

CAUSES AND CONSEQUENCES OF REVERSED SEXUAL SIZE DIMORPHISM IN RAPTORS: THE HEAD START HYPOTHESIS

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ABSTRACT.—Although a number of hypotheses have attempted to explain reversed sexual size dimorphism (RSD) in raptors, none has gained universal acceptance. Indeed, the function of RSD in predatory birds remains an enigma to many biologists. I present data on the behavioral development of recently fledged Northern Harriers (*Circus cyaneus*) that demonstrate that male fledglings develop more rapidly, and that they leave the immediate vicinity of their nests earlier, and with more flight experience, than do their female counterparts. I use these data, together with those from other published sources, to argue that RSD has evolved in raptors to enable the more rapid development of juvenile males.

My argument is based on the following line of reasoning: male raptors typically provide most, if not all of the prey for both their mates and young during much of the breeding season. Because of this, males, more so than females, must be especially proficient hunters if they are to breed successfully. Both sexes are under intense selection pressure to breed as early in life as possible. Males need to develop hunting skills more rapidly than females to do so. Larger size is not as important in male raptors as it is in other birds because the potentially lethal talons of raptors obviate any benefit accruing to small intra-gender differences in mass. If male raptors were larger, or even the same size as females, their more rapid development would place their female siblings at increased risk of siblicide. By being smaller than their sisters, males reduce this risk, thereby increasing their inclusive fitness, while at the same time enhancing their own development. I call this line of reasoning for the evolution of RSD the "Head Start Hypothesis."

Causas y consecuencias del dimorfismo invertido según el sexo en aves rapaces, la "Hipótesis del Pronto Desarrollo"

EXTRACTO.—Aunque numerosas hipótesis se han presentado para explicar el dimorfismo invertido según el sexo, en aves raptoras, ninguna ha ganado aceptación universal. La verdad es que la función de este dimorfismo en aves de rapiña permanece enigmática para muchos biólogos. Presento datos sobre el desarrollo de la conducta de crías, recientemente emplumadas, de las rapaces de la especie *Circus cyaneus*. Estos datos demuestran que las crías machos, recién salidas del nido, se desarrollan más rápidamente y dejan la inmediata vecindad del nido más pronto y con más experiencia en el vuelo que sus hermanas. Hago uso de estos datos, junto con otros procedentes de otras fuentes publicadas, para argüir que el dimorfismo invertido se produce en las rapaces para facilitar el rápido desarrollo de los machos jóvenes.

Mi argumento se basa en el siguiente razonamiento: las rapaces machos típicamente proveen la mayor parte, si no todo, de las presas tanto para sus parejas como para sus crías durante buen tiempo de la estación reproductora. Debido a esto, los machos, más que las hembras, deben ser especialmente proficientes en la cacería si es que han de procrear exitosamente. Tanto las hembras como los machos están bajo intensa presión de selección para reproducirse tan temprano en sus vidas como sea posible. Los machos necesitan desarrollar pericia en la caza más pronto que las hembras. El tamaño grande no es tan importante en los machos, como lo es en otra clase de aves, por que sus garras potencialmente letales obvian cualquier beneficio que el tamaño pudiera darles. Si las rapaces machos fueran más grandes, o aun del mismo tamaño que las hembras, su más pronto desarrollo total pondría a sus hermanas a un mayor riesgo de ser muertas por ellos. Siendo más pequeños que sus hermanas los machos reducen este riesgo, mientras promueven la sobrevivencia de sus parientes, y al mismo tiempo mejoran su propio desarrollo. Llamo a este raciocinio para la evolución del dimorfismo invertido "Hipótesis del Pronto Desarrollo."

[Traducción de Eudoxio Paredes-Ruiz]

For every complex problem there is a simple answer, and it is wrong.

