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Abbreviated inner primaries: a sex-linked dimorphism in the Acorn Woodpecker

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ABSTRACT. In at least 15 species of woodpeckers, the inner primaries of nestlings are reduced in size. This trait is polymorphic in Acorn Woodpeckers (*Melanerpes formicivorus*) at Hastings Reservation in central coastal California, where most nestlings (90.1%) had reduced first and second primaries, 9.8% had only a reduced first primary, and 0.1% had no reduced primaries. More males (11.1%) had large second primaries than did females (5.3%), and females with this trait were less likely to survive their first year of life. Smaller inner primaries may provide a temporary energetic savings for nestlings that facilitate faster growth, but, if so, why this trait is not more common among other cavity-nesting species remains unknown. This trait appears to be more ecologically interesting than previously suspected and warrants study in other species and populations of woodpeckers.

SINOPSIS. *Primarias internas más cortas: dimorfismo asociado al sexo en Melanerpes formicivorus*

Primarias reducidas en tamaño es una condición encontrada en pichones de al menos 15 especies de pájaros carpinteros. Dicha condición esta asociada a genes polimórficos en *Melanerpes formicivorus*. Encontramos esta condición en la mayoría de los pichones de esta ave en estudio que se condujo en la Reservación Hastings en California. La mayoría de los pichones en dicha localidad muestran reducción en la primera y segunda primaria. Un 10% muestra la reducción en la primera primaria y muy pocos no presentan la condición. La condición de una segunda primaria larga, es dos veces mas frecuente en los machos que en las hembras, y esta asociado a una supervivencia reducida entre las hembras durante su primer año de vida. Primarias internas reducidas pudieran proveer un ahorro metabólico para los pichones que pudiera facilitar el crecimiento de estos. Si este es el caso se desconoce la razón por la cual esta condición no es más común en otras aves que anidan en cavidades. La condición discutida es ecológicamente más interesante que lo previamente sospechado y amerita mayor estudio en otras especies de pájaros carpinteros.

Key words: inner primaries, molt, nestling growth, wing growth, woodpecker

Chapin (1921) was the first to point out a polymorphism among woodpeckers (family Picidae) in the growth of the first two inner primaries of nestlings. Of 30 species examined, the inner two primaries were reduced in size in 9, 15 exhibited reduction of the first but not the second inner primary, and 6 showed no reduction in either of the first two primaries. Nichols (in Chapin 1921) hypothesized that the gap in the wing created by the smaller inner primaries allowed young birds to position their heads to be fed more efficiently, an idea generated by the propensity for older nestlings to sometimes poke their heads through the wing gap formed in

part by the abbreviated inner primaries of other nestlings when attempting to obtain food from adults provisioning young at the nest.

The only substantive discussion of this phenomenon since Chapin's (1921) paper is in a note where Sibley (1957) pointed out that there would be no selection against reduced primaries if they are replaced before fledging (as stated by Chapin 1921). Further, Sibley (1957) suggested that the presence of this trait across species was likely to be a balance between the advantage it confers to nestlings and the presumed liability it becomes after fledging, mediated by the timing of replacement of the reduced feathers during the postjuvenile molt. Several subsequent mentions of this phenomenon (Short 1982, Winkler et al. 1995, Pyle and Howell 1995) confirm that reduced inner primaries are replaced prior to

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fledging, and that such replacement represents the beginning of the postjuvinal (formative) molt. del Hoyo et al. (2002) suggested that the molt of the inner primaries by nestling woodpeckers is, at least in some cases, an adaptation for hastening the postjuvinal molt so that it can be completed prior to dispersal or migration.

One of the species noted by Chapin (1921) as having both reduced first and second primaries was the Acorn Woodpecker (*Melanerpes formicivorus*). During our long-term study of this species at Hastings Reservation in central coastal California, we discovered that not all individuals in this population exhibit abbreviated growth of the inner primaries. Here we report on variation in this trait and its relationship to sex, survivorship, and annual differences in environmental quality. We also correct minor discrepancies regarding the fate of these reduced feathers in this species dating back to Chapin's (1921) initial report.

