NESTLING PROVISIONING BY AMERICAN DIPPERS NEAR JUNEAU, ALASKA

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ABSTRACT: The rate of food delivery by male American Dippers (Cinclus mexicanus) increased as the female spent more time brooding young chicks, although the delivery rate by male parents varied greatly when the female was not brooding. Males commonly delivered food more often than females when females were brooding, but nonbrooding females sometimes made more deliveries than their mates. Pairs differed in the relative numbers of food-delivery trips by male and female. Juvenile salmon, and salmon eggs in season, were often delivered to chicks on streams with salmon spawning runs, by both parents. Single parents raised chicks successfully in three cases. One male mated bigamously, but only one of his females was successful in rearing chicks, probably because of a severe infestation of bird-blowflies.

American Dippers (Cinclus mexicanus) typically nest in socially monogamous pairs, and both parents participate in parental care (e.g., Kingery 1996). Only the female incubates eggs and broods young chicks (Kingery 1996, pers. obs.), but reports in the literature differ as to the roles of male and female in caring for nestlings (Willson and Hocker 2008). Here we report on the relative contributions of males and females during the nesting cycle at six nests in southeastern Alaska in 2008. We note the ability of single parents to raise chicks successfully and one case of bigamy. Because there is circumstantial evidence that the availability of small fish may influence some aspects of dipper biology (Obermeyer et al. 2006, Willson and Hocker 2008), we also recorded the frequency of adults' delivering fish to nests.

STUDY AREA AND METHODS

We studied nesting American Dippers in streams near Juneau, Alaska (58° 18′ N 134° 25′ W), from 2004 through 2008. This region supports temperate rainforest with numerous small coastal streams used by dippers. We banded adults with individually distinctive combinations of color bands (Willson and Hocker 2008). In 2008 we focused mainly on six nests, observing food-delivery rates of pairs in which at least one adult was banded. We recorded delivery rates of males and females during the early part of the nestling period when females often brooded young chicks (also recording the brooding times of the females) and after brooding ceased. Males typically feed incubating and brooding females in the nest, as well as nestlings (Kingery 1996, pers. obs.) We also recorded visits to nests in which the adults brought small juveniles and eggs of salmon. In addition, we observed a nest at which the male alone was feeding chicks. All nest watches were in units of one hour, spread over most daylight hours (0600–2000) in June, July, and early August.

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			Brooding Not brooding										
Nest	Σ N (hrs)	M	F	Σ	N (hrs)	$M > F^a$	M	F	Σ	N (hrs)	$F>M^{\alpha}$		
SC	22	7.8	7.0	14.8	5	2	4.3	8.8	13.1	17	15		
$ML1^b$	18	4.9	5.6	10.5	8	4	5.3	8.4	13.7	10	5		
$ML2^c$	20	6.9	4.8	11.7	9	5	3.9	5.4	9.3	11	7		
SD	24	9.3	4.5	13.8	6	5	8.4	8.1	16.5	18	5		
GS	14	9.3	2.7	12.0	11	10	7.0	5.7	12.7	3	0		
LF	24						6.5	6.5	13.0	24	8		

Table 1 Average Food-Delivery Rates (Trips/Hour) of Male and Female American Dippers, During and After Brooding of Young Chicks

RESULTS

Delivery Rates

Average total delivery rates to nests with nestlings ranged from about 9 to 16 trips per hour, with no evident difference between times when the female was brooding and when she was not (Table 1). While the female was brooding, the male clearly made more trips than the female at three nests, slightly more at one nest, and slightly fewer at one nest (no data for one nest). When the female was not brooding, she made markedly more trips than the male at three nests, about the same at two nests, and fewer at one nest. There was no evident trend for males that delivered more often than their mates during the brooding phase to deliver less often than their mates after brooding ceased.

These patterns are corroborated by tallying each hour of observation according to which member of the pair made more trips (so that a few hours can not overwhelm the average). At the three nests with brooding females at which the average delivery rate of the male exceeded that of the female, in the majority of observation hours we recorded a higher rate by the male (Table 1). After brooding, at the three nests where females averaged more feeding trips, the female's rate was greater than the male's in over half the observation periods.

The relative rate of feeding by males during and after the brooding period varied from pair to pair. At three of five nests with data from brooding and nonbrooding periods, males markedly decreased their feeding rate when the female was not brooding; at one nest the rate decreased slightly, and at the remaining nest the rate changed little. Females usually increased their delivery rate when not brooding, at least to some degree (Table 1).

