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Mass, Reproductive Biology, and Nonrandom Pairing in Cooper's Hawks

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Several aspects of the ecology of many bird species are correlated with body mass of individuals, including fecundity (Ankney and MacInnes 1978, Aldrich and Raveling 1983), parasite load (Hurtez-Bousses et al. 1997), wintering distribution (Nolan and Ketterson 1983), molt (Cobley and Prince 1998), and predation risk (Lima 1986). In breeding birds of prey, body mass has been used to examine some of these themes and also to investigate the relationship of an individual's mass to the quality of its breeding territory (Newton et al. 1983, Korpimäki 1990) and to mate choice (Bowman 1987, Marti 1990, Bortolotti and Iko 1992). These studies underscore the importance of body mass in demographic and behavioral patterns in birds (Sauer and Slade 1987, Harvey and Bradbury 1991).

The Cooper's Hawk (*Accipiter cooperii*) is a medi-

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um-sized raptor that breeds in forest and urban landscapes throughout Wisconsin in some of the highest nesting densities known for the species (Rosenfield et al. 1995, 1996). Many breeding sites are used for multiple years, especially by males (Rosenfield and Bielefeldt 1996a). Cooper's Hawks exhibit one of the highest degrees of reversed sexual-size dimorphism among raptors; females average about one-third larger than males, although they may weigh more than twice as much as some males during the breeding season. As in other raptor species, a marked division in breeding duties occurs between the sexes, with females being responsible for most of the incubation and brooding and males providing most of the food for the pair and the young during the nesting season (Rosenfield and Bielefeldt 1991, 1993; Bielefeldt et al. 1998).

As part of an 18-year (1980 to 1997) study of the nesting ecology of Cooper's Hawks in Wisconsin (Rosenfield and Bielefeldt 1993, 1996a; Bielefeldt et al. 1998), our capture efforts have yielded body masses from 429 different individuals (201 males and 228 females), including data from multiple captures of many birds. Our objectives are to (1) describe intra- and interyear patterns of variation in body mass in breeding birds, (2) examine the potential for age-related and site-related variation in the mass of breeding birds, (3) investigate potential links between body mass of adults and hatching date and production of offspring, and (4) explore the possibility of nonrandom mating using body mass as an index of size.

Our long-term data set may provide an instructive look at the significance of body mass in breeding falconiforms because it cuts across several generations of nesting individuals (Rosenfield et al. 1995, Rosenfield and Bielefeldt 1996b) in various habitats under presumed temporal variation in environmental conditions (e.g. prey availability). Our results also show that body mass in Cooper's Hawks is significantly associated with several aspects of their nesting ecology in ways not documented previously in the congeneric Eurasian Sparrowhawk (*A. nisus*; Newton et al. 1983) nor in other raptors (Bowman 1987, Korpimäki 1990, Marti 1990).

Study area and methods.—During 1980 to 1997, we trapped breeding Cooper's Hawks at 91 nesting areas on two study sites, one in central Wisconsin near the city of Stevens Point, and the other in the Kettle Moraine State Forest in southeastern Wisconsin. We also captured adults at 35 other nesting areas, mostly in the southern half of the state (Rosenfield and Bielefeldt 1996a). Adult hawks were captured near their nests at different stages of the breeding season, including preincubation (ca. mid-March through late-April), incubation (ca. late April to early June), and brood rearing (ca. mid-June to early July). Captured adults ($n = 429$) and nestlings were individually marked with U.S. Fish and Wildlife Service alumi-

num bands. Seventy-eight birds were recaptured and weighed as breeding adults in one or more years subsequent to initial capture, including 12 of 15 hawks originally marked as nestlings (Rosenfield and Bielefeldt 1992).

We measured body mass of adults to the nearest 1 g with a balance-beam scale and unflattened wing chord and tail length to the nearest 1 mm. Thirty-eight 14-day-old nestlings with trace amounts or no food in their crops were weighed to the nearest 1 g with a spring scale in 1997. When necessary, we subtracted the estimated mass of food in the crop from total mass (<10% of birds had detectable food in their crops, and no adult had more than one-quarter of its crop full).

