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ALLOPARENTING IN THE RARE SICHUAN JAY (*PERISOREUS INTERNIGRANS*)

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Abstract. Over 3 years we observed the breeding behavior of four groups of the Sichuan Jay (*Perisoreus internigrans*), a poorly known Chinese endemic restricted to fragments of high-altitude spruce–fir forest on the east side of the Qinghai–Tibetan Plateau. The first seven known nests of this species were well hidden in tall conifers at 3350–3700 m above sea level, and clutches were initiated in cold, snowy conditions in late March and early April. Only the presumed breeding males fed incubating females, but all members of a group (mean size 3.8) regularly fed nestlings and fledglings. We contrast this pattern of alloparenting with that seen in the two other species of *Perisoreus*: alloparenting is restricted to the fledgling period in the Gray Jay (*P. canadensis*) and entirely absent in the Siberian Jay (*P. infaustus*). The differences may be explained by differences in the defensive capabilities of the three species and/or by differences in the abundance and capabilities of their potential nest predators.

Key words: *Sichuan Jay*, *breeding biology*, *cooperative breeding*, *allofeeding*, *feeding rate*, *helping behavior*, Perisoreus internigrans.

Cuidado Aloparental en la Especie Rara *Perisoreus internigrans*

Resumen. Durante tres años, observamos el comportamiento reproductivo de cuatro grupos de *Perisoreus internigrans*, una especie poco conocida y endémica de China que se encuentra restringida a fragmentos de bosque de coníferas ubicados a gran altitud en el lado este de la meseta de Qinghai y Tibet. Los primeros siete nidos descritos de esta especie estuvieron bien escondidos en coníferas altas en una región que se encuentra a 3350–3700 m sobre el nivel del mar. Las nidadas fueron iniciadas bajo condiciones climáticas frías cuando aun había nieve a fines de marzo e inicios de abril. Sólo los machos que se presumían reproductivos alimentaron a las hembras que estaban incubando, pero todos los miembros del grupo (tamaño promedio 3.8) alimentaron regularmente a los polluelos. Contrastamos este patrón de cuidado aloparental con el que se observa en otras dos especies de *Perisoreus*, en las que el cuidado aloparental se restringe sólo al periodo que sigue la salida de los polluelos del nido (*P. canadensis*) o está completamente ausente (*P. infaustus*). Las disparidades entre las tres especies pueden ser explicadas por diferencias en las capacidades de defensa de estas especies y/o por diferencias en la abundancia o capacidades de los posibles depredadores de sus nidos.

INTRODUCTION

The Sichuan Jay (*Perisoreus internigrans*) is a rare permanent resident of montane coniferous forests in western and central China rarely observed since the type specimen was collected in 1908 (Thayer and Bangs 1912). The species is associated with old-growth coniferous forest and is apparently restricted to the southeastern portion of the Qinghai–Tibet Plateau between 33° and 35° N, 97.5° and 105° W (Sun et al. 2001). In the past 30–40 years, nearly all of the Sichuan Jay's habitat has been heavily logged and fragmented, leading to its classification as vulnerable (IUCN 2003). Moreover, the conservation of this species is severely handicapped because only preliminary work has been devoted to determining its population status and habitat requirements (Jing et al. 2006).

The breeding and social biology of the Sichuan Jay are also of considerable theoretical interest. Group-living Corvidae are well known for the alloparenting behavior of nonbreeders, usually offspring from previous nestings that have not yet dispersed from the natal territory (Brown 1987). Contrary to widespread belief, however, delayed dispersal of a bird does not automatically lead to alloparenting. Strickland and Waite (2001) pointed out that although once begun allofeeding apparently continues invariably into the fledgling period, only 10 of 20 group-living corvids begin alloparenting at the earliest opportunity, in the nest-building period (assistance with nest building and the pre-laying feeding of the breeding female). Others begin only at the beginning of the incubation period (feeding the incubating female on the nest) or not until the nestling period (feeding of nestlings, removal