In general, the proportion of feeding trips made by the male increased with the female's brooding time per hour (r = 0.702, p = 0.000, n = 41 hours for all nests pooled). This pattern held at three nests individually (ML2, r = 0.698, p = 0.037, n = 9; SD, r = 0.825, p = 0.043, n = 6; GS, r = 0.723. p = 0.004, n = 11) and was marginally significant at another nest

^aNumber of observation hours in which the indicated sex made the most trips to the nest.

^bFirst brood of pair ML.

^cSecond brood of pair ML.

(SC, r = 0.797, p = 0.106, n = 5). Thus, males often increase their feeding rate as the female's brooding time increases.

The male's deliveries did not increase with the female's time spent brooding at one of the two nests of a bigamous male (ML1 in Table 1). His second nest was about 1 km upstream of the focal nest, and the date at which its chicks hatched was apparently similar. This nest failed, however, when the chicks' primary feathers were just beginning to emerge from the sheaths. The failure occurred before we could accumulate several hours of nest watching, so we could not determine the male's relative attentiveness at his two nests. This nest's failure was undoubtedly at least partly due to a severe infestation of bird-blowflies (probably *Protocalliphora aenea*; T. Whitworth pers. comm.); there were over 350 bird-blowfly larvae (with blood visible in their guts) in the nest with three dead chicks, one of which was markedly smaller than the others (28 versus 41 and 42 g). This male eventually raised a second brood with his remaining partner (ML2) and then increased his delivery rates when she brooded more.

Deliveries of Fish to Chicks

Juvenile salmon and salmon eggs were delivered to five of six nests in 2008, but the rates differed from nest to nest (Table 2). Often, more than one fish was included in a single delivery. Males delivered fish or eggs more often than females at three nests, less often than females at one nest, and at similar frequency at one nest. A female was observed to pluck salmon alevins (tiny hatchlings with yolk sac attached) from the gravel in one stream in June and both eat them herself and deliver them to her chicks.

Single Parents

At one nest in 2008, the female disappeared early in the nestling phase and the male successfully reared three chicks by himself, for at least the last nine days of the nestling period. His rate of food delivery to the nest was 12.9 trips per hour (n=8 hours), including an average of four fish per hour, which compares favorably with the rates posted by pairs at other nests in 2008 (Table 1).

Table 2 Average Rates of Delivery of Fish and Fish Eggs to American Dipper Nests per Hour of Observation

	M	ale	Fe	Female		
Nest	Fish	Eggs	Fish	Eggs		
SC ML1 ML2 SD GS LF	0.2 3.3 3.1 0.3 0 0.5	3.95	1.5 2.6 1.3 0.2 0 0.1	2.0		

In 2005, a widowed female also raised at least three chicks successfully, with an average delivery rate of 13.3 trips per hour (n=4 hours), including 1.3 deliveries of fish per hour. This rate, however, was lower than that of most pairs observed that year (post-brooding rates of 18-28 trips per hour at seven nests with at least 4 observation hours each; 11 trips per hour at one nest). One other widowed female is known to have fledged a brood successfully (Willson and Hocker 2008).

Chick Feeding at the Time of Fledging

The fledging of sibling dippers is often spread over two or even three days. During this time, both parents attend chicks both inside and outside the nest. In June 2008 we observed a nest at which the chicks repeatedly walked from the nest onto the nesting ledge or fluttered down to a rocky outcrop and later re-entered the nest. One temporary fledgling was seen to bathe and forage briefly. The female was aggressive toward this fledgling, pecking it and butting it with her head, and standing tall and sleek in an aggressive posture. The chick eventually re-entered the nest, flying up about 2 m. Both parents fed this chick and its siblings, on the ledge or outcrop or in the nest. By late the next day, all four chicks were outside the nest. In five years of observing dippers, this was the first time we saw fledglings re-enter their nest.

DISCUSSION

Delivery Rates of Males and Females

Pairs clearly differed in the balance between the sexes in food-delivery work, as previously suggested (Hann 1950, Willson and Hocker 2008). When females were brooding young chicks, males often made more food deliveries than females, and the female in some cases made more trips than the male when she was not brooding. In general, the more a female brooded the chicks during the early part of nestling care, the higher the delivery rate by her mate.

