J. Avian Biol. 40: 412–418, 2009
doi: 10.1111/j.1600-048X.2008.04490.x

Received 30 January 2008, accepted 5 November 2008

Evidence that tufted puffins *Fratercula cirrhata* use colony overflights to reduce kleptoparasitism risk

Gwylim S. Blackburn, J. Mark Hipfner and Ronald C. Ydenberg

G. S. Blackburn (correspondence) and R. C. Ydenberg, Centre for Wildlife Ecol., Simon Fraser Univ., Burnaby, BC V5A 1S6, Canada. E-mail: gwylim@zoology.ubc.ca. – J. M. Hipfner, Canadian Wildlife Service, Delta, BC V4K 3N2, Canada. – Present address of GSB: Dept. of Zool., Univ. of British Columbia, Vancouver, BC V6T 1Z4, Canada.

Predation, foraging and mating costs are critical factors shaping life histories. Among colonial seabirds, colony overflights may enhance foraging or mating success, or diminish the risk of predation and kleptoparasitism. The latter possibility is difficult to test because low predation or kleptoparasitism rates could be due either to low danger or to effective counter-tactics by prey. Tufted puffins *Fratercula cirrhata* breeding at a large colony in British Columbia, Canada, deliver several loads of fish each day to their nestlings and are targets for kleptoparasitism by glaucous-winged gulls *Larus glaucescens*. In the present study, we documented the ecological conditions under which overflights occurred in order to assess when overflights were made and to statistically isolate the effect of overflights on kleptoparasitism risk at this site. Load-carrying puffins engaged in overflights under ecological conditions associated with relatively high rates of kleptoparasitism. Further, when ecological factors determining risk were statistically controlled, overflights were correlated with marginally lower chances of kleptoparasitism than when the risk factors were ignored. The results suggest that breeding puffins at this site use overflights for kleptoparasite avoidance. This tactic is used sparingly, suggesting it is costly. Costs of overflight behaviour might contribute to the impact of kleptoparasitism on the breeding success of tufted puffins.

Prey organisms use a wide variety of tactics to evade predators (Caro 2005), pathogens and kleptoparasites (Moore 2002). Interest in antipredator behaviour has recently been re-energized by the realization that predators have powerful 'non-lethal' effects on entire populations of prey who by their anti-predator behaviour transmit effects to other trophic levels and so through entire ecological communities (Brown and Kotler 2007, Kotler and Brown 2007, Cresswell 2008). Obviously, the intensity of anti-predator behaviour should depend on the level of risk posed, but measuring the risk is problematic: mortality may be low not because of low predation risk but because antipredator behaviour is effective (Ydenberg et al. 2007). Lank and Ydenberg (2003) pointed out that the mortality in any ecological situation results from the interaction between the level of danger and the intensity of antipredator behaviour employed. They carefully distinguished between the level of mortality that would be observed if no antipredator tactics were employed (which they called 'danger') and actual mortality ('risk'). Here we use the word 'risk' to refer to the realized probability of kleptoparasitism, and the word 'danger' to refer to the probability that would obtain if puffins employed no anti-kleptoparasite tactics.

Several colonial alcid (Alcidae) species commonly make 'overflights' at their breeding colonies (e.g. Piatt and Kitaysky 2002; reviewed in Gaston and Jones 1998). Overflights are circuits made in flight in front of the colony, and include repeated circuits by individuals as well as the coordinated ''wheeling'' of thousands of birds. Colony overflights have been hypothesized to serve diverse purposes including searching for mates or burrows, strengthening pair bonds, exchanging foraging information, and avoiding predators or kleptoparasites (Grant 1971, Harris 1980, Lowther et al. 2002). In this study we investigate the significance of overflights by provisioning tufted puffins *Fratercula cirrhata* at Triangle Island, British Columbia, as a tactic to reduce the risk of kleptoparasitism by gulls.

Tufted puffins are underwater pursuit foragers, and as such have bodies and wings that are subject to a functional compromise between flying and swimming (Pennycuick 1987), which lowers take-off ability and manoeuvrability in the air. They are thus vulnerable to aerial attack by predators and kleptoparasites at their breeding colonies. During the extended nestling period (6 to 8 weeks), parents deliver on average 3–5 bill loads of fish to their young each day (Piatt and Kitaysky 2002). Loss of food loads to kleptoparasites might pose substantial costs for breeding puffins.

