INFLUENCE OF THE TRAILING-EDGE NOTCH ON FLIGHT PERFORMANCE OF GALLIFORMS

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ABSTRACT.—Trailing-edge notches, formed by shortened first secondaries, characterize the wings of most galliforms. I investigated the function of these notches with comparative measurements of notch size taken from extended-wing specimens and with experimental studies of model wings of four representative species. Pheasants, quail, and turkeys, all of which use flight to escape predators, have wide wings and deep notches. Grouse with dark flight muscles have long, narrow wings with small trailing-edge notches and typically fly relatively long distances from one foraging site to another. Grouse with light colored flight muscles have short, broad wings with large trailing-edge notches and mostly fly from ground to canopy or from branch to branch to reach their food. Model wings of two pairs of galliforms with different wing shapes were used in the experiments. White-tailed Ptarmigan (*Lagopus leucurus*) and Sage Grouse (*Centrocercus urophasianus*) have small notches, high aspect ratios, relatively heavy wing loadings, low maximum lift coefficients, and dark pectoral muscles. In contrast, Wild Turkey (*Meleagris gallopavo*) and California Quail (*Callipepla californica*) have deep notches, low aspect ratios, relatively light wing loadings, high lift coefficients, and light colored pectoral muscles. Experiments using model wings in a water flow tunnel show that the trailing-edge notch increases the maximum lift-to-drag ratio and stabilizes airflow around the wing, but reduces the maximum lift coefficient. Thus, the trailing-edge notch increases performance in vertical and slow flight but reduces efficiency in level flight. Such a function is consistent with the suite of differences these birds show in muscle color, wing shape, and predominant mode of flight. *Received 17 November 1995, accepted 27 February 1996.*

BIRD WINGS EXHIBIT morphological adaptations for different kinds of flight (Rayner 1988, Norberg 1989). Regardless of the species, slots between the primaries increase the lift-to-drag ratio by increasing lift and reducing drag (especially induced drag) that results from deflection of an air stream around a tilted wing. Such conclusions about the functional significance of wing slots come primarily from the established correlation between deep slotting and slow, level flight that characterizes birds with wings that are broad at the tip. Wind-tunnel experiments support these conclusions (Vinogradov 1951; Hofton 1978; Tucker 1993, 1994).

Galliforms have deep slots between their primaries and a large alula, but they rarely have been used as subjects for aerodynamic studies (Shtegman 1953, Shestakova 1971). Furthermore, no study of the aerodynamics of galliforms has addressed the functional significance of the large notch on the trailing edge of the wing that is formed by a short first secondary. This feature is exhibited by all galliforms and is quite evident when the wing is fully extend-ed. However, only Shestakova (1971) has noted the existence of this notch in various galliforms and some gulls.

In this paper, I present comparative data on the size of the trailing-edge notch for 31 species of galliforms. I also present results of experiments that show how this notch influences gliding performance in the wings of four species with different wing shapes.

MATERIALS AND METHODS

Measurements of wing length, wing breadth, and trailing-edge notch size were taken from 220 extended-wing specimens of 31 galliform species (Table 1). I calculated notch size (in %) as:

$$(WB - WB_{S1})/WB, \qquad (1)$$

where WB_{S1} is the distance between the leading edge of the wing and the tip of the first secondary, and WB is wing breadth measured from the leading edge of the wing to the tip of the fifth secondary. I chose the fifth secondary for these measurements because in some birds (e.g. turkeys) the wing notch is formed by several shortened secondary feathers. Wing length is the distance from the proximal end of the humerus to the tip of the longest primary, measured along a line parallel to the leading edge of the wing. Throughout this paper, means are reported ± 1 SD.

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Four species of galliforms were chosen for flight-performance experiments based on extremes of wing shape (see Fig. 1) and body size within the order: White-tailed Ptarmigan ([*Lagopus leucurus*]; Tetraoninae; subadult male specimen); Sage Grouse ([*Centrocercus urophasianus*]; Tetraoninae; adult male); Wild Turkey ([*Meleagris gallopavo*]; Meleagridinae; adult female); and California Quail ([*Callipepla californica*]; Odontophorinae; adult male). I refer to them as "model" species. Other species of galliforms provide more extreme examples of wing-shape variation, but my choices were limited by the availability of frozen specimens at the University of Washington Burke Museum for use in creating models of wings.

