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LITERATURE CITED

- ALLEN, R. W., AND M. M. NICE. 1952. A study of the breeding biology of the Purple Martin (*Progne subis*). *Am. Midl. Nat.* 47:606-665.
- DAVIDAR, P. AND E. S. MORTON. 1992. Living with parasites: prevalence of a blood parasite and its effects on survivorship in the Purple Martin. *Auk* 110:109-116.
- HAMILTON, W. D. 1990. Mate choice near or far. *Am. Zool.* 30:341-352.
- HAMILTON, W. D., AND M. ZUK. 1982. Heritable true fitness and bright birds: a role for parasites? *Science* 218:384-386.
- MORTON, E. S. 1987. Variation in mate-guarding intensity by male Purple Martins. *Behaviour* 101: 211-224.
- MORTON, E. S., L. FORMAN, AND M. BRAUN. 1990. Extra-pair fertilizations and the evolution of colonial breeding in Purple Martins. *Auk* 107:275-283.
- MORTON, E. S., AND R. L. PATERSON. 1983. Kin association, spacing and composition of a post-breeding roost of Purple Martins. *J. Field Ornithol.* 54:36-41.
- STUTCHBURY, B. J. 1991. The adaptive significance of male subadult plumage in Purple Martins: plumage dyeing experiments. *Behav. Ecol. Sociobiol.* 29:297-306.
- WAGNER, R. H., M. D. SCHUG, AND E. S. MORTON. 1996a. Condition dependent control of paternity by female Purple Martins: implications for coloniality. *Behav. Ecol. Sociobiol.* 38:379-389.
- WAGNER, R. H., M. D. SCHUG, AND E. S. MORTON. 1996b. Confidence of paternity, actual paternity and parental effort in Purple Martins. *Anim. Behav.* 52:123-132.

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COOPERATIVE BREEDING IN GRAY JAYS: PHILOPATRIC OFFSPRING PROVISION JUVENILE SIBLINGS¹

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Abstract. We present evidence for cooperative breeding in Gray Jays (*Perisoreus canadensis*), a species characterized by delayed dispersal but long thought not to exhibit the life-history tactic of helping. Our findings to date suggest that the alloparental care of younger siblings by philopatric yearlings is confined to the post-fledging period of nutritional dependence. We encourage other workers to investigate whether helping may be confined to this period in other semi-social species as well. Ongoing work is aimed at evaluating the fitness consequences of helping in our study population.

Key words: cooperative breeding, delayed dispersal, helping, Gray Jay, *Perisoreus canadensis*.

The Gray Jay (*Perisoreus canadensis*) is conspicuous among the Corvidae for its apparent lack of cooperative breeding (Strickland 1991, Strickland and Ouellet 1993). The failure to detect cooperative breeding in this species, and in its Eurasian congener (Siberian Jay, *P. infaustus*; Blomgren 1971, Lindgren 1975, Ekman et al. 1994), is unexpected because these jays are characterized by delayed dispersal (Strickland and Ouellet 1993), the necessary but not sufficient precursor of cooperative breeding (Koenig et al. 1992), and because cooperative breeding is thought to be a phylogenetically conserved trait in corvids (Edwards and Naem 1993, Cockburn 1996).

We were prompted to renew our search for cooperative breeding in Gray Jays by the apparently skeptical suggestion that alloparental care of younger siblings may occur during the post-fledging period of nutritional dependence (Ekman et al. 1994). Here, we document the discovery of helping during that period and encourage workers to search for, and examine the fitness consequences of, this form of cooperation in other semi-social species.

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METHODS

We studied Gray Jays in Algonquin Provincial Park, Ontario, Canada. Data collection took place during April–May 1994, March–June 1995, and April–May 1996. Air temperature ranged from -6 to 30°C , snow and rain occurred on several days, and snow cover persisted into April each year.

Social groups of Gray Jays occupy year-round, all-purpose territories, where they store surplus food (Strickland and Ouellet 1993, Waite and Ydenberg 1996). These caches are exploited extensively during winter and sometimes are used by adults to provision nestlings and fledglings. The typical social group in our study area is a mated pair, which may be accompanied by a nonbreeder who is either an offspring or an unrelated immigrant. This group composition arises several weeks post-fledging. The dominant brood-member evicts its subordinate siblings and remains on the natal territory, where parental facilitation apparently enhances survival (Ekman and Rosander 1992). Surviving siblings settle singly with unrelated pairs. During the nest-building phase of the subsequent breeding season, about 20% of mated pairs are accompanied by a nonbreeder, ~75% of which are philopatric offspring (unpubl. data).

