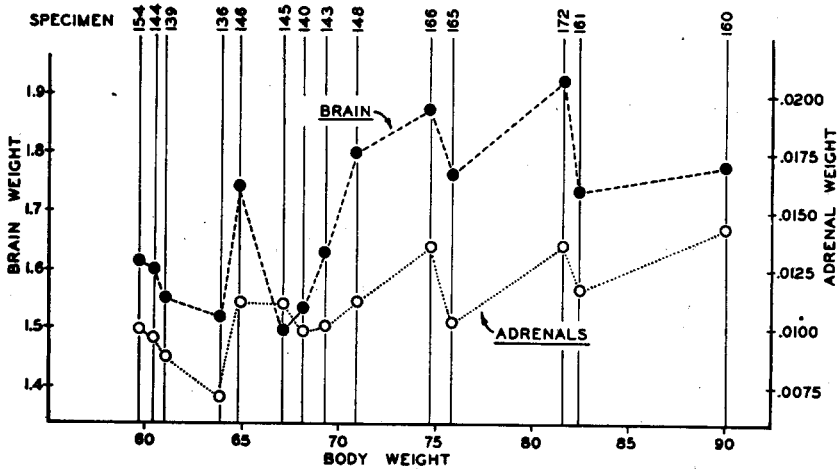


Fig. 35. Brain and adrenal weights of 14 domestic bronze turkey chicks; all weights are in grams. Within this sample, the coefficient of correlation between the weights of the brain and adrenals in individual birds is $.636 \pm .159$.

is a distinct parallelism in the "ups and downs" of these weights, which is quite independent of body size. The data were plotted on a scatter graph, and the coefficient of correlation determined as $.636 \pm .159$, which is relatively high. No similar correlation exists between any of the other paired weights, even pituitary and brain. What the relationship between the adrenals and brain may be, I cannot say. This point has only an indirect bearing on the present problem, but it is mentioned for its possible interest in the field of experimental embryology.

DISCUSSION OF ANATOMICAL AND PHYSIOLOGICAL DIFFERENCES

We have seen that wild, domestic and hybrid turkeys differ functionally in a number of respects and anatomically in several others. It is now possible to point out one or two ways in which structure and function may be interrelated.

Of the anatomical differences, the most significant in explaining differential behavior are those relating to the comparative development of the brain and endocrine glands. Since the nervous and endocrine systems jointly exercise almost complete control over the functioning of an organism, the possible effects of differences in the development of these two systems upon behavior are obvious. The larger size of the brain, adrenals and pituitary in *silvestris* undoubtedly has a bearing upon wild behavior in the individual bird. The following example, while largely speculative, illustrates one way in which this may operate.

The freezing reaction in wild turkey chicks is induced by a nervous stimulus transmitted to the brain through the ear or eye; the stimulus releases an innate or instinctive action. Being a "fear" reaction, it is almost certain that the sympathetic as well as the central nervous system is stimulated. Stimulation of the sympathetic system is known to release a "charge" of adrenalin, the size of which may well be dependent upon the size of the adrenal glands, as well as upon the strength of the stimulation. The resulting action of the bird, which Lorenz would call the innate perceptory pattern of behavior, might therefore be affected by (1) the inherent neuron pathway stimulated, (2) the strength of the stimulation, and (3) the amount of adrenalin secondarily re-

leased. It does not seem too far afield to point out that a violent fear reaction in humans often is evidenced in "freezing," the cause of which is primarily a strong stimulation of the sympathetic system.

The failure of domestic chicks to display a similar reaction might be due to a dulling of the senses of perception, that is to a weaker initial stimulation of the central nervous system by the danger call of the hen (connected perhaps with the smaller size of brain), and/or to a lesser amount of adrenalin released when the sympathetic network is secondarily stimulated. Differences in the fear reactions of adults may be similarly controlled. As previously stated, this is speculative reasoning and presents only one possible way in which the differences in brain and adrenal development might affect behavior.

The impossibility of predicting gland activity from gland size, however, is brought out when we consider pituitary functions. The pituitary has been shown to control the time of breeding and probably the initiation of molting in birds. In various laboratory animals, and in man, the initiation of sexual development is known to depend indirectly upon pituitary activity; the same is probably true of birds. As regards these three physiological functions, we have seen that the domestic turkey attains sexual maturity at an earlier age, breeds earlier each season, and undergoes more extensive molting during the first year than does *silvestris*. A possible explanation is that the hypophysis of the domestic turkey has a *lower threshold of stimulation* than that occurring in the wild bird. Although an earlier response of the gland to environmental and internal influences is indicated, there is nothing to suggest lessened hypophyseal secretion, even though the pituitary in domestic birds is smaller than in *silvestris*.

