vided field assistance. J. Maata contributed to experimental design. J. Savage and S. Whiting (Universities of Missouri and Minnesota Poultry Sci. Deps., respectively) supplied *Coturnix* eggs. This paper is a contribution of the Missouri Agricultural Experiment Station, Project 272, Journal Series 11,365.

## LITERATURE CITED

ANDERSSON, M., AND C. G. WIKLUND. 1978. Clumping versus spacing out: experiments on nest predation in Fieldfares (*Turdus pilarus*). Anim. Behav. 26:1207–1212.

BURGER, J. 1984. Grebes nesting in gull colonies: protective associations and early warning. Am. Nat. 123:327–337.

BURGER, J. 1987. Physical and social determinants of nest-site selection in Piping Plover in New Jersey. Condor 89:811–818.

ELLIOT, R. D. 1985. The exclusion of avian predators from aggregations of nesting Lapwings (*Vanellus vanellus*). Anim. Behav. 33:308–314.

HEISEY, D. M., AND T. K. FULLER. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. J. Wildl. Manage. 49:668–674.

GIBSON, F. 1971. The breeding biology of the American Avocet (*Recurvirostra americana*) in central Oregon. Condor 73:444–454.

GÖRANSSON, G., J. KARLSSON, S. G. NILSSON, AND S. ULFSTRAND. 1975. Predation in relation to antipredator aggression and nest density: an experimental study. Oikos 26:117–120.

GÖTMARK, F., AND M. ANDERSSON. 1984. Colonial breeding reduces nest predation in the Common Gull (*Larus canus*). Anim. Behav. 32:485–492.

HAMILTON, R. B. 1975. Comparative behavior of the American Avocet and the Black-necked Stilt (Recurvirostridae). Ornithol. Monogr. 17:1–98.

MARTIN, T. E. 1987. Artificial nest experiments: effects of nest appearance and type of predator. Condor 89:925–928.

MAYER, P. M. 1990. Conservation biology of Piping Plovers in the northern Great Plains. M.S.thesis, Univ. of Missouri, Columbia, MO.

MAYFIELD, H. 1961. Nesting success calculated from exposure. Wilson Bull. 73:255–261.

PAULSON, D. R., AND W. J. ERCKMANN. 1985. Buff-breasted sandpipers nesting in association with Black-bellied Plovers. Condor 87:429–430.

PRINDIVILLE GAINES, E., AND M. R. RYAN. 1988. Piping plover habitat use and reproductive success in North Dakota. J. Wildl. Manage. 52:266–273.

RODGERS, J. A., JR. 1987. On the antipredator advantages of coloniality: a word of caution. Wilson Bull. 99:269–271.

SORDAHL, T. A. 1981. Predator-mobbing behaviour in the shorebirds of North America. Wader Study Group Bull. 31:41–44.

SORDAHL, T. A. 1986. Evolutionary aspects of avian distraction display: variation in American Avocet and Black-necked Stilt antipredator behavior, p. 87–112. *In* R. W. Mitchell and N. S. Thompson [eds.], Deception: perspectives on human and nonhuman deceit. State Univ. of New York Press, Albany, NY.

U.S. FISH AND WILDLIFE SERVICE. 1985. Endangered and threatened wildlife and plants; determination of endangered and threatened status for the Piping Plover: final rule. Fed. Register 50:50726–50734.

WIKLUND, C. G. 1979. Increased breeding success for Merlins (*Falco columbarius*) nesting among colonies of Fieldfares (*Turdus pilarus*). Ibis 121:109–111.

WIKLUND, C. G., AND M. ANDERSSON. 1980. Nest predation selects for colonial breeding among Fieldfares (*Turdus pilarus*). Ibis 122:363–366.

*The Condor* 93:755–757


# OBSERVATIONS OF RAVENS PREYING ON ADULT KITTIWAKES[1]

JOHN KLICKA AND KEVIN WINKER
*Bell Museum of Natural History, 10 Church Street, SE, Minneapolis, MN 55455*

*Key words: Predator-prey interaction; Common Raven;* Corvus corax; *Black-legged Kittiwake;* Rissa tridactyla.

From 9 May–15 August 1990 we participated in ongoing U.S. Fish and Wildlife Service research at Cape Peirce (58°35′N, 161°45′W), Togiak National Wildlife Refuge, in the northern Bristol Bay region of southwestern Alaska. Within the area of heaviest seabird nesting densities at Cape Peirce (ca. 3 km of linear cliff face), four Common Raven (*Corvus corax*) pairs were known to be nesting and an additional nesting pair was suspected. Due to this high density of breeding ravens, walking along the cliff-top perimeter for any distance without observing ravens patrolling (Birkhead 1974) for seabird eggs was unusual. As a result, numerous opportunities were available to observe interactions between ravens and Black-legged Kittiwakes (*Rissa tridactyla*). Here we report individual Common Ravens exploiting adult Black-legged Kittiwakes as a food

[1] Received 10 October 1990. Final acceptance 7 February 1991.

source. We note that human disturbance was not a factor in these reported observations.

