The Condor 99:345–352
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FACTORS AFFECTING THE SUCCESS OF COLONY DEPARTURE BY THICK-BILLED MURRE CHICKS[1]

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Abstract. Young Thick-billed Murres leave their natal colony while still incapable of flight, jumping directly to the sea. The brief period of transition from cliff ledge to open ocean results in significant mortality. At Coats Island, Northwest Territories, Canada, we investigated the effects of predation by gulls, murre nest site characteristics, and adult murre aggression on the likelihood that chicks departed to sea. Approximately 20% of chicks that jumped from the cliff failed to depart successfully to sea. Live chicks were rarely taken by predators. Most mortality was caused by drowning, as a result of aggression by adult murres. However, chicks accompanied by defending parents usually were unaffected by aggression from other adult murres. As a result, the most important cause of chick mortality at colony departure was the separation of chick and parent before reaching the sea. Chicks landed alone because either they or their parent were knocked from the nest ledge during fights with neighbors as they moved to the jump site, or because chicks struck cliff ledges during the descent to the water. Apparently, the nearer the nest site was to the edge of the ledge, and the fewer obstructions below the jump site, the greater the departure success of chicks. Site characteristics that determine success during departure may differ from those associated with success in incubation and chick-rearing. Hence the effect of breeding site on reproduction may be incorrectly assessed if departure success is not taken into account.

Key words: *Thick-billed Murre, colony departure, nest site,* Uria lomvia.

INTRODUCTION

The young of several species of auks leave the breeding colony while only partially grown and incapable of flight (for review see Sealy 1973, Ydenberg 1989). The transition from the breeding site to the sea is typically a hazardous event, exposing the chick to a brief window of vulnerability between the safety of the breeding site and the sea. Most investigations of seabird reproductive success have emphasized events during the incubation and chick rearing periods, with little emphasis on the survival of chicks during colony departure (Harris and Birkhead 1985). However, Spear and Nur (1994) have recently emphasized that reproductive success measured up to colony departure may not give a good measure of subsequent recruitment.

Among murres (*Uria* spp.), chicks depart from the colony at 15–25 days old and at 12–27% of adult body mass. In many studies, survival to a minimum age of 15 days has been taken as equivalent to colony departure and reproductive success has been assessed on that basis (Birkhead 1977, Birkhead et al. 1985, Hatchwell 1991). As a result, conclusions regarding the influence of nest site characteristics, food resources, and the age and experience of breeding pairs on offspring survival often have been based on survival during incubation and chick rearing only, without reference to survival during the actual departure. This has been the case despite the fact that some studies have found that 15–20% of chicks surviving to age of departure failed to depart successfully to sea (Tuck 1960, Greenwood 1964, Williams 1975).

Mortality at departure may have important selective consequences for murre reproduction. Moreover, those characteristics of nest sites that are associated with a high survival rate of eggs and chicks to age at departure are not necessarily those that are associated with success during the actual departure process. In this paper, we present information on the mortality of Thick-billed

[1] Received 1 December 1995. Accepted 16 November 1996.

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Murre, *Uria lomvia,* chicks during colony departure and the effect that such mortality may have on reproductive success in relation to breeding site characteristics.

Our study was designed to determine the proportion of chicks that departed successfully to sea, and to identify factors contributing to their mortality, both on the sea and on the cliff. We investigated the effects of four factors: (1) Glaucous Gull predation, (2) nest site characteristics, (3) aggression by adult murres, and (4) parent and chick behavior. Because we were able to watch detailed behavior on the cliff prior to departure, as well as events taking place after the chicks had jumped, our results provide the most detailed analysis to date of causes of mortality during murre chick departure.

METHODS

The study was conducted on Coats Island, Northwest Territories, Canada (62° 30′N, 83° 00′W) during 1990, 1991, and 1993. Murres nested on exposed cliff ledges from just above the reach of highest waves to 80 m. The colony consisted of approximately 33,000 pairs of Thick-billed Murres and 15 pairs of Glaucous Gulls (Gaston et al. 1993).

THE CHICK DEPARTURE PROCESS

Thick-billed Murres breed in dense colonies on exposed cliff ledges. They make no nest and incubate their single egg on bare rock. Chick departure activity at colonies peaks in the late evening, and this timing is thought to have evolved in response to terrestrial and avian predators. Synchronous departures may dilute the impact of predators by swamping their ability to respond to sudden food availability (Kay 1947, Greenwood 1964, Daan and Tinbergen 1979), and the low light conditions in the late evening may make it difficult for sight-hunting predators to locate departing chicks (Tuck 1960).