I measured flight performance by steady-state (constant velocity) lift and drag characteristics of various wings. Active flight in these species may not be characterized by this particular dynamic condition, but any differences in the coefficients associated with wing lift and drag are presumed to apply to flapping, at least for fast forward flight. Lift (C_l) and drag (C_d) coefficients are defined by the following relationships:

$$C_l = L/(0.5\ \rho\ SU^2), \quad \text{and} \quad (2)$$

$$C_d = D/(0.5\ \rho\ SU^2), \quad (3)$$

where L is the measured lift force, D is the measured drag force, ρ is the density of the fluid medium, S is the plainform area of the wing, and U is the fluid velocity relative to the wing. Lift and drag coefficients were measured for model wings. Models were cut from 0.2-mm thick brass foil and soldered to a metal rod 2.5 mm in diameter and about 130 mm long. All models had a width of 30 mm (length varied from 46 to 62 mm depending on species). Each model was slightly bent around the axis of the metal rod, and the space between the leading end of the model wing and the rod was filled with glue. The bending created camber in the models. The top of the curvature was 10 mm behind the leading edge of a model wing, and the height of the curvature, measured as the distance from a line connecting the leading and trailing edges of a model wing to the top of the curvature, was approximately 4 mm. The patterns used for preparing the models were images (reduced by photocopy) of freshly thawed wings that had been pinned in a fully extended position.

Lift and drag coefficients are functions of the Reynolds number:

$$Re = UL/\nu, \quad (4)$$

where U is defined as above, L is the length of the wing chord, and ν is the kinematic viscosity of the fluid medium of the wing. Consequently, scale models were prepared so that in the testing apparatus (see below), each model had a Reynolds number relatively similar to that of real wings.

Lift and drag forces were measured in a water flow

TABLE 1. Trailing-edge notch size and wing length-to-breadth ratio of galliforms. Values are means (with SD in parentheses).

Species	n	Notch size (% of wing breadth)	Wing length-to-breadth ratio
Turnicidae			
Turnix sylvatica	3	12.36 (4.93)	1.77 (0.04)
Phasianinae			
Tetraogallus himalayensis	1	18.14	1.81
Alectoris chukar	3	36.62 (3.54)	1.69 (0.01)
Francolinus sephaena	3	35.45 (1.60)	1.62 (0.02)
F. africanus	4	24.98 (2.29)	1.86 (0.05)
F. swainsonii	2	47.34 (5.64)	1.57 (0.01)
Perdix perdix	6	30.17 (2.34)	1.91 (0.01)
P. dauurica	1	36.36	1.78
Coturnix coturnix	3	21.57 (2.04)	2.25 (0.05)
Lophura ignita	1	35.71	1.58
Gallus gallus	3	38.11 (2.67)	1.48 (0.07)
Phasianus colchicus	13	30.86 (3.20)	1.71 (0.10)
Odontophorinae			
Colinus virginianus	15	32.49 (3.76)	1.61 (0.05)
Callipepla squamata	2	35.06 (3.46)	1.63 (0.07)
C. californica	9	31.84 (3.76)	1.66 (0.05)
C. gambelii	2	37.37 (0.58)	1.62 (0.01)
Meleagridinae			
Meleagris gallopavo	4	31.40 (2.04)	1.47 (0.10)
Tetraoninae (light and intermediate flight muscles)			
Dendragapus falcipennis	2	26.50 (3.23)	1.95 (0.11)
D. canadensis	10	21.82 (4.29)	1.95 (0.09)
D. obscurus	19	23.24 (3.31)	1.90 (0.07)
Bonasa bonasia	14	24.52 (2.67)	1.94 (0.07)
B. umbellus	22	28.94 (2.49)	1.88 (0.10)
Tetraoninae (dark flight muscles)			
Lagopus lagopus	21	22.09 (1.89)	2.09 (0.05)
L. mutus	14	20.68 (3.08)	2.35 (0.08)
L. leucurus	8	19.60 (2.86)	2.12 (0.09)
Tetrao tetrix	1	18.87	2.08
T. urogallus	3	20.67 (1.29)	2.05 (0.16)
T. parvirostris	10	15.17 (2.52)	2.24 (0.11)
Centrocercus urophasianus	10	18.06 (3.54)	2.24 (0.16)
Tympanuchus phasianellus	4	19.25 (2.49)	2.16 (0.05)
T. cupido	7	20.76 (3.17)	2.05 (0.10)