—H.L. Mencken

I introduce my contribution to the Hamerstrom Festschrift with an epigram from Mencken for several reasons. First, Frederick Hamerstrom lived by this credo, and attempted to instill it in his intellectual offspring. Second, Mencken's terse remark certainly applies to the question at hand; to wit, why do predatory birds exhibit reversed sexual size dimorphism (RSD)? And third, Dean Amadon (1975) used this quote to introduce his contribution on the subject of RSD in the Journal of Raptor Research almost two decades ago.

Few would argue that in most species of raptors (i.e., Falconiformes and Strigiformes as recognized by traditional avian taxonomists, see A.O.U. 1983 for North American examples), females are larger than males. However, a consensus on the adaptive value of RSD remains elusive. Indeed, the literature on the subject, which dates from the 13th Century (Wood and Fyfe 1943), is crammed with alternative hypotheses that propose to explain RSD. My own reprint collection on the subject numbers in the hundreds, and Walter (1979), Mueller and Meyer (1985), and Mueller (1990) list more than a dozen hypothetical explanations for the phenomenon. In general, all of the extant hypotheses, most of which can be categorized as ecological, physiological, anatomical, or behavioral adaptations (Table 1; cf., Mueller and Meyer 1985, Mueller 1990), refer to selective forces acting on breeding adults. The latter also appears to be true of hypotheses aimed at explaining RSD in several other avian families (cf., Jehl and Murray 1986).

My purpose here is not to review these hypotheses, nor is it to explain why none has managed to gain overwhelming acceptance. Rather, it is to propose that we investigate the possibility that selective forces acting on developing young and nonbreeding subadults, as well as those acting on breeding adults, are responsible for RSD. Specifically, I use my own research on Northern Harriers (*Circus cyaneus*), along with that of other researchers working on other predatory birds to argue (1) that RSD has important consequences for the developmental biology of raptors and (2) that these consequences need to be considered when attempts are made to determine the cause of RSD in predatory birds. Finally, I propose a new working hypothesis for the evolution of RSD, and suggest ways in which it might be tested.

METHODS

During the summers of 1974–79 I studied the behavioral development of recently fledged Northern Harriers on the 40 000-ha Buena Vista Marsh in Portage County, central Wisconsin, the same site used by Fred and Frances Hamerstrom for their long-term studies of harriers and Greater Prairie Chickens (*Tympanuchus cupido*; Hamerstrom 1986, Hamerstrom and Hamerstrom 1973). Portions of the marsh, which are currently managed for prairie chickens, provide prime nesting habitat for harriers (Hamerstrom 1986, Bildstein 1988). Between 1959 and 1983, 9.6 ± 6.3 (mean \pm SD) pairs of harriers nested on the marsh, including 25, 12, and 25 pairs in 1974, 1977, and 1979, respectively (Hamerstrom 1986). I studied the development of at least 14 unmarked fledglings at five nests in 1974, two individually marked fledglings (one male and one female) at a single nest in 1977, and 29 individually marked fledglings (11 males and 16 females) at seven nests in 1979. In 1977 and 1979, prior to fledging, juveniles were sexed and aged (Hamerstrom 1986) and individually marked by bleaching four adjacent primaries or rectrices (Ellis and Ellis 1975). All marked individuals were watched for from 1–12 hr at least every other day from several days before fledging (i.e., the time of their first brief hovering flights over the nest) until they left the nest area and began to hunt on their own several weeks later (Beske 1982). In 1974, unmarked fledglings were watched for from 30 min to 4 hr 1–4 times a week. Observations, which totaled more than 700 hr over the course of the three breeding seasons, were made using 7 \times binoculars and a 15 \times telescope at distances of from 100–250 meters. In 1974 I watched fledglings from the back of a pick-up truck parked on the side of the road, and in 1977 and 1979 I watched them from a portable, lightweight, 2.5-m tower (Bildstein 1980) that I moved among the nest sites.

