available to wrens for shelter or warmth. I did not record air temperatures, but three consecutive nights were clear with strong (10–25 knot) winds from the east. Air temperatures at the nearest National Weather Service station (Quillayute; approximately 55 km to the southeast and at an elevation comparable to Tatoosh) were recorded as (date; max./min. degrees F): 28 December, 32/16; 29 December, 29/19; 30 December, 26/20; 31 December, 28/9; 1 January, 32/10 (U.S. Dep. of Commerce 1978, 1979). On my trips to the island on 16–21 March and 26–29 April 1979, I found neither wrens nor the other two conspicuous, resident passerines, Song (*Melospiza melodia*) and Fox (*Passerella iliaca*) sparrows.

My observations on subsequent trips suggested the following recolonization pattern. No wrens were seen or heard in 1979 (*n* = 12 visits), 1980 (*n* = 9), 1982 (*n* = 10), or 1983 (*n* = 12). In 1981, wrens were heard in February and March, but were neither seen nor heard on the subsequent seven visits. In 1984, wrens were heard in mid-March, and on nine of 10 visits between then and mid-November. The density of singing males (five) was roughly about 50% of the previous maximum. Wrens have been conspicuous on all (six) 1985 trips to date. The other passerines of interest were active at a feeder that was established in October, 1979, and had returned to pre-freeze abundance by late June, 1980 (G. B. van Vliet, pers. comm.).

These observations are compatible with what is known of Winter Wren biology. Bent (1948, and references therein) recorded a number of invasions or extinctions on habitable islands in Alaska. In Europe, the same species occupies similar vegetation-dense habitats (Armstrong 1955). Although few data exist on fluctuations in insular populations, on the mainland, wrens seem especially susceptible to cold weather, and show precipitous population declines during severe winters (Batten 1980, Williamson 1981). On Tatoosh, the 6-year interval noted between extinction, presumably due to some combination of cold and starvation, and recolonization probably indicates the difficulties experienced by a relatively sedentary species in invading nearby habitable terrain that is isolated by a water gap. For instance, the coldest weather in western

Washington's history occurred in January, 1950. On Tatoosh, the maximum recorded temperature between 13–18 January was 28°F, and the minimum was 14°F (U.S. Dep. of Commerce 1950). Wrens were abundant in 1956 (F. Richardson, pers. comm.). From 16–18 December 1964, air temperatures on Tatoosh were generally below freezing, ranging from 33–14°F (U.S. Dep. of Commerce 1964). I heard wrens in June, 1968. I know of no records of disappearance of Winter Wrens from mainland sites during any of these intervals.

Extreme climatic events, such as freezes, are recognized as important determinants of island avifaunas. Winter Wrens can be abundant, permanent, and conspicuous residents on islands like Tatoosh. In the last decade, however, they have been absent as breeders 50% of the time (1979–1984) and, since 1950, I estimate that breeding wrens have been absent a maximum of about 40% of the years.

LITERATURE CITED

ARMSTRONG, E. A. 1955. The Wren. Collins, London.
BATTEN, L. A. 1980. Some recent bird population changes in Britain. Ibis 122:420.
BENT, A. C. 1948. Life histories of North American nuthatches, wrens, thrashers and their allies. U.S. Natl. Mus. Bull. 195.
JEWETT, S. A., W. P. TAYLOR, W. T. SHAW, AND J. W. ALDRICH. 1953. Birds of Washington State. Univ. of Washington Press, Seattle.
U.S. DEPARTMENT OF COMMERCE. 1950, 1964, 1978, 1979. Climatological Data, Washington. Weather Bureau.
WILLIAMSON, M. 1981. Island populations. Oxford.

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BEHAVIOR AT A PINYON JAY NEST IN RESPONSE TO PREDATION

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Predation is a major cause of nest failure in a population of Pinyon Jays (*Gymnorhinus cyanocephalus*) that inhabit Flagstaff, Arizona (Marzluff 1983). Jays in this population reduce predation by nesting colonially, concealing their nests (Marzluff 1983), and grouping fledged young in a creche that is guarded by sentinels (Balda and Balda 1978). Typically, they mob predators and desert their nests (Clark and Gabaldon 1979) after acts of predation. I report here the response of one pair of jays to the partial removal of their brood by an American Crow (*Corvus brachyrhynchos*). The predation event spanned a two-day period, which enabled me to contrast the parents' behavior during the event with their behavior before the event. I also compare their behavior to the behavior of other jays that were not detected by predators.

Individuals in the study population have been color-banded since 1972. The nesting attempt described herein was begun on 13 May 1983 by a four-year-old male and a three-year-old female in their second breeding season together. The nest was placed 8.5 m high in a 10-m ponderosa pine tree (*Pinus ponderosa*). Five eggs were laid, all of which hatched on 30 May.