tunnel. The flow tunnel provided a uniform flow of relatively low turbulence intensity (ca. 5%). The working section of the tunnel was square in cross section, with sides of 0.2 m and a length of 1.2 m. The flow in the working section had all four boundaries fixed. During the measurements I placed each model such that its center was in the center of the working section. Apart from the model, there was only a piece of rod approximately 7 cm long in the flow. This rod connected the model to the force trans-
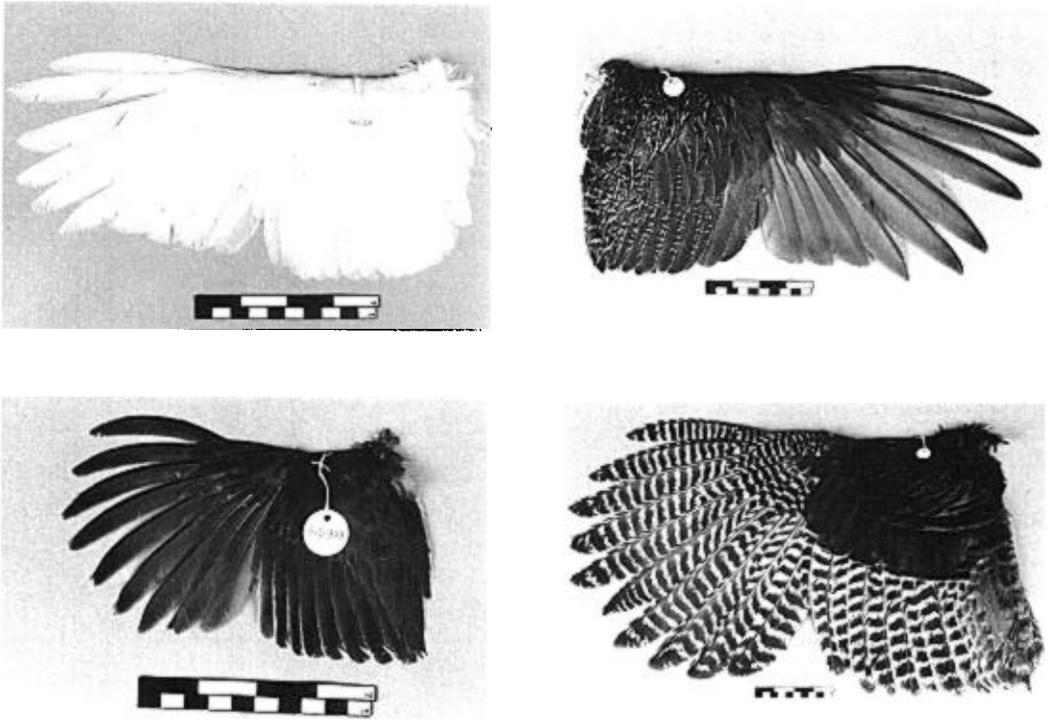
FIG. 1. Extended-wing specimens used as models for the experiments. White-tailed Ptarmigan (*Lagopus leucurus*; upper left); Sage Grouse (*Centrocercus urophasianus*; upper right); California Quail (*Callipepla californica*; lower left); and Wild Turkey (*Meleagris gallopavo*; lower right). Scale under each wing is in inches (upper) and cm (lower).

ducer. Use of a water flow tunnel provides high resolution of lift and drag forces, which, as long as the Reynolds number is similar (see below), gives useful data for lift and drag coefficients. Water speed in the flow tunnel was 0.5 m/s.

If models are perfectly scaled, then the Reynolds numbers of the models and the wings they represent will be equal. Due to the limited size of the flow tank, constant flow velocity, and the need to keep model geometry similar to the real wing geometry, models were made such that the greatest breadth of each was 30 mm. Thus, the Reynolds number of all models was the same, viz. $Re = 1.5 \times 10^4$. This is somewhat lower than the Reynolds numbers for the real wings (White-tailed Ptarmigan, $Re = 12.5 \times 10^4$; Sage Grouse, $Re = 19.5 \times 10^4$; Wild Turkey, $Re = 33.5 \times 10^4$; California Quail, $Re = 9.0 \times 10^4$) at a presumed flight speed of 15 m/s, a value available for the Ring-necked Pheasant (*Phasianus colchicus*; Rayner 1985). Despite the differences between these figures, the models are still useful for the experiments because $Re = 1.5 \times 10^4$ is within the performance range of real wings. Reynolds number increases proportionally with flight speed between takeoff and fast forward flight. Also, as long as geometric similarity is maintained, the drag coef-

ficient remains stable and constant across Re values of 5×10^3 to 5×10^5 (Vogel 1983).

