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EVIDENCE FOR AERODYNAMIC ADVANTAGES OF TAIL KEELING IN THE COMMON GRACKLE

SCOTT HICKMAN

The behavioral function of tail keeling in the Common Grackle (*Quiscalus quiscula*) has been thoroughly documented as a male flight display (Bent 1958; Ficken 1963; Wiens 1965; Maxwell 1970; Wiley 1976a, 1976b). The purpose of this study is to determine if keeling functions aerodynamically as well.

STUDY AREA AND METHODS

The data used in this study were collected through field observations of flying Common Grackles. A total of 3507 nonbreeding season observations was recorded from August 1974 through February 1975. Breeding season observations totaled 1415 and were recorded from March 1975 through May 1975. Observations were recorded in the vicinity of Bloomington–Normal, McLean Co., Belleville, St. Clair Co., and Carbondale, Perry Co., all in Illinois.

Each observation was a record of the configuration of the rectrices of a flying bird and its concomitant flight status. The tail configuration was recorded as one of four possible degrees of keeling: (1) flat tail—tail forms one plane (180°), (2) shallow keel—slight depression of midline rectrices folds the tail into a shallow V of approximately 160°, (3) medium keel—increased depression of central rectrices folds the tail into a deeper V of approximately 120°, (4) deep keel—complete depression of central rectrices in which the tail is folded into a deep V of less than approximately 110°. These 4 categories were selected because they represent the maximum number of keeling positions I could accurately distinguish. Observations which I could not clearly assign to any of these categories were disregarded.

In addition to a flying grackle's degree of keeling, I also recorded the following 14 characteristics: (1) sex—male or female; (2) season—breeding or nonbreeding; (3) relative wind direction—wind direction relative to bird flight direction; (4) wing speed—m/sec; (5) wind character—steady or gusty; (6) bird braking—yes or no; (7) bird banking—yes or no; (8) bird angle—ascending, descending or level flight; (9) company—bird accompanied or alone; (10) bird flight—flapping or gliding; (11) tail spread—tail fanned or not; (12) tail molting—yes or no; (13) entering roost—whether or not the bird was entering a roost; (14) leaving roost—whether or not the bird was leaving a roost.

I treated the 14 characteristics of bird status as independent variables and degree of tail keeling as the dependent variable. For mathematical analysis the 4 degrees of keeling (flat, shallow, medium and deep) were assigned the values 0, 1, 2 and 3, respectively. Stepwise multiple regression analysis was used to determine which independent variables, and/or combinations of independent variables, could account for a significant proportion of the variability in keel depth. Pearson product-moment correlations were also calculated. One-way analysis of variance was used to test for significant differences between mean degrees of tail keeling associated with each value of an independent variable. The breeding season and nonbreeding season data were treated separately, then pooled, for all statistical tests.

RESULTS

The results of the stepwise multiple regression analysis are shown in Tables 1, 2 and 3 for the nonbreeding season, breeding season and com-

TABLE 1

PARAMETERS ASSOCIATED WITH KEELING DURING THE NONBREEDING SEASON

Step and df	Independent variable	R^2	F	F^a
1	Tail spread	0.368	1965	12.10
2	Company	0.426	1305	7.60
3	Banking	0.479	1077	5.91
4	Molting	0.487	845	5.00
5	Braking	0.494	648	4.52

[a] F value that must be exceeded to attain $P < 0.001$.

bined seasons data, respectively. These tables indicate the maximum cumulative percent variance accounted for (R^2) by independent variables. Table 4 indicates what mean keel depths are associated with various independent variable values.

Deep keel was displayed only during the breeding season and only by males. During the breeding season 50% of all observed males had their tails in deep keel. Deep keel was the only tail shape used more by one sex than the other.

Medium keel was rarely used by either sex. Only 4.5% of observed males and females showed medium keel.

Only nonbreeding season data are used to analyze shallow keel. This is because frequent sexual display of deep keel by males during the breeding season under virtually all conditions consistently increased the average keel depth correlated with each independent variable. This masked the actual relationship between aerodynamic factors and shallow keel.