My results reported here were based on 20.6 h of nest observations over six days (10.6 h before predation and 10.0 h after predation). I observed the nest from a distance of 15 m in a canvas blind. Before predation, I watched the nest for 4.6 h on the morning of 13 June, for 4.0 h after noon on 14 June, and for 2.0 h before noon on 15 June. Following predation, I watched the nest for 2.0 h before noon on 15 June, for 3.0 h after noon on 15 June, and for 5 h before noon on 16 June.

On 15 June, both parents arrived in the nest tree together at 08:24, and proceeded to feed and clean the 16-day-old young. They departed 2 min later, and an adult American Crow appeared at the nest at 08:58. All nestlings begged from the crow, as they would from their parents (see McArthur 1982 for a description of begging). The crow jabbed one young bird repeatedly in the head and neck region until it was dead. During this time, all nestlings called harshly. The crow then grasped the dead young with its bill and carried it from the nest. The crow's visit lasted about three minutes.

While the parents were still gone, the crow returned to the nest at 09:22 and killed another nestling. A Steller's Jay (*Cyanocitta stelleri*) discovered the crow there and, with crest erect, approached to within 0.3 m of it while uttering the *shook* scolding call (Brown 1964). The Steller's Jay called approximately 90 s before the crow departed with the dead young. Both Pinyon Jay parents returned as the crow was leaving, mobbed it, and chased it out of sight. I heard Pinyon Jays scolding in the area for the next 41 min. Afterward, both parents returned to the nest where they fed and cleaned the remaining three nestlings. I heard scolding in the area for 10 min following this nest visit. The parents returned separately once more before I ceased watching at 12:00.

The parents' behavior changed in two ways after they discovered the predator. (1) Each remaining young was fed twice as long after the predator located the nest (before predation: $\bar{x} = 9.32$ s/h, $n = 3$ observation periods; after predation: $\bar{x} = 18.78$ s/h, $n = 3$ observation periods; $P = 0.13$, Mann-Whitney U test). This was due to the male feeding slightly more per visit after predation (median = 88.0 s, $n = 7$ visits) than before predation (median = 71.0 s, $n = 6$ visits; $P = 0.33$, Mann-Whitney U test), and to parents bringing food to the nest more often following predation (median = 1.33 visits/h, $n = 3$ observation periods) than before predation (median = 1.25 visits/h, $n = 3$ observation periods; $P = 0.04$, Mann-Whitney U test). (2) The parents remained in the nest area for long periods between visits to the nest. I define "nest area" as the area where I could vocally or visually locate the pair from the blind (a circle of approximately 200-m radius around the nest). Parents remained in the nest area for 11.5% of the observation period before predation, but for 84.0% of the period following predation ($P = 0.04$, Mann-Whitney U test).

Feeding appears to have increased in response to predation, not as a result of caring for fewer, or older young. In the study population, time spent feeding each nestling varied inversely with brood size ($r = -0.41$, $n = 29$ nests, $P = 0.014$). The observed feeding rate following predation ($\bar{x} = 177.92$ s/offspring/h), however, was above the upper limit of the 99% confidence interval around the mean feeding rate at other nests with three similar-aged young ($\bar{x} = 19.8 \pm 5.9$ s/offspring/h, $n = 7$ nests). At nests that naturally had three young, I never saw males feed their offspring as long per visit as at this nest ($\bar{x} = 14.52$ s/offspring, SD = 4.84 s, $n = 6$ nests), and I observed only one female to exceed the feeding duration of the female at this nest ($\bar{x} = 6.83$ s/offspring, SD = 3.31 s, $n = 5$ nests).

More attentiveness also was inconsistent with reduced brood size or ageing of the nestlings. Normally, attentiveness of smaller broods is greater than large broods ($r = -0.36$, $n = 32$ nests, $P = 0.02$); however, I never before observed parents remaining for long periods in the nesting area after leaving the nest. The observed percent attentiveness (84%) was not within the 99% confidence interval for attentiveness at nests with three young (0.0%–25.6%, $n = 8$ nests), or for attentiveness of the entire population (6.4%–24.8%, $n = 32$ nests). Attentiveness typically decreases as nestlings age from 15 days to fledging ($r = -0.46$, $n = 55$ days, $P = 0.000$).