Colony overflights have been described as a means of evasion by puffins facing attack, but if so, what would we expect to observe? The most basic prediction of a positive association between overflights and kleptoparasitism could be interpreted in one of two ways. The first is that overflights increase the risk of kleptoparasitism. Alternatively, overflights may be an effective but costly means of reducing the risk, and used predominantly when kleptoparasitism danger is high. Clarifying the ecological context will help to distinguish between these alternative interpretations.

Previous work has focussed on the behaviour of kleptoparasites and predators, with little consideration given to counter-strategies by puffins (Grant 1971, Harris 1980, Rice 1987). There are few data connecting variation in puffin behaviour to that of kleptoparasite or predator activity (but see Addison et al. 2007), and none on its association with environmental conditions that might affect the level of danger. In the present study, we documented the ecological conditions under which overflights occurred in order to statistically isolate the effect of overflights on kleptoparasitism risk at this site.

Methods

Fieldwork

We observed nesting tufted puffins during July and August, 2001, at Puffin Rock, on the southeast corner of Triangle Island. Triangle Island is located about 45 km northwest of Vancouver Island, British Columbia, Canada (50° 52′N, 129° 05′W). Provisioning adults at this site are sometimes kleptoparasitized by glaucous-winged gulls *Larus glaucescens* (Cassady St. Clair et al. 2001) that patrol the airspace above the puffin burrows and attempt to intercept landing puffins. Attacks are also occasionally made by gulls that are on the ground. We measured and flagged a study plot 25 × 50 m in size on a grassy slope with tufted puffin burrows. The plot had a shallow slope on the top half, and steepened toward a cliff at the bottom edge. The plot area encompassed a group of puffin burrows for which all puffin approaches and landings could be easily observed from a blind located on a facing slope approximately 100 m from the study plot. Observation shifts were typically two to four hours long and were distributed roughly evenly throughout daylight h (05.00–22.00) on clear days. Adult puffins were not individually banded, and we estimated based on nestling presence that at least 45 pairs of puffins nested on the study plot. Mean (±SE) burrow re-visitation time was 98 (±6) min. for the only instances (n = 11) in which a burrow was confirmed to be visited more than once during a 4 h observation shift. Assuming equal male and female contributions to food provisioning (Creelman and Storey 1991), this indicates burrow visits by individual pair members were typically separated by at least 2 × 98 min. = 3.2 h. This is a conservative estimate, because in most cases burrows were not visited more than once during a 4 h observation shift. We conclude that individual tufted puffins were unlikely to visit the study plot more than once in a single observation shift.

All food bearing individuals were easily spotted from the blind as they approached the study plot due to their distinctive bill loads of up to several fish. Overflights consisted of circular or figure-8 shaped circuits about 100–300 m in diameter in front of the study plot and were fully visible from the blind. All gull chases occurred within about 25 m of the slope as puffins decelerated to land. A single observer (GSB or JMH) visually tracked food-bearing puffins with binoculars, counted the number of overflights and landing attempts that occurred within the study plot, and noted whether they were chased by gulls. We assigned individuals to one of three overflight categories, based on whether they made zero ("0"), one to four ("1–4"), or five or more ("≥5") overflights prior to landing. Preliminary observations suggested that these categories reflect zero, average, and high puffin investment, respectively, in overflight behaviour at this site (GSB pers. obs.). We scored approaches as successful food deliveries (puffins entered burrows with food loads intact) or as kleptoparasitic events (puffins lost the food due to pursuit by a gull).