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of fecal sacs, mobbing of nest predators). Even more challenging to neat definitions of what constitutes an alloparenting species, a few small jays live in groups but delay the behavior to the fledgling period. The two congeners of the Sichuan Jay, the palearctic Siberian Jay (*P. infaustus*) and the nearctic Gray Jay (*P. canadensis*), take the confusion one step further insofar as they share a highly unusual system of juvenile dispersal but, surprisingly, given their apparent ecological similarites, have unexpectedly different alloparental behaviors. In both species, dominance struggles within a brood give rise in early summer to two classes of juveniles. Dominant juveniles, almost never more than one from the same brood in *P. canadensis* (Strickland 1991, unpubl. data) but sometimes two or three in *P. infaustus* (Ekman et al. 1994), remain in the family group on their natal territory whereas evicted juveniles perish or establish themselves as immigrants in family-like groups with unrelated adults elsewhere. Furthermore, the Gray and Siberian Jays are among the handful of birds in which nonbreeders, even those still with their parents, do not feed nestlings (Brown 1987). Allofeeding has never been observed at any stage of the nesting cycle in *P. infaustus* (Blomgren 1964, 1971, Ekman et al. 1994, 2002) and is confined to the fledgling period in *P. canadensis* (Waite and Strickland 1997, Strickland and Waite 2001). Given these peculiarities of the better-known species of *Perisoreus* and the morphologically distinct and possibly ancestral position of the Sichuan Jay within the genus (Goodwin 1976, but see Ericson et al. 2005), we were especially interested in documenting any alloparenting behavior in the Chinese endemic and investigating any intrageneric differences we might find.

METHODS

STUDY AREA

Field studies were carried out in two areas previously logged, the Kache Forestry Farm in Zhuoni county of southern Gansu province (34° 27′ N, 103° 26′ E), which is the northernmost known location for the Sichuan Jay, and the Hongyan Forestry Farm in Jiuzhaigou county of northern Sichuan province (33° 03′ N, 103° 43′ E), near the middle of the species' distribution. At both study sites the topography is mountainous; altitudes range from 2800 to 3800 m. Growing mainly on north-facing slopes, the patchy mature coniferous forest is dominated by several species of spruce and fir, principally *Abies fargesii*, *Picea wilsonii*, and *P. retroflexa*, but also includes *P. purpurea*, *A. faxoniana*, *A. squamata*, and *A. ernestii.* Rhododendrons (*Rhododendron* spp.) are the major understory vegetation, and in mature forest 75% of the ground is covered by mosses. South-facing slopes are treeless, bearing only grasses and low shrubs. Snow depths occasionally reached 100 cm in shaded areas, were often 10 cm in nesting areas when nestlings hatched, and snow fell as late as early June.

Both study sites had been logged for several decades until 1998, when logging was stopped to protect remaining pristine forests. At Zhuoni all trees of diameter at breast height >30 cm had been removed, although this criterion varied by forest patch for a maximum overall objective of 40% harvest to be met. At Jiuzhaigou, trees were clear-cut in 10- to 20-ha patches (mean 12 ha), over ~30% of the available forest. About 30% of the logged land had been replanted with spruce (*Picea* sp.) grown to a diameter of approximately 5–8 cm and height of 2–5 m at the time of the study. Other logged areas had thick growth of willows (*Salix* spp.), honeysuckles (*Lonicera* spp.), and seabuckthorns (*Hippophae* spp.).

STUDY POPULATIONS

At both study areas we attracted Sichuan Jays to bait stations consisting of squares of pigskin, ~15 × 15 cm, the fat still attached, nailed to trees in conspicuous locations, 200 m apart, and protected under wire mesh. Daily patrols of the stations permitted us to approach the otherwise wary jays. Captures, in a portable walk-in trap or mist nets, were continued until we encountered no more unbanded individuals at the bait or in groups of birds already marked. All group members were fitted with one or more colored bands and almost always with a lightweight radio transmitter taped to the base of the central rectrices. Models used were the Holohil PD-2 (3.8 g, battery life 6 months) in 2001 and Holohil BD-2 (1.8 g, battery life 14 weeks) from 2002 to 2004. In practice, one functioning transmitter per group allowed us to locate and approach the birds, after which we attempted to follow the (cohesive) groups and maintain visual contact from ~20 m. Not counting 4 hr average daily commuting time by jeep and/or on foot, we spent an average of 6 hr per day, 6 days per week from March through May in our study areas, plus summer visits of 10 to 20 days, 2001–2004.