The jays' increased attentiveness helped them to detect a crow (presumably the same individual) when it came the next day. The crow entered the nest tree at 11:06, and after 2 min it grabbed at one nestling, which gave one harsh squawk. Immediately thereafter, the parents gave *rack* and *racka* calls (Berger and Ligon 1977), in response to which the crow left the nest without removing any young. The parents followed the crow and continued to mob it for 5 min. The crow returned to the nest tree 12 min later, attempting to seize another nestling. Again I heard *racka* calls. Upon hearing the vocalizations of the young, the parents and two other Pinyon Jays, flew into the nest tree and violently mobbed the crow, occasionally

striking it on the back with feet and bills. The adults uttered begging-like *quays* (Balda and Bateman 1973), in addition to normal mobbing *racks* and *rackas*. The nestlings vocalized continuously. The parents forced the crow from the nest for 90 s. It then returned to the nest, grasped one young alive in its bill, flew to the ground 10 m from the nest, and killed it. During this time, the crow was unresponsive to continued mobbing and dive-bombing by the parents. It left the area at 11:30, 3.5 min after taking the young jay. The remaining two young departed the nest prematurely (age 17 days, instead of 21 days) during the intensive mobbing at the nest. Twenty minutes after the crow left the area, both parents returned, uttering soft *near* calls (Balda and Bateman 1971), to which the fledglings vocally responded with various squawks, whistles, and begging. The young were, in this manner, lead away from the nest.

The preceding observations bring out an adaptive aspect of mutual parent-young communication that was demonstrated in this population by McArthur (1982). The harsh squawk given by the young jays apparently functioned as a distress call that alerted parents, other Pinyon Jays, and even Steller's Jays to the presence of a predator at the nest. This resulted in mobbing which, at least temporarily, delayed predation. The harsh begging *quay* of the parents may have signaled the young to leave the nest, although it may also be a displacement behavior early in the nesting cycle (Balda and Bateman 1973). Normal mobbing by parents does not promote such behavior; instead, it causes the young to crouch and remain motionless and silent in the nest (Balda and Balda 1978).

Ensuing parental behaviors (mobbing and increased nest area attentiveness) increased parental fitness. The parents were able to quickly respond to the distress calls of their young, force the predator from the nest, and provide a means of escape for two of their remaining three young. It is significant that one of these young survived to become a breeder because, of 35 other fledglings produced in the study flock in 1983, only three became breeders.

My results suggest that memory is adaptive in predation events such as the one I report. Remembering the nest location, as well as its status (empty or not), would aid the predator in its return to a previously located, but not emptied, nest. Remembering that a predator, who is likely to return, located the nest would be adaptive for parents because changing their behavior may increase their fledging success.

LITERATURE CITED

BALDA, R. P., AND J. BALDA. 1978. The care of young Pinyon Jays and their integration into the flock. J. Ornithol. 119:146–171.

BALDA, R. P., AND G. C. BATEMAN. 1971. Flocking and annual cycle of the Pinyon Jay, *Gymnorhinus cyanocephalus*. Condor 73:287–302.

BALDA, R. P., AND G. C. BATEMAN. 1973. Unusual mobbing behavior by incubating Pinyon Jays. Condor 75:251–252.

BERGER, L. R., AND J. D. LIGON. 1977. Vocal communication and individual recognition in the Pinyon Jay. Anim. Behav. 25:567–584.

BROWN, J. L. 1964. The integration of agonistic behavior in the Steller's Jay *Cyanocitta stelleri* (Gmelin). Univ. Calif. Publ. Zool. 60:223–328.

CLARK, L., AND D. GABALDON. 1979. Nest desertion by the Pinyon Jay. Auk 96:796–798.

MARZLUFF, J. M. 1983. Factors influencing breeding success and behavior at the nest in Pinyon Jays. Unpubl. M.Sc. thesis, Northern Arizona Univ., Flagstaff, AZ.

McArthur, P. D. 1982. Mechanisms and development of parent-young vocal recognition in the Pinyon Jay (*Gymnorhinus cyanocephalus*). Anim. Behav. 30:62–74.

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SAGE THRASHERS REJECT COWBIRD EGGS

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Actual and potential hosts of brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) can be classified as either rejecters or accepters of cowbird eggs (Rothstein 1975, 1982a, b). Few North American species show intermediate responses (Rothstein 1982a). Rothstein (1982b) reasoned that once the rejection behavior appears in a species, it has such a high adaptive value that it is rapidly fixed. Whatever the cause, this dichotomy between accepters and rejecters makes it possible to determine the response of a given species by experimentally manipulating the contents of relatively few nests.

It is desirable to continue accumulating evidence on the responses to brood parasitism of untested species because no absolute criteria that explain why some species are rejecters and others accepters have yet been identified (Rothstein 1975). Although Rothstein (1975) failed to find a strong relationship between taxonomy and response to non-mimetic parasitic eggs, knowledge of the host response in all members of a family would be useful because many variables related to morphology, behavior, and evolutionary history would be somewhat controlled.