I used Chi-square extended median tests and student's *t*-tests to examine the extent of gender-related differences in the behavioral development of fledgling harriers (Siegel 1956, Sokal and Rohlf 1969). Because singleton juveniles are known to develop more slowly than harriers with siblings (Scharf and Balfour 1971, see also Nelson 1977 for a similar phenomenon in Peregrine Falcons *Falco peregrinus*), and because all but two of the fledglings I watched had siblings (the exceptions being the singleton female mentioned above, and a male whose sibling disappeared less than 6 d after his fledging), I limited statistical analysis to broods with more than one nestling.

RESULTS

In 1977 and 1979, 64% (7 of 11) of the marked males and 88% (14 of 16) of the marked females survived to fledging. Males with siblings fledged at 29 ± 2.1 d, while females with siblings fledged at 32 ± 3.8 d ($t = 2.33$, $N = 19$, $P < 0.05$). The sole singleton female fledged at 35 d. Males in all-male broods ($N = 4$) fledged 1.8 d earlier than those in mixed-gender broods ($N = 3$), while females in all-female broods ($N = 4$) fledged 1.4 d later than those

Table 1. Some of the more popular hypotheses for reversed sexual size dimorphism in raptors based on selective forces acting on breeding adults. Readers interested in the full array of possibilities should consult Mueller and Meyer (1985) and Mueller (1990).

Ecological hypotheses

There are many variations, but, in general, these hypotheses suggest that because raptors of different size feed on prey of different size, RSD acts to reduce food competition in breeding pairs (Storer 1966, Snyder and Wiley 1976, Newton 1979, Andersson and Norberg 1981, Temeles 1985, but see Mueller and Meyer 1985).

Physiological and anatomical hypotheses

Large females lay larger (better?) eggs than do small females (Reynolds 1972, Selander 1972, Cade 1982).

Large females better protect developing follicles during hunting than do smaller females (Walter 1979).

Large females are better incubators than are small females (Snyder and Wiley 1976, Cade 1982).

Large females are better able to withstand periods of food shortage during incubation than are small females (Lundberg 1986).

Small males spend less energy providing food for their young than do large males (Balgooyen 1976).

Behavioral hypotheses

Large females are better protectors of their nests than are small females (Storer 1966, Reynolds 1972, Cade 1982).

Small males are better protectors of their nests than are large females (Andersson and Wiklund 1987).

Large females are better preparers of food for their nestlings than are small females (Andersson and Norberg 1981).

Large females prevent small males from eating their own young (Amadon 1959).

Large females are better able to form and maintain pair bonds than are small females (Mueller and Meyer 1985, Mueller 1990).

in mixed-gender broods ($N = 10$). Sample sizes, however, were too small to permit statistical analyses.

Once they had fledged, both sexes remained in the vicinity of their nests for an additional two to three weeks, during which time they were fed by their parents. Fledglings were almost always seen perched, usually on fence posts in family groups within 50 m of each other. First flights from the nests typically were brief, vertical springs into the air as a parent, usually the female, returned with food. Within several days of such initial flights, fledglings flew to

Table 2. Flight activities of fledgling Northern Harriers on the Buena Vista Marsh, 1977 and 1979.

TYPE OF FLIGHT	PERCENT OF TOTAL	
	FLEDGLING WITH SIBLINGS	SINGLETONS
Toward adult carrying prey	12	8
Toward sibling carrying prey	2	
To nest for prey	4	2
Toward adult without prey	8	8
Toward sibling without prey	3	2 ^a
In tandem with sibling	17	2 ^a
Other ^b	54	78
Total number of flights	758	444

^a With fledgling from another nest.

^b Mostly wide, circular "exercise" flights.

meet returning parents with food, which was always transferred aerially to the first fledgling that approached. Although many flights were directed at obtaining prey, either from returning parents or from siblings who had already obtained it from their parents, most flights appeared to be exercising events in which the birds flew in wide circles, either in tandem or by themselves, before returning to their initial perch site (Table 2). Fledglings spent little, if any, time hunting, and although several individuals pounced on and played with inanimate objects, I never saw a fledgling capture live prey during this period.