METHODS

Nestlings were generally banded at about 21 d of age when feathers are actively growing and the relative size of the inner primaries of most individuals is evident. Although fledging does not take place until 30–32 d of age (Weathers et al. 1990), brood reduction is rarely late in the nestling period (Stanback 1991) and thus all birds banded were assumed to have fledged. During processing, we recorded body weight and whether the size of the inner two primaries was clearly small relative to the other primaries or about the same size. In addition, several nestlings were observed and measured during fall 2004 to determine the pattern of growth by inner primaries. Young birds for which the status of the inner primaries was not yet clear were not included in the analysis. All nestlings have adult male-like crown plumage (Spray and MacRoberts 1975), and thus sex was determined by observation following the formative molt 2–4 mo postfledging (Koenig et al. 1995). For a subset of individuals not surviving to this stage, sex was determined using molecular methods (Koenig et al. 2001).

Acorn Woodpeckers are cooperative breeders and young generally delay dispersal until at least the spring following fledging (Koenig and Mumme 1987). Thus, nestlings were assumed to have survived through their first year if still

present in the study area as of February the year following fledging. The mean number of young fledged per bird and per group was determined based on all groups for which data were available for each year of the study, excluding fall nests that only occur in years of particularly good acorn crops (Koenig and Mumme 1987). The size of the fall acorn crop was estimated during each year of the study using the mean number of acorns counted in 30-s visual surveys of 250 oaks throughout the study area (Koenig et al. 1994a,b, unpubl. data).

RESULTS

Chapin (1921) stated that the small inner primaries are molted “as soon as [the longer primaries] have attained their full length” and are then replaced by a quill “as large as that of adults.” We found this description basically accurate for Acorn Woodpeckers, except that the initial set of juvenal-plumage inner primaries is replaced before fledging and well before the other primaries have attained full length (as stated correctly by Short [1982] and Winkler et al. [1995]). Following Howell et al.'s (2003) suggested modifications of the Humphrey and Parkes (1959, 1963) molt terminology, we call this replacement the preformative molt and the replacements formative feathers. The remainder of the formative molt in this species takes place 2–4 mo postfledging and involves only the head and body feathers (Spray and MacRoberts 1975, Pyle and Howell 1995).

The juvenal primaries, consisting of feathers with shafts much smaller in diameter than the normal primaries, erupt with the rest of the plumage at about day 10 posthatching. The juvenal feathers grow to 15–20 mm in length over several days and are then replaced by the formative feathers of normal diameter that push out the juvenal feathers between days 16 and 20 (Fig. 1). The formative feathers are thus delayed by about a week relative to the other (juvenal) primaries and are only about 55–60% the length of the third primary at the time of fledging (Fig. 2).

The size of the inner primaries was determined for 1487 nestlings banded between 1988 and 2004. Of all nestlings examined, 1340 (90.1%) had reduced inner first and second primaries, 146 (9.8%) had a reduced first but not second primary, and 1 (0.1%) had no reduced primaries.

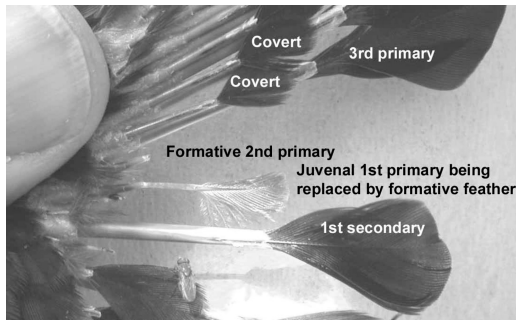


Fig. 1. Right wing of a 20-d-old nestling Acorn Woodpecker as the juvenal primaries are being replaced by the formative feathers. Note that in this individual the juvenal first primary is still attached to the emerging formative feather, while the juvenal second primary has just broken off and is no longer present.

The latter bird was combined with birds having only one reduced primary and collectively referred to as birds with a “large” second primary in contrast to the more common category of birds with a “small” second primary. The 147 nestlings with large second primaries were distributed among 114 broods, 19 of which had 2 nestlings with large second primaries and 7 of which had 3 nestlings with large second primaries. In individuals lacking a reduced second primary, the juvenal-plumage second primary is as large

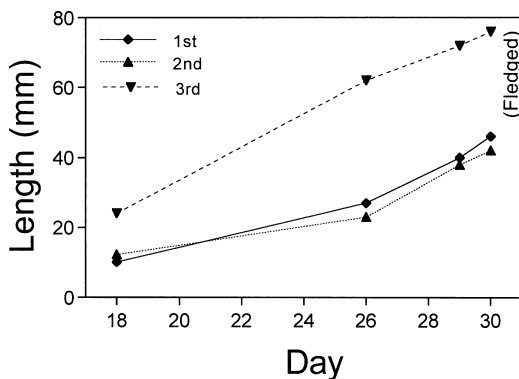


Fig. 2. Growth of the first three primaries in a representative nestling Acorn Woodpecker starting on day 18, shortly after the formative first and second primaries emerged, until fledging on day 31. The day before fledging, the formative first and second primaries were 61% and 55% the length of the third primary.

