SIH, A. 1982. Foraging strategies and the avoidance of predation by an aquatic insect, *Notonecta hoffmani*. Ecology 63:786–796.

SNEDECOR, G. W., AND W. G. COCHRAN. 1967. Statistical methods. Iowa State Univ. Press, Ames, IA.

STEIN, R. A., AND J. J. MAGNUSON. 1976. Behavioral response of crayfish to a fish predator. Ecology 57: 751-761.

SULLIVAN, K. A. 1984. The advantages of social foraging in Downy Woodpeckers. Anim. Behav. 32: 16–22.

WAITE, T. A. 1986. Experimental studies of foraging and anti-predator behavior in some captive birds of a winter bark-foraging guild of temperate deciduous woodland. M.S.thesis, Ohio State Univ., Columbus, OH.

WERNER, E. E., J. F. GILLIAM, D. J. HALL, AND G. G. MITTELBACH. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology 64:1540–1548.

The Condor 89:940–943

COLONY DEPARTURE OF FAMILY GROUPS OF ANCIENT MURRELETS[1]

IAN L. JONES[2] AND J. BRUCE FALLS
Department of Zoology, University of Toronto, 25 Harbord St., Toronto, Ontario M5S 1A1, Canada

ANTHONY J. GASTON
Canadian Wildlife Service, Ottawa, Ontario K1A 0E7, Canada

Key words: Ancient Murrelet; Synthliboramphus antiquus; *coloniality; predation; behavior; Alcidae.*

The behavior of young seabirds at departure from the colony is critical for their survival and for the reproductive success of their parents. The young of several alcid species depart their nest site when partly grown and receive parental care on the sea later. Murres (*Uria* spp.) and the Razorbill (*Alca torda*) have semiprecocial young which are fed at the nesting ledge for 15 to 30 days (Gaston 1985), before leaving with the male parent (Scott 1973; Gaston and Nettleship 1981; S. Wanless and M. P. Harris, pers. comm.). The *Synthliboramphus* murrelets have precocial young which accompany their parents to sea a few days after hatching (DeWeese and Anderson 1976, Sealy 1976, Murray et al. 1983). Colony departure behavior of murre and Razorbill chicks has been described in detail (Tuck 1961, Greenwood 1964, Gaston and Nettleship 1981), but there is little information on the departure behavior of murrelets. In this note we describe the colony departure behavior of Ancient Murrelets (*S. antiquus*) at Reef Island, Queen Charlotte Islands, British Columbia. This island supports a colony of 5,000 pairs of Ancient Murrelets (Gaston, unpubl.).

METHODS

Fieldwork was carried out in May and June of 1984, 1985, and 1986. We monitored attendance of burrows by adults by placing small rectangular plastic strips in the entrances of 45 burrows. These were displaced as birds entered. We marked 16 adults in burrows with fluorescent paint on their flank or back to measure incubation shifts. We checked the burrows regularly by feeling for the presence of pipping eggs or chicks. Vocalizations of adults and chicks were recorded using a Marantz PMS-220 cassette recorder and miniature microphones (Realistic 33-1052 and 33-1056). We monitored departure behavior near the burrow by listening to the vocalizations and other sounds of family groups from a blind in a dense part of the colony. Using a dim flashlight, we made brief observations of about 20 family groups just as they emerged from their burrows. We observed departures from several burrows using a Star-tron MK-303A night vision scope, though this was generally of little use in the extremely dark conditions within the colony. Using the scope we made extensive observations of the behavior of departing family groups on the sea below the colony, where viewing conditions were better.

RESULTS

Adult Ancient Murrelets tended to enter their burrows more frequently towards the end of their incubation period. Chicks began calling from at least the time of the first cracks in the eggs, which appeared 4 to 11 days before hatching ($\bar{x} = 6.20 \pm 1.58$ SD days, $n = 20$). However, parents normally did not vocalize while alone in the burrow with chicks. Complex vocalizations were normally restricted to the period just following the return of the off-duty member of the pair. Parents entered burrows several times ($\bar{x} = 2.55 \pm 0.76$ times, $n = 31$) and brooding changeovers occurred ($\bar{x} = 0.89 \pm 0.60$ times, $n = 9$) during the 1 to 4 days ($\bar{x} = 2.19 \pm 0.70$

[1] Received 21 January 1987. Final acceptance 27 April 1987.

