

Brood amalgamation and alloparental care in the Least Sandpiper, *Calidris minutilla*

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Least Sandpipers (*Calidris minutilla*) were studied on the Queen Charlotte Islands, British Columbia, over five breeding seasons. Brood amalgamation and care of foreign chicks occur regularly, though at low incidence, among the approximately 90 breeding pairs there. Such behavior is probably important to chick survival and has little impact on adult fitness. Brood amalgamation and alloparental care appear to be widespread in calidridine sandpipers.

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Des Bécasseaux minuscules (*Calidris minutilla*) ont été observés au cours de cinq saisons de reproduction dans l'archipel de la Reine-Charlotte, Colombie-Britannique. La fusion de différentes couvées et l'adoption d'oisillons voisins ont été observées régulièrement, quoique rarement, chez les quelque 90 couples d'oiseaux étudiés. Un tel comportement favorise probablement beaucoup la survie des oisillons et a peu d'impact sur la contribution démographique (fitness) des adultes. La fusion des couvées et les soins alloparentaux semblent des phénomènes communs chez les calidridinés.

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Introduction

Care of foreign offspring (alloparental care) is known for over 150 species of birds (Wilson 1975; Reidman 1982; Skutch 1987). The colonial stilts and avocets express this through brooding foreign chicks and detecting and mobbing predators (Glutz et al. 1975; Hamilton 1975; Bie and Zijlstra 1979; Johnsgard 1981; Cramp 1983; Sordahl 1986; Skutch 1987). Alloparental care in noncolonial shorebirds sometimes results when more than one female lays eggs in a nest, and one or more of the females incubates the eggs or provides post-hatching care (McGillp and Morgan 1931; Glutz et al. 1975; Hale 1980; Walters and Walters 1980; Burbridge and Fuller 1982; Nethersole-Thompson and Nethersole-Thompson 1986). Care-giving to unrelated shorebird chicks assumes various forms, such as brooding, leading, feeding, and predator deterrence² (Wormald 1910; Rittinghaus 1961; Pulliainen 1970; Glutz et al. 1975, 1977; Marcström and Sundgren 1977; Cramp 1983; Flemming 1987). Indeed, interspecific "adoption" has even been observed (Grobe 1977; Hildén 1977; Breihagen 1984). Thus, alloparental care appears to be widespread in noncolonial shorebirds. We report on several instances of alloparental care in a typical calidridine, the Least Sandpiper (*Calidris minutilla*). Most alloparental care in this species results from broods amalgamating in habitat patches where families congregate after hatching. Other instances reflect misdirection of the species' strong parental drive. Alloparental care probably occurs regularly in this species in suitable habitat and increases chick survival. This is the first report of such behavior for *C. minutilla*. Based on scattered published observations we suggest that it occurs regularly among calidridine sandpipers.

Materials and methods

We studied Least Sandpipers over five breeding seasons (1984–1988) in the Delkatla Wildlife Sanctuary, a 190-ha marsh at Delkatla Inlet, Masset, Queen Charlotte Islands, British Columbia, where about 90 pairs nest. We banded most breeding adults and chicks with aluminum and color bands. Incubating adults were captured with a drop trap or hand net. Most chicks were banded immediately after they hatched and before they left the nest. Information on the fates of nests and broods, brood movements, brood attendance, and parental behavior was gathered daily in May–June of 1987 and 1988.

Results

Most nests were in well-drained upland areas, but families gathered in four other areas after chicks hatched. These areas were moist and low lying, with dense vegetation, soft substrate, and small bodies of water (e.g., channels). Such posthatching movements and concentrations of families in undefended feeding areas are typical of northern scolopacids (Miller 1983, 1985). Adult Least Sandpipers tending chicks react strongly to predators. Upon human approach, for example, parents fly around the intruder while uttering loud calls (Miller 1984, 1985; see Cramp 1983; Gochfeld 1984; Sordahl 1986). This behavior alerts other parents, which may participate. Such parental "alarm" responses cause chicks to hide or move away. Parents' responses to predators wane as chicks mature. The responses are generally stronger in males than in females. Males also tend chicks for longer than females do, remaining until after chicks fledge (Miller 1985; see Gratto-Trevor 1991).

We observed six cases of brood amalgamation:

1. On 12 June 1987 we located and banded a brood of three 1-day-old chicks tended by their unbanded parents. The next day the group included a 5-day-old chick from nest 87-24, then about 90 m distant; that chick and its parents had been banded previously. On 15 and 16 June this chick plus two or more chicks from the original brood were attended by the unbanded

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²For components of parental care see Walters (1984).

adults in the same area (we judged the adults to be the same on the basis of their location, behavior, and voice). On 16 June we captured a fifth chick (unbanded when captured) that was being led away by one of the unbanded adults. Thus, on that date the group contained at least four chicks from three different broods, under the care of the original unbanded adults. The first foreign chick was still with the unbanded male in the same area on 27 June. It subsequently fledged.

2. On 24 June 1987 the banded adults 87-52 were tending their 2-day-old chicks about 70 m from the nest. The brood included a 4-day-old chick (banded) from nest 87-61, which was 35 m away from nest 87-52. That chick was not seen again and presumably did not fledge, though its parents continued to raise its siblings. Adults 87-52 subsequently split their brood and led them to different brood-rearing areas, unusual behavior for a calidridine but typical of the Common Snipe, *Galinago gallinago* (Cramp 1983). All the young fledged.

3. On 26 June 1988 male 88-24 was with a nearly fledged chick (banded) from nest 88-98. He showed typical parental "alarm" at our presence and landed repeatedly near the chick as it retreated from us. The male was about 120 m south of its own nest from which two chicks hatched on 13 June and subsequently disappeared (it presumably died). The chick was 300 m south of where it had been with its parents on 13 June, at about 3 days of age. The chick was not seen again.