Forces were measured separately with a strain-gauge transducer (sensitivity 2×10^{-3} N) as one arm of a Wheatstone bridge (see Lanyon 1976). The output was amplified and collected by a PC computer. For lift measurements, the wing was mounted to the force transducer with its sensitive axis normal to the flow; for drag, the sensitive axis was parallel to the flow. For all models, lift and drag forces were measured at six angles of attack: 0, 5, 10, 15, 20, and 25 degrees. At each angle of attack, 2,000 samples were measured over 10 s and averaged. To reduce error, five measurements were made before water flow was started, five during the stable flow, and five after the flow was stopped. The mean of the 10 electric potential measurements (five measurements each before the flow was started and after it was stopped) was considered to be the "0 force" condition. This mean value was subtracted from the mean of the five measurements that were taken when flow was stable, and the difference between these two means was then converted to a force. By measuring the "0 force" condition before and after measuring the lift and drag forces, errors in measurements were reduced. Measure-

ments were first made on wing models without notches. Then, notches were cut in each model, and the measurement cycles were repeated. The area of each cut piece was calculated by weighing it ($\pm$ 0.001 mg) and using foil thickness and specific gravity of the metal.

I used differences in pectoral muscle color as an index of differences in power output and resistance to fatigue among galliforms. White muscles have higher power output but are less resistant to fatigue. Galliform muscles that are white or intermediate in color are composed predominately of glycogen-loaded white fibers (Norberg 1989). For example, glycogen-loaded white fibers constitute >80% of all muscle fibers in the pectoral muscles of Ring-necked Pheasants and Spruce Grouse (*Dendragapus canadensis*). This similarity suggests that the proportion of red and intermediate fibers varies among galliforms by about only 20%. Because galliforms are thought to be monophyletic, all species within the order are likely to share similar types of red and intermediate muscle fibers. When muscle fiber types are the same, differences in muscle color might correlate with differences in the proportions of these fiber types and, thus, differences in muscle function that are related to the ecology of the respecitve species.

While preparing museum specimens I recorded pectoral muscle color according to a visual scale. This scale had three grades: dark or red (e.g. *Lagopus*), intermediate (e.g. *Dendragapus*), and light or white (e.g. *Bonasa*).

RESULTS

DIFFERENCES AMONG GALLIFORMS IN WING GEOMETRY AND NOTCH SIZE

Wing narrowness (length-to-breadth ratio) and notch size vary widely among the 31 species studied (Table 1). Ptarmigan and grouse (Tetraoninae) have narrower wings and smaller notches than other galliforms. The range of wing length-to-breadth ratios for grouse and ptarmigan is 1.88 to 2.35, compared with 1.47 to 1.91 in all other species except Common Quail (*Coturnix coturnix*), which is migratory and has long, narrow wings (length-to-breadth ratio of 2.25).

Notch size varies between 15.17% and 28.94% of wing breadth in the tetraoninae and between 24.98% and 47.34% in most other galliforms except three species: Small Buttonquail (*Turnix sylvatica*), Common Quail, and Himalayan Snowcock (*Tetraogallus himalayensis*; Table 1). The systematic position of buttonquails is not clear. Most authors treat them as galliforms, but some place them with Gruiformes and others in the Turniciformes. The Common Quail is a migrant
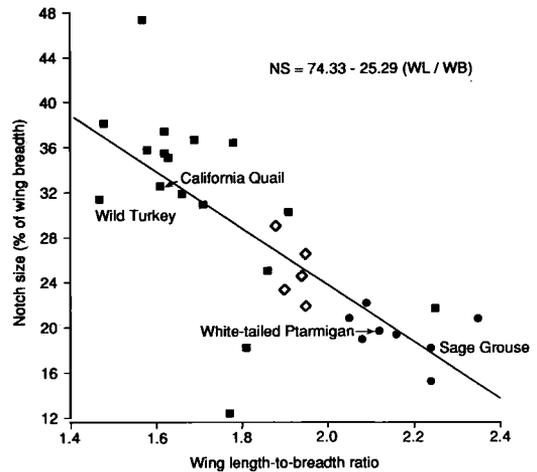
FIG. 2. Relationship between notch size and wing length-to-breadth ratio for 31 galliforms. Circles are tetraonids with dark pectoral muscles, diamonds are tetraonids with light pectoral muscles, and squares are other galliforms.

that undergoes long, strait flights. The Himalayan Snowcock is characterized by downhill gliding instead of active flapping flight. Despite these exceptions, I found a strong negative correlation between notch size and the ratio of wing length to wing breadth ($r = -0.76$, $n = 31$, $P < 0.001$; Fig. 2). Galliforms with short, wide wings have deeper notches.

The differences in wing shape and notch size between grouse and other galliforms could be related to differences in the frequency and duration of flights performed by the two groups. Flight is a critical element of foraging behavior in grouse and ptarmigan, especially in winter, when they feed on buds and foliage in trees. To reach these foods, forest grouse must make vertical flights to limbs and frequent short flights from limb to limb, and ptarmigan must fly from one foraging site to another. Other galliforms fly less often, using flight primarily to flee from predators.