Not all sites allow the chick a clear jump to the sea. Consequently, the chick may have to walk some distance before reaching an adequate launching site: in this journey the chick is accompanied, but not led, by its male parent. Upon reaching the edge, the chick may hesitate for several minutes before jumping. Prior to jumping, the chick and its parent interact on the nest site by head bowing and vocalizing (Gaston and Nettleship 1981). When the chick finally leaps from the ledge it is followed closely to the water by the accompanying parent (Pennycuick 1956, Gaston and Nettleship 1981).

Chicks are unable to fly at colony departure, but they flap vigorously and their primary covert feathers enable them to glide to the sea. Typically, the chick and parent land almost simultaneously and within a few meters of one another. After landing on the sea, the chick calls loudly and the adult rushes towards it and greets it with a growl. They touch bills and frequently circle one another before starting to swim away from the colony, the parent leading and the chick swimming at its side. Only the male parent departs to sea with the chick (Bradstreet 1979), behavior also found in the Razorbill *Alca torda* and Common Murre *Uria aalge* (Harris and Birkhead 1985). Female Thick-billed Murres return to the nest site intermittently for several days following the departure of the chick (Gaston and Nettleship 1981). However, even if the chick fails to depart successfully, the male rarely returns to the nest site (Gaston, unpubl. data).

At murre colonies where chicks must cross beaches or rock slopes to reach the sea, much of the fledging failure is caused by gull and fox predation while chicks are on land (Williams 1975, Hatch 1983). However, at colonies where chicks jump directly into the sea, the causes of chick failure have not been identified, despite detailed descriptions of the fledging process (Pennycuik 1956, Greenwood 1964).

DATA COLLECTION

We observed chick departures from cliff vantage points approximately 40 m above the sea. Chick departures peaked between 19:00 and 22:00 at Coats Island and we concentrated our observation effort during this period. Similar departure peaks have been well documented at other colonies (Cullen 1954, Daan and Tinbergen 1979, Gaston and Nettleship 1981). Observers watched for chicks launching themselves from the cliff and monitored their departure for the subsequent 5 min after landing, using 8× binoculars. Preliminary observations in 1990 indicated that the fate of 87% of chicks (n = 15) could be determined within the first 5 min after landing and that chick survival on the water was determined largely by whether the chick and the parent reunited on the sea immediately after landing. Chicks typically landed with a defending adult that we assumed to be the parent. Because we did not always see the chick depart

directly from the nest site, we cannot be certain that this was always the case. However, more detailed observations carried out on the cliff face in 1993 confirmed that 96% of defending adults (n = 87) that landed with chicks were indeed the parents that had been brooding the chick.

Observers watched chicks descending to the sea and recorded whether the chick landed: alone, with a defending adult, with a defending adult and other birds, or apart from the defending adult (i.e., > 3 m between birds). As each chick swam out to sea, we estimated the number of adult murres present within a 5 m radius surrounding it. These adults were attracted to calling chicks and quickly formed aggregations paying evident attention to them. We termed these aggregations "mobs." We also recorded whether chicks swam either in circles, towards the cliff, or out to sea. As defending adults departed with the chick, we recorded whether the parent: made no attempt to defend the chick, rushed mobbers but made no contact (mild defense), or rushed mobbers and made contact (aggressive defense). Finally, we recorded whether the chick successfully departed to sea, was taken by a gull, or was attacked and drowned by mobs.

In 1993, we observed the events leading up to departure on nesting ledges, but did not follow what happened on the water, except to observe whether or not chicks united with their parents. In some cases we used two observers at the same site so that the actions on the cliff and the water could be adequately observed. Thus, information from 1993 was not directly comparable with that obtained in previous years, but was complementary, because in most cases we saw the actions leading up to departure and knew with precision whether the parent (i.e., the bird that had been brooding the chick) departed with the chick and whether they united on the water. In addition, several adults and chicks were banded and marked with blue ink on the breast so that we could be sure of their actions in the event that the departure went wrong. Some parents were of known gender. On the nest ledge itself, we recorded if the chick and/or adult were knocked off the ledge prematurely by other birds. During the jump, we recorded whether the chick struck cliff ledges during its descent to the sea and if the parent was able to accompany the chick to the water. Finally, we recorded whether the chick and parent reunited on the water.

