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Source: *The Auk*, Vol. 118, No. 4 (Oct., 2001), pp. 934-943

Published by: American Ornithologists' Union

Stable URL: <http://www.jstor.org/stable/4089843>

Accessed: 27-05-2015 18:34 UTC

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DOES KLEPTOPARASITISM BY GLAUCOUS-WINGED GULLS LIMIT THE REPRODUCTIVE SUCCESS OF TUFTED PUFFINS?

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ABSTRACT.—Interspecific kleptoparasitism (food stealing) occurs in many seabird species and can sometimes significantly affect host individuals and populations. We investigated effects of kleptoparasitism by Glaucous-winged Gulls (*Larus glaucescens*) on a population of Tufted Puffins (*Fratercula cirrhata*) in which almost all chicks die before fledging in some years. Rates of kleptoparasitism were estimated during two seasons and compared with several spatial and temporal factors that have been predicted to influence kleptoparasitism rates both within and among seasons. Kleptoparasitism rates increased from 2% in the first year to 19% in the second, whereas puffin fledging success declined precipitously from 81% in the first year to 11% in the second. Within years, kleptoparasitism rates increased with number of puffins returning with fish, decreased during fair weather, and were unaffected by tidal height. Spatially, those rates increased with puffin burrow density and declined with angle of the nesting slope. Gull kleptoparasitism success increased during foul weather and at higher puffin nesting elevations. Despite those associations, survival of puffin chicks was not influenced by kleptoparasitism activity near their nests although it increased with a combination of low elevation and high slope at the nesting burrow. Neither kleptoparasitism nor predation by gulls were exceptional relative to other seabird colonies and they were unlikely to cause reproductive failures that characterize puffins at that site. Other factors, particularly food shortages at sea, merit further attention in explaining those failures. *Received 12 November 1999, accepted 27 March 2001.*

INTERSPECIFIC KLEPTOPARASITISM is relatively common in seabirds (Brockmann and Barnard 1979, Furness 1987), but frequency and effects of that behavior vary both among and within species. Gulls, with their opportunistic foraging strategies, are frequent kleptoparasites (Duffy 1982, Barnard and Thompson 1985), and puffins, which nest in highly concentrated colonies and return at predictable intervals conspicuously carrying their prey, epitomize suitable kleptoparasitism hosts (*sensu* Brockmann and Barnard 1979). Thus, kleptoparasitism by gulls (Family Laridae) and closely related skuas (Family Stercorariidae) has been well-studied in Atlantic puffins (*Fratercula arctica*), but effect of that behavior on puffin reproductive success varies. Nettleship (1972) reported that piracy, and associated avoidance of gulls by puffins, can severely limit puffin food deliveries and, ultimately, reproductive success. However, other researchers suggested that kleptoparasitism by gulls only exacerbates extrinsic food shortages (Harris 1984, Furness 1987), found that it affects puffins only where

they nest in low densities (Harris 1980), or discounted its effect on puffin populations altogether (Evans 1975, Pierotti 1983, Hudson 1985, Rice 1985). For some seabirds, predation by gulls on host eggs or chicks may impose a more significant limitation on reproductive success (Gilchrist et al. 1994, Becker 1995, Castilla 1995) and that has resulted in culling programs at several seabird colonies (Thomas 1972, Blokpoel and Spaans 1991). However, those programs have sometimes been initiated in the absence of a causal link between gull behavior and host population success (Harris and Wanless 1997).

Despite considerable work on kleptoparasitic effects on Atlantic Puffins, almost nothing is known of the interactions between gulls and the Pacific-dwelling Tufted Puffin (*Fratercula cirrhata*), for which there is some indirect evidence of a negative effect by gulls. Populations of Glaucous-winged Gulls (*Larus glaucescens*) have increased several-fold in recent decades along the southwestern coast of British Columbia (Verbeek 1986, Reid 1988) and increasing gull populations may generally destabilize kleptoparasitic (Furness 1987) and predatory

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(Russell and Montevechi 1996) relationships. Concurrently, the population of Tufted Puffins on the provincial Ecological Reserve of Triangle Island, British Columbia (50°52'N, 129°05'W), the stronghold of that species in Canada (Vermeer 1979), has exhibited almost complete reproductive failures in more than half of its recent breeding seasons (Vermeer et al. 1979, Rodway et al. 1990, C. C. St. Clair pers. obs.). Those failures may be linked to periodic scarcity of sandlance (*Ammodytes hexapterus*), a favoured prey of Tufted Puffins (Vermeer et al. 1979). However, several other factors, including kleptoparasitism and predation by Glaucous-winged Gulls, may also be important (G. Gilchrist and I. Jones pers. comm.). Although gulls frequently attack puffins on Triangle Island (Vermeer 1979), there has so far been no attempt to quantify extent or effect of that behavior.