We recorded for each approach six ecological factors hypothesized to contribute to kleptoparasitism danger (see Nettleship 1972, Cassady St. Clair et al. 2001), including the slope grade of each burrow (two categories: steep or shallow), the number of puffin arrivals, gulls present (number of gulls on or in the air over the study plot), gull pursuits (total pursuits by gulls per load-carrying puffin landing), wind direction (four categories: North, East, South, or West), and wind speed (km/h). Slope grade was recorded for each individual landing. The number of puffin arrivals, gulls present and the number of gull pursuits were counted during 15 min intervals and the tally assigned to each approach occurring during that interval. Interactions between puffins and gulls typically involve only those gulls in the immediate vicinity of the study area despite the presence of hundreds of gulls on nearby slopes (GSB pers. obs.). We therefore included in our gull presence estimate all gulls patrolling the air space immediately above the study plot or on the ground within the study plot perimeter during each 15 min period. Gull pursuit rate was recorded as the total number of chases of load-carrying puffins over or on the study area in each 15 min period. Regional wind estimates were obtained from the climate archives of Environment Canada (www.climate.weatheroffice.ec.gc.ca). These are recorded each hour by an automated weather station located on Sartine Island, 10 km east of Triangle Island, and were assumed to reflect wind direction at our study site since both islands are in exposed locations. We assigned to each puffin approach the wind direction (four categories, each encompassing 90° and centred on one of the four cardinal directions) and wind speed during the hour in which it occurred.

Data analysis

To examine relationships between kleptoparasitism danger factors, overflights, and kleptoparasitism events we used logistic regression models in SYSTAT 12 (Systat Software Inc., 2007). The parameter coefficients (log odds) in the models are statistically independent from each other, and comparable to the slope coefficients of linear models. We exponentiated the coefficients to obtain estimates of the change in odds of the dependent factor occurring given a one-unit increase in each continuous factor, or an increase across categories in each categorical factor (Hosmer and Lemeshow 2000). One category from each of the three categorical factors served as a reference level for comparison with the remaining categories: zero (overflights), shallow (slope grade), and North (wind direction).

We analyzed the data in three steps. We first examined how overflights varied with ecological danger factors. We next estimated the odds of kleptoparasitism occurring as a combined function of the number of overflights made and the ecological factors we measured. Finally, we evaluated the contributions of ecological factors (hypothesized to raise the danger) and overflights (hypothesized to counter heightened danger) to the observed level of kleptoparasitism.

Overflight model

If puffins estimate the likelihood of kleptoparasitism by assessing a number of ecological danger factors and engage in overflights to diminish the risk, then overflights should correlate independently with each factor in the direction of increasing danger. In contrast, if overflights have a function unrelated to kleptoparasitism evasion, no such relationships should be evident. The overflight model estimated the average odds that load-carrying tufted puffins performed overflights (either "1–4" or "≥ 5") relative to making a direct landing (i.e. zero overflights) for each of the six measured ecological factors. We tested for each factor the hypothesis that it contributed significantly (i.e. a change in odds significantly different from 1.00) to the explanatory power of the total model.

Previous work at Puffin Rock (Cassady St. Clair et al. 2001) revealed that slope grade correlated negatively with the number of kleptoparasitism events experienced by incoming puffins, probably because puffins can more easily and quickly enter the burrow, and can take flight more easily on steep slopes (see also Nettleship 1972). We therefore predicted that puffins landing on the steep portion of the plot would be less likely to engage in overflights than those landing on the shallow portion. We predicted that overflights would decrease with the number of puffins arriving at the study area, since kleptoparasitism risk to individual puffins is diluted when they arrive in groups (Harris 1980, Rice 1987). Puffins landed with greater control when wind blew down rather than up the face of the breeding slope, and they manoeuvred less well in strong wind. In contrast, gulls patrolled the colony with apparently greater control during upslope wind (Gilchrist et al. 1998, GSB pers. obs.). Hence, we predicted that overflights would increase when wind was upslope (South winds) and would increase with wind speed. Finally, we included the number of gulls present and pursuit rate by gulls as direct indices of kleptoparasitism danger. We predicted that if puffins judge kleptoparasitism danger by assessing gull numbers or pursuit activity level near the breeding slope, an increase in either factor would result in an increased number of overflights.

Kleptoparasitism model

To evaluate whether the ecological danger factors we measured were indeed indices of kleptoparasitism, we estimated the average odds of kleptoparasitism occurring as a combined function of the number of overflights made and the six ecological factors we measured. We tested whether each factor contributed significantly (i.e. a change in odds significantly different from 1.00) to the explanatory power of the total model and whether the correlations were in the same direction as in the overflights model.