I limit my conclusions, therefore, to the following. Wildness in turkeys is inextricably tied up with the functioning of the central and sympathetic nervous systems and with the secretions of the pituitary and adrenal glands; the thyroid may well be involved also. Demonstrable differences in the size of the brain and of the glands doubtless affect their function, although in precisely what ways cannot be stated. Differences in function may well be present that are not reflected in size. But in these two coordinated systems of physiological control must lie the fundamental differences between wildness and domesticity. The next steps toward understanding the actual interrelationships between hormones and nervous impulses, as they affect behavior in turkeys, will of necessity be experimental in nature.

Of the other anatomical differences in turkeys, plumage color probably has no relation to wildness, and body size and the characteristics of the tarsi may likewise be of no significance. The nature of the head ornamentation in males, and the age at which the wattles and caruncles reach full development, are significant as surface reflections of physiological processes going on within the bird. The extent of molt in young specimens has a similar value. For those who seek external manifestations of wildness in turkeys, I would suggest the limited molts and the limited development of the secondary sex characters of the head as the most likely criteria. At least, these are visible characters which I have found consistently associated with wild behavior.

CONCLUSIONS

ENVIRONMENTAL ADAPTATION IN TURKEYS, AND THE INFLUENCES OF SELECTIVE FORCES

Wildness as an adaptive condition.—Wildness was defined early in this report as the sum of the various behavior patterns and other inherent adaptations which permit the successful existence of free populations of turkeys. According to this definition, the

only full measure of wildness is the relative success of established populations. I reiterate this concept here. Wildness is the inherited condition by which turkeys as individuals, and collectively as populations, are adapted to live successfully in a natural environment.

In attempting to explore the complex nature of this adaptive condition in turkeys, I have compared various characteristics of *M. g. silvestris*, of which free populations are demonstrably successful in the Ozarks, with characteristics of hybrid and domestic turkeys whose populations are partially or entirely unsuccessful there. Differences of several types have been shown between individual birds of the three strains. Some of these appear to have no fundamental relation to wildness; color of plumage, body size and characteristics of the tarsi seem to fall in this category. There are other differences, the significance of which is not clear, as for example the differential flocking habits of wild and hybrid birds. In what ways sexual segregation and size of flock are associated with the wild condition I cannot say. But the majority of the points of distinction appear to be connected, directly or indirectly, with relative wildness and domesticity. In review, these concern the following topics: (1) wariness and tolerance of disturbance; (2) the age of attaining sexual maturity, and the related development of secondary sex characters in males; (3) the timing of the breeding cycle; (4) behavior of hens and chicks in response to threatened danger, and the differential behavior of chicks in the laboratory (as shown in the experiments of Gerstell and Long); (5) the extent of molts in young birds; and (6) the relative size of the brain and some of the endocrine glands. This list of differences is indeed heterogeneous in character. It is doubtless incomplete, presenting only a few, perhaps a small percentage, of the actual differences that may be found to exist between the wild and tame strains. The heterogeneity of the list reflects, in fact, its incompleteness.

Even though my data are scattered, the fundamental distinction between the strains has been quite clearly indicated. Wildness and domesticity are two heritable, physiological complexes; their dissimilarities stem primarily from differences in the form and function of the nervous and endocrine systems in the individual turkey. Certain resultant differences in behavior have been shown to affect the survival of both young and adult birds; these distinctions are therefore of adaptive significance. Differences in molt, in age of maturity, and perhaps even in flocking habits, I interpret as non-adaptive, secondary manifestations of the significant physiological complexes. Such non-adaptive expressions of internal conditions in themselves probably have little if any bearing upon survival, but they may be useful "indicators" of the associated adaptive functions in behavior.

The wild condition is not only favorable in the evolutionary sense to free-living populations—it seems to be immediately essential. Birds so endowed follow a pattern of behavior that promotes the survival of the individual as well as of the race. Wild turkeys are wary and shy, which are advantageous characteristics in eluding natural and human enemies. They breed at a favorable season of the year. The hens and young automatically react to danger in ways that are self-protective. Reproductive success is high. Collectively these and associated actions and reactions literally adapt the native wild birds to existence in their ancestral environment. As a consequence, we find that populations of *silvestris* are tenacious and thrifty under adversity and are readily responsive to protection and management.

Birds of the domestic strain, on the other hand, are differently adapted. Many of their physiological reactions and psychological characteristics are favorable to existence in the barnyard but may preclude success in the wild. What Crile calls the "tranquil

temperament" is one of these. Tranquility is doubtless an asset in domesticated flocks but may be a highly deleterious character in independent populations that are exposed to poaching and predation. Other types of innate reactions, such as the early period of breeding, may be of equal importance in limiting the natural productivity of free populations. Early breeding is considered an advantage on commercial turkey farms; it is even selected for (Asmundson, 1941). But in the wild, the advanced reproductive cycle throws the period of hatching into cool weather and a time of possible food shortage that may sharply delimit juvenal survival. Domestic turkey chicks scatter rather than hide in response to the warning note of the hen; further losses of young to predation may result from this disadvantageous reaction. In such ways as these are domestic turkeys physiologically maladjusted to existence in the wild. And, as we have seen, they do not so exist.