We made detailed observations during the breeding season in one territory during both 1994 and 1995. The adults had occupied the territory since 1992. All jays were color-banded. In the spring of 1994, the territory was occupied by a mated pair (female, WOL; male, ROS), along with a son (GOS) from the 1993 breeding season. Three fledglings were produced in 1994, including ROG. Multilocus minisatellite DNA fingerprinting confirmed that WOL and ROS were the parents of GOS and the three fledglings. In October, WOL disappeared following an injury and was replaced by a first-year female (WOB) from an adjoining territory. In the spring of 1995, the territory was occupied by ROS, the same breeding male; ROG, his philopatric son; and WOB, stepmother to ROG. ROS and WOB produced one (female) fledgling, LOS.

In 1994, we conducted focal watches of the three fledglings for 56 hr during nine days between 1 May (seven days post-fledging) and 6 June. In 1995, we conducted 60 hr of observation on 13 days during the nestling period (15 April [2 days post-hatch] to 3 May [one day pre-fledge]) and 94 hr on 16 days post-fledging (between 4 May and 7 June). In 1996, we made observations in a different territory in which a yearling male (YOS) accompanied his putative father (TOY) and stepmother (ROY), but did no provisioning. In this case, we conducted 24 hr of observation on four days during the nestling period (three days post-hatch to one day pre-fledge) and 60 hr on 10 days post-fledging (2–17 May). Observational records were taken ad libitum at the nest during the nestling phase (1995 and 1996) or while maintaining virtually continuous visual contact with the (socially cohesive) juvenile(s) during the post-fledging phase. Data were collected for the adults as well whenever they were in view. Data were recorded using a microcassette recorder or notebook.

RESULTS

In 1994 and 1995, the yearling nonbreeders made substantial contributions, provisioning the recently fledged

young with both retrieved caches and regenerating food. In 1994, the son, GOS, made 77 of 344 (22%) total feeds distributed among his younger siblings. Of the remainder, the mother, WOL, made 123 (36%) and the father, ROS, made 144 (42%) feeds. This extensive provisioning by the helper occurred despite parental aggression towards him (52 recorded supplanting attacks and chases), which decelerated across days ($r_s = -0.79$, $P = 0.04$, two-tailed; overall rate: 0.9 interactions hr^{-1}). No significant trend across days emerged in the proportion of feeds performed by GOS ($r_s = 0.33$, $P = 0.42$). Provisioning by all three adults was still occurring on 13 May (19 days post-fledge), but had stopped by 6 June.

In 1995, the philopatric offspring (ROG) was consistently supplanted and chased upon approaching the nest, and was never observed to provision the sole nestling, his putative half-sibling, LOS. The father (ROS) made 38 feeds and the mother (WOB) made 8 feeds. However, in the 25-day period beginning one day after LOS fledged, the older sibling, ROG, made 129 of 329 (39%) total observed feeds. The mother made only 36 (11%) feeds, whereas the father made 164 (50%) feeds. On a daily basis, ROG's provisioning effort (number of feeds) typically exceeded that of the mother (14 of 15 days; sign test: $P < 0.001$), but not the father (5 of 15 days; $P = 0.30$). As in the previous year, the rate of parental aggression towards the helper diminished across days ($r_s = -0.81$, $P < 0.001$; overall rate: 0.2 hr^{-1} ; 19 total interactions), and no significant temporal trend emerged in the proportion of feeds performed by ROG ($r_s = -0.20$, $P = 0.47$). Provisioning was last seen 26 days post-fledge.

In 1996, the yearling nonbreeder (YOS) was chased by the adults on the three occasions when it approached the nest. It was never observed to provision the sole nestling, his putative half-sibling, which was fed 12 times by each parent. Likewise, YOS was never observed to provision the young during the post-fledging period, when the father made 90 feeds and the mother made 100 feeds.

In 1994, GOS made several contributions classifiable as antipredator behavior. While uttering stereotypical mobbing calls, he performed five of seven recorded swoops or powered flights directed towards solitary red squirrels (*Tamiasciurus hudsonicus*) that had approached to within a few meters from his younger siblings. In 1995, ROG participated in at least one of two recorded episodes of mobbing of a Long-eared Owl (*Asio otus*). We suspected, but were unable to confirm, that both of these birds also gave alarm calls. In 1996, no consistent attempt was made to collect similar data.