A nesting area was defined as an area about 800 m in diameter that was occupied by breeding birds in one or more years (Rosenfield and Bielefeldt 1992). A nesting area was considered reoccupied when we found a new nest in a subsequent year within 400 m of the original nest on the site. Fidelity was thus defined as reoccupancy of the same nesting area by the same marked adult in a subsequent year (Rosenfield and Bielefeldt 1996a).

To evaluate possible site effects on body mass, we assessed quality of nesting areas by the frequency of occupancy during a 10-year period (Newton and Marquiss 1982, Korpimäki 1990); nesting areas used by at least three different males, or used by one individual male for at least three years, were categorized as relatively "good" nesting areas. Relatively "poor" nesting areas were those that met neither of these criteria. We also categorized the intensive study sites at Stevens Point and Kettle Moraine as relatively "good" sites because they have shown high nesting densities and levels of productivity comparable to historic figures for the eastern United States, as well as for elsewhere in Wisconsin (Rosenfield et al. 1995, Bielefeldt et al. 1998).

Hatching dates were determined by backdating from estimated nestling ages based on plumage development of known-age birds (Palmer 1988, Bielefeldt et al. 1998). Brood sizes were determined by climbing to nests in the mid-nestling stage when young were about 16 days of age. Unless stated otherwise, all correlation analyses involving adult mass, brood size, and nesting phenology are based on data gathered at the mid-nestling stage. Phenological measures were treated in terms of each nest's departure (in days) from the median hatching date for all nests studied in a given year. For correlation analyses of adult mass and nestling mass, we measured nestling mass per nest as the sum of mean male nestling mass and mean female nestling mass in mixed-sexed nests. Nests that contained only one sex of nestling were omitted from this analysis. We also obtained fledgling counts at nests that were revisited opportunistically for other purposes (Rosenfield and Bielefeldt 1993) and used these counts in correlation a-

nalyses with adult masses obtained at the mid-nestling stage.

We investigated the possibility of nonrandom mating by size using body mass and wing chord of adults at the mid-nestling stage (Newton et al. 1983, Korpimäki 1990, Marti 1990). Although we are aware of the pitfalls of using mass as a surrogate for size (Piersma and Davidson 1991), mass has been considered to be the most accurate univariate measure of body size in birds (Cade 1960, Marti 1990). In our samples of adults captured at the nestling stage, wing chord and tail length were significantly correlated with mass in both sexes (males, $n = 159$; wing, $r_s = 0.39$, $P < 0.0005$; tail, $r_s = 0.20$, $P = 0.01$; females, $n = 210$; wing, $r_s = 0.22$, $P = 0.001$; tail, $r_s = 0.17$, $P = 0.03$). Therefore, we used body mass as an index of size in all further analyses that were significantly correlated with body mass.

We used z-standardization on body masses to create a distribution with a mean of 0 and a standard deviation of 1. Standardized masses of each bird were then categorized as small ($z < -0.43$), medium ($-0.43 < z < 0.43$), or large ($z > 0.43$). This allowed us to classify pairs of hawks into one of nine categories (e.g. small male/small female, small male/medium female, etc.), which permitted contingency analysis (Marti 1990). In this and other methodologies, we have adopted many of the analytical approaches used by other researchers (Newton et al. 1983, Bowman 1987, Korpimäki 1990, Marti 1990) to facilitate discussion of our results. All variables were tested for normality, and nonparametric tests were used as appropriate.

Results.—The mean change in mass for 48 adult males between first ($\bar{x} = 336 \pm$ SE of 3.2 g) and last ($\bar{x} = 333 \pm 3.2$ g) captures (one year or more later) during the nestling stage was only 0.9% (paired $t = 1.57$, df $= 47$, $P = 0.12$). Similarly, for 30 adult females captured (582 ± 7.6 g) and recaptured (585 ± 5.9 g) during the nestling stage in different years, the mean change in mass was only 0.5% (paired $t = -0.60$, df $= 29$, $P = 0.55$). We also compared mass at the nestling stage among breeding adults recaptured 1, 2, and 3 or more years after initial capture. Mean mass changes in all temporal categories again were not significant for either sex, ranging from 0.07 to 1.4% for males (all $P > 0.10$) and from 0.4 to 1.6% for females (all $P > 0.40$). Thus, age-related variation in body mass of breeding adults during the nestling stage was negligible.