Chicks rarely jumped alone while one or both parents remained on the nest site. In these cases, we recorded whether the chick on the water was claimed by other adults, and simultaneously observed the behavior of the parents on the nest site.

STATISTICAL ANALYSIS

We used stepwise logistic regression to examine the factors influencing the success or failure of departing chicks. Logistic regression is useful in a wide variety of applications in which the assumption of multivariate normality is not satisfied and the logistic model equation is justified (e.g., when the dependent variable is binary). We entered independent variables into our logistic model in a stepwise manner using BMDP Statistical Software. Selection of variables was based on maximum likelihood ratios. At each step, the change in the log-likelihood (loss function) resulting from the addition of an independent variable was evaluated using the goodness-of-fit chi-square statistic. If there was a significant improvement in the model, the variable was included. Probability values are presented for each variable at the step at which they were added to the model.

We carried out two logistic regression analyses. The first tested for factors influencing the survival of all departing chicks. Independent variables included: year, date, time at departure between 18:00 and 22:00 hours, the presence or absence of a defending adult during departure, and the size of mobs attacking chicks. In the second regression analysis, we only included those chicks that had landed with presumed parents (n = 239). We made this distinction to examine the influence of parental behavior on chick departure. Independent variables included: the time of departure between 18:00 and 22:00, the distance between defending adult and chick upon landing, the number of adult birds accompanying the defending adult and chick from the cliff, the intensity of adult defense on the water, and the number of murres attacking in mobs on the sea.

We used chi-square goodness-of-fit tests to examine differences in fledging success between years, in the behavior of chicks on the sea in relation to how they landed, and in the success of chicks in relation to the interactions of murres on the nesting ledge prior to the departure.

TABLE 1. Outcome of Thick-billed Murre chicks departing from Coats Island colony based on chicks landing at sea.

Year	n	Proportions		
		Reunification and departure to sea	Taken by gull	Mobbed and drowned
1990	114	76.3	2.6	21.1
1991	178	86.5	0.0	12.9
1993[1]	99	79.7	—	—

[1] Success in 1993 refers to chicks that reunited with their parent. Chicks were not monitored subsequent to landing.

TABLE 2. Factors affecting whether murre chicks successfully depart to sea. Data for 1990–1991.

Variable[a]	χ^2	P
Year	0.08	0.78
Date	0.05	0.82
Time[b]	0.25	0.61
Adult present	134.53	<0.01
Mob size	5.28	0.02

[a] Stepwise logistical regression analysis.
[b] Within our evening observation period.

RESULTS

OBSERVATIONS ON THE WATER

Approximately 20.2% of the 391 departing Thick-billed Murre chicks that we observed failed to depart successfully to sea (Table 1). There was no significant difference in success among years ($\chi^2_2 = 5.86$). In all years of this study, we observed two distinct behavior patterns towards chicks among adults present on the sea. The first consisted of birds that approached unaccompanied chicks without aggression and attempted to lead them to sea. The second and more common behavior consisted of individuals that circulated in groups and attacked unaccompanied chicks and departing pairs. Most of the chicks that died drowned because of adult aggression. Chicks were repeatedly struck on the back or head, and pulled under water. Few live chicks were taken by gulls (Table 1). Patrolling gulls sometimes descended on mobs of adults in an attempt to take chicks, but they were rarely successful (3 of 13; 23%) because of the aggressive defense of mob members.

Analyses of data from 1990 and 1991 indicated that neither year, date, nor time at departure (within our observation period) had a significant influence on departure success (Table 2). The most important factor influencing success was whether or not the chick landed alone (i.e., no immediate reunion with parent). Only 21% of chicks that landed alone (1990 and 1991 combined, $n = 53$) were eventually joined by a defending adult and departed to sea (Table 3). There was no significant difference in failure rates of chicks that landed with a presumed parent, with a parent and other adults, or apart from the presumed parent (Table 3; $\chi^2_2 = 1.24$).

For chicks that landed with a parent, only the intensity of parental defense and the size of mobs influenced chick departure (Table 4). If the adult defended the chick, others appeared to lose interest and moved off. Despite this observation, mob size still had an effect on the departure success of accompanied chicks (Table 4). Interference and aggression by large mobs (> 10 birds) on the water increased the likelihood of a chick and adult getting separated during departure. In one example, an apparent parent (it had greeted the chick and they had touched bills) rushed a large mob but became separated from the chick and never reunited with it.

