THE EFFECT OF MOLTING ON THE GLIDING PERFORMANCE OF A HARRIS' HAWK (*PARABUTEO UNICINCTUS*)

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ABSTRACT.—The maximum lift-to-drag ratio of a Harris' Hawk (*Parabuteo unicinctus*) gliding in a wind tunnel at 10.5 m/s dropped from 10.5 before the onset of molting to a low of 7.2 when missing primary wing feathers left gaps in the wing tips (36 days after onset). It then rose to 10.5 again when the new feathers were complete (172 days after onset). The decrease in wing span and area due to the missing primaries can theoretically account for only 39% of this drop. The changed shape of the wing-tip slots could account for the remainder by increasing induced drag and profile drag. Loss of feathers other than the primaries did not have a major effect on the hawk's wing and body shape. *Received 19 February 1990, accepted 24 July 1990.*

THE WING feathers generate almost all of the aerodynamic force that keeps a bird aloft in flight, yet these feathers fall out during molting. However, the effect of molt on flight performance is unexplored. I was able to determine this effect for a Harris' Hawk (*Parabuteo unicinctus*) trained to glide freely in a wind tunnel during its molting period. Several studies describe the molting process in raptors (Snyder et al. 1987, Henny et al. 1985, Prevost 1983, Newton and Marquiss 1982, Houston 1975, and Stresemann and Stresemann 1966), but there appears to be no information on its effect on gliding performance.

THEORY

The term *gliding performance* refers to the maneuvers a bird is capable of while gliding. This paper describes *equilibrium gliding performance*, which restricts the bird to movement at constant speed along a straight path through air that does not accelerate. At equilibrium, the bird is capable of two maneuvers: it can glide at different air speeds (V), and it can glide along paths inclined at different angles (the glide angle, θ) to the horizontal.

The air speed, glide angle, and the bird's weight define three other useful quantities: aerodynamic lift (L), drag (D), and sinking speed (V_s), the rate at which the bird sinks vertically through the air. I use the ratio of lift to drag (L/D) to specify gliding performance. Further, I show the relations between L/D and the other quantities mentioned, and I explain the rationale for choosing L/D.

Many authors illustrate gliding performance with a "performance diagram" (nomenclature from Tucker 1987), which plots air speed against sinking speed (often plotted downward) (Fig. 1). Air speed and glide angle determine sinking speed:

$$V_s = V \sin \theta.$$

Speeds and sinking speeds of birds fall in a *performance area*. The upper boundary of this area is the *maximum performance curve*, sometimes called a glide polar or a superpolar (Pennycuick 1989), along which V_s has its minimum value for each V. A bird flying at a combination of air speed (V_0) and sinking speed that occurs on the maximum performance curve achieves maximum performance in the sense that when gliding through still air at speed V_0, it loses altitude at the minimum rate and travels the maximum distance before coming to earth. Only the upper left part of the maximum performance curve describes normal gliding, during which sinking speeds are less than 5 m/s.

Each point on the performance diagram represents a particular value of the ratio of lift to drag. This can be seen from the relation between lift, drag, and the glide angle. A bird that glides at equilibrium must generate an aerodynamic force directed upwards that equals its weight. (Weight, not to be confused with mass, is body mass [m] multiplied by gravitational acceleration [g].) Lift is the component of this aerodynamic force in a direction perpendicular to the glide path, and drag is the component in a direction parallel to the glide path. It follows that