Males progressed more rapidly than females in all measures of behavioral development. Males took more flights per hour, had longer flight times, and spent more time in the air than females (Fig. 1). Males took their first minute-long flight 9 d earlier than did females, and also first perched at least 50 and 400 m from their nest 4–6 d earlier than did their female counterparts (Fig. 2). By the time males were last seen in the vicinity of their nests, usually at between 43 and 47 d of age, they were spending more than 10 min of each hour in the air. Females, on the other hand were averaging less than 2 min of flight per hour at this age (Fig. 1).

Finally, although I was unable to determine with certainty when each bird left the immediate vicinity of its nest and began to feed on its own, none of the six males that I watched were seen in the vicinity of their nests after they had reached 47 d of age. On

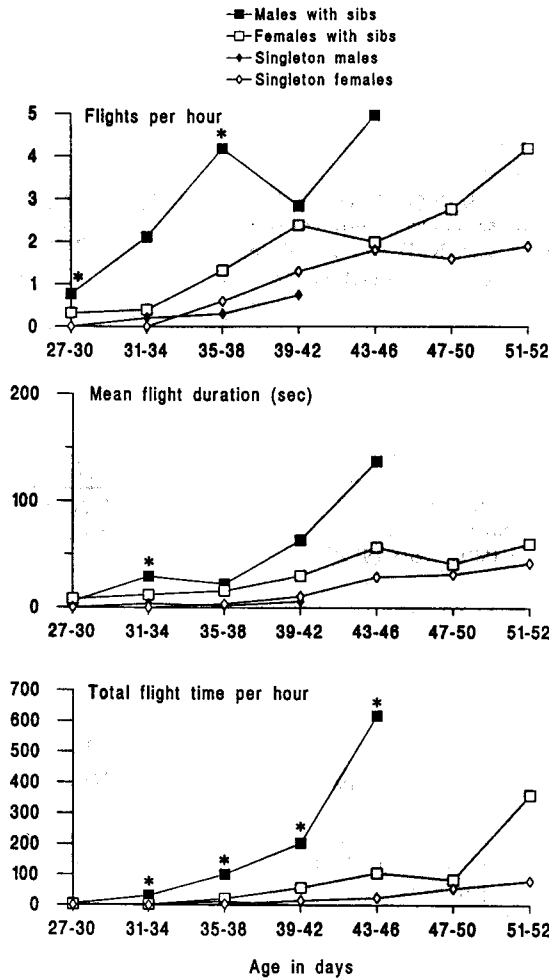


Figure 1. Gender-related differences in the numbers of flights per hour (top), mean flight duration (middle), and total time spent flying per hour (bottom), of fledgling Northern Harriers on the Buena Vista Marsh, central Wisconsin, 1977 and 1979. Significant differences between males and females at multibird nests using Chi-square extended median tests are indicated with asterisks. Data are based on observations of 8 male and 15 female fledglings during a total of 519 hr of observations in 1977 and 1979. Data for males end before those for females because males leave the nest area sooner than females.

the other hand, 9 of 14 females were seen for from 1-6 d beyond this age.

DISCUSSION

My observations clearly illustrate that in Northern Harriers, males develop flight more rapidly, and disperse from their nests earlier and with more flight

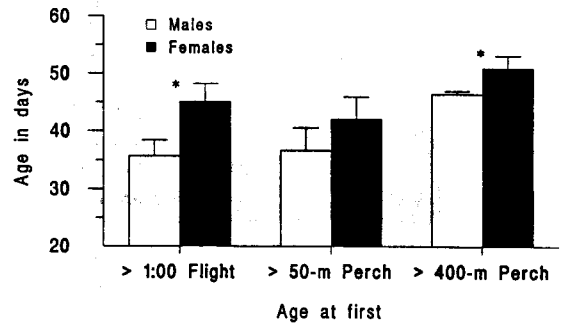


Figure 2. Age in days at which fledgling Northern Harriers first flew for longer than 1 min and perched at least 50 m and 400 m from their nests. Significant differences between males and females at multibird nests using Chi-square extended median tests are indicated with asterisks. Means are indicated by the bars and standard deviations by vertical lines.