The behavior of unaccompanied chicks differed from that of chicks departing with an adult ($\chi^2_2 = 212.2$, $P < 0.001$). Chicks that landed alone swam in circles or towards the cliff calling loudly (98%, $n = 44$). The continuous calling of

TABLE 3. Proportions of Thick-billed Murre chicks successfully departing to sea with an adult.

Jump outcome	Year	Reunification and departure (%)	n
Lands with defending adult	1990	93.8	65
	1991	96.9	98
Lands with defending adult and others	1990	100.0	14
	1991	100.0	36
Lands apart from defending adult	1990	90.9	11
	1991	93.3	15
Chick lands alone	1990	12.5	24
	1991	27.6	29

TABLE 4. Factors affecting the likelihood that murre chicks successfully departed to sea.

Variable[a]	χ^2	df	P
Time	0.26	1	0.61
Parent distance at landing	0.00	1	0.98
Number of adults at landing	2.66	1	0.10
Parental defense intensity	6.70	2	0.04
Mob size	7.83	1	0.01

[a] Stepwise logistical regression analysis.

unaccompanied chicks attracted swarms of adults on the water and appeared to intensify their aggression. In contrast, chicks that were accompanied by a defending adult were led directly out to sea and rarely called after the initial reunion (97%, n = 232).

INTERACTIONS ON THE CLIFF

Several factors determined whether the chick landed alone (Table 5). Fights often occurred on nesting ledges as departing pairs moved through the nest sites of other birds; as a consequence, six chicks were knocked off the cliff prematurely by fighting adults. After fights had ended, parents recognized the absence of their chicks and descended immediately to the sea, but reunion occurred in only one case (n = 12, Table 5). Parents also were knocked off ledges prematurely during fights. They returned to the nest site within a few minutes, but in two of three cases, the parent returned to an empty site because the chick had jumped in its absence; no reunion was seen (Table 5).

Chicks that struck lower ledges as they descended (n = 8) were never killed on impact and although dazed, all jumped again within a few minutes. However, they became separated from their parent, because the parents continued directly to the water. In most cases, these chicks and their parents failed to reunite on the sea (Table 5). Some chicks became trapped among breeding birds after landing on lower ledges, further delaying their second jump. Such delays may have contributed to the inability of parents and chicks to reunite on the water.

Several chicks jumped alone from the nest ledge despite the presence of an adult and the absence of interference from other birds. Some of these chicks may have landed previously from higher ledges, and we were witnessing the second jump to the sea. In most situations however (10 of 12 cases), our observations showed clearly that the chick initiated the departure and the parent remained on the site. Two of these chicks (17%) were later claimed on the sea by adult murres while the known parent remained on the nest site.

DISCUSSION

PREVIOUS OBSERVATIONS OF MURRE CHICK DEPARTURES

Some studies have concluded that parents leave the cliff prior to the departure of the chicks and that mobs of adult murres present on the sea below the colony consist of parents that are awaiting the descent of their chicks (Perry 1940, Tuck 1960, Daan and Tinbergen 1979). Our observations, and those of Gaston and Nettleship (1981), show that at colonies in Arctic Canada, Thick-billed Murre parents rarely precede their chicks to the water. Where the cliffs are high, it would be difficult for a parent to predict where its chick might land. Consequently, it seems likely that most Thick-billed Murre parents accompany their chick from the ledge.

CAUSES OF DEPARTURE FAILURE

Approximately 20% of Thick-billed Murre chicks that fledged at Coats Island failed to depart successfully from the colony. As they did not have to cross scree slopes or beaches to reach the sea, they did not experience high levels of predation during their departure. Glaucous Gulls did attack live chicks on the water but attempts were rarely successful due to the aggres-

TABLE 5. The percent of murre chicks in 1993 that reunited with their parent on the sea relative to interactions on the nesting ledge. n = total number of observations in each category.

	% reunited	n
Chick and parent jump together, did not strike cliff	97.5	81
Chick and parent jump together, chick struck cliff	12.5	8
Chick knocked off ledge prematurely	16.7	6
Parent knocked off ledge prematurely	33.3	3
Chick jumped alone	16.7	12

sive defense of adult murres. Instead, gulls scavenged chicks that were already dead and floating on the sea.