On 27 May (ca. 10:00 hr), a group of kittiwakes were gathering nest material (vegetation and mud) at the margin of a small brackish pond approximately 120 m from camp. The gathering of nest material had been in progress for much of the morning, and birds were constantly arriving and departing. The group's size remained at around 200 individuals. Suddenly, the group flew up, circling and calling loudly. Perhaps one minute later, a Common Raven lifted off from where the kittiwakes had been, carrying in its bill what appeared to be a kittiwake without its head. It carried the body in the direction of the nearest cliff nest. About 10 min later it returned and picked up a kittiwake head, recognizable as such in binoculars. Upon examining the area where the raven had lifted off, only a few neck feathers and a little blood were found. No other ravens were seen in the area during this observation. The disturbed kittiwakes did not harass the raven, but continued circling and calling until settling down and resuming the gathering of nest material at a different location nearby. No carcass was seen in the area during observation before the outcry; head removal with the presence of fresh blood suggests that the kittiwake was killed by the raven. The body of a kittiwake was found on the nearest cliff nest (ca. 250–300 m from the kill site) when we looked an hour later.

On 19 June, JK was at an observation point used for daily monitoring of nests of kittiwakes, Common Murres (*Uria aalge*), and Pelagic Cormorants (*Phalacrocorax pelagicus*) in a colony that was located approximately 100 m distant, across a small bay. At this date, an estimated 60–70% of kittiwake nests still contained eggs; no chicks had yet been hatched. During a 2-hr period around mid-day, a local raven pair was on patrol in this colony. Although visual contact was not continually maintained, the clamor of alarm calls from nesting kittiwakes was a constant indicator of each raven's position. The raven's nest, containing three large chicks (age approximately 25–30 days), was located on a rock shelf 20 m above a steep grassy slope roughly 40 m above the sea. At 13:00 hr the kittiwakes made an outcry nearby, and an adult raven was seen making repeated passes over a ledge of nesting kittiwakes. The ledge, on the northern periphery of the colony, was only about 10 m above and located diagonally to the raven nest. The raven was apparently trying with little success to dislodge the cornermost group of approximately five incubating gulls from their nests. The uppermost gull held its ground through several aerial attacks, rearing back slightly in a defensive posture while keeping the eggs covered. No blows (bill thrusts) were exchanged although the kittiwake was clearly in a position to do so. The raven, apparently intensifying and focusing its attack, then perched on the cliff face less than a half meter above this kittiwake nest, and the two birds briefly exchanged "bill thrusts." At this point the raven seized the gull in the head region, whipped it out of the nest in a wide arc, and drove it to the grassy slope below. After a brief tussle on the ground the raven subdued the kittiwake by straddling its breast and pinning the wings by placing a foot on each wrist. The raven then proceeded to pluck the still living gull, beginning on the neck and breast. Much of the kittiwake was eaten immediately. After about 20 min, smaller portions of the gull, including the head, were delivered in the bill to the nestlings above. At no time during or after the attack was any mobbing behavior displayed by other kittiwakes towards the raven.

The nest site tenacity displayed by this kittiwake seemed unusual, as the majority of kittiwakes observed abandoned their nests when closely approached by ravens. However, Petersen and Sigman (1977) documented ineffective nest defense by kittiwakes, noting that kittiwakes were sometimes tossed off the nest by individual ravens, with subsequent loss of eggs or young. Haggblom and Mendenhall (1990) noted one case of an incubating kittiwake successfully fending off an attacking raven. This was accomplished by "lunges" at the raven from the incubating position. Kittiwakes respond to raven attacks on the nest by either defense or abandonment. Given the very real threat of death by choosing to defend the nest, nest abandonment upon attack may be the best choice among experienced gulls.

Although we have only two observations suggesting that solitary ravens take adult kittiwakes as prey items, circumstantial evidence suggests it may be a fairly frequent event. On numerous occasions we observed adult ravens flying low near the cliff tops with only the detached head of a kittiwake in their bill, carried much the way an egg would be. The fresh appearance of the heads (clean, white, fresh red blood) suggests that they were from recently killed birds rather than scavenged from washed up carcasses. Given the likely risks involved in subduing an adult kittiwake, this behavior seems unusual in that eggs and chicks from a number of seabird species seemed plentiful at this time.

Montevecchi (1979) reported active defense of nesting areas by kittiwakes, with chases and even physical attacks on ravens. Our observations of nesting kittiwakes at Cape Peirce indicate more passive behavior. The antipredator behavior we witnessed, although less passive than that described by Cullen (1957), was less aggressive than the physical attacks described by Montevecchi (1979) or the "post-attack" circling and dive-bombing observed by Parmelee and Parmelee (1988). The aggressive responses we did observe usually occurred after a nest had been depredated, and generally consisted of a feeble chase by the nest "owner" and perhaps a few neighbors as the raven flew off with egg in bill. Such chases were usually only a few seconds in duration and in no case was physical contact observed.