NEST OBSERVATIONS AND SEX DETERMINATION

Nests were found by radio tracking at the onset of the egg-laying period when brooding females stay on the nest for longer periods and become less mobile. We designate nests by study area (Zhuoni or Jiuzhaigou), territory (1 through 5), and year (2001 through 2004). We observed the first nest (Zh-1-01) from a blind on the ground, upslope, but used a video system with a ground-based monitor to facilitate surveillance and to minimize disturbance at subsequent higher and less accessible nests. Only one bird was seen to incubate at each nest and was therefore assumed to be the (only) breeding female. Similarly, only one bird was observed to feed the incubating female in each group, and we inferred it to be the breeding male. We assigned no sex to the group's remaining members (all presumed to be nonbreeders because of their obviously subordinate social relations with the apparent breeders). We observed four nests for a total of 89 hr during the incubation period and five nests for a total of 160.5 hr during the nestling period, mostly between mid-morning and mid-afternoon. We were also able to observe two broods and quantify provisioning behavior for a total of 30.5 hr up to 10 days into the fledgling period. After that we could no longer reliably maintain visual contact with family groups. For calculations and comparisons of provisioning and visitation rates at various stages of the nesting cycle, we used the definitions of Strickland and Waite (2001).

RESULTS

BASIC BEHAVIOR AND DESCRIPTION

In our two study areas we color-banded 34 Sichuan Jays, including 4 nestlings and the 14 intensively studied adults and nonbreeders composing the 4 family groups whose 7 nestings we observed. Breeding adults and nonbreeders of unknown age had straw-colored or pale yellow bills (with small greenish or black streaks) that contrasted sharply with the dark heads. At fledging, the bills of young birds appeared whitish or light gray with small black areas. By 40 days after fledging, juveniles' bills had darkened to black but with pale yellow at the tip and between the nares. No older birds of known age were observed, and we have no information on the age at which Sichuan Jays acquire their pale bills.

Except when the female was incubating, all members of a social group normally foraged together, moving through the forest at middle heights, and were seldom more than 30 m apart. We often observed Sichuan Jays placing small food items in bark crevices or under arboreal moss or lichens, but we were unable to gather quantitative information on food storage and recovery because of the birds' wariness, the height of the trees, and the difficulty of following birds on steep slopes (often >30%) at high altitudes.

SOCIAL ORGANIZATION

At the beginning of each breeding season we observed five social groups (two at Zhuoni, three at Jiuzhaigou) for a total of eight "group-springs," including those associated with the seven nests we observed. Two groups consisted of a pair plus one nonbreeder, two consisted of four birds (two nonbreeders), and one group whose nest was not observed consisted of five birds, presumably including three nonbreeders. The mean group size was thus 3.8 ($n = 5$). Membership in these groups was extremely stable with only one female disappearing and no nonbreeders arriving at or dispersing from Jiuzhaigou during or between the three breeding seasons of the study. At Zhuoni one nonbreeder died during the incubation period. The mean April–May home range of our four groups was 0.53 km^2 (Jing et al. 2006), but because many large areas of seemingly suitable habitat were unoccupied, the overall density of the Sichuan Jay in our study areas was only about 1 km^{-2}.