Most mortality was caused by the drowning of chicks as a result of aggression by adult murres. During departure evenings at Coats Island, large rafts of adult murres congregated on the sea below the colony. Similar groups of adults have been observed at other colonies (Pennycuick 1956, Tschanz 1959, Greenwood 1964, Daan and Tinbergen 1979). At Coats Island, some of these adults approached chicks without aggression and attempted to lead them to sea. These birds may have been parents searching for chicks from which they had become separated. However, most chicks refused to accompany the soliciting adults, suggesting that chicks could recognize their parents. In these circumstances, chicks did not carry out typical interactions with the adult (e.g., touching bills), and continued to swim in circles instead. In rare instances, soliciting adults bonded with unattended chicks and led them to sea. These instances involved unusual persistence on the part of the adult, because chicks repeatedly swam away from them. Fisher and Lockley (1954) witnessed similar behaviors and emphasized that unaccompanied murre chicks occasionally departed with, "the adult which most persistently answered its calls." These observations suggest that some unaccompanied murre chicks may be adopted on the water during departure. Adoptions prior to departure have been documented among Thick-billed Murres in situations where chicks have fallen from nest sites to lower ledges (Gaston, unpubl. data.). Hence, the possibility of adoption on the water cannot be discounted.

Our observations suggested that only a small proportion of birds on the sea were parents searching for chicks. The more common behavior consisted of adults who attacked unaccompanied chicks and departing pairs. This aggression by adult murres on the water was the most important cause of chick mortality at departure. Aggression by conspecific adults towards departing chicks also has been observed among Common Murres (Greenwood 1964). Greenwood suggested that the response of parents and chicks towards aggressive adults influenced their departure success. Such aggression also occurs in Northern Gannets (*Morus bassanus,* Nelson 1967) and Ancient Murrelets (*Synthliboramphus antiquus,* Jones et al. 1987, Gaston 1992), however the role of aggressive conspecifics in determining the outcome of chick departures among these species is unknown. At Coats Island, the size of mobs affected the likelihood of a chick departure going wrong. Parental defense against attacking adults increased departure success, because aggressive mobs lost interest in well-defended chicks. Most adult aggression was directed towards unattended chicks and as a result, chicks that landed alone rarely succeeded in departing to sea.

Although the proximal cause of observed mortality was often aggression from mobs, the fate of most chicks was actually determined by interactions on the cliff during departure which determined whether they were accompanied to sea by a parent.

WHY DID MURRE CHICKS LAND ALONE?

To reach the edge of the ledge and achieve a clear jump to the sea, chicks from certain sites must move, with their parent, past the nest sites of other birds. Fights between adults often occurred in response to this trespassing, and both chicks and parents were sometimes knocked from ledges prematurely during these interactions. Fights were most common on broad, densely occupied ledges. In contrast, sites on narrow ledges allowed chicks to jump directly to the sea without harassment by neighbors. In addition, a chick hesitating at the edge of a broad ledge supporting many breeding sites was vulnerable to being struck by adults landing on or departing the ledge. We conclude, as did Greenwood (1964) for the Common Murre, that nest sites in the interior of dense ledges are a disadvantage during chick departure.

The suitability of a nest site also may depend upon the absence of obstructions in the descent path of the chick. Of those chicks that failed to depart, 26% struck ledges during their descent. Although no chicks were killed outright, most eventually landed alone on the sea and were mobbed. Based upon these findings, we expected chicks to assess obstacles below the departure site before jumping and this appeared to be the case. On ledges with obvious obstructions below, we observed chicks descend to lower ledges and more rarely, up to higher rock outcrops. This behavior was clearly differentiated from their "launching" leap, as chicks scrambled cautiously during this time. Moving to a better jump site

increased the probability of fights occurring between adults and increased the likelihood that the parent and chick would become separated on the cliff. Hence, chicks leaving sites without a direct jump to the sea likely have a lower chance of successful departure.