MORPHOLOGICAL FLIGHT PARAMETERS OF THE MODEL BIRDS

Several morphological measurements are useful in comparative analyses of flight performance in birds (Rayner 1988, Norberg 1989). Among the most important are wing loading and aspect ratio. Wing loading (in N/m²) is defined as:

TABLE 2. Wing loading, aspect ratio, and trailing-edge notch size for the specimens used to make the model wings.

Species	Wing loading (N/m²)	Aspect ratio	Notch size (% of wing area)
Lagopus leucurus	74.12	9.36	1.57
Centrocercus urophasianus	121.52	5.79	1.64
Meleagris gallopavo	87.19	4.23	4.11
Callipepla californica	59.43	3.67	2.16

FIG. 3. Plot of wing loading vs. body mass for the four model species relative to expected relationship (curve) based on an allometric equation calculated for galliforms by J. M. V. Rayner (pers. comm.).

$$\text{wing loading} = Mg_n/S, \qquad (5)$$

where M is body mass in kg, g_n is acceleration due to gravity (i.e. 9.81 m/s²), and S is the total wing area (the planar area of both wings and that part of body between the leading and trailing edges of the wings in m²). Wing loading determines important flight characteristics such as speed and maneuverability. Birds with heavy wing loading fly at high speed and have a large turning radius. Aspect ratio is defined as:

$$AR = b^2/S, \qquad (6)$$

where b is wingspan (in m), and S is total wing area (in m²). Aspect ratio determines cost of transport, or the ratio of power to speed. Birds with a high aspect ratio use less energy per unit of distance flown (i.e. less power) to generate the same horizontal speed compared with birds with low aspect ratio (Rayner 1988).

The White-tailed Ptarmigan has the highest aspect ratio of the four models and a fairly heavy wing loading (Table 2). The aspect ratio for Sage Grouse is lower, but it still is much higher than that of the Wild Turkey and Common Quail. Wing loading of the Sage Grouse is exceptionally high, whereas the California Quail has the lightest wing loading. Wild Turkeys have somewhat greater wing loading than White-tailed Ptarmigan. However, when size is taken into account, wing loading changes proportionally to $M^{0.201}$ in galliforms (J. M. V. Rayner pers. comm.). Thus, Wild Turkeys actually have much lower wing loading than expected by allometry (Fig. 3).

Another important morphological parameter that can be used for comparative study of closely related species is the color of the pectoral muscles. In galliforms it may indicate relative abundance of fast-twitch oxidative-glycolytic fibers and fast-twitch glycolytic fibers. Fibers of

the first type are red, whereas fibers of the second type are white. These types of fibers have different biochemistry that results in differences in contraction frequency and speed as well as resistance to fatigue. Red fibers have lower frequency and speed of contraction, but much higher resistance to fatigue than white fibers (Norberg 1989). Therefore, muscles with a high proportion of red fibers are suited for sustained (horizontal) flight, but white muscles are adapted for short, powerful bursts (take off, vertical flight). Wild Turkey and California Quail have much lighter colored pectoral muscles than do White-tailed Ptarmigan and Sage Grouse.

Grouse and ptarmigan with red pectoral muscles (i.e. *Lagopus*, *Tetrao*, *Tympanuchus*, and *Centrocercus*) have smaller trailing-edge notches than those with white or intermediate pectoral muscles (i.e. *Dendragapus* and *Bonasa*; $\bar{x} = 19.46 \pm 2.01\%$, $n = 9$ vs. $\bar{x} = 25.04 \pm 2.79\%$, $n = 5$, respectively; $t = 4.32$, df $= 13$, $P < 0.001$) and wings with larger length-to-breadth ratios ($\bar{x} = 2.15 \pm 0.10$ vs. $\bar{x} = 1.92 \pm 0.03$; $t = 4.76$, df $= 13$, $P < 0.0005$).

The four model species form two pairs, each with different wing characteristics and pectoral muscle colors. White-tailed Ptarmigan and Sage Grouse have high wing loading, high aspect ratio, and red pectoral muscles, which serve their long, straight flights at high speeds. In contrast, Wild Turkey and California Quail have low wing loading, low aspect ratio, and white pectoral muscles that are better suited for slower, more powerful and maneuverable flights. Their short, broad wings are better suited to frequent short (and vertical) flights because they generate more

TABLE 3.   Maximum lift coefficients of the model wings, maximum lift-to-drag ratios (L/D), angles of attack at which they occur, and increase in lift-to-drag ratios with wing notching.