Studies of other kleptoparasitic relationships suggest that population-level effects of kleptoparasitism are mediated through a variety of factors that influence both rate and success of individual kleptoparasitic events. From those studies, several predictions can be made. First, gull activity may track number of puffins returning with fish to equalize per puffin risk of being attacked (Rice 1987). That correlation may also occur because gulls follow diel cycles of puffin activity, attacking most often in the morning when puffin returns are likely to be highest (Vermeer 1979). Second, gulls may not track puffin activity well (Hudson 1985), and may instead be affected by meteorological or tidal conditions that influence gull foraging success directly (e.g. Furness 1987, Bélisle and Giroux 1995), or by stormy weather when surface feeding is difficult. Third, poor visibility may also make it easier for gulls to ambush incoming puffins (Furness 1987). Finally, gull activity and success may vary with nesting-slope topography, increasing on shallower slopes where puffins are more vulnerable (Nettleship 1972, Wilson 1993), and either decreasing (Grant 1971) or increasing (Furness 1978) at higher elevations according to puffin escape tactics. We examined relationship between Glaucous-winged Gulls and Tufted Puffins nesting on Triangle Island to (1) quantify frequency and nature of kleptoparasitism on adults and predation on chicks, and compare those to other kleptoparasitic relationships; (2)

identify factors responsible for variation in rates and success of kleptoparasitism; and (3) assess potential effect of kleptoparasitism on puffin reproductive success by measuring chick survival.

METHODS

The study took place on Triangle Island, the outermost island of the Cape Scott archipelago, 46 km northwest of Vancouver Island, during summers of 1995 and 1996. Most of the breeding puffins on the island nest on the steep, hairgrass (*Deschampsia caespitosa*) covered slopes of Puffin Rock, a 90 m hummock connected to the rest of the island by a low-tide isthmus. Glaucous-winged Gulls nest along the ridge tops above and among puffin burrows where they can easily survey incoming puffins. Gulls typically kleptoparasitize puffins by waiting until a puffin approaches its burrow and then lunging or flying toward it and attempting to grasp it by the wing, tail or head, and then shaking it, sometimes violently, until it drops its fish. Gulls frequently patrol puffin burrows at other times and probe in and around burrow entrances, apparently looking for displaced eggs or chicks and dropped fish.

Frequency of kleptoparasitism and predation.—Observations of puffin and gull activity took place on one southeast-facing nesting slope of Puffin Rock visible from a blind ~100 m away on an opposite-facing slope. To reference observations and burrow locations, we placed a grid over the accessible portion of the southeast slope over an area of approximately 40 × 100 m with flags at 10 m intervals. During the puffin nestling period (30 June–16 August, 1995, and 29 June–15 August 1996), we observed the slope for periods of 1–8 h per day. Those periods were spread approximately equally over the daylight hours (0600–2200 h). We recorded kleptoparasitism and predation by gulls by *ad libitum*, continuous sampling (Martin and Bateson 1986) of the gridded area, including the air above it. For each kleptoparasitism event, we recorded the following variables: date, time, number of gulls involved, type (attack or chase, see below), location of closest contact between the gull and puffin (air or ground), approximate two-dimensional grid location, and success or failure. We captured and marked three gulls in 1995; two others were identifiable by unique markings in both years, so in some instances we knew the identity of the kleptoparasite. An attack was defined as an event involving contact between the gull(s) and puffins, and chases were those without contact. Because it was often difficult to tell when small fish had been dropped, we recorded events as successful only when we observed a gull eating pirated fish and that was easily determined by spotting scope or binoculars. In 1996, we also recorded the escape substrate

TABLE 1. Frequency and success of kleptoparasitism (kp) events recorded on the observation slope in 1995 and 1996. Superscripts refer to G-tests comparing years for the variables indicated. Because multiple comparisons are made with the same data set, the reader may wish to interpret alpha conservatively at $P = 0.01$.