To test our hypothesis that overflights were a counter-kleptoparasitism tactic, we needed to disentangle the effects of 'danger' and the counter-measure on kleptoparasitism risk. If puffins were sensitive to kleptoparasitism danger and used overflights to mitigate this danger, then overflights should be associated with lower kleptoparasitism risk when the danger is statistically controlled for than when it is ignored. We therefore compared the model of kleptoparasitism as a function of overflights alone to the model that included ecological factors. We predicted that overflights would be correlated with decreased odds of kleptoparasitism when the ecological factors (i.e. danger indices) were included in the model compared to when they were excluded.

Results

We recorded 3,272 approaches during 126.25 observation hours compiled between 7 July and 23 August 2001. There were a total of 505 15 min sample periods, with an average of 6.48 approaches per period (range: 0–53). Each hour of the day between 06.00–22.00 h was represented by at least four separate observation shifts, providing coverage of all hours of the day when puffins were most active. Supplementary analyses including time of day as a factor (not shown) indicated our results pertain to all daylight hours; despite a slight positive effect on overflight occurrence, time did not alter any of the qualitative relationships in the overflight model and did not contribute significantly to the kleptoparasitism models. We excluded this factor from further analyses and focussed on the ecological factors predicted to directly affect kleptoparasitism risk (see Methods).

We observed 396 pursuits by gulls but kleptoparasitism was rare, occurring only 36 times, or on 1.1% of all approaches. Tufted puffins made overflights on just 10.8% (352/3272) of approaches, but most kleptoparasitic events (23/36, or 64%) occurred following overflights (Fisher's Exact Test, $P < 0.001$, Fig. 1). Puffins were kleptoparasitized on 13.5% (23/352) of all approaches with overflights,

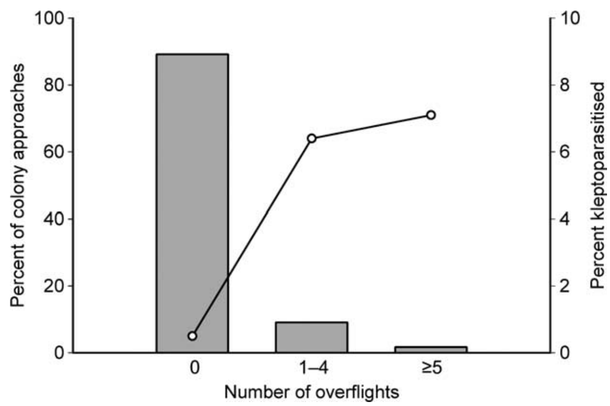

Figure 1. The distribution of colony approaches by load-carrying puffins among three overflight categories (bars), and the proportion of kleptoparasitic events within each category (points).

compared to only 0.5% (13/2920) of approaches on which they made direct landings, different by a factor of 27.

Overflight model

Overflight behaviour changed in relation to five of the measured factors as predicted if it is a response to kleptoparasitism danger (Table 1). The odds of overflights significantly (1) decreased with increasing puffin arrivals, (2) increased during periods of high wind speeds, (3) increased during periods of upslope (South) winds, (4) increased during periods of increased gull pursuits, and (5) were lower in steeper habitats. Gull presence did not change the odds of overflights, and was excluded from the final model, which therefore contained five independent factors. This model had a significantly better fit to the data than a reduced model lacking the ecological danger factors (Likelihood ratio test $\chi^2_{14} = 335.03$, $P < 0.001$). None of the effects differed significantly between the two overflight categories ("1–4 vs. 0" and "≥ 5 vs. 0"). There may be no true difference between the overflight categories in this regard, or we may have failed to detect differences that truly exist. Not only may our overflight categories not accurately represent transitions in puffin evasive behaviour, but categorical data are less suitable than are continuous data in this assessment. Consequently, we consider our conclusions regarding different degrees of overflight behaviour to be tentative.