Gray Jays routinely engage in sentinel behavior. Sentinels detect both predators and conspecific territorial intruders. In 1994, GOS performed 21% (4 of 19) of the observed (2–7 min) bouts of sentinel duty. In contrast, in 1995 ROG performed none of 12 bouts of sentinel duty. In 1996, no attempt was made to collect such information.

DISCUSSION

Our findings constitute the first evidence for cooperative breeding in Gray Jays, a species characterized by delayed dispersal but long thought not to be coopera-

tive (Strickland 1991, Strickland and Ouellet 1993). In our study population, alloparental care of younger siblings by philopatric yearlings, when it occurs, appears to be confined to the post-fledging period of nutritional dependence. Until this discovery, the compelling question about helping in Gray Jays was how to explain its absence. Why would parents start treating their philopatric offspring despotically at the onset of the breeding season, following nearly a year of extended parental care? Why would the parents apparently not allow their mature young to help feed the nestlings as do the parents of so many other species in seemingly similar demographic circumstances?

Unfortunately, any meaningful analysis of the inclusive fitness consequences of helping cannot be accomplished using our long-term data set; we have no way of knowing whether mature offspring present on the natal territory during the breeding season prior to 1994 actually helped their parents provision the fledglings. Now that helping is known to occur, our future work will be aimed at evaluating the indirect and direct fitness consequences of helping.

Finally, we encourage other workers to pay increased attention to the post-fledging period. This period has been largely ignored in studies of cooperative breeding, which have usually been done on populations in which helping during the nestling stage is prevalent (Heinsohn et al. 1990). Our findings prompt the suggestion that helping may be restricted to the post-fledging period in other semi-social species (e.g., Western Scrub-Jay, *Aphelocoma californica*, in southern Mexico, Burt and Peterson 1993). If so, studies focusing on this period should help elucidate conditions favoring cooperative breeding in such species, and should fill remaining gaps in our knowledge of the phylogenetic distribution of cooperative breeding.

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LITERATURE CITED

- BLOMGREN, A. 1971. Studies of less familiar birds. No. 162. Siberian Jay. *Br. Birds* 64:25–28.
- BURT, D. B., AND A. T. PETERSON. 1993. Biology of cooperative-breeding Scrub Jays (*Aphelocoma coerulescens*) of Oaxaca, Mexico. *Auk* 110:207–214.
- COCKBURN, A. 1996. Why do so many Australian birds cooperate: social evolution in the Corvidae?, p. 451–472. *In* R. Floyd, A. Sheppard, and P. de Barro [eds.], *Frontiers of population ecology*. CSIRO Publishing, Melbourne, Australia.
- EDWARDS, S. V., AND S. NAEEM. 1993. The phylogenetic component of cooperative breeding in perching birds. *Am. Nat.* 141:754–789.
- EKMAN, J., AND B. ROSANDER. 1992. Survival enhancement through food sharing: a means for parental control of natal dispersal. *Theor. Pop. Biol.* 42:117–129.
- EKMAN, J., B. SKLEPKOVYCH, AND H. TEGELSTRÖM. 1994. Offspring retention in the Siberian Jay *Perisoreus infaustus*: the prolonged brood care hypothesis. *Behav. Ecol.* 5:245–253.
- HEINSOHN, R. G., A. COCKBURN, AND R. A. MULDER. 1990. Avian cooperative breeding: old hypotheses and new directions. *Trends Ecol. Evol.* 5:403–407.
- KOENIG, W. D., F. A. PITELKA, W. J. CARMEN, R. L. MUMME, AND M. T. STANBACK. 1992. The evolution of delayed dispersal in cooperative breeders. *Quart. Rev. Biol.* 67:111–150.
- LINDGREN, F. 1975. Iakttagelser rörande lavskrikan (*Perisoreus infaustus*)—huvudsakligen dess häckningsbiologi. *Fauna Flora* 70:198–210.
- STRICKLAND, R. D. 1991. Juvenile dispersal in Gray Jays: dominant brood member expels siblings from natal territory. *Can. J. Zool.* 69:2935–2945.
- STRICKLAND, D., AND H. OUELLET. 1993. Gray Jay. *In* A. Poole, P. Stettenheim, and F. Gill [eds.], *The birds of North America*, No. 40. Academy of Natural Sciences, Philadelphia and American Ornithologists' Union, Washington, DC.
- WAITE, T. A., AND R. C. YDENBERG. 1996. Foraging currencies and the load-size decision of scatterhoarding Grey Jays. *Anim. Behav.* 51:903–916.