Most studies that have examined the influence of nest site characteristics on murre reproductive success have concentrated on the egg laying and chick brooding periods. Murres nesting on broad ledges in the center of dense groups are most successful in raising chicks to the age of departure (Birkhead and Nettleship 1984, Hatchwell 1991, deForest 1993), in part because interior nest sites experience less gull predation and accidental dislodgment of eggs (Birkhead 1977, Spear 1993, Gilchrist and Gaston, in press). However, our results suggest that nest sites in the interior of dense ledges are at a disadvantage during chick departure. Thus, the optimal nest site may be a trade-off between the benefits of dense nesting and the proximity to the edge of the ledge at chick departure. Hence, the relative quality of breeding sites cannot be assessed solely on the basis of the proportion of chicks reared to the age of departure.

In some cases, chicks jumped alone from ledges despite the presence of a parent on the ledge and the absence of interference from other birds. In four of these cases, the parent attempted to keep the chick from jumping by obstructing the chick with its wings as it moved to the edge of the ledge. Similarly, Greenwood (1964) observed that three of 37 Common Murre chick departures failed when chicks jumped alone while the parent remained on the nest site. In a further four cases at Coats Island, the chick was abandoned immediately upon landing. Murre chicks typically depart with the male parent, and it is possible that these failures occurred when chicks initiated departures while the female parent was present. If so, such failures may have been the result of poor coordination between the parents (possibly young, inexperienced birds) during the departure evening.

WHY ARE DEPARTING CHICKS ATTACKED BY ADULTS?

At Coats Island, color bands visible on some mobbing adults showed that they included 3- and 4-year-old birds. Few Thick-billed Murres of this age successfully rear a chick (deForest 1993). Hence some, perhaps the majority, of mob birds were failed or nonbreeding adults. This has been suggested for Common Murres (Harris and Birkhead 1985) and Ancient Murrelets (Jones et al. 1987) that attacked departing chicks on the water close to colonies.

Aggression towards young by adult conspecifics is adaptive for many organisms (for review see Hrdy and Hausfater 1984). Infanticide may increase the resources available to the killer or its lineage by facilitating access to mates, nest sites, or food resources (Hrdy 1974). However, this resource competition hypothesis has been difficult to document in the field (see reviews by Hrdy 1974, Mock 1984). At some Arctic breeding colonies, suitable nest sites may be limited for young Thick-billed Murres and perhaps by killing departing chicks, mobbing adults increased their access to mates and/or nest sites the following year. This is a tenuous explanation because it assumes that separation or death of the chick on the water influences the male's assessment of the nest site and that this increases the probability that he chooses a new mate or nest site the following season. This is unlikely considering that murres often return to the same nest site after several successive years of breeding failure (deForest 1993). Furthermore, at Coats Island, attacking adults were most interested in chicks that were already alone and calling on the sea (i.e., after male assessment of the departure was determined). In addition, chicks were rarely killed outright by a single bird, but were killed instead by the successive attacks from different individuals. Thus, it does not seem possible that the potential selective benefits resulting from the death of a chick could be accrued to a single individual.

It is possible that the aggression of adult murres towards chicks on the sea served no adaptive purpose for the attackers, and that this behavior was a byproduct of hormonal influences that stimulated adults to respond aggressively to the distress calls of chicks. Aggression towards distressed murre chicks could be an adaptive behavior among breeding murres nesting densely on cliff ledges where foreign chicks may fall or wander onto their nest sites, particularly during the confusion of departure evenings (see above). If so, reproductive hormones present in failed or nonbreeding murres could induce an aggressive response towards foreign chicks on the sea. This could explain why the distress calls of chicks on the sea attracted adults

and appeared to intensify mob aggression. Although this explanation is speculative, aggression towards chicks would not necessarily be selected against if the costs and risks associated with this behavior, which appear minimal, were outweighed by the future benefit of the behavior when expressed in the proper context by breeding birds on nesting ledges.

ACKNOWLEDGMENTS

We thank Thomas Alogut, Leah deForest, Garry Donaldson, Mark Hipfner, and Marco Passeri for assistance with the field work. We also thank Ian Jones, Ron Ydenberg, Jamie Smith, and two anonymous reviewers for comments on earlier drafts of the manuscript. The research was funded in part by the Orville Erickson Memorial Scholarship (Canadian Wildlife Federation), Canadian Wildlife Service (operating grant to AJG and University Support Grant to HGG), the Natural Science and Engineering Research Council of Canada, and the Northern Science Training Program of the Department of Indian and Northern Affairs. Assistance with organization and logistics was provided by the Polar Continental Shelf Project of the Department of Energy, Mines, and Resources, and the Science Institute of the Northwest Territories Iqaluit Research Centre.

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