experience, than do females. Although post-fledging behavior has been examined in detail in only a few species of raptors, in general, the behavioral patterns I observed in fledgling harriers appear to be similar to those of other species of raptors, including the Osprey (*Pandion haliaetus*; Edwards 1989), Spanish Imperial Eagle (*Aquila heliaca*; Alonso et al. 1987), Eurasian Sparrowhawk (*Accipiter nisus*; Wyllie 1985), Sharp-shinned Hawk (*A. striatus*; Delannoy and Cruz 1988), and Red-tailed Hawk (*Buteo jamaicensis*; Johnson 1986). In general, recently fledged raptors tend to spend most of their time within several hundred meters of the nest waiting for their parents to return with food. Most appear to spend relatively little time hunting on their own during this period, and it is not unusual for a bird to leave the vicinity of the nest and parental care, without having caught a single prey item.

The tendency for males to fledge earlier than their female counterparts appears to be typical of many raptors (Table 3). Similarly, in the two studies that I am aware of that report dispersal times for males and females, male Peregrine Falcons dispersed approximately 4 d earlier than their female siblings (Sherrod 1983); while fledgling male Australasian Harriers (*Circus aeruginosus approximans*) were more "precocious," and left the nest territory about a day earlier than their female counterparts (Baker-Gabb 1978). In captive-reared Eastern Screech-Owls (*Otus asio*), males were more active than young females throughout a 20-week post-fledging period (Ritchison et al. 1992). Overall, then, it appears that my observations of fledgling Northern Harriers in

Table 3. Examples of species for which gender-specific differences in fledging age have been reported.

SPECIES	AGE AT FLEDGING (DAYS)		REFERENCE
	MALES	FEMALES	
Peregrine Falcon	41	44	Sherrod 1983
Sharp-shinned Hawk	24	27	Platt 1976
	28	32	Delannoy and Cruz 1988
Cooper's Hawk (<i>A. cooperii</i>)	30	32-34	Meng 1951
European Sparrowhawk	26	30	Newton 1978
	28	28-30	Wyllie 1985
Hen Harrier	33	38	Balfour 1957
Northern Harrier	29	32	This study
Harris' Hawk (<i>Parabuteo unicinctus</i>)	45	48	Bednarz and Hayden 1991
Bald Eagle (<i>Haliaeetus leucocephalus</i>)	78	82	Bortolotti 1986
Crowned Eagle (<i>Stephanoaetus coronatus</i>)	107	115	Brown 1966

central Wisconsin are similar to those for fledgling raptors elsewhere.

Why do male raptors develop faster than females? I believe that the selective forces acting on males to develop rapidly are greater than those acting on females, and that RSD is the result of this gender-specific difference in selection pressure. Specifically, I argue below that selection favors smaller males because such males develop more rapidly and disperse more quickly, and in better condition, from their nest sites, and that this, in turn, enhances and accelerates their development into breeding adults. I term this explanation for RSD the Head Start Hypothesis.

THE HEAD START HYPOTHESIS AND THE EVOLUTION OF RSD IN RAPTORS

Most raptors hatch their young asynchronously, a phenomenon that has been linked to both sibling competition and brood reduction in a number of species of birds (Lack 1968, but see Magrath 1990 for a thorough review and alternative explanations for hatching asynchrony). And, indeed, both siblicide and brood reduction are common in a number of species of raptorial birds (Newton 1979, Mock 1984). In most instances, smaller siblings, which are dominated by larger sibs, suffer higher mortality as a result of competition for food (cf., Edwards and Collopy 1983). However, in predatory birds, small males reach asymptotic masses and develop flight more rapidly than larger females (Beebe 1960, Moss 1976, Newton 1979, Collopy 1986, Ritchison et al. 1992). In Eurasian Sparrowhawks, for example, sex-specific differences in growth are such that while females outweigh males at fledging, fledgling males

are actually heavier than adult males (i.e., they have already reached asymptotic mass), while fledgling females are considerably lighter than their adult counterparts (Moss 1976). In Golden Eagles (*Aquila chrysaetos*), nestling males grow and develop at such an enhanced rate that they metabolize as much energy as do their larger female counterparts (Collopy 1986).