Ravens regularly prey on kittiwake chicks and eggs (Petersen and Sigman 1976; Montevecchi 1979, Haggblom and Mendenhall 1990, pers. obs.). The observations reported here, together with those of Parmelee and Parmelee (1988) involving the effective use of coordinated hunting tactics by a pair of ravens at nearby Chagvan Bay, suggest that in southwestern Alaska adult kittiwakes may be a regular component of the raven's summer diet.

We thank Mike Hinkes and Dave Fisher of the U.S. Fish and Wildlife Service, Togiak NWR, for allowing us the opportunity to conduct fieldwork at Cape Peirce and for providing logistic support. The Dayton Natural

History Fund of the Bell Museum assisted with travel expenses. We thank David Parmelee for his advice and encouragement.

LITERATURE CITED

BIRKHEAD, T. R. 1974. Utilization of guillemot (*Uria aalge*) colonies by jackdaws (*Corvus monedula*). Ornis Scand. 5:71–81.

CULLEN, E. 1957. Adaptations in the kittiwake to cliff-nesting. Ibis 99:275–302.

HAGGBLOM, L., AND V. M. MENDENHALL. 1990. Chapter 5: Cape Peirce. *In* V. M. Mendenhall [ed.], Monitoring of populations and productivity of seabirds at St. George Island, Cape Peirce, and Bluff, Alaska. Unpubl. rep., U.S. Fish and Wildlife Serv., Togiak Natl. Wildl. Refuge, Dillingham, AK.

MONTEVECCHI, W. A. 1979. Predator-prey interactions between ravens and kittiwakes. Z. Tierpsychol. 49:136–141.

PARMELEE, D. F., AND J. M. PARMELEE. 1988. Ravens observed killing roosting kittiwakes. Condor 90: 952.

PETERSEN M. R., AND M. J. SIGMAN. 1977. Field studies at Cape Perice, Alaska—1976, p. 633–693. *In* Environmental assessment of the Alaskan continental shelf, Annual reports of principal investigators, Vol. 4. NOAA, Environ. Res. Lab., Boulder, CO.

*The Condor* 93:757–759


# THE ROLE OF EGG-CAPPING IN THE EVOLUTION OF EGGSHELL REMOVAL[1]

KIM C. DERRICKSON AND IAN G. WARKENTIN[2]
*Department of Zoological Research, National Zoological Park, Smithsonian Institution, Washington, D.C. 20008*

*Key words: Behavior; eggs; nest; egg-capping; eggshell removal.*

The adaptive value of removing eggshells from the nest after hatching has been interpreted as an antipredator function, based solely on the classic experiments of Tinbergen and his colleagues on Black-headed Gulls (*Larus ridibudundus*; Tinbergen et al. 1963, Tinbergen 1963). Although Tinbergen et al. briefly mentioned several other potential costs that may have favored eggshell-handling behaviors, these costs have been ignored. While predation may explain eggshell-removing behavior in species whose nests are relatively exposed, it is more difficult to accept predation as an explanation in species with well-concealed nests, especially cavity nests. For these species, the other adaptive reasons may be valid and should be reconsidered. Here, we present evidence implicating one of the other potential costs, "egg-capping." Egg-capping occurs when the empty eggshell from a recently hatched egg slips over an unhatched egg, thereby preventing the "capped" egg from hatching, either by mechanically interfering with pipping or with gas transport across the eggshell. That egg-capping was found to occur, even at a low frequency, despite the existence of eggshell-handling behaviors, strongly implicates egg-capping as a selective force favoring the evolution of eggshell-handling behaviors. We briefly describe instances of egg-capping in six species: Gadwall (*Anas strepera*), Merlin (*Falco columbarius*), Purple Martin (*Progne subis*), Tree Swallow (*Tachycineta bicolor*), Clay-colored Robin (*Turdus grayi*), and Northern Mockingbird (*Mimus polyglottos*). We speculate on the absence of other such observations from the literature and further discuss the significance of these observations in relation to the evolution of eggshell handling.

Egg-capping was observed in one Northern Mockingbird nest during studies conducted from 1979–1990. In this nest, the halves from the first egg that hatched each slid over respective parts of the two other eggs in the nest. Although cracks were evident on these two eggs, egg-capping was missed during a quick inspection of the nest. That egg-capping had occurred became apparent when, during a subsequent nest check, the background color of the eggs was noted to change abruptly at the cracks and, furthermore, egg dimensions were noted to be larger than measurements taken shortly after laying. One egg, initially measured 25.2 × 17.4 mm, was now 26.6 × 17.6 mm, and the other egg, initially 25.9 × 17.8 mm, was now 27.8 × 17.9 mm. Neither of the capped eggs hatched. The egg that hatched was the first egg laid and did not differ in dimension or mass from the other eggs.

A total of 144 nests have been examined in the mid-Atlantic region of the United States. Of these nests, 129 eventually contained eggs and 79 reached the nestling stage. Thus, egg-capping occurred in 0.8% of the nests with eggs and 1.3% of the nests in which it potentially could have been observed. Northern Mockingbirds are multi-brooded, potentially producing 2–

[1] Received 16 October 1990. Final acceptance 11 April 1991.

[2] Order of authorship was randomly determined.