We tabulated body mass at three stages of the breeding season within years for independent sets of adults captured over 18 years. Males lost mass as the season progressed from the preincubation ($\bar{x} = 360 \pm 5.6$ g, $n = 31$), to incubation ($\bar{x} = 346 \pm 3.8$ g, $n = 27$), to nestling ($\bar{x} = 331 \pm 1.8$ g, $n = 143$) stages ($F = 22.37$, df $= 2$ and 198, $P < 0.0005$). Mean loss of mass over the season was 8% in males. Body mass of females also declined significantly from the prein-

cubation ($\bar{x} = 634 \pm 9.8$ g, $n = 20$), to incubation ($\bar{x} = 609 \pm 10.0$ g, $n = 8$), to nestling ($\bar{x} = 581 \pm 3.1$ g, $n = 200$) stages (Kruskall-Wallis test, $H = 23.56$, df $= 2$, $P < 0.0005$), averaging 9% over the course of these stages. For individual birds captured at both the preincubation and nestling stages in different years, mass loss between the two stages again was significant for males ($P = 0.007$, $n = 15$) and females ($P = 0.003$, $n = 9$), averaging about 6% in both sexes.

Based on quality of nesting areas (see *Study area and methods* section), the body mass of adults during the nestling stage did not differ significantly between good and poor sites (162 marked males at 54 good sites vs. 47 poor sites; $t = -0.51$, $P = 0.612$; 188 marked females at 54 good sites vs. 32 poor sites; Mann-Whitney $U = 261.5$, $P = 0.55$). The mean difference in mass of birds on good versus poor sites ranged from 0.6 to 3.1%. To further evaluate site effects, we compared mass on two study sites with high densities of breeders with that at other nesting areas in the state. We reasoned that birds from the two high-density sites would be heavier. However, we found no significant difference in mass for birds nesting in high-density sites (males, $\bar{x} = 332 \pm 6.1$ g, $n = 14$; females, $\bar{x} = 591 \pm 9.7$ g, $n = 12$) versus other sites (males, $\bar{x} = 328 \pm 2.3$ g, $n = 70$; females, $\bar{x} = 571 \pm 6.0$ g, $n = 68$; males, $t = 0.63$, df $= 82$, $P = 0.528$; females, $t = 1.34$, df $= 78$, $P = 0.185$).

For analyses of adult mass in relation to hatching date, brood size, and fledgling production, body mass was derived from captures of adults at the nestling stage of breeding. Pair mass was the sum of male and female mass in cases where we caught both adults at a nest. Male mass ($r_s = 0.23$, $n = 159$, $P = 0.001$), female mass ($r_s = 0.28$, $n = 183$, $P < 0.0005$), and pair mass ($r_s = 0.51$, $n = 97$, $P < 0.0005$) were significantly correlated with hatching date. Thus, within a given year, birds of higher individual mass and pair mass tended to exhibit earlier hatching dates (and thus earlier clutch-completion dates) compared with the respective median dates in our sample. Likewise, male mass, female mass, and pair mass were positively correlated with brood size (Spearman rank correlation, all Ps ≤ 0.04) and with the number of young fledged per nest (Spearman rank correlation, all Ps ≤ 0.02).

Mass of adult males was significantly correlated with mean mass of their male nestlings ($r = 0.73$, $n = 10$, $P = 0.03$) and their female nestlings ($r = 0.76$, $n = 6$, $P = 0.05$). Mass of adult females was significantly correlated with mean mass of their male nestlings ($r = 0.85$, $n = 7$, $P = 0.02$) but not with that of their female nestlings ($r = 0.65$, $n = 8$, $P = 0.06$). Pair mass also was correlated with the combined mean mass of male and female nestlings ($r_s = 0.88$, $n = 7$, $P = 0.02$).

Finally, the mass of seven male offspring that subsequently were captured as breeding adults was significantly correlated with the mass of their fathers (r_s

TABLE 1.   Number of mated pairs ($n = 104$) of Cooper's Hawk's by size categories in Wisconsin, 1980 to 1997. Values in parentheses are body mass in g ($\bar{x} \pm$ SE, range).