Grackles that were braking, tail spreading, banking, ascending or with

TABLE 2

PARAMETERS ASSOCIATED WITH KEELING DURING THE BREEDING SEASON

Step and df	Independent variable	R^2	F	F^a
1	Sex	0.228	416	12.10
2	Entering roost	0.302	305	7.60
3	Bird angle	0.320	221	5.91
4	Banking	0.331	174	5.00
5	Wind direction	0.341	145	4.52

[a] F value that must be exceeded to attain $P < 0.001$.

TABLE 3
PARAMETERS ASSOCIATED WITH KEELING FOR COMBINED DATA

Step and df	Independent variable	R^2	F	F[a]
1	Season	0.218	1373	12.10
2	Braking	0.273	926	7.60
3	Sex	0.315	757	5.91
4	Company	0.349	659	5.00
5	Banking	0.375	592	4.52
6	Entering roost	0.387	524	4.02
7	Leaving roost	0.394	479	3.72
8	Bird angle	0.409	427	3.48
9	Wind direction	0.413	385	3.30

[a] F value that must be exceeded to attain $P < 0.001$.

tails in molt often used shallow keel. Sixty-three percent of all braking, 64.9% of all tail spreading, 85% of all banking, 44.7% of all ascending and 42.2% of all tail molting birds used shallow keel. This shallow keel differed significantly ($P \leq 0.01$) from the nearly flat tail seen in the remaining contexts (Table 4). Flat tail was noted in only 24% of all braking, 23% of all tail spreading, 17% of all banking, 37% of all ascending and 22% of all tail molting grackles.

Eighty-six percent of all grackles flying into a head wind used flat tail. This represents at least 11% more use than flat tail generated with any other wind direction. Flat tail was also the configuration most used for level, non-maneuvering flight such as when flying to or from a roost. Approximately 90% of all grackles entering or leaving a roost possessed flat tail and 88% of all grackles recorded as flying level and not banking had their tails in a flat position.

DISCUSSION

Aerodynamic factors account for variability in keel depth. Table 1 shows that tail spread (usually associated with landing), banking, tail molting and braking are significant predictors of keel depth during the nonbreeding season. Similarly, Table 2 indicates that bird angle, banking and wind direction account for variance in keel depth during the breeding season and braking, banking, bird angle and wind direction are predictors of keel depth when the seasonal data are pooled. This is evidence that tail keeling has aerodynamic functions.

The most likely aerodynamic uses of tail keeling are stall prevention and improvement of stability. Grackles observed to be landing, banking, taking off, or with tails in molt typically possessed shallow keel. These are

TABLE 4
KEEL DEPTHS ASSOCIATED WITH VARIOUS INDEPENDENT VARIABLES (NONBREEDING SEASON)

Independent variables	$\bar{x}$	SE	N
Braking			
No	0.12*	0.0070	2953
Yes	0.90*	0.0250	555
Tail spread			
No	0.11*	0.0065	2905
Yes	0.90*	0.0239	601
Bird angle			
Level	0.40*	0.0337	66
Descending	0.30*	0.0091	3125
Ascending	0.80*	0.0235	317
Banking			
No	0.20*	0.0079	3202
Yes	1.0*	0.2150	305
Molting			
No	0.41*	0.0075	3072
Yes	0.80*	0.0344	436

* Significant at $P < 0.001$.

all conditions during which birds are susceptible to stall and/or are unstable.

Landing birds are flying slowly and in danger of stalling since lift is directly proportional to air speed. Birds typically prevent stalls during landing by spreading and depressing the flat tail which draws the airflow down and caudally from the dorsal surfaces of the wings. This keeps the airflow from breaking away from the wing surfaces and prevents stalling (Pennycuick 1972). Landing grackles, however, did not usually possess a flat tail. Grackles that were landing were most often recorded as tail spread and braking. The correlations in the results section and Table 4 indicate that these grackles used shallow keel rather than the flat tail described above. Shallow keel may be more effective in stall prevention than flat tail since depression of the central rectrices may funnel air downward from the wings more effectively.