Variable	1995	1996
Hours of observation	173	174.5
Total chases** (% successful) ^{ns}	227 (3)	321 (2)
Total attacks** (% successful) ^{ns}	144 (18)	239 (21)
Percentage chases on ground ^{ns} (% of successful chases occurring there) ^{ns}	68 (67)	86 (100)
Percentage attacks on ground ^{ns} (% of successful attacks occurring there) ^{ns}	81 (84)	88 (98)
Percentage escapes into air (% of successful kp with aerial escapes)		74 (100)
Mean (\pm SD) no. of gulls/kp event ^{ns}	1.2 (0.44)	1.2 (0.41)
Percentage of chases with interference (% of these that were successful)		3 (0)
Percentage of attacks with interference (% of these that were successful)		10 (25)

* $P < 0.05$, ** $P < 0.01$.

of the puffin (air or burrow; the water was far below the nesting slope and not easily visible) and interference by other gulls with a primary kleptoparasitizing individual.

Factors influencing kleptoparasitism frequency and success.—To monitor abundance and foraging success of puffins, we counted the number of puffins returning with and without fish once during each hour of observation. For consistency, those data were collected during a 10 min period from two grid squares (10 \times 20 m) that were easily observed from the blind. To provide a relative measure of kleptoparasitism frequency, we recorded the number of gulls present in the grid squares during the count and recorded any chases or attacks that occurred. Prior to those counts, we also counted the number of puffins standing on the nesting slope in three (1995) or two (1996) grid squares adjacent to return rate squares. We collected qualitative data on cloud cover (five categories) and obtained Environment Canada weather data from the automated buoy at nearby Sartine Island (14 km to the southeast) for three other variables: temperature, wind speed, and wind direction. We added an additional wind direction variable, "northwest wind direction," to recognize the prevailing weather patterns: 180 for high pressure systems from the northwest grading symmetrically on both sides of the compass to 0 for the stormy weather from the southeast. Finally, we determined tidal heights for each hour of observation using the program XTide (Flater 1996).

Effects of kleptoparasitism on puffin success.—As a measure of effect of gulls on puffins, we monitored the growth and fledging success of a sample of puffins from the observation grid. In 1995, we located an active burrow (i.e. one containing a chick, adult, or warm egg) early in the chick-rearing period as near as possible to each of 41 grid flags, marked its entrance with a small flag, dug an access hole to the nesting chamber and covered it with a wooden shingle and sod, and then returned every 10 days to record chick survival. In 1996, we repeated that pro-

cedure with 32 of our original burrows, replaced inactive burrows, and added a burrow at most grid flags for a total of 79 burrows. We considered puffin chicks to have fledged if they were at least 219 g with a wing length of 131 mm when they were last measured because this size exceeds the 95% confidence interval of 45 dead (presumably starved) chicks found on Puffin Rock in the 1995 season. In 1996, too few puffins fledged for meaningful comparisons, so we used measurements taken on 19 July as a cut-off date to compare chick survival. On that date roughly half the chicks had perished (the remainder were two to three weeks old), therefore using that cut-off point maximized the power of our statistical comparisons of chick survival.

Because slope topography and burrow position potentially influence kleptoparasitism rates and puffin fledging success, we quantified several slope attributes at grid flags and monitored burrows. At each grid flag, we measured the direction of the steepest downslope and then applied trigonometry to the vertical and horizontal distances between grid-marked points to determine elevation and slope-angle at each flag. Elevations were quantified relative to the highest point on the southwest end of the ridge. At each burrow, we measured distance and height difference (for elevation) to the nearest grid flag, height of the tallest hairgrass on each of four sides surrounding the entrance (a measure of exposure), slope (by triangulation over 10 m horizontal), and number of puffin burrows within a 5 m radius. Later we also tallied number of kleptoparasitism events referenced to each grid square as a more direct measure of effects of kleptoparasitism activity on puffin fledging success.

RESULTS

Frequency of kleptoparasitism and predation.—Chases were proportionately more common than attacks in both years (Table 1; Likelihood

ratio $\chi^2 > 6.0$, $df = 1$, $P < 0.014$ for both years), but a higher proportion of attacks were successful ($\chi^2 > 6.4$, $df = 1$, $P < 0.012$ for both years). Both behaviors increased in frequency in 1996 (Table 1), although their relative success rates were unchanged. During kleptoparasitism attempts, gulls typically lunged or flew at puffins just before they entered their burrows. Thus, both chases and attacks were much more common on the ground (Table 1; $\chi^2 > 6.7$, $df = 1$, $P < 0.01$ for each year and behavior) and that is also where the majority of successful kleptoparasitism events occurred (Table 1; $\chi^2 > 6.0$, $df = 1$, $P < 0.013$). In 1996, kleptoparasitism attempts in the air were virtually never successful, although trends for an increase in both proportion and success rate of ground kleptoparasitism in 1996 were not significant (Table 1). Escape data from 1996 also suggest that puffins have an advantage in the air; harassed puffins were more likely to escape into the air than into their burrows (Table 1; $\chi^2 = 12.4$, $df = 1$, $P = 0.0004$) and puffins always fled into the air after successful kleptoparasitism. Gulls typically approached puffins singly (Table 1) and, in 1996, when interference by other gulls occurred during a kleptoparasitism event, it usually involved only one additional individual (mean additional individuals = 1.31, $SD = 0.67$, $n = 36$). Interference had no effect on the success rates of attacks (Table 1; $\chi^2 = 0.13$, $df = 1$, $P = 0.72$) or chases ($\chi^2 = 0.41$, $df = 1$, $P = 0.52$).