Kleptoparasitism model

All ecological factors contributed significantly to the model, but puffin arrivals and wind speed did so only when included separately. We present results from both versions of the model (Table 2), the first ("Ecological Factors 1" [EF1]) with puffin arrivals excluded and the second ("Ecological Factors 2" [EF2]) with wind speed excluded. There was no interaction between these two factors. Each model version significantly improved the fit of the model to the data compared to a model in which both wind speed and puffin arrivals were excluded (Likelihood ratio test: [EF1] $\chi^2_1 = 7.13$, $P = 0.008$, [EF2] $\chi^2_1 = 6.64$, $P = 0.01$]), and the two versions explained similar levels of variation in the data (AIC = [EF1] 264.8, [EF2] 265.3; Likelihood ratio test: [EF1] $\chi^2_9 = 150.98$, $P < 0.001$, [EF2] $\chi^2_9 = 150.49$, $P < 0.001$). The relationship between kleptoparasitism and all other ecological variables was qualitatively similar in both models, except for a non-significant effect of westerly wind in EF2 (Table 2). The odds that load-carrying tufted puffins were kleptoparasitized (i.e. kleptoparasitism risk) generally changed as predicted with each of the six measured ecological factors. As in the overflights model, the odds of kleptoparasitism occurring significantly decreased with increasing slope grade and puffin arrivals, and significantly increased during upslope (South) wind, increasing wind speed, and higher pursuit rates by gulls. Surprisingly, increased gull presence correlated with decreased odds of kleptoparasitism, perhaps explaining the nonsignificant contribution of gull presence to the overflight model.

We assessed the contribution of the ecological factors to kleptoparasitism risk relative to that of overflights by comparing kleptoparasitism models with and without the ecological factors. If puffins assessed the ecological factors and performed overflights when kleptoparasitism danger was high, we would expect overflights to be correlated with decreased odds of kleptoparasitism when the ecological factors are controlled for (i.e. for a given level of danger, overflights reduce the probability of kleptoparasitism). The kleptoparasitism models that included all ecological factors significantly improved the fit of the data compared to the model that included only overflights (Likelihood ratio test: [EF1] $\chi^2_7 = 91.81$, $P < 0.001$, [EF2] $\chi^2_7 = 91.32$, $P < 0.001$]). There was a decrease in the odds of overflights in the kleptoparasitism models that included ecological factors compared to the model that included overflights alone, but the overlapping 95% confidence intervals (CI) within overflight levels between the models suggests this difference was non–significant (Table 2). However, the models are distinct if 90% CI are compared (90% CI for "1–4" level: 2.14–8.31 (EF1), 2.09–7.99 (EF2), 8.41–27.98 (overflights alone); 90% CI for "≥ 5" level: 0.53–5.36 (EF1), 0.52–5.17 (EF2), 6.53–45.30 (overflights alone). No qualitative results

Table 1. Statistical analysis of overflights, giving odds ratios of 1–4 vs. 0 overflights, and 5 or more vs. 0 overflights occurring given a one-unit increase in the three continuous ecological factors, or a change of factor level in the two categorical factors (from shallow to steep slope grade and northerly to other wind directions).

Factor		Coefficient (B)	SE	Z	P	Odds ratio (95% CI)
				1–4 vs. 0		
Puffin arrivals	No./15min	−0.042	0.008	−5.18	<0.001	0.96 (0.94–0.97)
Wind speed	km/h	0.028	0.006	4.77	<0.001	1.03 (1.02–1.04)
Wind direction	East	0.835	0.401	2.08	0.037	2.31 (1.05–5.06)
	South	1.336	0.177	7.54	<0.001	3.80 (2.69–5.38)
	West	0.676	0.191	3.54	<0.001	1.97 (1.35–2.86)
Gull pursuits	No./15min	0.105	0.034	3.13	0.002	1.11 (1.04–1.19)
Slope grade	Steep	−0.393	0.141	−2.79	0.005	0.68 (0.51–0.89)
				≥5 vs. 0		
Puffin arrivals	No./15min	−0.107	0.029	−3.72	<0.001	0.90 (0.85–0.95)
Wind speed	km/h	0.025	0.012	2.13	0.033	1.03 (1.00–1.05)
Wind direction	East	0.236	1.091	0.22	0.829	1.27 (0.15–10.73)
	South	1.990	0.398	5.00	<0.001	7.32 (3.35–15.98)
	West	0.772	0.535	1.44	0.149	2.16 (0.76–6.18)
Gull pursuits	No./15min	0.243	0.055	4.44	<0.001	1.27 (1.15–1.42)
Slope grade	Steep	−0.818	0.291	−2.82	0.005	0.44 (0.25–0.78)

Table 2. Statistical analysis of kleptoparasitism, giving odds ratios of kleptoparasitism occurring for a one-unit increase in the three continuous ecological factors, or for a change of factor level in the three categorical factors (from zero to one or more overflights, shallow to steep slope grade, and northerly to other wind directions).