Table 1. Number (%) of nestling Acorn Woodpeckers of known sex with large and small second primaries.

Size of second primary	Males	Females	Total	% Male
All birds ^a				
Small	423 (88.9)	412 (94.7)	835 (91.7)	50.7
Large	53 (11.1)	23 (5.3)	76 (8.3)	69.7
Total	476	435	911	52.3
Sex determined using molecular methods ^b				
Small	41 (87.2)	77 (92.8)	118 (90.8)	34.8
Large	6 (12.8)	6 (7.2)	12 (9.2)	50.0
Total	47	83	130	36.2

^a Difference between the sexes: χ^2 contingency test = 10.2, $df = 1$, $P < 0.01$.

^b Difference between the sexes: χ^2 contingency test = 1.1, $df = 1$, $P > 0.05$.

as the other primaries and is not replaced in the preformative molt along with the first primary. Presumably, no replacement occurs in individuals lacking either reduced inner primary, but this was not confirmed in the single such individual identified during our study.

Of 1487 nestlings, we determined the sex of 911 either by observation ($N = 781$) or using molecular markers ($N = 130$). For the complete sample, males (11.1%) were significantly more likely to have large second primaries than females (5.3%; Table 1). This comparison combines any differences during the nestling stage with possible survivorship differences after fledging because the sex of most birds was not determined until after the rest of their formative molt in the fall. Using only birds sexed with molecular markers (thus avoiding any subsequent survival effect), males were still 78% more likely to have large second primaries than females (Table 1). Although no longer statistically significant, this is consistent with our previous result suggesting that large second primaries are more frequent among male than female nestlings.

In addition to this sex bias, there was a tendency, although not significant, for smaller nestlings to have large second primaries compared to larger nestlings in the same brood. This was determined by comparing pairs of nestlings of the same sex (determined either by observation or molecular methods) within broods differing by the most body weight at the time of banding. Of 198 such comparisons possible, nestlings were the same size in 171 (86.4%). However, among pairs differing in the size of the second primary, there were 18 cases where the

Table 2. The size of second primaries (N , % of total) among paired nestling Acorn Woodpeckers of the same sex according to relative body weight at time of banding.^a

Size of second primaries	Males	Females	Total
Both the same	88 (82.2)	83 (91.2)	171 (86.4)
Heavier nestling large; smaller nestling small	7 (6.5)	2 (2.2)	9 (4.6)
Heavier nestling small; smaller nestling large	12 (11.2)	6 (6.6)	18 (9.1)
Total	107	91	198

^a Binomial test comparing the total number of pairs in the "heavier nestling large" category to the "heavier nestling small" category: $z = 1.54$, two-tailed $P = 0.12$.

heavier nestling had a small second primary and the lighter nestling a large second primary and 9 cases where the situation was reversed (Table 2).

Subsequent to fledging there was no difference in survival rates of males that differed in inner primary size. However, females with large inner primaries were 37% less likely to survive to February of their second year than females with small inner primaries, a significant difference (Table 3).

Nestlings with a large second primary were detected in each year of our study ($N = 17$) except the first (1988) when only 9 nestlings were examined. Excluding 1988, the percentage of birds lacking a reduced second primary ranged from 5.0% in 2004 to 22.5% in 1990. Annual differences were inversely, but not significantly, correlated with annual productivity, with the proportion of nestlings with large second

primaries smaller in years when the population produced more fledglings per bird ($r_s = -0.34$, $N = 17$, $P = 0.18$) and per group ($r_s = -0.40$, $N = 17$, $P = 0.11$). Productivity during the spring is closely related to the prior fall's acorn crop, which was also inversely, but not significantly, correlated with the proportion of nestlings having large second primaries ($r_s = -0.30$, $N = 17$, $P = 0.23$).