Observations of marked gulls suggests that frequency and success of kleptoparasitism is highly variable among individuals. Number of events performed by each individual ranged from 0 to 87 (mean = 27.7 ± 33.7 , $n = 7$) per year. Individual success rates ranged from 0 to 25% for chases (mean = 6.4 ± 10.1 , $n = 6$) and 0 to 33% for attacks (mean = 14.3 ± 16.2 , $n = 6$).

In addition to kleptoparasitizing adults, gulls also targeted puffin offspring by walking around on the nesting slope and probing in burrows. In 1995, we saw only two chicks consumed in that way. In the first case, a gull stabbed repeatedly at the ground above a burrow, tearing a hole in the burrow ceiling, then pulled out the live puffin chick from within and swallowed it whole. In the second case, we saw a gull eating a puffin chick, but could not tell if the chick was initially alive and where it had come from. In 1996, chick consumption by gulls

was much more common, but it may have represented scavenging more than predation. We saw 28 puffin chicks being eaten by gulls; four of those were dead when discovered by the gull, one was alive and actively tried to escape, but we could not tell whether the others were initially alive or dead. Four chicks were pulled from their burrows, eight were already outside a burrow on the ground, and the others (16) were first observed in the bill of a gull. Other species may also prey on puffin offspring. One fledgling puffin chick was apparently killed by a Peregrine Falcon (*Falco peregrinus*) (identifiable by the characteristic head and wing remains), we saw one egg dug out and eaten by a Common Raven (*Corvus corax*) and a giant race of deer mice (*Peromyscus maniculatus triangulatus*) or Townsend's vole (*Microtus townsendi cowani*) may have been responsible for the tooth marks and predated eggs we found in puffin burrows near the observation slope in 1996. In 1995, we saw gulls eat two other puffin eggs and one was taken directly from a burrow. On one occasion, we saw a gull apparently kill an adult puffin after grabbing it by the head and shaking it.

Despite the higher frequency of kleptoparasitism and predation in 1996, puffin activity was not similarly heightened as we had predicted. In return-rate counts, mean number of puffins standing on the reference grid squares decreased by 23% in 1996 and number of puffins landing decreased by 40% (Table 2). There were over three times as many return rate counts in 1996 than in 1995 during which no puffins returned (Table 2). Fewer puffins returned with food in 1996, although proportion of returning puffins observed with food did not differ between years (Table 2). However, a greater number of unscored puffins (i.e. we did not know whether or not they were carrying fish) in 1995 may obscure a similar decrease: if all unidentified puffins in both years are assumed to be carrying food (food-laden puffins tend to dart directly into their burrows making it difficult to detect fish), proportion with food actually decreased by as much as 30% (Table 2). Relative to number of returning puffins observed with food in each year, significantly more puffins were approached by gulls in 1996 (Table 2). That equates to an eight fold increase in percentage of food-carrying puffins that

TABLE 2. Puffin counts and return rates (during a 10 min period) collected from adjacent pairs (10×20 m) of grid squares. Means are given \pm SD, and superscripts indicate either independent *t*-tests (for means that are first arcsine-transformed for percentages) or *G*-tests (for counts and overall percentages) for differences between years. Again, multiple comparisons promote a more conservative interpretation of significance values.

Variable	1995	1996
Number of counts (number with kp data)	185 (182)	199 (183)
Mean number of standing puffins** (range)	24.8 ± 21.2 (0–99)	19.2 ± 18.1 (0–82)
Mean number of returning puffins*** (range)	15.5 ± 14.6 (0–66)	9.2 ± 10.8 (0–47)
Number of counts with no returning puffins** (%)	12 (6.4)	41 (21)
Mean number of puffins returning with fish*	1.47 ± 1.67	1.15 ± 1.60
Mean percentage of returning puffins with food ^a (mean maximum percentage)**	24 ± 31 (38 \pm 30)	20 ± 27 (27 \pm 30)
Total number of puffins with food approached by gulls** (mean percentage per return rate count***)	9 (2.4 \pm 13.8)	29 (18.8 \pm 36.0)

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

^a not significant ($P > 0.05$).

were chased or attacked during return-rate counts (Table 2).