$$L = mg \cos \theta,$$

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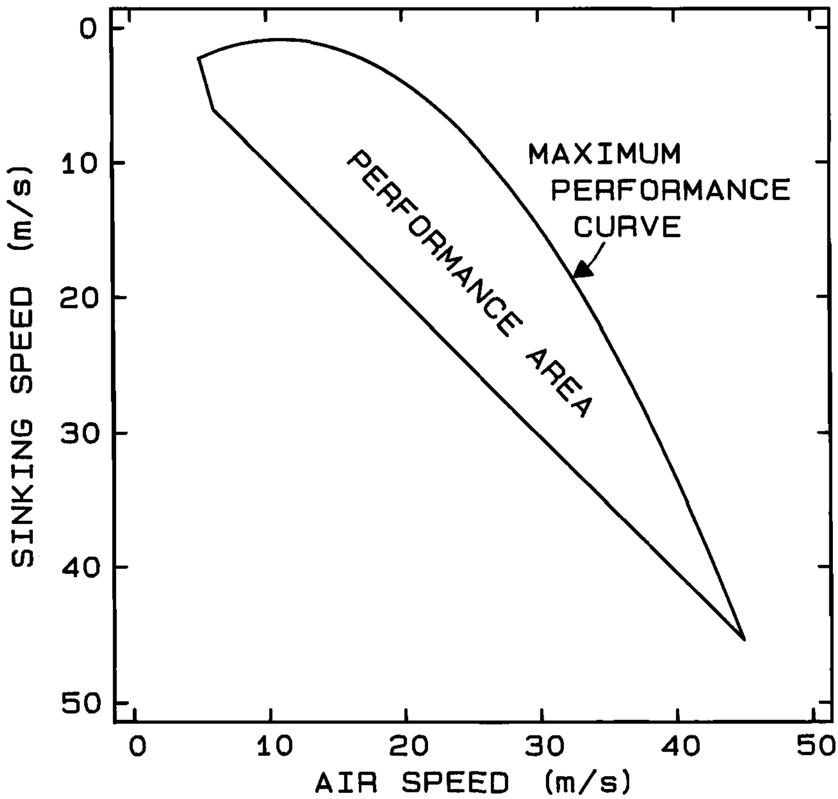

Fig. 1. Theoretical performance diagram for a hypothetical gliding bird (see Tucker 1988 for theory). The bird normally glides at sinking speeds of <5 m/s, so only a small region at the upper left of the performance diagram represents normal flight.

and

$$D = mg \sin \theta.$$

Because θ is normally less than 10° for birds that are gliding at maximum performance, $\cos \theta$ is approximately 1. With this approximation,

$$L = mg,$$
$$L/D = 1/\sin \theta,$$

and

$$L/D = V/V_s.$$

The last equation shows that points on the performance diagram with the same L/D value lie on a straight line that passes through the origin.

The ratio of lift to drag is a useful measure of gliding performance because a single L/D value can describe maximum performance over a wide range of speeds. For example, a straight line through the origin of the performance diagram for a Harris' Hawk (Tucker and Heine 1990) describes maximum performance with reasonable accuracy at airspeeds between 8 and 15 m/s (Fig. 2). Other gliding birds have similarly shaped maximum performance curves (Tucker and Heine 1990).

The air speed and glide angle of a bird can be measured when the bird glides at equilibrium in a wind tunnel. If the bird has air speed V_0 and glide angle θ_0, it remains motionless relative to the earth when the air through which it glides flows upward at speed V_0 and angle θ_0. This situation can occur naturally in updrafts, in which case the aerodynamic and gravitational forces on the bird are identical to those when the bird glides at the same speed and angle through still air.

When a wind tunnel is tilted around a horizontal axis perpendicular to the direction of air flow, the tunnel can move a column of air upward at the desired speed and angle. Birds