The most popular explanation for this phenomenon is that gender-specific growth substantially reduces or nullifies the likelihood of males being out-competed by their larger female sibs (Newton 1979, Bortolotti 1986, see also Werschkul and Jackson 1979). There are two problems with this initially attractive and seemingly plausible explanation. First, where raptor siblicide has been examined in detail (cf., Newton 1979), it usually occurs in young nestlings, and almost always within the first half of the nestling period, while male raptors continue to develop behaviorally more rapidly throughout the nestling and fledgling periods, long after this period of vulnerability. Second, and perhaps more importantly, in species of birds where males are larger than females, nestling males almost always require more food than nestling females (e.g., Howe 1977, Cronmiller and Thompson 1981, Linden et al. 1984, Teather 1987, Teather and Weatherhead 1989, see also Slagsvold 1982), at least in part because they, too, typically grow more rapidly than their female counterparts (cf., Linden et al. 1984, Teather 1987). Thus gender-specific differences in adult size alone are not necessarily responsible for gender-specific differences in nestling growth. Nestling males tend to grow and develop faster than nestling females regardless of their relative adult sizes. Viewed in

their entirety, these data suggest that siblicide alone does not explain why small males develop more rapidly than large females.

Why then, do male raptors develop so rapidly? One alternative explanation is that rapid growth and development enables males to breed at an earlier age than they would otherwise be able to do, and that rapid growth and development in females is not equally advantageous.

Most raptors, including Northern Harriers, exhibit delayed maturation, and fail to breed during their second calendar year. Larger species tend to defer breeding longer than do smaller species, and within species (including harriers; Schmutz and Schmutz 1975), males tend to defer longer than do females (Newton 1979). In many non-raptorial birds, delayed maturity has been linked to low reproductive success at earlier ages, in part because of the inferior foraging abilities of younger birds (e.g., Amadon 1964, Lack 1968, Ashmole 1971, Newton 1979, Bildstein 1984). Presumably, hunting skills of younger birds are insufficient to ensure successful breeding, since delayed breeding is more costly to overall fitness than is reduced fecundity (Mac Arthur and Wilson 1967).

Although the development of hunting behavior in recently fledged and prebreeding-age raptors has yet to be studied in detail in most species, evidence suggests that raptors in pre-definitive plumages forage decidedly less efficiently than do adults (Mueller and Berger 1970, Barnard 1979, Bourne 1985, Bildstein 1987). Indeed, Newton (1979) has suggested that "insufficient skill in foraging" may be responsible for the fact that most raptors fail to breed until they are at least 2 yr old.

During both incubation and brooding, male raptors typically provide most, if not all, of the prey for both their mates and developing young (Newton 1979). Females, on the other hand play a major role in providing food for developing young only after brooding has ceased, and females never provide food for both their young and their mates. Thus, becoming a proficient hunter before attempting to breed should be more important for males than for females. Existing data support this notion. In four of the five species in which sexual bimaturation (*sensu* Wiley 1974) has been reported (Northern Goshawks [*Accipiter gentilis*], Red-shouldered Hawks [*Buteo lineatus*], Northern Harriers, and Peregrine Falcons, but not Eurasian Sparrowhawks), males initiate breeding in later years than do females (Newton 1979).

Direct support for the idea that the more rapid

development of male raptors enables them to develop hunting skills more rapidly than their female counterparts is scarce. Nevertheless, evidence suggests that birds that fledge and disperse earlier are better prepared for their first winter than are later fledging birds (Hunt and Hunt 1976, Martin 1987, Nilsson and Smith 1988), and that earlier fledging enhances the likelihood of breeding the following spring (Hochachka 1990). Although none of these studies describe the impact of early fledging for males and females separately, all of them support the notion that earlier fledging dates can affect an individual long beyond its survival to independence (cf., Boag and Alway 1980). In addition, several studies suggest that nestling condition is more likely to affect the eventual breeding success of males than of females (Smith et al. 1989, Hochachka and Smith 1991).