Species	Max. lift coefficient		Max. L/D		Angle of attack[a]		% increase[b]
	No notch	Notched	No notch	Notched	No notch	Notched	
Lagopus leucurus	0.69	0.61	3.96	5.98	5	5	33.8
Centrocercus urophasianus	0.64	0.56	2.40	2.61	10	10	8.0
Meleagris gallopavo	0.80	0.76	4.57	5.23	5	10	12.6
Callipepla californica	0.70	0.65	4.81	5.12	5	10	6.1

[a] At maximum lift-to-drag ratio (L/D).
[b] Increase in maximum L/D with wing notching.

power on the upstroke, facilitating takeoff, landing, and steep climbs at low forward speed.

The wing notch sizes of White-tailed Ptarmigan and Sage Grouse are similar (Table 2). This suggests that such a structure is less important for galliform birds with relatively high aspect ratios and heavy wing loading. In contrast, the wing notch sizes of California Quail and Wild Turkeys are much larger. These comparisons suggest that birds with short, rounded wings should derive more benefit from the wing notch than do longer-winged species.

LIFT-TO-DRAG COEFFICIENT RATIOS IN WINGS WITH AND WITHOUT NOTCHES

The trailing-edge notch increased the maximal lift-to-drag ratio in all the model wings (Fig. 4). However, this increase was small in Sage Grouse, Wild Turkey, and California Quail but reasonably large in White-tailed Ptarmigan (Table 3). The angle of attack of maximal lift-to-drag ratio did not change in White-tailed Ptarmigan and Sage Grouse, but it increased in Wild Turkey and California Quail after notches were created experimentally.

All wing models also had smaller standard deviations of lift and drag coefficients after the trailing-edge notches were created (Fig. 4). I tested for the effect of the notch, angle of attack, and species, and for the interaction of species and notch, on coefficients of variation (CV) of the lift and drag measurements (Table 4). Coefficients of variation for measurements of lift were significantly affected by only two factors: (1) increasing the angle of attack from 0° to 25° progressively reduced the CV, and (2) notches reduced the CV by 53.4% regardless of species. Coefficients of variation for measurements of drag were significantly affected by all four factors (Table 4). The relationships of CV to the angle of attack and the presence of the notch

were the same as those for lift measurements. In addition, notching decreased the CV for measurements of drag to a different extent in different species (White-tailed Ptarmigan, 70.2%; Sage Grouse, 25.1%; California Quail, 21.3%; and Wild Turkey, 0.1%).

The inverse relationships between angle of attack and the CV for lift and drag measurements may be related to the means of the forces increasing with an increase in angle of attack.
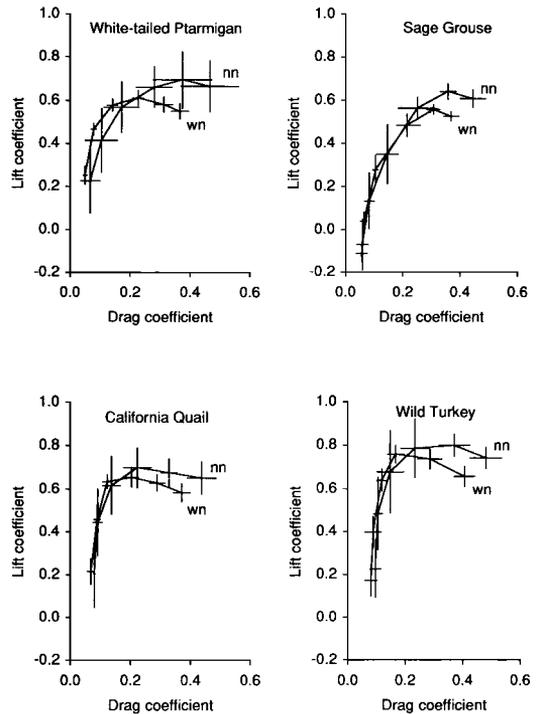
FIG. 4.   Plot of lift vs. drag coefficients for the model wings. Each curve is based on independent measurements (indicated by standard deviations) made at six angles of attack. From left to right: 0°, 5°, 10°, 15°, 20°, and 25°; nn is model with no notch, wn is model with notch.

TABLE 4. Effect of wing notching and angle of attack on the CV of lift and drag measurements of model wings.