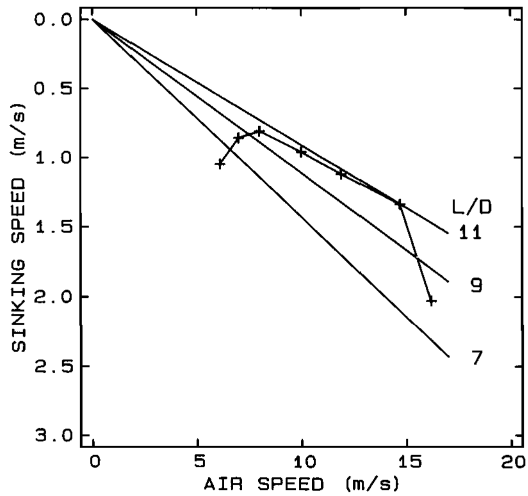

Fig. 2. Performance diagram for a Harris' Hawk gliding in a wind tunnel. Each straight line connects points that correspond to a constant ratio of lift to drag. Points marked with + are on the maximum performance curve.

trained to glide freely in the column are at equilibrium when they are motionless relative to earth. However, the column is not identical to a natural air mass because it is has a smaller cross-sectional area. This difference causes boundary effects that influence drag, but the boundary effects can be corrected.

METHODS

The Harris' Hawk, a male whose gliding performance was studied by Tucker and Heine (1990), hatched in captivity on 15 May 1988 and molted to adult plumage between 15 June and 4 December, 1989. During the molting period, it lived in an outdoor cage (6.1 m long, 2.8 m wide, and 3.4 m high) and was fed mice and rats *ad libitum*. I collected the large primary feathers as they were shed and identified them as 5–9 from photographs taken of the bird before it molted. The 10 primary feathers on a hawk's wing are conventionally numbered from 1 (nearest the secondary feathers) to 10 (on the leading edge of the wing).

At intervals during the molting period, the hawk flew in a wind tunnel (described by Tucker and Heine 1990) at a speed equivalent to 10.5 m/s in air at sea level in the U.S. standard atmosphere (von Mises 1959). Standard sea level air has a density of 1.23 kg/m^3, and the air density during the observations did not change significantly from 1.18 kg/m^3.

I started the bird flying at an angle where it could remain motionless relative to the tunnel for at least 1 s. *Motionless* means that it did not change position faster than 1 cm/s. Then I tilted the tunnel toward horizontal in ¼° steps until the hawk no longer remained motionless. Instead, it drifted downwards and backwards while gliding, then it moved forward by flapping and began to glide again. I repeated this process several times to confirm that the hawk's behavior was repeatable, and then I noted the shallowest tunnel angle (θ) at which the hawk remained motionless. The hawk's body mass did not change significantly from 0.702 kg during these observations.

I corrected measured drag for boundary effects by adding the following term to drag:

$$(mg)^2/(4C\rho V^2),$$

(derived from Tucker and Heine 1990) where C is the cross-sectional area of the wind tunnel (1.5 m^2) and ρ is the air density. Corrected drag is given by

$$D = mg(\sin \theta + mg/(4C\rho V^2)).$$

Since the correction term is constant, L/D depends only on the tunnel angle:

$$L/D = 1/(\sin \theta + 0.00846).$$

The hawk lost primaries 5–8 on each wing between 15 June and 21 July. The matching feathers on each wing molted within a day or two of one another. Except for primary 6, the new primaries on July 21 were nearly as long as the original feathers. The new primary 6, however, was short and left an obvious gap (Fig. 3). Seen from the side in flight, the anterior edge of the gap was about half a feather-width ventral to the posterior edge (i.e. the trailing edge of primary 7, which formed the anterior edge of the gap, was ventral to the leading edge of primary 5, which formed the posterior edge of the gap).

This arrangement of primaries 7 and 5 was markedly different from that of the fully feathered wings in flight. When the feathers are complete, the trailing edge of each primary overlaps beneath and touches the leading edge of the next posterior feather, except at the distal ends of primaries 6 through 10 in the Harris' Hawk. These ends form the separated tip slots typical of soaring hawks and vultures, and the anterior feather tips are above the posterior tips. Thus, the trailing edge of the feather that forms the anterior edge of a slot is dorsal to the leading edge of the feather that forms the posterior edge of the slot—just the opposite of the gap that appeared during molting.