4. On 1 July 1988 a 3-year-old male and banded female of unknown age, from nearby nests 88-62 and 88-92, respectively, were close to one another. The male vigorously displayed towards us in protecting its 5-day-old brood. The female was tending her 1-day-old brood of three chicks but was quiet and undemonstrative. We believe that her mate had deserted her the previous day after we captured and banded him, which seemed to cause him great distress. On 2 July, male 88-62 again displayed diversionary and "alarm" behavior at our approach while he tended five chicks, two from his nest and three from nest 88-92. Female 88-92 was then standing quietly about 20 m away. We released the chicks after measuring them, and the male approached and brooded them all for 7 min. The female was not seen again.

The male tended the five chicks until 16 July. Two of his chicks and all three of the foreign chicks fledged. The male was also observed tending a nearly fledged chick from a nearby nest (88-61) in the same area on 13 July.

5. On 1 July 1988 we captured a banded chick (88-43) for measurement. Its father (2+ years old) was in attendance. Moments after releasing the chick, another male (from nearby nest 88-44) landed beside the chick and led it into cover. The relationship did not endure, however, and male 88-43 was subsequently in sole attendance on his chicks. The chick in question did not fledge, but its siblings did.

6. In 1988 we documented the takeover of a brood by a pair that had lost two clutches to predation. The incident concerned pairs 88-21 and 88-02. Male 88-21 was 2+ years old, had fledged four chicks in the previous year, and was an extremely attentive parent, allowing exceptionally close approach by human observers. We banded his mate in 1988 so do not know if she was paired to him in 1987. Four young hatched from this pair's nest on 13 June, about 100 m from the nearest brood-rearing area.

Adults 88-02 were also paired in 1987, when they successfully fledged young. The male was 4+ years old and the female 3+ in 1988. In that year they initiated a clutch on 12 May but it was depredated on 25 May. They initiated a

replacement clutch on 30 May but it was depredated 14–16 June. The replacement clutch was about 70 m from nest 88-21.

Pair 88-21 began leading their brood to the brood-rearing area on 13 June and reached it on 15 June. On 16 June we saw female 88-02 brooding two of the chicks while her mate and female 88-21 responded with typical "alarm" to our approach. Male 88-21 stood quietly nearby. The next day female 88-21 flew aggressively at female 88-02 several times. Over the next few days female 88-21 showed typical parental responses to us. Male 88-21 remained in the vicinity until 20 June but was calm and undemonstrative in our presence. He then moved to near his nest and remained there until 29 June. Pair 88-02 successfully fledged three chicks. The female deserted her brood after 8 days and the male after 17, typical periods for this species (Miller 1985).

Discussion

Alloparental care in the Least Sandpiper results from the high density of family groups in brood-rearing areas. We judge such care to be important to chick survival, as we noted that several chicks fledged after receiving only alloparental care. Chicks must incur only minor costs in an alloparental relationship. In contrast, adults care for young by brooding, leading, following, and monitoring them, and by predator detection and deterrence. Even so, the incremental cost of tending extra chicks must be small (Walter 1984; Rohwer and Freeman 1989). There may even be some benefits to tending extra chicks, e.g., through spreading of predation risk or from enhanced vigilance due to the larger number of individuals (Parmelee and MacDonald 1960; Eadie et al. 1988). Even if adoption carries a cost to the adult it may be even more costly to abandon a foreign chick, as it must be difficult to locate and identify it in the concealing brood-rearing habitat, and to segregate or abandon it without also abandoning the original brood (Eadie et al. 1988).

After hatching, many northern scolopacids concentrate in productive areas away from nest sites. Contacts between unrelated adults and chicks in such areas must be common, as evidenced by frequent mention of adoption and brood amalgamation (Brown 1938; Parmelee and MacDonald 1960; Heldt 1966; Parmelee et al. 1967, 1968; Soikkeli 1967; Hildén and Vuolanto 1972; Jehl 1973; Hale 1980). Shorebirds are well known for their "broodiness," which must also predispose them to be attracted to and care for unrelated chicks. Two species show striking examples of this: (i) male Pectoral Sandpipers (*Calidris melanotos*), a polygynous species with no known paternal role in incubation or brood rearing, defended and otherwise attended to newly hatched chicks (Parmelee et al. 1967, 1968); and (ii) Ruddy Turnstones (*Arenaria interpres*) brooded willow catkins (Parmelee and MacDonald 1960)!

We conclude that Least Sandpipers and related species are predisposed to brood amalgamation and alloparental care because of several factors: precociality, with reproduction limited by egg production, not chick rearing; strong "broodiness"; mixing of broods in undefended brood-rearing areas, where densities can be high; and breeding synchrony. There would seem to be little selective value to individual recognition of chicks by parents, as the costs to adopting adults are so low and would be counterbalanced in any case by the difficulty of abandoning foreign chicks. The evolutionary impact of the costs to adopting parents is poorly understood for animals generally (Walters 1984): in the Hawaiian monk seal

(*Monachus schauinslandi*), for example, most females spend a great deal of time nursing foreign pups, yet suffer no apparent negative effects (Boness 1990). This subject merits further study in shorebirds.

Brood amalgamation is probably a regular feature of the breeding biology of high-latitude northern shorebirds. Because of this, and in light of the arguments advanced above, it is likely that chicks are adapted to compensate adopting adults tolerantly, and adopting adults are adapted to be at least tolerant of foreign chicks, if not actually solicitous towards them.

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