Forces of selection operating on captive hybrid stocks.—One important point regarding the degree of wildness in hybrid stocks remains to be explained. The hybrids in Missouri have been shown to be intermediate between *silvestris* and the domestic strain in nearly all aspects of anatomy and behavior. Only in some external morphological traits do they closely resemble *silvestris*, and these have no bearing on relative wildness. In their ecological relations, hybrid populations are also intermediate. Under complete protection and in favorable environmental conditions they persist in low density populations, which the domestic strain is unable to do, but they are far less thrifty and productive than are native populations. For all practical purposes we can consider the hybrids little more than half wild.

Returning to the breeding method by which these stocks have been derived, it was shown that the Lost Trail strain had passed through ten successive generations of backcrossing to wild-living gobblers, which theoretically should render the present stock in excess of 99 per cent wild. A partial explanation for the failure of the wild pen breeding plan actually to derive this high degree of wildness has been offered, namely, that some of the gobblers enticed into the pens were themselves hybrids. Yet in my opinion this is not the full explanation. A large number of the breeding males were, if not pure *silvestris*, still perceptibly wilder than the hens. Some additional factor is involved. I postulate that the mixed stock on the game farm is subject to a powerful selective force, which favors domesticity and prevents the accumulation of the genes for wildness in captive populations. There is considerable evidence that such a force may exist.

Wildness is definitely an unfavorable characteristic in captive birds. As previously stated, no one to my knowledge has successfully raised pure eastern wild turkeys on a production basis. The nervous temperament and violent reactions of wild turkeys fit them poorly for existence in confinement. It is difficult to induce captive native turkeys to breed and to produce fertile eggs. Many birds, both young and adults, kill themselves in violent efforts to escape. The strain seems to be even more susceptible to common poultry diseases than is the domestic turkey. Mosby and Handley (p. 125) report that of 30 native chicks hatched at the Virginia game farm from eggs confiscated from nests, only two were raised to maturity. Similar efforts in Missouri have been equally unproductive. In all, the difficulties of handling confined populations of *silvestris* are so great as to render their propagation unprofitable. That, of course, is why breeders have turned to the "indirect approach" to wildness, by the use of the wild pen breeding method.

It is not really surprising that the native turkey should be difficult to raise. Many of our wild gallinaceous birds, including nearly all the grouse and some quails, are

equally difficult to propagate artificially. There is no reason to expect wild turkeys to be any more tractable.

Hybrid strains can be propagated, although they are more difficult to handle than domestic turkeys. Since, under artificial conditions, mortality is so much higher among wild than among domestic turkeys, we should expect to find that the difficulties of raising hybrid strains increase when the hens are backcrossed to wild males. This is exactly the situation encountered on game farms. Since the Lost Trail unit is a private concern, hatching and mortality figures are not available to me, but it is generally agreed that propagation difficulties of all sorts multiplied when the wild pen mating system was adopted. Gerstell and Long actually measured the difference in mortality between strains of two degrees of wildness on the Pennsylvania game farm. They state (p. 17): "Up to the time of release at the approximate age of sixteen weeks, the losses among the [wild mated] class totalled approximately thirty-eight per cent as compared to only twelve per cent in the [game farm] type." Normal mortality on the game farm, therefore, seems to be roughly proportional to the degree of wildness of the stock.

In a hybrid game farm population, individual birds are probably heterozygous for most or nearly all of the numerous genetic factors which control wildness. This heterozygosity is constantly maintained when hybrid females are backcrossed to wild males. There would be no reason to expect uniformity among the birds in the exact degree of wildness; according to the laws of chance, some individuals should be wilder than others. That this occurs is indicated by the variability of the hybrids in the size of the brain and endocrine glands, which I have presumed to be criteria of wildness. Examination of figures 32 and 33 in particular discloses greater variability among the hybrids than among the domestic birds in the weights of the brain and the adrenals. The sample of domestic turkeys, drawn from pedigreed stock, represents a pure strain, hence uniformity would be expected. The scattering of the hybrids on these graphs suggests a decided lack of uniformity in the genetic factors which control brain and endocrine development and hence indirectly control wildness.