The loss of other wing and body feathers did not cause large gaps in the wings or make the body surface look rough. The loss of primary 9 left a narrower gap than the loss of primary 6, and without a raised posterior margin. Occasionally, a secondary feather fell out while the new feather was 1 or 2 feather widths shorter than its final length. The covert feathers on the undersides of the wings were noticeably thin. The hawk had a patchy appearance because the new feathers were colored differently from the old.

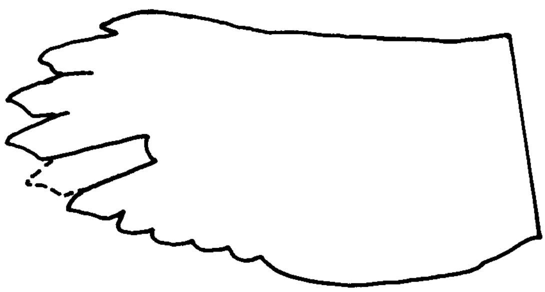

Fig. 3. A fully spread wing of a Harris' Hawk, showing the gap left by the missing primary 6. The dotted line shows the outline of the normal feather. The straight line at the base of the wing represents a distance of 18.4 cm. The wing outline is traced from a photograph of a fully feathered gliding bird.

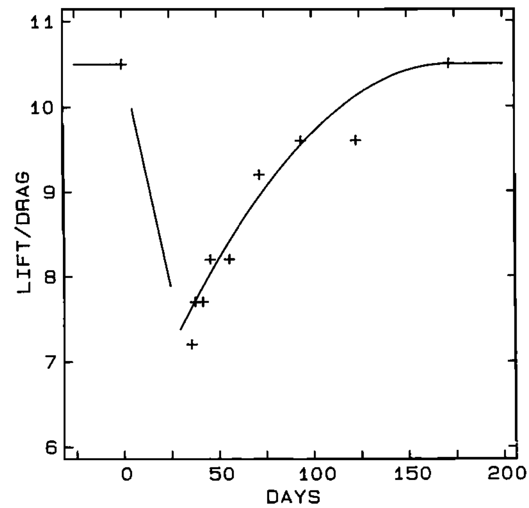

Fig. 4. Lift-to-drag ratios of a gliding Harris' Hawk during molting. Molting began on day 0 and was complete before day 172.

Both old and new feathers appeared smooth and unbroken throughout the molt.

The tail maintained its normal length as new feathers gradually replaced old ones. No gaps were visible in the tail because the hawk kept its tail folded during flight. The feather conditions and maximum L/D values during the period from pre- to postmolt are summarized in Table 1 and Figure 4.

Discussion

Molting degrades gliding performance over a period that correlates with (1) the appearance of gaps in the wing tips caused by missing primary feathers, and (2) the temporary shortening of the primary feathers until the new primary feathers reach their final length. These changes reduce the wing area and span, and they change the shape of the wing tips. Their effect on maximum gliding performance can be evaluated by comparing the observed L/D values with predictions from a gliding theory for the Harris' Hawk (Tucker and Heine 1990).

The changes in wing area and span alone cannot account for all of the decline in L/D. The fully feathered hawk in this study had a wing span of 0.86 m when gliding at maximum performance at a speed of 10.5 m/s in the wind tunnel (Tucker and Heine 1990). The theoretical maximum L/D for these conditions is 11.0. The loss of the primary feathers caused reductions in wing area and span that I estimate were less than 0.01 m^2 and 0.1 m, respectively. These reductions would in theory reduce L/D to 88% of the theoretical maximum. The lowest L/D during molting was 69% of the premolt value. In addition, the hawk probably can compensate somewhat for the reduced wing area and span by extending its wings.