	Notching		Angle of attack		Species		Notching and species	
	F	P	F	P	F	P	F	P
Lift	7.77	0.008	30.43	<0.001	2.81	ns	0.23	ns
Drag	20.48	0.001	34.09	<0.001	3.91	0.016	8.94	<0.001

Because the CV is a ratio of standard deviation to the mean, increasing the means will lower the CV if the SD does not change. Drag increases through the whole range of angles of attack, and lift increases through most of the range, and then levels off or slightly decreases. Also, the rate of change in lift and drag is not constant through the range of angles of attack (Fig. 1). For example, a minor error in positioning the model wing for a small angle of attack (close to 0°) will have a large effect on lift measurements and a small effect on drag measurements. When the angle of attack is close to 25°, the opposite is true.

Despite other factors, wing notches significantly reduced the CV of lift and drag measurements. This suggests that wings with trailing-edge notches should be more stable in flight, and that their performance should be more predictable. Trailing-edge notches also reduced the maximum lift coefficients (Table 3). The maximum lift coefficients of models without notches were inversely related to the amount of their reduction ($r = -0.84$, $n = 4$, $P = 0.16$). This indicates that long wings that produce less lift (e.g. Sage Grouse and White-tailed Ptarmigan) lose proportionately more lift with the addition of a notch than do short, round, high-lift wings (e.g. turkey and quail). However, they also lose proportionately more drag, so the lift-to-drag ratio of long wings increases more than that of short wings. Therefore, trailing-edge notches make takeoff easier by improving the lift-to-drag ratio, but they also increase the energetic cost of forward flight by decreasing lift, thus forcing birds to fly faster.

The angle of attack at maximum lift-to-drag ratio is probably stable regardless of the presence or absence of a notch in long-winged birds (Sage Grouse, White-tailed Ptarmigan), but it increases in short-winged birds (Wild Turkey, California Quail). The increase in angle of attack in birds with short, rounded wings should increase lift (at the expense of some increase in drag) and, thus, increase vertical acceleration during take off. Therefore, notches may help such birds to ascend faster.

DISCUSSION

My comparative data show that galliforms display a wide variety of trailing-edge notch sizes and wing shapes (Fig. 2). In general, galliforms of all groups except Tetraoninae have the shortest wings and deepest notches found in the order. Bonasa and Dendragapus have intermediate notch sizes and intermediate wing length-to-breadth ratios. Other grouse (Lagopus, Tetrao, Tympanuchus and Centrocercus) and the migratory Common Quail have the longest wings and smallest notches found in the order, and all, except the quail, have dark pectoral muscles, whereas the other 22 species have light or intermediate colored pectoral muscles.

Although the flight performance data were collected for fixed wings in steady flow, differences in lift and drag characteristics should apply to fast forward flight with reduced frequencies (see Norberg 1989) less than 0.5 Hz. The reduced frequency parameter ($2\pi f L/U$) for these birds in forward flight is about 0.65 (calculated for Ring-necked Pheasant, $f = 9$ Hz; Greenewalt 1962: table 13). Despite a rough approximation (the pheasant has an intermediate body mass, so its speed is probably higher than the speed of California Quail and White-tailed Ptarmigan but lower than that of Wild Turkey and Sage Grouse; the opposite is true for wing-beat frequency), the calculated reduced frequency parameter is only slightly higher than the generally accepted cutoff. Thus, the results of the experiments still are likely to apply to the flight of model species. However, in take off or landing, some caution should be used in interpreting differences in steady state aerodynamic coefficients.

The differences in wing geometry and notch size are related to the ecology and behavior of different species. Except for the grouse and ptarmigan, which use flight between bouts of for-

aging, most galliforms use flight primarily to flee from predators. Thus, because the main element of their flight is vertical (takeoff and ascending), level flight is not so important. In contrast, flight is an important part of the foraging behavior of grouse and ptarmigan, and the relative importance of level flight varies dramatically in species with dark versus light (or intermediate) pectoral muscles. Grouse with a higher proportion of red fibers in the pectoralis major fly relatively long distances from one foraging site to another, but then they either walk on the ground or perch on branches to feed. These grouse use level flight primarily to reach food patches. However, grouse with light or intermediate pectoral muscle fibers do not fly long distances. Rather, they use vertical flight primarily from ground to canopy, or slow flight from branch to branch, to reach their food. The grouse with white and intermediate fibers and short, broad wings have deep trailing-edge notches that increase both their lift-to-drag ratio and the angle of attack at which their wings are more efficient.