DISCUSSION

As reported by Chapin (1921), we found that most nestling Acorn Woodpeckers had reduced first and second inner primaries. However, this character is polymorphic, with 9.8% of nestlings at Hastings Reservation exhibiting reduced first but not second primaries and 0.1% no reduction in the size of either inner primary. This condition is due to a set of temporary juvenile primaries that are present for about a week before the eruption of the normal-sized (formative) first and (usually) second primaries (Fig. 1). As a result, inner primaries in this population exhibit delayed growth, temporarily leaving a gap in the wings of nestlings (Fig. 2) that is filled approximately a week after fledging.

We found that males were significantly more likely to exhibit the rarer large second primary phenotype than females. In addition, female nestlings with large second primaries had lower survivorship during their first year of life than females with the more common small second primary phenotype. This suggests a fitness disadvantage to the rare large second primary phenotype, at least among females, and further contributes to the overall bias of the trait toward males.

Table 3. Differences in survival until February of their second year (N , %) by nestling Acorn Woodpeckers that differed in the size of their second primary.

Sex size of second primary	Survived	Died	Total	% Survived
Males ^a				
Small	332 (89.2)	91 (87.5)	423 (88.9)	78.5
Large	40 (10.8)	13 (12.5)	53 (11.1)	75.5
Total	372	104	476	78.2
Females ^b				
Small	295 (96.1)	117 (91.4)	412 (94.7)	71.6
Large	12 (3.9)	11 (8.6)	23 (5.3)	52.2
Total	307	128	435	70.6

^a Difference between survivorship of small and large males: χ^2 contingency test = 0.3, $df = 1$, $P > 0.05$.

^b Difference between survivorship of small and large females: χ^2 contingency test = 4.0, $df = 1$, $P < 0.05$.

Even within sexes, large second primaries tended to be more frequent among lighter nestlings within broods, although the difference was not statistically significant. Because dominance is correlated with nestling size in this population (Stanback 1994), this result suggests a possible fitness disadvantage to the extent that this trait is associated with slower nestling growth or with eggs laid later in a clutch. However, it is also possible that this trait is condition-dependent and occurs when nestlings are fed less or generally receive poorer care. This latter hypothesis is supported by the inverse correlations found between both annual productivity and the prior fall's acorn crop and the frequency of nestlings with large second primaries. These relationships were not, however, statistically significant.

Our results support Chapin's (1921) suggestion that the gap in the wings of nestlings created by smaller inner primaries is exploited by siblings to facilitate begging for food from adults late in the nestling period when young are projecting out of the nest hole. However, it seems unlikely that natural selection would favor a trait that provides a benefit to siblings. Given the extent of sibling competition in this species and among nestling birds in general (Stanback 1991, Mock and Parker 1998), the cost to a nestling of having a trait that potentially improves the chances of nest mates obtaining food from adults is likely greater than the indirect fitness benefit of enhancing the survival of genetically related siblings.

Sibley (1957) assumed that the postjuvinal (formative) molt was complete and that the smaller inner primaries were completely replaced prior to fledging. This first assumption was also the basis of del Hoyo et al.'s (2002) hypothesis that the replacement of the inner primaries was an adaptation for hastening the formative molt prior to dispersal or migration. Neither of these assumptions is correct for Acorn Woodpeckers. The formative molt does not involve replacement of the remiges (other than the reduced juvenal primaries under discussion here; Spray and MacRoberts 1975, Pyle and Howell 1995), and the inner primaries that are replaced are not fully grown at the time of fledging (Fig. 2). Furthermore, most fledgling Acorn Woodpeckers neither disperse nor migrate. Sibley (1957) further suggested that the reduced growth "lessens the physiological drain associated with feather

growth" and "probably makes it easier for the nestling to fold the wing." Whether either of these assertions is true remains to be determined, but, to the extent that they are, we predict that nestlings with reduced inner primaries might grow faster and be more successful than those without such primaries, predictions supported to some extent by our results. In any case, our findings indicate that the length of inner primaries has fitness consequences beyond the nestling period in terms of the survival of females during their first year.

In summary, 90% of nestling Acorn Woodpeckers exhibit delayed growth of the second primary. Large second primaries are more common in male than in female nestlings and are associated with reduced survivorship among females. The proximate mechanisms by which these consequences are expressed remain unclear, although it appears possible that the metabolic savings of reduced inner primary growth may play a role in the possibly faster growth rate and higher postfledging survivorship exhibited by females with this trait. Clearly, more detailed examination of other species of woodpeckers would improve our understanding of both the proximate and ultimate causes of variability in this intriguing trait.

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