NESTS AND PRODUCTIVITY

We located the first known nest of the Sichuan Jay at Zhuoni in 2001 and six more at Jiuzhaigou from 2002 to 2004. All nests were bulky twig platforms close to the trunk and hidden by dense foliage in the upper part of coniferous trees (mean nest height 14.9 m) on steep north-facing slopes at elevations ranging from 3350 to 3700 m. Estimated dates of clutch completion ranged from 21 March to 19 April (mean 6 April). Clutch size was three in all six nests at which we could determine it. Of those 18 eggs, 13 (72.2%) hatched, and 4 (22.2%) nestlings fledged. One inaccessible nest was abandoned during the incubation period when the female disappeared, and three other nests failed to fledge any young. Causes of nest failure remained unclear, but chicks died from a cause other than predation in three of the six nests whose contents we could see, including two of the three nests where we observed allofeeding intensively (Table 1). At one nest, the female was observed to cover the eggs 96% of the time (43.5 hr), and several females gave soft raspy calls (presumably begging) for minutes at a time, possibly indicating they were experiencing nutritional stress. The incubation period (time from laying to hatching of the last egg) was 22 days at one nest, and the nestling period was 25 days at another nest.

TABLE 1. Feeding visitation rates and contribution of allofeeders at Sichuan Jay nests.

	Unassisted nest[a] (total/mean)	Assisted nests[b] (total/mean)
Number of nestlings	1.67	2.69
Number of nonbreeders	0	2
Hours observed	47	99.5
Total feeding visits to nest	32	252
Known feedings by breeders	32 (100%)	126 (56%)
Known feedings by nonbreeders	—	101 (44%)
Feeding visits to the nest per hour by breeders	0.68	1.41
Total feeding visits to the nest per hour	0.68	2.53
Feeding visits to the nest per nestling per hour by breeders	0.41	0.52
Total feeding visits to the nest per nestling per hour	0.41	0.94

[a]The single nonbreeder at this nest (Zh-1-01) disappeared during the incubation period, and one of the two chicks died in the nest at the age of 5 days.

[b]Nests J-3-02 and J-4-04 combined. The three chicks in J-3-02 died in the nest at the ages of 16, 17, and 19 days.

FEEDING OF INCUBATING FEMALES, NESTLINGS, AND FLEDGLINGS

We did not observe nest building but saw six feedings of two presumed breeding females by their putatively exclusive mates up to 16 days (mean 6 days) before the laying of the female's first egg. At four nests watched for 89 hr during the incubation period we saw nine feedings of the incubating females by their apparently exclusive mates for an overall rate of 0.10 feedings per hour (i.e., barely once per day, at least from the mid-morning to mid-afternoon when we tended to make most of our observations). On five of these occasions one or more of the nonbreeders accompanied the male to the nest but did not feed the incubating female. Five days before the eggs hatched at one nest, two nonbreeders made separate visits to the nest (male not present) but did not feed the female. The day before hatching one of these nonbreeders visited the nest, and the sitting female quickly seized food from its bill. In contrast, 10 days earlier, the female, screaming and quickly joined by the male, had vigorously chased the same two nonbreeders away from the nest over a distance of 30 m. We witnessed no other signs of breeders' hostility towards nonbreeders at any time during the nesting season.

During the nestling period we watched five nests for 160.5 hours. The sole nonbreeder at Zh-1-01 had disappeared during the incubation period, leaving the adults to feed the nestlings unassisted (Table 1). At both J-3-02 and J-4-04 two nonbreeders were present, helped remove fecal sacs, and accounted for 44% of the visits in which nestlings were fed (Fig. 1). At J-3-02 the three nestlings died in the nest, but, with each reduction in brood size, there was a partial compensation in nest-visitation frequency by both breeders and allofeeders (i.e., feeding visits per hour fell but feeding visits per hour per nestling rose; Table 1). Nevertheless, the proportion of visits accounted for by the allofeeders remained relatively constant (rising from 0.44 when there were three nestlings to 0.55 when two remained and 0.50 when only one remained). We watched two more nests, J-4-03 and J-3-04, for only 6 and 8 hr during the nestling period and were not able to quantify the feeding visits by nonbreeders, although we observed at least one allofeeding at each of them. One of the remaining nests, J-3-03, was abandoned with its intact clutch of three eggs during incubation for unknown reasons (all adults and nonbreeders still alive afterward), and the seventh nest (J-5-03) also failed during the incubation period when the breeding female disappeared. Overall, the allofeeding of nestlings was observed at all four of the nests with associated nonbreeders that reached the nestling period.