[2] Present address: Dept. of Biology, Queen's University, Kingston, Ontario K7L 3N6, Canada.

days, $n = 80$) between the hatching of the chicks and their departure.

Ancient Murrelets' most frequent vocalization, the *chirrup,* is short and individually distinctive (i.e., variability within individuals < variability between individuals, see Jones 1985; Jones et al. 1987). Adults in burrows normally gave continuous complex vocalizations. The first *chirrup* calls not combined in more complex calls occurred only a few hours before departure of the family group from their burrow. Usually only one parent was present in the burrow with the chicks by day, and the calling and subsequent departure followed the arrival of the second parent after dark. Four of 32 departures for which the number of parents present was known involved only one parent. The occurrence of departures peaked sharply about 3 hr after sunset (Fig. 1).

Departure was preceded by intense vocalization in the burrow, which lasted up to 21 min ($\bar{x} = 4.0 \pm 4.7$ min, $n = 19$). After a period of increasingly intense vocalizations involving more *chirrup* calls and fewer other calls, the parents emerged from the burrow, faced its entrance and called as the chicks emerged. Occasionally one parent followed the chicks out of the burrow. The parents shuffled downslope towards the sea, flew from the slope 1 to 10 min after emerging ($\bar{x} = 4.3 \pm 2.3$ min, $n = 33$) and called one to 95 times ($\bar{x} = 20 \pm 17$ times, $n = 34$) during this period. Some parents took flight within 1 m of the burrow; others accompanied their chicks for more than 40 m. Of 19 departures where the distance was known, eight (42%) involved accompaniment of less than 3.5 m, seven (37%) of between 3.5 and 9.5 m, and four (21%) of more than 9.5 m. Calls by parents provoked emphatic calls by the chicks, which followed closely until the parents took flight. The parents flew from the slope 0 to 3.5 min apart ($\bar{x} = 0.70 \pm 0.75$ min, $n = 9$). The chicks then made their way rapidly and silently to the sea. We made observations of departures from burrows located near the sea and up to 100 m above sea level, but in no case did the parents accompany the chicks all the way from the burrow to the sea.

During the peak of departures hundreds of adults frequented the sea surface 15 to 200 m from shore below the colony. The calls of these adults formed a chorus audible high up on the nesting slopes. After descending the nesting slopes virtually without vocalization, the chicks began intense calling after they entered the sea.

Adults on the sea exhibited three forms of behavior towards chicks: aggression, complete lack of attention, and attachment to chicks in a protective manner. We saw groups of up to six adults silently approaching solitary chicks and behaving aggressively towards them. These adults either dove and surfaced from directly beneath the chicks, sometimes colliding with them, or followed closely behind chicks and pecked at their backs. These encounters usually lasted only a few minutes and no chicks were observed to be injured.

Parents and chicks used vocalizations to locate one another on the water. Adults giving the *chirrup* call every 15 to 20 sec were observed swimming back and forth close to shore, avoiding some chicks and apparently reuniting with and leading others away. Marked birds were not observed, so relationships between adults and chicks were tentatively inferred from behavior. We observed seven events which we interpreted as reunions of single parents and their chicks, and four apparent reunions of more than one adult or one chick. In most cases, the adults and chicks initially vocalized and rapidly rushed towards one another. Afterwards, the chicks followed their presumed parents closely and responded to their calls. Family groups apparently maintain their cohesion by frequent vocalization, since both adult and young Ancient Murrelets can individually recognize and approach each other's calls (Jones et al. 1987).

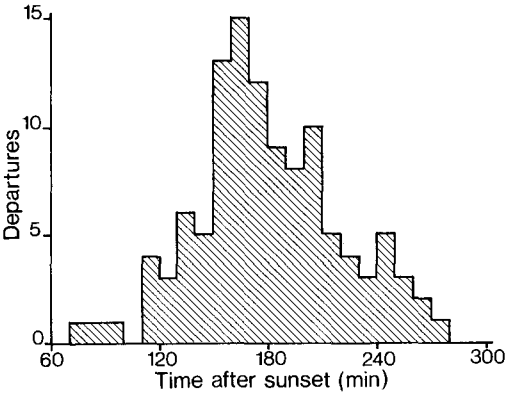

FIGURE 1. The timing of 110 family group departures from a 30 × 40 m study plot at Reef Island (1984 and 1985).