Model	Factor		Coefficient (B)	SE	Z	P	Odds ratio (95% CI)
Ecological Factors 1 (Puffin arrivals excluded)	Puffin overflights	1–4	1.438	0.413	3.49	<0.001	4.21 (1.88–9.46)
		≥5	0.518	0.706	0.73	0.464	1.68 (0.42–6.70)
	Wind speed	km/h	0.033	0.013	2.66	0.008	1.03 (1.01–1.06)
	Wind direction	East	2.560	0.871	2.94	0.003	12.93 (2.35–71.29)
		South	2.837	0.658	4.31	<0.001	17.06 (4.70–61.94)
		West	1.899	0.867	2.19	0.029	6.68 (1.22–36.53)
	Gull pursuits	No./15min	0.380	0.086	4.42	<0.001	1.46 (1.24–1.73)
	Gulls present	No./15min	−0.236	0.088	−2.69	0.007	0.79 (0.67–0.94)
	Slope grade	Steep	−1.536	0.385	−3.99	<0.001	0.22 (0.10–0.46)
Ecological Factors 2 (Wind speed excluded)	Puffin overflights	1–4	1.407	0.408	3.45	0.001	4.08 (1.83–9.09)
		≥5	0.497	0.697	0.71	0.475	1.64 (0.42–6.44)
	Puffin arrivals	No./15min	−0.080	0.033	−2.41	0.016	0.92 (0.87–0.99)
	Wind direction	East	2.483	0.862	2.88	0.004	11.98 (2.21–64.92)
		South	2.210	0.679	3.26	0.001	9.12 (2.41–34.47)
		West	1.123	0.832	1.35	0.177	3.07 (0.60–15.69)
	Gull pursuits	No./15min	0.432	0.091	4.74	<0.001	1.54 (1.29–1.84)
	Gulls present	No./15min	−0.252	0.090	−2.80	0.005	0.78 (0.65–0.93)
	Slope grade	Steep	−1.559	0.384	−4.06	<0.001	0.21 (0.10–0.45)
Overflights alone	Puffin overflights	1–4	2.730	0.365	7.47	<0.001	15.34 (7.50–31.39)
		≥5	2.845	0.589	4.83	<0.001	17.20 (5.43–54.53)

for any of the other ecological factors change when we examine 90% CI. We conclude there is marginal support for our prediction of a decrease in the odds of kleptoparasitism when overflights are examined in their ecological context. There was no significant difference in odds of kleptoparasitism between the "1–4" and " ≥5" overflight categories and the " ≥5" and "0" overflight categories in either model including ecological danger factors (Table 2), suggesting kleptoparasitism risk was similar among these pairs of categories.

Discussion

Our results support the hypothesis that load-carrying tufted puffins at Puffin Rock engaged in colony overflights to reduce the risk of kleptoparasitism by glaucous-winged gulls. The probability of kleptoparasitism was independently correlated with most of the ecological factors we measured (Table 2), showing that these factors were reliable indices of danger, and for nearly all of these factors puffins performed overflights in the manner predicted of evasive behaviour (Table 1). The occurrence of overflights was negatively correlated with the number of puffins arriving at the colony, as expected if synchronous arrivals diluted kleptoparasitism risk (Harris 1980; see Roberts 1996 for a review). Puffins were also less likely to perform overflights when approaching the steep portion of the study plot or during low or downslope (North) winds, each of which presumably gave them greater flight control and reduced vulnerability to kleptoparasites. Finally, the odds of overflights occurring increased with pursuit rate by gulls.