Factors affecting kleptoparasitism frequency and success.—Data were tallied for comparing rates of kleptoparasitism in two ways, temporally as hourly totals, and spatially as grid marker totals. In the first subset, we investigated effects of the actual density of returning puffins, predictability of returning puffins, weather conditions, and tidal height on the hourly rates of kleptoparasitism (attacks plus chases) using multiple regression. We measured puffin density as number of puffins returning with food as well as the total number of puffins returning during each observation hour. For "puffin predictability," we used hourly averages of number of puffins returning with fish in each season to generate diel patterns of puffin activity. The best-fit significant relationship between those variables was linear in 1995 ($R^2 = 0.38$, $df = 1$ and 14, $P = 0.01$) and cubic in 1996 ($R^2 = 0.82$, $df = 1$ and 12, $P < 0.001$). To analyze effects of weather, we first used principal components analysis to reduce the five weather var-

iables to two orthogonal factors that explained 68% of their variance (Table 3). The first factor corresponded roughly to good weather (relative factor loadings indicated high temperatures, low wind speed, low cloud cover, and northwest wind direction) and the second to foul weather (low temperatures, strong southeast winds, higher cloud cover). We added "year" as a dummy variable to account for obvious differences between the two seasons, but did not examine interaction terms because we were more interested in testing the hypothesized main effects.

Of the seven independent variables analysed, four contributed significantly to variation in the rates of kleptoparasitism activity (Table 4). Kleptoparasitism rates increased with number of puffins actually returning with fish as well as with number predicted to return by hourly averages. Kleptoparasitism also decreased during good weather although it showed no measurable increase during foul weather. Total number of puffins returning with food and tidal height also did not contribute significantly, though those small effects were in the predicted directions. Inclusion of the four significant factors (Table 4) yielded a regression model that explained only 20% of the variance in gull activity ($R^2 = 0.192$, $F = 21.8$, $df = 3$ and 346, $P < 0.001$), indicating that several unmeasured factors are relevant to rate of kleptoparasitism activity. Hourly percentages of successful kleptoparasitism events increased during foul weather ($\beta = 0.121$, $t = 2.46$, $P = 0.014$), but no other factor contributed significantly to proportion of successful events ($\beta < 0.036$, $t <$

TABLE 3. Principal components analysis used to reduce five weather variables to two factors explaining 68% of their variance.

	Factor 1	Factor 2
Eigen value	2.26	1.12
Percent variance explained	45.2	22.3
Temperature	0.500	-0.461
Wind speed	-0.223	0.831
Cloud cover	-0.592	0.184
Wind direction	0.875	0.353
Northwest wind direction	0.918	0.235

TABLE 4. Stepwise multiple regression statistics predicting hourly rates of kleptoparasitism activity (attacks plus chases). Beta represents correlation coefficients adjusted for their units of measurement in the final model. Factors are listed in order of their entry in the regression equation with ΣR^2 indicating the cumulative proportion of the variance explained by addition of each significant variable.

Factor	β	<i>t</i>	<i>P</i>	ΣR^2
Number of puffins with food	0.228	4.42	<0.001	0.078
Good weather	-0.195	-3.91	0.001	0.133
Year	0.219	4.42	<0.001	0.162
Puffin return predictability	0.202	3.70	<0.001	0.192
Foul weather	0.076	1.49	0.135	
Total number of puffins returning	0.030	0.52	0.602	
Tidal height	-0.003	-0.07	0.947	

0.73, $P > 0.46$). Foul weather alone explained only 1% of the variance in kleptoparasitism success ($R^2 = 0.012$, $F = 6.06$, $df = 1$ and 406, $P = 0.014$).