	Females		
Males	Small (531 ± 5.8, 461–562)	Medium (588 ± 1.7, 569–606)	Large (632 ± 4.3, 607–701)
Small (308 ± 2.1, 276–320)	16	11	7
Medium (329 ± 0.9, 321–338)	6	20	10
Large (354 ± 2.1, 339–388)	5	13	16

$= 0.86$, $P = 0.03$). Further comparisons that are not appropriate for statistical analyses (because of small sample sizes) include 18 birds captured as breeders (four mother-son, three mother-daughter, and two father-daughter combinations). In each case, parent and offspring were mutually below or above the mean mass (male $= 332$ g, female $= 582$ g) for our population. That is, they were consistent with results from correlations of parent-offspring masses evaluated statistically above.

Within 104 independent pairs of adults captured during the nestling stage, male and female masses were positively correlated ($r_s = 0.35$, $P = 0.003$). Pairing by size class was nonrandom ($\chi^2 = 15.1$, df = 4, $P = 0.04$) in that larger males tended to pair with larger females, and smaller males tended to pair with smaller females (Table 1). In both sexes, the mean mass of large birds was about 15 to19% heavier than that of small birds.

Discussion.—Captures of 429 breeding Cooper's Hawks revealed significant correlations among adult mass, nesting phenology, and productivity. However, we detected no site-related or age-related effects on adult mass. In males, we also failed to detect an age-related effect (as indexed by eye color) on brood size or their mates' clutch size (Rosenfield and Bielefeldt 1997). In males, at least, mass rather than age thus appears to be associated with the results presented here. Pairing among adults with respect to size was significantly nonrandom. We speculate that some of our results are the outcome of heritability of body mass.

Some of our findings contrast with results from the few other similar studies of raptors. For example, mass of both male and female Cooper's Hawks declined significantly from the preincubation to nestling stages of the breeding cycle, whereas Eurasian Sparrowhawks (Newton et al. 1983), Barn Owls (*Tyto alba*; Marti 1990), and Boreal Owls (*Aegolius funereus*; Korpimäki 1990) exhibited a qualitatively similar decline in mass over the course of the nesting season for breeding females but not for breeding males. Newton et al. (1983) found no significant change in mass of male Eurasian Sparrowhawks over the breeding season. In contrast, our results on the congeneric Cooper's Hawk document a seasonal decline in mass of males. Thus, generalizations about intray-

ear trends in mass of male raptors, and the behavioral and physiological factors that may affect these trends (Newton et al. 1983, Korpimäki 1990), should be made with caution.

During the nestling stage, mass of male Cooper's Hawks ranged from 274 to 421 g ($\bar{x} = 332 \pm 1.8$ g, $n = 159$) and that of females ranged from 455 to 722 g ($\bar{x} = 582 \pm 3.0$ g, $n = 210$). Within this span of larger and smaller birds, heavier individuals tended to have earlier laying dates than did smaller birds and also tended to have significantly larger brood sizes. The correlations among mass of breeding adults, nesting phenology, and reproductive output thus appear to derive (Newton et al. 1983), at least in part, from the respective mass of each sex. These relationships also held when we combined male and female masses of mated pairs in phenological and reproductive analyses.

We were unable to detect site-related or age-related effects on phenological or reproductive patterns. To the extent that our analyses permit, relationships between mass, phenology, and reproduction seem not to have been compromised by age and site effects. Newton (1986) also reported that the heaviest female Eurasian Sparrowhawks tended to begin laying earlier and to produce larger clutches. It seems reasonable that heavier birds could afford to nest earlier, when food supplies might be limited, and also might withstand brief food shortages more readily, than would lighter birds (Newton 1986). Perhaps an earlier initiation of nesting allows more opportunity to renest should first clutches fail. Earlier nesting also might enhance survival of juveniles (Newton 1989) and provide a longer period of time for them to develop foraging and flight skills before the onset of migration.

We suggest that size (i.e. mass) in Cooper's Hawks has a heritable component. In both males and females, interyear variation in mass at the nestling stage was minimal, on the order of 1% on average. The small variation in mean mass across years in adults implies a heritable element to size. Furthermore, mean loss of mass on an intrayear basis between the preincubation and nestling stages was virtually identical for males that were above (8.3%, $n = 7$) or below (8.2%, $n = 7$) the median mass of these birds at the preincubation stage. A comparable anal-

ysis for nine females showed a similar loss of mass of 5.4 and 7.5% for smaller and larger females, respectively.