The Mimidae have several features that make the family a good group for study of response to brood parasitism. In particular, they have at least four of the six characteristics suggested by Rothstein (1975) as contributing to the formation of rejection behavior. Their eggs are unlike cowbird eggs, their beak is large, their nest is large and easily found, and they practice good nest sanitation (Bent 1948). Yet, three North American mimids accept eggs of the Brown-headed Cowbird: Northern Mockingbird (*Mimus polyglottos*; Rothstein 1975), Le Conte's Thrasher (*Toxostoma lecontei*), and California Thrasher (*T. redivivum*; Rothstein, pers. observ.). Among North American mimids, three species eject cowbird eggs from their nests: Gray Catbird (*Dumetella carolinensis*), Brown Thrasher (*T. rufum*; Rothstein 1975, 1982a), and Crissal Thrasher (*T. dorsale*; Finch 1982). A neotropical mimid, the Chalk-browed Mockingbird (*Mimus saturninus*), is also known to eject parasitic eggs (Mason 1980, Fraga 1982).

The Sage Thrasher (*Oreoscoptes montanus*) may have accepted a cowbird egg in the only known case of parasitism (Friedmann 1963), but most of the evidence suggests that this species may be a rejecter. Rich (1978) found no cowbird eggs in 21 Sage Thrasher nests in an area frequented by cowbirds, where at least two other sympatric species were parasitized. Also, Rich (pers. observ.) has examined about 40 other thrasher nests in Bingham and Blaine counties, Idaho, and found neither cowbird eggs nor nestlings. In Mono County, California, both cowbirds and Sage Thrashers are locally common and sometimes forage at the same horse corrals (Rothstein et al. 1980). Rothstein has seen a large number of fledgling cowbirds being fed by other passerine species, but has seen none associated with Sage Thrashers.

We experimentally parasitized Sage Thrashers to determine their responses to cowbird eggs. We wanted to determine whether few cases of parasitism are reported because Sage Thrashers are not parasitized or, in part at least, because they remove cowbird eggs before observers find them. The differing appearances of cowbird and Sage Thrasher eggs indicate that a bird could distinguish between them easily. Cowbird eggs are white with numerous small brown and gray spots, whereas Sage Thrasher eggs are blue-green with red-brown blotches.

We located Sage Thrasher nests in basin big sagebrush (*Artemisia tridentata tridentata*) habitat in Blaine County, Idaho, during April and May, 1984. Nest contents were manipulated between 08:00 and 14:00, with most manipulations being performed between 09:00 and 10:00. At each nest, we exchanged or added an artificial cowbird egg quickly and then left the area so as to minimize disturbance of adult thrashers. These eggs were made of plaster of Paris and measured 21.1 × 16.3 mm. They were identical to eggs in Rothstein's (1975) study and closely resembled real cowbird eggs found in southern Idaho (Rich, pers. observ.). Nests were checked between 1 h and several days after the manipulation to determine responses. Unless noted otherwise, all nests were subjected to only one experimental manipulation.

In ten nests, we removed a thrasher egg and replaced it with an artificial cowbird egg. Five of these nests were found during egg-laying, and five were found during incubation. Although most natural cowbird parasitism occurs during the host's egg-laying period, nest stage has little or no relation to response in most rejecter species (Rothstein 1976, 1977), a trend also indicated by our results. Nine of the 10 eggs were ejected. The tenth egg remained in the nest, which was deserted. The last nest was the only one where there had been only a single egg laid at the time of manipulation. At an eleventh nest, we added an artificial cowbird egg to a clutch of four eggs. This egg was also ejected along with two thrasher eggs, and the nest was subsequently deserted.

Cowbird eggs were usually ejected quickly, but not always immediately; artificial cowbird eggs were still present at one nest after 2 h and at another after 3 h. The earliest known ejections occurred within 1, 2, and 3 h, and two within 4 h, although in no case did we watch a bird remove an egg. Only one of 17 ejected eggs was found, and that was at a distance of 3 m from the nest. The egg bore no evidence of pecking, thereby matching previous findings that most species that eject eggs do so by holding eggs in their bills, rather than by spiking them (Rothstein 1975).

We performed nine additional experiments with two types of eggs intermediate between cowbird and Sage Thrasher eggs to get some indication of the factors that Sage Thrashers use to distinguish among egg types. Single, real, thrasher eggs that were painted to resemble cowbird eggs were ejected from four nests. These results suggest that the difference in size between thrasher (24.8 × 16.8 mm, Bent 1948, p. 429) and cowbird eggs (21.8 × 16.8 mm, Bent 1958, p. 451) is not a necessary releaser for rejection behavior.

Artificial eggs identical in size to the artificial cowbird eggs, but colored an immaculate blue (identical to egg type "S" in Rothstein 1982a), were accepted at two of five nests. Birds at three of these nests were incubating and had ejected artificial cowbird eggs 44 to 48 h before the blue egg