In a second analysis of kleptoparasitism rates, we tallied number of kleptoparasitism events referenced to each grid marker and used multiple regression to tease apart contributions of slope angle, elevation, and puffin burrow density (measured from the nearest monitored burrow). We analyzed years separately to avoid pseudoreplicating grid squares. Significant models were produced in both years (year 1, $R^2 = 0.53$, $df = 5$ and 41; year 2, $R^2 = 0.37$, $df = 2$ and 42), primarily through the positive effect of increasing burrow density on kleptoparasitism rates ($P < 0.001$ in both years). Slope angle was negatively correlated with kleptoparasitism activity in 1995 ($P < 0.001$) and a similar trend was evident in 1996 ($P = 0.087$). Elevation did not contribute to kleptoparasitism frequency in either year after other effects were removed ($P > 0.35$). None of those variables influenced grid-specific success rates of kleptoparasitism attempts (year 1, $R^2 = 0.07$, $df = 3$ and 34, $P > 0.49$ for each variable; year 2, $R^2 = 0.02$, $df = 3$ and 38, $P > 0.24$). However, it is possible that by tallying kleptoparasitism success per grid square and lumping chases and attacks, we missed a slight effect of topography on success of individual events. Comparing instead mean grid coordinates of successful and unsuccessful attacks indicated that successful attacks occurred at higher vertical grid coordinates in 1996 (Mann-Whitney *U*-test, $P = 0.03$) with a similar trend in 1995 ($P = 0.09$). Vertical grid location had no effect on chase success in either year ($P > 0.55$). Because slope angle decreases with increasing elevation of grid coordinates ($R^2 = 0.49$, $df = 1$ and 44, $P < 0.001$), that result

may indicate that puffins are also more vulnerable to successful attack on shallower slopes.

Effect of kleptoparasitism on puffin fledging success.—Puffin fledging success on the observation slope differed markedly in the two years. Among monitored burrows that initially contained a chick, 81% (33/41) produced a fledgling in 1995, but reproductive success was very poor in 1996 when only 11% (8/79) of chicks survived to 14 August and all of those were relatively light (<265 g). Clearly, fledgling success declined as kleptoparasitism rates increased the second year (*G*-test, $G = 48$, $P < 0.001$), but a causal effect of kleptoparasitism cannot be assumed. Better evidence of such a relationship might be derived from a nest-level analysis.

To perform that analysis, we grouped nests according to fledgling success and used logistic regression to assess effect of several variables describing nest characteristics: slope, elevation, mean height of grass surrounding each burrow, puffin burrow density within 5 m, and sum of kleptoparasitism events referenced to the nearest grid square. For a few missing values (4–7 values per variable), we substituted nearby locations (elevation), grid row means (slope), or overall means (grass height, burrow density, and kleptoparasitism frequency) and then centered all variables on their means for analysis. Because elevation and slope were strongly and negatively correlated ($R^2 \geq 0.44$, $df \geq 40$, $P < 0.001$ in both years), we combined this measure with a PCA and termed it *inaccessibility*. That term reflects the high factor loadings for low elevations and high slopes that explained most of the variation among measured burrows for these two variables (1995 = 85%, 1996 = 83%).

Among the four remaining main effects and their three biologically plausible two-way interactions (i.e. excluding grass height), only in-

accessibility contributed significantly to the year-specific models predicting chick success (1995: $\chi^2 = 7.1$, df = 1, $P = 0.008$; 1996: $\chi^2 = 2.78$, df = 1, $P = 0.10$). We assessed model fit by comparing observed to predicted frequencies in each decile of probability (Hosmer and Lemeshow 1989), expecting that a good fit would yield a high probability of obtaining those differences by chance. Our model fit the data reasonably well in 1995 (Hosmer-Lemeshow $\chi^2 = 7.13$, df = 7, $P = 0.42$) when it correctly classified 83% of cases, but quite poorly in 1996 (Hosmer-Lemeshow $\chi^2 = 14.6$, df = 8, $P = 0.068$) when it correctly classified 66%. Kleptoparasitism frequency did not enter the model in either year, but those rates were actually $2.3 \times$ higher in grid squares of successful chicks in 1995 ($t = 1.68$, df = 39, $P = 0.11$) with a much lesser difference of 15% in 1996 ($t = 0.75$, df = 77, $P = 0.45$).

DISCUSSION

Frequency of kleptoparasitism and predation.—Successful kleptoparasitism on Triangle Island nearly always involved attacks on the ground by single gulls. Although other seabird kleptoparasites typically chase or intercept hosts in the air without touching them (Furness 1987), ground attacks by gulls on puffins were more common, presumably because most gulls lack the maneuverability to catch puffins in the air (Grant 1971, Harris 1984, but see Hudson 1985). The eight-fold increase in success of attacks over chases indicates that gulls must actively dislodge food from puffins. Interference by other gulls did not improve success of attacks or chases, in contrast to several other species in which group attacks are more likely to yield fish (Arnason and Grant 1979, Osorno et al. 1992, Oro and Martinez-Vilalta 1994, Bélisle and Giroux 1995). Finally, there was some evidence, from the few gulls we could identify, that gulls differed in their propensity for kleptoparasitism, perhaps as a function of age (Verbeek 1977, Steele and Hockey 1995) or specialization.