We observed 18 family groups at sea by day, all believed to have left the colony the previous night. Chicks remained within a few centimeters of their accompanying adults and responded to adult calls by calling and moving closer. Fifteen of the family groups were observed in the early morning (<4 hr after sunrise) 4 to 11.5 km from Reef Island and moving rapidly away from land. In 1984, three family groups were seen in mid-afternoon at a murrelet staging area near Reef Island.

Adults and chicks are vulnerable to predation during departure. Bald Eagles (*Haliaeetus leucocephalus*) were significant predators of adult murrelets at Reef Island, as they are at other colonies in the Queen Charlotte Islands (Vermeer et al. 1984). Numerous murrelet carcasses were found under roost trees, and eagles were active and apparently hunting on moonlit nights. Adults may be particularly vulnerable during departure because they remain on the surface longer and call repeatedly. Furthermore, the imperative departure of the chicks means the process must often occur on moonlit nights when activity at the colony is otherwise reduced, making the departing parents even more conspicuous. We observed predation of chicks by deer mice (*Peromyscus maniculatus*) on several occasions. Chicks left alone in two burrows were killed and partly eaten. Several chicks were killed by mice on the nesting slope while on the way to the sea after the flight of their parents.

We frequently observed and heard Northern Sawwhet Owls (*Aegolius acadicus*) on the nesting slopes

during the departure of family groups. Although no predation was actually observed, it seems likely that the owls prey on the departing chicks. Saw-whet Owls seemed to be attracted to the sounds of family groups about to depart from their burrows, and we found owl pellets containing down, probably from Ancient Murrelet chicks. On two occasions we saw chicks taken by large fish a few meters off shore. One chick was harassed by a harbor seal (*Phoca vitulina*), which tossed it into the air several times, but without apparent harm. We found the remains of two chicks, likely captured or scavenged after departure, in pellets of Glaucous-winged Gulls (*Larus glaucescens*) at a colony near Reef Island.

DISCUSSION

Our observations of the colony departure of Ancient Murrelets differ from previous reports in several respects. For example, Willett (1915) noted parents calling from the sea to lure their chicks from the burrow and Heath (1915) described parents leading their chicks downslope for hundreds of meters, both from observations made at Forrester Island, Alaska. Sealy (1976) stated that the chicks began coming down the nesting slopes 30 to 45 min before the nightly arrival of adults at Langara Island, British Columbia. We found that the parents invariably led their chicks from the burrow, usually for a short distance, before flying from the nesting slope. The first departures at Reef Island commenced shortly after the first arrivals at the colony at dark. It appears that the topography of the colony may influence the distance that parents accompany their young. There is considerable variability of this behavior between colonies: where the terrain is flat both parents normally accompany their chicks for considerable distances (M. Lemon, pers. comm.). The colony at Reef Island is situated on steep seaward facing slopes, so most chicks merely proceed downhill to reach the sea. Gaston et al. (in press) provided evidence that illumination from the direction of the sea, as well as slope, may provide orientation cues for the chicks. This may reduce the need for guidance for more than a few meters at Reef Island. The risk of predation presumably creates selection for the parents to leave their precocial chicks where and when they are able to successfully navigate to the sea. Xantus' Murrelets (*S. hypoleucus*), a species closely related to Ancient Murrelets, leave their precocial chicks after leading them downslope in open habitat for 2 m or less (Murray et al. 1983), an even shorter distance than observed for Ancient Murrelets. In either species a lengthy period of vocalization on the slope could attract predators, and thus would not be advantageous unless critical for the seaward orientation of chicks.

Departing family groups of Ancient Murrelets synchronize their activities using vocal signals. Chicks do not hear their parents' separate *chirrup* calls until the evening of departure. The call probably functions as a signal to the chicks that departure is about to occur, and as a similar coordinating signal between the parents. The system of mutual recognition by calls makes it possible for the family group to separate and then relocate one another later (Jones et al. 1987). Ancient Murrelets' departure in the first few hours of darkness, peaking about 50 min after the first arrivals at the colony, allows time for family groups to reunite and move well offshore before dawn.