Partly because of their at least initially larger broods, the nests of the two intensively observed assisted pairs were visited more than four times more frequently than the one unassisted nest (i.e., 2.53 feeding visits hr^{-1} vs. 0.68; Table 1). When the comparison is made in terms of visits to the nest per nestling per hour, the two intensively observed allofed broods were fed, on average, more than twice as often as the brood whose parents were unassisted (0.94 feeding visits per hour per nestling vs. 0.41).

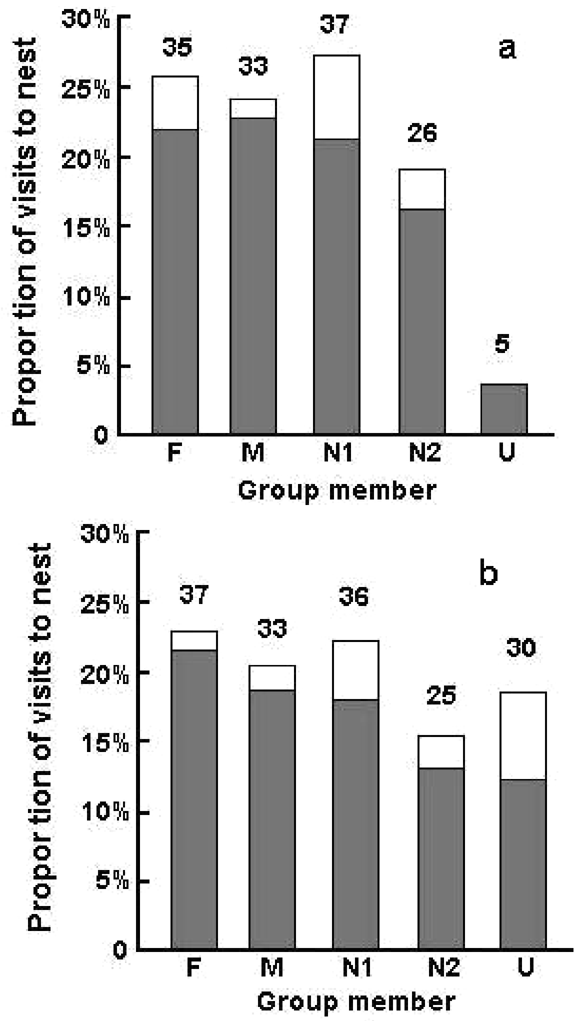

FIGURE 1. Proportion of visits to nest by each group member during the nestling period. Gray bars refer to visits in which food was delivered, white to visits in which food was not delivered. F, breeding female; M, breeding male; N1, nonbreeder 1; N2, nonbreeder 2; U, unknown, visitation could not be attributed to a specific individual. Total visits by each bird given by numbers above bars. (a) Nest J-3-02 (two allofeeders); (b) nest J-4-04 (two allofeeders).

Furthermore, since the breeders at assisted nests accounted for more than half (56%) of the feeding visits, there is no indication they benefited by having their "load lightened" (Hatchwell 1999) through the contributions of allofeeders. Rather, they seemingly kept making feeding visits at a rate that, if anything, was greater (0.52 feeding visits per hour per nestling) than the rate observed at the unassisted nest (0.41 feeding visits per hour per nestling). Allofeeding by the two nonbreeders therefore had the effect of approximately doubling the nest-visitation rate that the parents would have achieved unassisted.