The number of kleptoparasitism events we observed increased by one-third in 1996. However, number of puffins returning decreased so that proportion of returning puffins approached by gulls actually increased eight-fold from 2.5–19%. Similar interannual variation in

the rates of kleptoparasitism occurred over eight years on the Isle of May (Harris 1984) and both populations approach the 2–30% range reported among other populations of Atlantic Puffins and their kleptoparasites (Nettleship 1972, Arnason and Grant 1978, Furness 1978, Harris 1984). The high degree of variation that occurs within populations suggests that kleptoparasitism frequency is mediated primarily through stochastic phenomena, like food availability, rather than by gradual trends in the population sizes of gulls or puffins.

Despite increase in gull activity, success rates were similar between the two years and were generally low at 3% for chases and 20% for attacks. Our conservative definition of success, in which gulls had to be observed eating dropped fish, almost certainly underestimates the actual effect on puffins; Arnason and Grant (1978) estimated that as much as 30% of fish dropped by Atlantic Puffins was not retrieved from where it had fallen in vegetation. But even with that correction, proportion of puffins that were approached by gulls and also lost their fish is likely less than the mean value of 28% reported by Furness (1987) from a review of 28 kleptoparasitic relationships in which gulls and terns were the parasites. Thus, neither proportion of puffins approached by gulls nor their success rate was exceptional in this study, even during the markedly higher activity in the second year.

Apparent predation of puffin chicks by gulls was uncommon in the first year and may have actually represented scavenging in the second year when many chicks were likely already dead or starving. Starving chicks may approach gulls probing in their burrows after mistaking them for a returning parent (Harris 1984) or may linger at burrow entrances where they are vulnerable to attack (Nettleship 1972). Eggs, too, are likely taken by gulls, ravens, or mice only after they have been displaced or abandoned by parents because healthy chicks and actively incubated eggs are typically more than an arm's length from the burrow entrance (C. C. St. Clair pers. obs.). Nonetheless, at least one apparently healthy chick was excavated and eaten by a gull. Ravens and crows (Family Corvidae) undoubtedly take eggs occasionally at this and other sites (Harris 1984), but predation by mice is unknown elsewhere, and requires study at Triangle Island. Killing of adult puffins by Glaucous-winged Gulls must be

very rare, but larger gull species appear to take adult puffins more often (reviewed by Harris 1984, Russell and Montevercchi 1996).

Factors influencing kleptoparasitism frequency and success.—Several temporal factors exerted some influence on the hourly rates of kleptoparasitism, though they explained only one-fifth of their total variation. There were higher rates of kleptoparasitism when more puffins returned with fish, a finding common to other studies (Rice 1987, Oro and Martinez-Vilalta 1994) and perhaps an extension of requisite host concentration that appears to be necessary for evolution of kleptoparasitic relationships (Brockmann and Barnard 1979). Because gulls did not respond to the total number puffins returning with food, it appears that they recognize laden puffins and assess profitability of waiting for kleptoparasitism opportunities. However, gulls must also have some ability to remember or predict when food returns are likely to be highest as evidenced by their partial correspondence with the hourly averages of the number of puffins returning with fish. Lack of a tidal effect on kleptoparasitism rates was surprising because we frequently saw invertebrate parts in regurgitated gull pellets, and intertidal feeding by Glaucous-winged Gulls is generally concentrated during low tides (Irons et al. 1986). Moreover, kleptoparasitism frequency by other pirate species decreases at low tides when intertidal prey are available (Brockmann and Barnard 1979, Bélisle and Giroux 1995). Perhaps the lower food quality of many invertebrates (e.g. Murphy et al. 1984) favors hunting them only when fish from kleptoparasitism or surface foraging is not available, masking a predictive effect of tide on kleptoparasitism frequency. Conversely, one would expect few correlations with environmental conditions if only a few specialist gulls were responsible for the bulk of the kleptoparasitism activity.

Good weather caused a decrease in kleptoparasitism frequency. That effect may have been mediated through improved visibility and foraging success experienced by surface-feeding gulls under those conditions. Similarly, poor visibility increases kleptoparasitism rates in a raptor guild, presumably through its effects on host concentration and food availability (Temeles and Wellcome 1992). Gulls may also have avoided kleptoparasitism in good weather because good visibility made it more

difficult to ambush returning puffins (Furness 1978) or because it was correlated with wind direction. Northwest winds that typically accompanied good weather on Triangle Island may have precluded hovering on the updraft of the southeast facing observation slope. Although we observed puffins on a northwest facing slope to test that idea, too few puffins returned to be able to compare gull activity.