For example, the Willow Ptarmigan (*Lagopus lagopus*), which has red pectoral muscles, feeds on willows (*Salix schwerinii, S. rorida*) and chosenia (*Chosenia arbutifolia*) twigs and buds during winter in northeastern Russia (Andreev 1980, Drovetski 1992b). The willow and chosenia thickets where ptarmigan forage are situated on river islands and along the banks of braided river channels. During foraging birds walk along patches of thickets and pick twigs and buds from bushes and snow. After passing through a patch of willows, a flock of ptarmigan must fly to reach another willow patch, which usually will be situated on another river island or along another channel. Thus, Willow Ptarmigan perform several flights of several hundred meters a day. They fly through open places at a fast pace and at low altitude. Because these flights are relatively long, the most expensive component is not takeoff and landing, but rather level movement.

In the same region, the Hazel Grouse (*Bonasa bonasia*), which has white pectoral muscles, feeds in trees but in denser, more continuous forests (Andreev 1980; Drovetski 1992a, 1992b). Unlike Willow Ptarmigan, Hazel Grouse forage mostly by perching on branches in the canopy, and extremely rarely by walking to branches that can be reached from the snow. Each bird spends 3 to 8 min on one branch and then flies to an-

other branch in the same tree, or to a neighboring tree in the same canopy. During one foraging bout a Hazel Grouse visits 6–12 branches. Flights within foraging bouts are short and slow, and a flock does not move more than 300 m during a single bout of foraging. Thus, the majority of the energy Hazel Grouse spend in foraging flights is invested in vertical movements and in the frequent takeoffs and landings required to move from branch to branch. Furthermore, Hazel Grouse land and feed on such small branches that they can not jump from them with their feet to aid in takeoff. This places even greater demands on their wings for acceleration. For these short bursts of flight, white muscle fibers; short, broad wings; and deep trailing-edge notches are the best compromise.

I used model wings of two pairs of galliforms with different flight characteristics in my experiments. White-tailed Ptarmigan and Sage Grouse represent species with small notches (Fig. 2). They have high aspect ratios, heavy wing loading for their size, low maximum lift coefficients, and dark pectoral muscles (Tables 1–3). These are all adaptations for relatively long, fast, straight and efficient flight (Rayner 1988, Norberg 1989). In contrast, the Wild Turkey and California Quail, which represent species with deep notches (Fig. 2), have low aspect ratios, relatively light wing loading, high lift coefficients, and light pectoral muscles (Tables 1–3). These features are adaptations to powerful short flights and maneuverability (Rayner 1988, Norberg 1989).

Short, wide wings can generate as much lift as long, narrow wings of the same area only by increasing the angle of attack (Vogel 1983). However, higher angles of attack generate increases in both profile and induced drag. My results show that the trailing-edge notches in galliform wings increase the maximum lift-to-drag ratio by improving air flow around the wing. Notches had a similar effect on all four species, i.e. increasing the maximum lift-to-drag ratio and stabilizing air flow around the wing. However, the trailing-edge notch slightly reduced the maximum lift coefficient (Fig. 2). This reduction in maximum lift is presumably more detrimental to species characterized by relatively long flights than to species that spend a high percentage of their flight time in landings and takeoffs, times when the angle of attack must be great.

The experimental data show a tradeoff in flight

performance of galliforms associated with the trailing-edge notch. The notch reduces maximum lift, but increases the lift-to-drag ratio and stabilizes airflow around the wing. This means that an increase in the ability to take flight and climb fast, and in the ability to maintain height during a slow flight, may be achieved at a cost of reduced efficiency in level flight. Galliforms that experience relatively long and fast level flights should benefit more from a high-lift (i.e. high-efficiency) wing. In such species the trailing-edge notch should be smaller. In short flights, when vertical movements become a large component of each flight, increasing the lift-to-drag ratio becomes more advantageous. In this circumstance selection should favor larger trailing-edge notches.

Compared with other volant birds, galliforms spend small amounts of time in the air, rarely fly long distances, and have pronounced trailing-edge notches. The comparative analysis within the order supports the results of experiments and suggests that wing geometry and size of the notch result from of a compromise between what is optimal for level flight and what is optimal for frequent takeoff and vertical flight. Grouse that spend much time in level flight have small trailing-edge notches, whereas those whose flight is characterized by frequent takeoffs and landings, and by vertical movement, have deep trailing-edge notches. One may ask why ptarmigan and other long-winged galliforms have any trailing-edge notch. The answer, I think, lies in the fact that even those grouse with relatively long, narrow wings fly very little compared with other birds. Thus, relative to other species, long-winged galliforms spend a considerable amount of their flight time in takeoff, where the notch is helpful.

Whereas the trailing-edge notch improves maximum lift-to-drag ratio of the extended wing, the notch could be even more important for a powered upstroke. The possibility that it creates a separate wing should be examined by photography, and, if confirmed, be explored by further work in wind tunnels or flow tanks.

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