When high mortality is suffered by a mixed group of confined birds, which vary in degree of wildness, is it not logical that the greatest loss probably occurs among the wildest birds? If the likelihood of such differential mortality is granted, there follows a corollary sequence of ideas that adequately explain the situation actually found in hybrid stocks. After a certain number of backcrosses to wild males have been made, a point must be reached where the forces of selection, which strongly favor domesticity, balance the gains in relative wildness made by the backcrosses, since the wildest birds of each generation are largely lost. The degree of wildness in the stock as a whole fluctuates thereafter around an intermediate point of dynamic equilibrium. Backcrossing of hens from Lost Trail farm to wild males might continue indefinitely without making the strain any wilder, since the resultant annual gains in wildness are not cumulative. It would be impossible, therefore, ever to approach complete wildness in artificially propagated turkeys. As previously noted, the actual degree of wildness found to exist in the Lost Trail strain is little better than 50 per cent, as measured by the rough criteria at my disposal. The logic of this roundabout deduction is borne out by the fact, which I repeat again, that artificial production of a pure strain of *silvestris* never has been accomplished by any game breeder, and it is not reasonable to expect that strains of equal wildness could be "derived" and subsequently produced in numbers through the backcrossing procedure. The wild pen breeding method, to be fully effective, would have to be accompanied by artificial selection in the pens for wildness, which in itself would soon lead to extermination of the captive stock.

Be it admitted, however, that if wild pen breeding were not followed, confined hybrid strains would tend rapidly toward virtually complete domesticity. The process of backcrossing to wild males definitely produces a wilder strain of hybrids than could be obtained by the usual inbreeding methods.

Such rapid alteration of the genetic constitution of a group of organisms by a selective force, as has been postulated here, would only be possible in a heterozygous population. The classic experiments of Johannsen showed that selection is highly effective in genetically mixed populations but inoperative in pure lines. Haldane, as quoted by Dobzhansky (1937), demonstrated that selection can proceed most rapidly at intermediate stages in relative gene frequencies. Both of these conditions for the optimum operation of selective forces are met in the game farm turkeys.

Selection in the wild.—In free-living populations, the selective forces are reversed. All the evidence presented here has suggested that wildness is strongly adaptive under natural conditions, and we can safely assume that as an inherited condition it is favored by the forces of selection. In the wild, differential mortality among individuals and differential rates of productivity would tend to eliminate traits of domesticity. When, therefore, a hybrid population becomes established, the average degree of wildness of the individual bird should increase over a period of generations. Ultimately, the population should approach *silvestris* in behavior and in productivity. The following case is presented as indirect evidence that such progressive change actually occurs.

In the region north of Drury Refuge in Taney County, there are reported to have been released in the late 1920's a large number of domestic and some hybrid turkey hens. This activity was undertaken by local sportsmen in an effort to bolster the declining wild turkey population. There are no reliable records of the immediate results; but they must have been unsatisfactory, for the project was soon abandoned. Considerable hybridization with the resident native stock probably occurred, however, for the birds of that area now show more variability in their morphological characters than any local population known to me in the state. There are all shades of tail coverts and rectrix tips from Pinkish Buff to the normal Cinnamon Brown. Some birds display traces of albinism. Some have "frosted" body plumage resembling the domestic Naragansett strain. Yet the present population is high, and in behavior the birds resemble the native strain. They are wary and alert; the winter flocks segregate sexually; the gobbling season is approximately that of *silvestris* on Caney Mountain Refuge. I believe that tendencies of domestic behavior gradually have been eliminated from the hybrid population by forces of selection favoring wildness, whereas some morphological traits, which were introduced concomitantly, have persisted, since they are independently segregated from wildness and have no strong selective value of their own.

If these hypotheses are correct, we no longer can look upon the hybridized state in turkeys as being a static condition. Under normal circumstances, stocks derived from hybrid origin probably are heterozygous for most of the genes which control wildness, hence are highly subject to selective influences. The direction which the processes of selection will take is governed by the external circumstances in which the hybrids exist—whether in pens or in the wild.

Such being the case, all established hybrid populations, as for example those on Blue Spring and Deer Run refuges, should over a period of time tend to become progressively wilder. The alteration will undoubtedly proceed most rapidly on areas where remnants of native stock exist, as on the north end of the Blue Spring area; there, natural backcrossing to *silvestris* can occur. As a management practice, the deliberate

introduction of live-trapped, wild gobblers into hybridized populations would be a practical way of hastening the genetic rehabilitation of such populations.

The original domestication of *M. g. gallopavo* was probably a gradual selective process by which the genetic constitution of the wild bird was modified to bring about a physiological adaptation to symbiotic existence with man; the very fact of the domestic turkey's subsequent tenure of the barnyard has tended to sustain these modifications. And conversely, the wild condition in native turkeys is constantly and very effectively maintained by the influence of an opposite set of selective factors in the natural environment.

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