In the fledgling period we followed the broods from J-4-03 and J-4-04 for 30.5 hr in the 10 days after departure from the nest and recorded 71 feedings, a rate of 2.33 feeding visits per hour per fledgling). Nonbreeders accounted for 13 of

26 feedings in which we could identify the feeder. Thus, after fledging, both adults and nonbreeding allofeeders apparently doubled their rate of visiting individual juveniles (from a combined rate of 1.11 feeding visits per hour per fledgling to 2.33). We did not observe fledglings in the summer when they presumably achieve nutritional independence and when broods might break up through intrabrood dominance struggles as in the Gray Jay (Strickland 1991) and the Siberian Jay (Ekman et al. 1994). No banded fledgling was observed with its parents on the natal territory at the beginning of the following breeding season. Nor did we see any new nonbreeders that might have been expelled from territories elsewhere.

DISCUSSION

BASIC BEHAVIOR

The congeners of the Sichuan Jay are well known for their extraordinarily early nesting in cold and snowy late-winter conditions when no sources of food are obvious (Strickland and Ouellet 1993, Blomgren 1964, 1971). Our observations confirm that the Sichuan Jay also nests very early in cold, high-altitude, and seemingly foodless conditions. Further similarities with the other *Perisoreus* spp. are the Sichuan Jay's permanent residency in a subalpine habitat with a strong component of spruce, its conspicuous arboreal food-storing behavior, and the apparently very low mortality rate of territory-holding adults.

DELAYED DISPERSAL AND ALLOPARENTING

We did not witness the retention of young Sichuan Jays on their natal territories or the appearance of nonlocal (i.e., unbanded) first-year birds on territories belonging to unrelated adults. Nor could we learn the origin of the long-term nonbreeders that we saw closely associating with breeders. We do not know, therefore, whether some juvenile Sichuan Jays leave their natal groups to become closely associated with unrelated breeders or whether one or either of the models proposed to explain this dispersal pattern in Gray and Siberian jays (Strickland 1991, Kokko and Ekman 2002) applies to the Sichuan Jay as well. Whatever their origin, however, nonbreeders seemed much more prominent in the Sichuan Jay than has been reported in its congeners. Mean group size at the beginning of the breeding season was 3.8, and there were no unaccompanied pairs ($n = 8$). By contrast, at the start of the breeding season Strickland and Waite (2001) reported a mean group size of 2.2 in the Gray Jay with 78.7% of all pairs unaccompanied ($n = 647$), and Ekman et al. (1994) reported corresponding figures of 2.5 and 59.5% in the Siberian Jay ($n = 42$).

With one possible exception, the feedings of the female we observed before egg laying and during incubation in the Sichuan Jay were exclusively by the breeding male, as in the Gray Jay (Strickland and Ouellet 1993) and Siberian Jay (Blomgren 1964). We found the rate of feeding visits during the incubation period to be only 0.10 visits hr^{-1}, very similar to the rates reported for the other two *Perisoreus* spp. and on the order of 10× less frequently than in other corvids for which corresponding figures are available (Strickland and Waite 2001).

We discovered two major contrasts between the Sichuan Jay's breeding behavior and that of its congeners. First, breeding pairs of the Sichuan Jay did not exclude nonbreeders from the nest area as do the other *Perisoreus* spp. Second, nonbreeding Sichuan Jays began allofeeding and removing fecal sacs at the beginning of the nestling period, whereas allofeeding does not begin until the young have fledged in the Gray Jay (Waite and Strickland 1997), and it does not occur at all, even in the fledgling period, in the Siberian Jay (Ekman and Ericson 2006). In their survey of group-living corvids Strickland and Waite (2001) showed that the absence of allofeeding during the nestling period in some small group-living jays is associated with low body mass and a small complement of nonbreeders. They suggested that whether allofeeding was suppressed or enhanced in a given species depends on the abundance and capabilities of local predators on one hand and on the size and defensive capabilities of the potentially allofeeding species on the other. Other things being equal, allofeeding should be suppressed in small species with low complements of nonbreeders because it results in better nest concealment when such birds face abundant, undeterrable diurnal predators capable of capturing their young. Contrastingly, as an expansion on the original ideas of Skutch (1961) and Brown (1987), allofeeding is more likely in larger birds among which nonbreeders are more numerous because, under those circumstances, it will result in better detection of approaching nest predators and greater ability to repel them. Strickland and Waite (2001) suggested that potentially allofeeding Gray Jays are not allowed near nests but are permitted to feed fledglings because that species' most serious nest predator, the North American red squirrel (*Tamiasciurus hudsonicus*), poses only a minor threat after the young leave the nest. The conspicuously different, total suppression of allofeeding in the Siberian Jay (Ekman and Ericson 2006) may also be consistent with the predator-avoidance hypothesis. At least in northern Sweden, the Eurasian red squirrel (*Sciurus vulgaris*), is rare (DS, pers. obs; J. Ekman, pers. comm.), and the most serious predators the Siberian Jay faces are the Eurasian Sparrowhawk (*Accipiter nisus*) and the Northern Goshawk (*Accipiter gentilis*; Griesser 2003, Nystrand 2006). Unlike squirrels, these hawks continue to pose a danger to fledglings, possibly explaining why the allofeeding of both nestling and fledgling Siberian Jays has been selected against.