When kleptoparasitism rates were tallied spatially, it appeared that gulls concentrated their activity where puffin burrow density—and thus number of returning puffins—was greatest, an effect found also in Herring Gulls (*Larus argentatus*) and Atlantic Puffins (Hudson 1985). Kleptoparasitism rates also declined with increasing slope angle, as reported for other puffins (Nettleship 1972, Wilson 1993). That may have occurred because shallow slopes occurred at higher elevations where puffins had to fly farther over land to reach their burrows and taller grass there made it harder to see their burrows. Or it may be because puffins have more difficulty lifting off from shallow slopes once they have been attacked (Nettleship 1972). There was no evidence that elevation alone was important to kleptoparasitism frequency, although that may be important for aerial kleptoparasites where it affects chase distance to the sea (Furness 1978).

We found only weak predictors of kleptoparasitism success. Success increased during foul weather and at higher elevations. Although foul weather did not influence rates of kleptoparasitism, success may have been more likely then due to poorer visibility (*sensu* Furness 1978). Puffins, notable for their high wing-loading (Harris 1984), may have also had more difficulty maneuvering during foul weather when the wind tended to blow upslope (i.e. from the southeast). Gull success may have increased at higher elevations because it corresponded to a greater distance from the sea (making it more difficult for puffins to escape) or because it was correlated with shallower slopes that may favour gulls for a number of reasons (above).

Effect of kleptoparasitism on puffin fledging success.—Despite the association between heightened kleptoparasitism rates and lower chick survival in the second year, it did not appear that kleptoparasitism affected fledging success directly. Among attributes we measured, only inaccessibility was a significant determinant of

puffin fledging success, conferring higher success at lower elevations with steeper slopes. Grid-specific kleptoparasitism rates did not influence fledging success and, to the extent that a difference existed at all, it was in the opposite direction; kleptoparasitism rates were higher at the grid squares with higher chick survival, presumably because food deliveries were also more frequent there. Height of the grass surrounding the burrows, which might help to conceal landing puffins, was similarly unimportant.

There are a couple of potential explanations for the accessibility effect, which was more pronounced in 1995. One possibility is that burrows at higher elevations with shallow slopes are in poorer condition, due to thinner ceilings caused by the shallower slope, greater human visitation over many years, and proximity of nesting gulls that pull out and trample the vegetation. Although better burrow condition was related to higher chick survival in 1996 ($\chi^2 = 5.8$, $df = 2$, $P = 0.055$), the two were not related in 1995 ($\chi^2 = 0.12$, $df = 2$, $P = 0.94$) and elevation did not differ among three burrow condition categories in either year ($F < 0.91$, $P > 0.42$). A second possibility is that burrow location on the nesting slope correlates with parental quality. Some evidence for that suggestion comes from the fact that lower elevations were accompanied by higher burrow densities ($r^2 = 0.16$, $df = 1$ and 40, $P = 0.006$) which generally correlate with earlier breeding and higher fledging success (Harris 1984).

It seems likely that fledging success is primarily dictated by causes other than slope attributes or gull activity and those will require further study. Because puffins likely evolved under conditions of unpredictable prey (Kitaysky 1996), annual differences in food availability (Vermeer et al. 1979) more likely cause seasonal differences in reproductive success. Greater effects of kleptoparasitism might be realized if it increased in frequency (e.g. Nettleship 1972) or if foraging costs for puffins were to rise (e.g. Gorman et al. 1998) due, for example, to low prey availability. Thus, kleptoparasitism may slightly exacerbate poor food years for puffins (Harris 1984, Furness 1987), but gulls do not seem to cause, or substantially contribute to, reproductive failures that afflict puffins at that site.

ACKNOWLEDGMENTS

Financial and logistical support for this project were provided by Research Network Program Grants through the Wildlife Ecology Chair (jointly supported by Simon Fraser University, the Canadian Wildlife Service, and the Natural Science and Engineering Research Council of Canada), by an Izaak Walton Killam Memorial Postdoctoral Fellowship to C.C.S. and an NSERC operating grant to T.D.W. We thank G. Gilchrist and I. Jones for proposing a study on kleptoparasitism and securing the initial funding for it. D. Bertram, L. Cowan, J. Kendall, A. King, S. Romain, J. Salatas, R. Torres, A. Watt, and M. Wiley provided invaluable assistance and wonderful company in the field, and D. Bertram, S. Carroll, F. Cooke, E. Danchin, J. Dunn, S. Hannon, and D. Oro provided helpful comments on the subsequent analysis and manuscript.

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Associate Editor: E. Danchin