I have been able to find only one report in which the impact of fledging date has been examined in detail in predatory birds. However, that investigation also provides evidence in support of the Head Start Hypothesis. In an impressive 7-year study, involving more than 3700 nestling Eurasian Kestrels (*Falco tinnunculus*), Dijkstra et al. (1990) found that sex ratios (i.e., male : female) declined with hatching date, and, more importantly, that the probability of breeding as a yearling decreased with hatching date for males, but not for females, exactly as suggested by the Head Start Hypothesis.

Any hypothesis that attempts to explain RSD in raptors must also explain why most other species of birds fail to exhibit the same pattern. The Head Start Hypothesis appears to meet this requirement. Nestling raptors are clearly able to kill their siblings, and in a few species do so on a regular basis (Newton 1979). Parental raptors seem indifferent to the siblicidal actions of their offspring (Brown 1971, Steyn 1973). The data presented above demonstrate that male raptors grow and develop more rapidly than their female sibs. If males were also larger, or even if they were the same size as their female counterparts, their presumed more rapid growth and development (see above) would place their female siblings in an especially vulnerable position, not only with regard to siblicide, but also with regard to securing enough prey to fledge successfully. Given these circumstances, reversed size dimorphism enables males to grow and develop more rapidly without unduly threatening their female sibs.

Why, then, don't most other species of birds also exhibit RSD? First, the nestlings of many other species of birds are not normally threatened with

siblicide, nor do they appear to be as prone to starvation as raptors. Furthermore, large adult size in males appears to be more important in other species of birds than it is in raptors (Amadon 1959), possibly because the presence of potentially lethal talons in raptors negates any advantage accruing to a slight difference in mass. (A human example supports the validity of the latter supposition. While prize fighters [i.e., birds without talons] are carefully ranked by weight to equalize the combatants, small soldiers with automatic weapons [i.e., birds with talons] are just as threatening as larger ones.) That several other groups of birds exhibiting RSD (i.e., Sulidae, Stercorariidae) also engage in siblicidal brood reductions (Dorward 1962, Young 1963) lends additional support to the Head Start Hypothesis.

Given the paucity of published information on the behavioral development of fledgling raptors, as well as on the consequences of fledging dates in males and females, this paper, has been quite speculative. Although hypotheses that attempt to explain RSD in raptors are often difficult to test (Andersson and Norberg 1981), the Head Start Hypothesis offers several testable predictions. If the Head Start Hypothesis is true, then: 1) juvenile males should develop hunting skills earlier than their female counterparts. 2) Adult hunting ability should be a more important correlate of initial breeding in males than in females. 3) Early fledging within, as well as across, broods should enhance the probability of early breeding in male, but not female raptors. An experimental test of prediction 3 would be to restrain male fledglings near their nests until after their sisters had fledged, and then compare their flight behavior in subsequent weeks, as well as their breeding success in later years, with those of unconstrained males.

With these predictions in mind, I strongly recommend that additional studies be directed at the least studied portion of raptor life histories: the time between fledging and first breeding. In addition to continuing the long-standing Hamerstrom tradition of focusing one's efforts on pivotal life-history events (see Errington and Hamerstrom 1937), this strategy should foster a better understanding of a phenomenon that has remained unexplained for far too long.

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The comments of Dean Amadon, together with those of several anonymous referees, helped clarify and strengthen my arguments for the Head Start Hypothesis. I thank all of them for their efforts on my behalf. Nevertheless, many aspects of my interpretations are likely to remain in dispute until additional data are collected. I can only hope that my ideas will serve as a starting point for future efforts in this area. Hawk Mountain Sanctuary Contribution number 2.

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