Shallow keel may also reduce the instability encountered during landing. When used as an air brake the flat tail would create some directional instability to be controlled by the wings. However, shallow keel positions the ventral surface of the braking tail into a wedge, thereby giving the spread tail a guiding quality which increases landing precision. The dorsal surface of a tail in shallow keel could also aid in the development of increased landing precision as it may funnel the caudal airflow into a longitudinal axis and thereby minimize yaw.

Grackles normally used shallow keel while banking (Table 4). This may also be functionally interpreted in terms of stall prevention and increased flight stability. Birds are susceptible to stall during banking (Dalton 1977). Positioning the tail in shallow keel while banking may function to prevent stalls as described above. Stability is also reduced during banking because the bird's body passes through a vertical rather than horizontal plane. Airfoils are not parallel to the ground and are less efficient in resisting gravity and regulating yaw. Shallow keel, however, would increase the stability of a turn by making the tail a 2-plane surface that would funnel the airflow into a longitudinal axis and minimize yaw.

The mean keel depth used in ascending flight also approximated shallow keel (Table 4). Most ascending grackles were observed while taking flight. During take-off, air speed is slow and thus conducive to stall (Salt 1966). Shallow keel may prevent stalling during take-off in the same manner as proposed above for landing and banking.

Most grackles used shallow keel while their tails were in molt, this shallow keel being significantly deeper than that of grackles with tails not in molt (Table 4). Many birds with tails in molt had no full length rectrices. Such an abnormally short tail cannot provide the stability of a full length tail. Shallow keel would presumably help to regain the stability lost during tail molt.

Shallow keel seems to be the only recorded keel shape that is primarily aerodynamic in function. Deep keel was correlated with behavioral rather than aerodynamic conditions. This caused sex to account for more of the variability in the breeding season data than did any other independent variable (Table 2). This is in agreement with the conclusions of earlier researchers that keeling functions behaviorally. Medium keel was seldom used by Common Grackles of either sex. It seems to exist only as an intermediate position through which the tail passes when changing from shallow keel to deep keel or vice versa. Flat tail functions in several displays performed by this species (Ficken 1963; Wiley 1976a, 1976b). My results indicate that the aerodynamic situations during which grackles most often use flat tail are (1) when flying into a head wind, apparently because keels increase drag inordinately during head winds; and (2) in level and non-maneuvering flight, as when grackles fly to or from a roost. During these conditions the tail's aerodynamic importance is relatively minimal. The wings can supply all the lift, thrust and control required to maintain trim. The tail is then most efficiently positioned in a flat, narrow shape to minimize drag.

The aerodynamic uses proposed above for shallow keel are hypothetical functions based upon the correlations between shallow keel and conditions during which birds are unstable and/or susceptible to stall. These hypotheses are strengthened by unquantified observations which indicate that other birds, such as the Rock Dove (*Columba livia*) and Herring Gull (*Larus argentatus*) also use shallow (but U vs V shaped) keel under unstable conditions during which stall is likely.

I am publishing my conclusions even though I am uncomfortable with the degree to which they rely on pure correlations in the hope that researchers with wind tunnel access will properly test the aerodynamic functions proposed for shallow keel.

SUMMARY

This study indicates that tail keeling by Common Grackles functions aerodynamically as well as behaviorally. Deep keel functions behaviorally and is restricted to males. Medium keel was rarely observed. The primary function of shallow keel is probably aerodynamic, increasing stability during tail molt. Shallow keel probably also functions to prevent stalls during landing, banking and take-off. The Common Grackle showed flat tail in direct non-maneuvering flight and when flying into head winds.

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DEPT. BIOLOGY, ILLINOIS STATE UNIV., NORMAL, ILLINOIS 61761. (PRESENT ADDRESS: DEPT. BIOLOGY, COLL. LAKE COUNTY, GRAYSLAKE, ILLINOIS 60030 AND DEPT. BIOLOGY, UNIV. ILLINOIS AT CHICAGO CIRCLE, CHICAGO, ILLINOIS 60080.) ACCEPTED 5 MAR. 1981.