Our earlier study (Willson and Hocker 2008) found that early in the nesting cycle delivery trips by males exceeded those of females in 7 of 11 observation periods; after brooding ceased, relative rates of delivery during 60 observation periods were roughly equally divided among cases in which males delivered more often than females, less often than females, and about equally, with some variation among nests. For the Eurasian or White-throated Dipper (Cinclus cinclus), Tyler and Ormerod (1994) reported similar delivery rates by males and females during the nestling period, although females increased their rates as brooding ceased and then visited the nest slightly more often than their mates.

Relative and absolute rates of delivering food to nestlings are likely to vary with ambient temperatures and the concomitant need to brood the chicks, the nature and abundance of the food supply, and the number of chicks in the nest, among other factors. These provide useful topics for future work.

Polygyny

Bigamy is rare in American Dippers but has been reported previously (Price and Bock 1973, Marti and Everett 1978). The nest success of both females in four bigamous matings in Colorado was high for first broods (7 of 8 attempts) but considerably lower for second broods (4 of 8 attempts; Price and Bock 1973). Nevertheless, the number of fledglings attributed to bigamous males exceeded that attributed to monogamous males, while the females in bigamous and monogamous matings raised similar numbers of fledglings (Price and Bock 1973). In Utah Marti and Everett (1978) found that a bigamous male contributed to the successful rearing of two broods at each of his nests.

Polygyny is also recorded for the White-throated Dipper, in which it is sometimes quite common (Marzolin 1988, Tyler and Ormerod 1994, Wilson 1996). Polygynous males father more chicks than monogamous males (Wilson 1996). Primary females in polygynous matings had success similar to that of females in monogamous matings, but secondary females of polygynous males had broods smaller than those of monogamously mated females (Wilson 1996).

Delivery of Fish and Fish Eggs

The highest rates of fish delivery were on a stream noted for good salmon runs (especially chum, *Oncorhynchus keta*, and coho, *O. kisutch*), followed by those on a stream that has good runs of sockeye (*O. nerka*) and coho. Dippers nesting on the remaining streams did not have access to runs of anadromous fish but only to small populations of resident Dolly Varden (*Salvelinus malma*) or introduced brook charr (*S. fontinalis*). Both chum and sockeye enter freshwater streams at times that overlap with dipper nesting, so their eggs are available to nesting dippers. Dippers capture unburied, drifting salmon eggs and pluck shallowly buried eggs and alevins from the gravels. Circumstantial evidence suggests that availability of small fish may lead to greater chick mass at a given age, reduce the amount of brood reduction (progressive loss of chicks from the brood, usually beginning with the smallest), and increase the probability of a second brood being raised in the same season (Obermeyer et al. 2006, Willson and Hocker 2008).

Contrary to our previous findings (Willson and Hocker 2008), females did not deliver fish more often than males in 2008 (Table 2). The earlier study found that, at nests where fish were a relatively common prey, males provided 0.23 fish per trip while females delivered 0.41 fish per trip. The difference between this report and the previous one may be related to individual idiosyncrasies of parent birds foraging in differing circumstances. Perhaps a much larger sample size would permit detection of a consistent pattern, but the observed variation among pairs, locations, or years may be more interesting and ultimately more informative than any general trend.

Single Parents

Single parents, male or female, are clearly capable of raising chicks alone (Hann 1950, Kingery 1996). It seems likely, however, that single

males would not be able to do so until the nestlings acquired some ability to thermoregulate, because only females brood young chicks. Indeed, both in Hann's case and in ours, the successful solo males became sole providers in the latter part of the nestling period. In all of our single-parent cases, small fish were relatively abundant in the territory and were fed to nestlings fairly frequently at two of such nests that we were able to watch. It would be interesting to know if the abundance of fish facilitated the success of single parents. In both cases, there was a spread of at least two days between the fledging of the first and last chicks from the nest, but in some years the spread was just as wide at some nests with two parents (pers. obs.; Willson and Hocker 2008).

The ability of single parents to increase delivery rates to compensate for the absence of the other parent may differ, as seen in this report. Compensation is likely to be easier on productive reaches of streams where the density of prey near the nest is high and the body condition of the solo parent can be maintained. Also, the need to try to compensate may vary with brood size at the time one mate disappears. Our sample of single parents was too small to determine if their fledging success was less than at nests with both parents attending. In *C. cinclus* Tyler and Ormerod (1994) observed single parents delivering food at rates higher than those of individual mated birds, in general, but single parents did not match the combined rates of mated pairs, and their broods were small.

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