Also, for seven pairs of adults, pair mass was significantly correlated with the combined mean masses of their male and female nestlings, again in accord with a possible heritability of size and mass. Moreover, mass of seven male nestlings subsequently captured as breeders was positively correlated with the mass of their fathers. Masses of nine other parent-offspring sets were consistent with a positive relationship between parental size and offspring size.

Variation in the size of individual hawks within the population offers the opportunity for nonrandom mating with respect to mass. Mueller (1986) suggested that a size difference between the sexes, and hence the potential for nonrandom pairing, likely evolved in falconiforms because of the selective advantage of female dominance over males during pair formation. This hypothesis predicts that females should pair preferentially with small males. To date, studies have not supported this claim (Newton et al. 1983, Bowman 1987, Marti 1990), although Bortolotti and Iko (1992) showed mate choice in American Kestrels (*Falco sparverius*) based on condition or quality of individuals as revealed through mass scaled to body size.

Our data demonstrate that nonrandom mating with respect to body mass occurs in Cooper's Hawks in Wisconsin. An analysis using wing chord rather than body mass also showed significant nonrandom pairing for this same data set ($r = 0.23$, $P = 0.02$). Newton et al. (1983), using wing chord, and Bowman (1987) and Marti (1990), using body mass, were unable to document nonrandom mating in Eurasian Sparrowhawks, American Kestrels, and Barn Owls, respectively. The apparent tendency for large males to mate with large females and small females to mate with small males contradicts Mueller's (1986) hypothesis that large females should prefer to mate with small males. Our study is the third to show nonrandom mating in falconiforms (Bortolotti and Iko 1992, Olsen et al. 1998) and the first to demonstrate nonrandom pairing on the basis of mass per se (as well as wing chord) as an index of size.

Birds at the extremes of size and mass (small/large) appear to avoid mating with each other, whereas birds of relatively similar size (medium/medium) seem more likely to form pairs. Bortolotti and Iko (1992) suggested that some individuals exercise active mate choice, whereas others pair by default. For example, the presumed phenological and reproductive benefits of large/large pairs might provide a basis for nonrandom pairing with size as the proximate factor in such pairing. Only 3 of 15 nestlings subsequently detected as breeding birds (Rosenfield and Bielefeldt 1992, 1996b) hatched after the median hatching date for their natal year. The rela-

tive proportions of earlier and later hatching dates in these 15 birds were significantly different ($\chi^2 = 5.4$, df = 1, $P = 0.02$). Thus, it appears that breeding adults of greater mass (at the nestling stage), which also exhibit earlier nesting phenology, contribute a disproportionate share of recruits to subsequent breeding generations in the population we studied. Dzus and Clark (1998) also suggested that early hatching conveys advantages in recruitment, but our results are the first to show an explicit link between nonrandom pairing and recruitment in falconiforms.

It is also possible that the pattern of nonrandom pairing that we report is attributable in part to complementary factors such as territory quality (e.g. food availability), although we were unable to detect site effects. For example, as noted earlier, the proportional loss of mass between the preincubation and nestling stages was very similar for both sexes above or below the sample's median mass at the preincubation stage. Thus, absolute loss of mass was greater on average for heavier birds. It seems unlikely that larger birds on supposedly high-quality territories would exhibit a greater loss of mass than would smaller birds on supposedly poorer territories.

Differential timing of migration (in that segment of the Wisconsin population that migrates; Rosenfield and Bielefeldt 1993), with larger birds arriving and pairing on the breeding grounds before smaller birds appear, provides another possible explanation for the nonrandom paring that we observed. This hypothesis may be questionable because it presumes that our large sample of masses in Wisconsin is drawn mainly from migratory birds, and therefore that most of the birds in our sample were migratory. We were unable to examine this hypothesis or other alternative explanations of the observed patterns with our study design. We propose that heritability of body size (and hence mass) remains a tenable explanation for the pattern of pairing that we observed.

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