The predator-avoidance hypothesis may also be reconciled with the occurrence of allofeeding during both the nestling and fledgling periods of the Sichuan Jay. First, Sichuan Jays (102 g; Sun et al. 2001) are 40% and 21% heavier than Gray Jays and Siberian Jays, respectively (Dunning 1993). Second, our observations suggest that most breeding pairs of the Sichuan Jay seem to be accompanied by one, two, or even three nonbreeders (average 1.8 per pair and no unaccompanied pairs in our study).

Contrastingly, Ekman et al. (1994) found that during the breeding season only 4.8% of pairs of the Siberian Jay were accompanied by two or more nonbreeders and only 33.3% had one. In the Gray Jay the corresponding figures are even lower (1.1% and 20.2%; Strickland and Waite 2001). Compared to those of its congeners, therefore, groups of the Sichuan Jay are more formidable in terms of both the numbers and size of the individuals that compose them. Other things being equal, they should be more capable of confronting predators, and the consequences of betraying a nest location through extra provisioning traffic will be less serious. Furthermore, while we did not formally evaluate the abundance of nest predators in our study areas, those we detected, the Boreal Owl (*Aegolius funereus beickianus*), Sichuan Wood Owl (*Strix davidi*), Siberian weasel (*Mustela sibirica*), and a large flying squirrel (*Petaurista* sp.), seemed rare and, being mostly nocturnal, none of them is likely to use the provisioning of nestling or fledgling jays as a prey-location clue. Thus, the costs of allofeeding during the nestling period may be lower for the Sichuan Jay than for the other two species of *Perisoreus*.

It is also possible that allofeeding of nestlings may enhance the Sichuan Jay's nesting success. The high rate of nestling loss we observed, unrelated to predation and in spite of the approximate doubling of the feeding rate due to allofeeders, suggests that unassisted breeding is particularly difficult for this species. Alternatively, the poor nesting success we observed may be explained by our working at the lower edge of the Sichuan Jay's altitudinal range—where one might expect reproductive difficulties in an age of global warming in a genus whose subalpine nesting in late winter is made possible, at least in part, by cold weather preserving otherwise perishable food (Strickland and Ouellet 1993). Waite and Strickland (2006) reported erosion of the southern edge of the Gray Jay's range and plausibly linked it to warmer temperatures although, in contrast to what we observed at Zhuoni and Jiuzhaigou, they saw almost no deaths of nestlings unrelated to predation (Strickland and Ouellet 1993).

At the onset of the breeding season nonbreeders are frequent in all *Perisoreus* spp. and thus have the potential to engage in alloparenting. What has actually been observed in the three species, however, is strikingly different. Alloparenting does not occur at all in the Siberian Jay, starts only at the beginning of the fledgling period in the Gray Jay, and occurs through both the nestling and fledgling periods in the Sichuan Jay. We propose that these differences are probably best explained as adaptive responses to the different ecological circumstances faced by each member of the genus.

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