Another factor that could decrease L/D during molting is a change in the normal configuration of slots in the wing tips. These slots are thought by some to reduce induced drag (Pennycuick 1983, Withers 1981). The "induced drag factor" (also called the "span efficiency factor" in the aerodynamic literature) in the gliding theory adjusts the amount of induced drag produced by the wings at a given span. Figure 5 shows the effect of increasing the induced drag factor, and hence the induced drag, in a theoretical hawk with the reduced wing span and area mentioned above.

An increase in the induced drag factor of 45%, from 1.1 to 1.6, together with the reduction of

Table 1. Feather condition and lift-to-drag ratios (L/D) for a gliding Harris' Hawk during molting.

Day	Description	L/D
0	All feathers complete	10.5
36	Primaries 5–8 lost, gaps in wing tips	7.2
38		7.7
42		7.7
46	New primary 6 growing into gap	8.2
56		8.2
72	New primary 6 fills gap	9.2
94	Primary 9 missing	9.6
123	Primary 10 replaced, completing primaries. Underwing coverts, new tail feathers growing in	9.6
172	New feathers complete	10.5

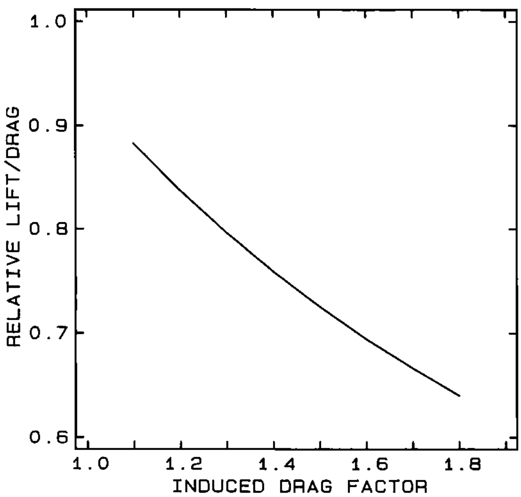

Fig. 5. The theoretical effect of the induced drag factor on the relative lift-to-drag ratio of a gliding Harris' Hawk. A relative value of 1 corresponds to the theoretical maximum lift-to-drag ratio of 11.0 for a fully feathered hawk gliding at 10.5 m/s with a normal induced drag factor of 1.1. The curve shows the relative lift-to-drag ratios for a molting hawk with a wing area reduced by 0.01 m^2, and a wing span by 0.1 m.

wing span and area, would account for the drop in L/D seen with molting. This change in the induced drag factor seems too high to be caused by the loss of the normal tip slots alone. According to theoretical calculations (Cone 1962), the loss of tip slots would increase the induced drag factor by only about 25%.

However, the gaps in the wing tips during molting also could increase the induced drag factor. The raised posterior edge of the gap suggests that primary 5 and the feathers behind it were producing higher than normal lift forces at the wing tips. Increased lift at the wing tips increases the induced drag factor (Pennycuick 1971, Tucker 1987). The gaps also could increase the profile drag of the wing (see Pennycuick 1989, Tucker 1987 for an explanation of profile drag). These changes, together with the changes in wing area, span, and tip slots, could plausibly account for the decline in gliding performance reported in this study.

There could be behavioral as well as aerodynamic components to the degraded gliding performance during molting. The molting hawk might have chosen to flap and glide rather than glide at equilibrium at shallow angles. My observations do not test this hypothesis. The hawk also might have forgotten how to glide at its maximum L/D between 15 June and 21 July, and then improved with practice. This explanation seems unlikely. Once trained, the nonmolting hawk never failed to glide at its maximum L/D of 10.5, even when it had not flown in the wind tunnel for several months.

Although the decline in gliding performance with molting was marked in the wind tunnel, it might not have much effect on a free-living bird. Harris' Hawks hunt in cooperative groups and usually capture their prey by flying from perches rather than soaring (Bednarz 1988). The feather loss that I have described has an unknown influence on flapping flight. It probably has only a small effect on high-speed gliding during a dive, when Harris' Hawks flex their wings, thereby covering up gaps left by missing feathers.

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