In Ancient Murrelets and murres (Tuck 1961, Greenwood 1964) large numbers of adults congregate on the sea below their colonies at the time of chick departure. These assemblies produce a considerable volume of vocalizations. A somewhat similar phenomenon has been reported for the noncolonial Marbled Murrelet (*Brachyramphus marmoratus,* Sealy 1975). Ancient Murrelet chicks may use the sound of the adults as a cue for seaward orientation (Gaston et al., in press). Once chicks reach the sea, the chorus of calls and the number of birds present become a potential impediment to reunion with parents.

Both murre (Tuck 1961, Greenwood 1964, Gaston and Nettleship 1981) and Ancient Murrelet chicks are harassed in a strikingly similar fashion by unrelated adults before they join their parents. This hostile reaction emphasizes the advantage to chicks of being able to recognize and approach their own parents rapidly. Aggression towards unrelated young is common in colonial species, probably because of strong selection for parents to direct care only to their own young. The response of unrelated adults to unaccompanied chicks is clearly very strong in alcids with precocial or semiprecocial young, but its function is obscure because parents seeking chicks do not participate in the behavior.

We are grateful for help in the field from Laurence Turney, Chris Risley, Paul Jones, David Noble, and Steve Smith. Thanks to Moira Lemon, Mike Rodway, G. Vernon Byrd, and K. Greg Murray for their comments on the manuscript. Logistical support for this study was provided by the Canadian Wildlife Service. Financial assistance was provided by a grant from the Canadian Wildlife Service support fund (KN 107-5-4130) and by NSERC operating grant A0898 to J. B. Falls.

LITERATURE CITED

DeWeese, L. R., and D. W. Anderson. 1976. Distribution and breeding biology of Craveri's Murrelet. Trans. San Diego Soc. Nat. Hist. 18:155–168.

Gaston, A. J. 1985. Development of the young in the Atlantic Alcidae, p. 319–354. *In* T. R. Birkhead and D. N. Nettleship [eds.], The Atlantic Alcidae. Academic Press, New York.

Gaston, A. J., and D. N. Nettleship. 1981. The Thick-billed Murres of Prince Leopold Island—a study of the breeding ecology of a colonial high arctic seabird. Can. Wildl. Serv. Monogr. Ser. No. 6.

Gaston, A. J., I. L. Jones, D. G. Noble, and S. A. Smith. In press. Orientation of Ancient Murrelet chicks during their passage from the burrow to the sea. Anim. Behav.

Greenwood, J. 1964. The fledging of the Guillimot *Uria aalge* with notes on the Razorbill *Alca torda.* Ibis 106:469–481.

Heath, H. 1915. Birds observed on Forrester Island, Alaska during the summer of 1913. Condor 17: 20–41.

Jones, I. L. 1985. The structure and function of

vocalizations and related behavior of the Ancient Murrelet (*Synthliboramphus antiquus*). M.Sc.thesis. Univ. of Toronto, Canada.

JONES, I. L., J. B. FALLS, AND A. J. GASTON. 1987. Vocal recognition between parents and young of Ancient Murrelets (*Synthliboramphus antiquus*). Anim. Behav. 35:1405–1415.

MURRAY, K. G., K. WINNETT-MURRAY, Z. A. EPPLEY, G. L. HUNT, AND D. B. SCHWARTZ. 1983. Breeding biology of the Xantus' Murrelet. Condor 85: 12–21.

SCOTT, J. M. 1973. Resource allocation in four syntopic species of marine diving birds. Ph.D.diss., Univ. of Michigan, Ann Arbor.

SEALY, S. G. 1975. Aspects of the breeding biology of the Marbled Murrelet in British Columbia. Bird-Banding 46:141–154.

SEALY, S. G. 1976. Biology of nesting Ancient Murrelets. Condor 78:294–306.

TUCK, L. M. 1961. The murres: their distribution, populations and biology—a study of the genus *Uria*. The Queen's Printer, Ottawa.

VERMEER, K., S. G. SEALY, M. LEMON, AND M. RODWAY. 1984. Predation and potential environmental perturbances on Ancient Murrelets nesting in British Columbia. ICBP Tech. Publ. 2:757–770.

WILLETT, G. 1915. Summer birds of Forrester Island, Alaska. Auk 32:295–305.