The basic data presented in Fig. 1 indicate that puffins making overflights experienced a risk of kleptoparasitism many times higher than those making direct colony landings, which might suggest that overflights increased rather than decreased the risk of kleptoparasitism. However, the relevant 'risk' is not the observed rate of kleptoparasitism, but the rate that would occur if puffins did not engage in evasive behaviour. Our prediction that kleptoparasitism would be more frequent if tufted puffins did not perform overflights is supported by the marginal decrease in the odds of kleptoparasitism occurring when overflights were examined in their ecological context compared to when they were examined on their own (Table 2, significant when 90% confidence intervals are compared; see Results). The presence of unmeasured danger factors might account for the weak difference we observed here. Alternatively, overflights might have only marginally diminished kleptoparasitism risk.

Puffins engaging in five or more overflights prior to landing apparently experienced similar odds of kleptoparasitism as those making direct landing attempts (i.e. without overflights) while puffins engaging in one to four overflights experienced slightly higher odds (Table 2). The simplest interpretation of this pattern is that multiple overflights effectively compensate for kleptoparasitism danger, equalizing the net risk of kleptoparasitism across different levels of danger. However, relatively few puffins made five or more overflights before attempting a landing (Fig. 1). This suggests the kleptoparasite evasion benefits of repeated overflights may be countered by other costs. Optimal flight cruising speed and angle with respect to wind direction are reported to govern flight efficiency in seabirds (Spear and Ainley 1997a, b), and both of these factors may be compromised during overflight behaviour. Energetic demands of overflights may be particularly acute for tufted puffins given the high ratio of body mass to wing area in this species (Spear and Ainley 1997a, b), but data are lacking on this issue.

Contrary to one of our predictions, the number of gulls in the air or on the ground within the study area did not influence puffin overflights. Cassady St. Clair et al. (2001) reported that the frequency of kleptoparasitic behaviour was highly variable among seven marked gulls at this site, which suggests gull presence might not accurately reflect kleptoparasitism danger. The surprising negative correlation in the present study between gull number and kleptoparasitism

(Table 2) further suggests that interactions among gulls such as interference (Steele and Hockey 1995, Ratcliffe et al. 1997, GSB pers. obs.) may diminish kleptoparasitism danger for load-carrying puffins. The correlation we observed between overflights and gull pursuit rate (Table 1) indicates puffins may base evasion decisions on more reliable cues of kleptoparasitism danger than mere gull presence.

Puffin arrivals were negatively correlated with the occurrence of overflights (Table 1) and kleptoparasitism (Table 2), which raises the possibility that puffins use overflights to synchronize their colony approaches (Grant 1971, Pierotti 1983). Clustered arrivals are known to occur in load-carrying Atlantic puffins (Merkel et al. 1998). There was no obvious relationship between the number of overflights performed and the occurrence of clustered arrivals in the present study, and many individuals who performed overflights landed alone, suggesting that this behaviour may have limited utility in coordinating colony approaches at Puffin Rock. However, we lack the individual landing data required to fully assess clustered arrivals or a synchronizing role of overflights. Research in this direction will allow us to distinguish whether overflights are an individual or group-level kleptoparasite evasion strategy. This distinction is important since interactions between the benefits of group living and costs of predator attraction to large groups are probably among the central forces determining the evolution of coloniality (review: Danchin and Wagner 1997). To the extent that overflights occur independently from clustered colony arrivals, kleptoparasitism of tufted puffins may represent a cost of presumably colony-derived foraging or nesting advantages that is paid at an individual level.

A shortcoming of our data is that neither puffins nor gulls were individually marked. Our data might therefore be biased if: (1) there are consistent differences among individuals in evasive or pursuit behaviour, and (2) if these differences did not fairly represent the variation in behavioural differences among individuals across a properly replicated sample. We cannot quantify this potential bias. It seems likely that all puffin pairs that were actively provisioning a chick are approximately equally represented (see Methods). The number of gulls present varied from 1 to 20, but we could not identify how many individuals actually pursued puffins. Some identifiable individuals prove that several gulls exhibited kleptoparasitic behaviour, as has previously been observed at this site (Cassady St. Clair et al. 2001). Overall, the data appear to reflect temporally independent responses from a large sample of puffins to at least several different kleptoparasitic gulls.

Our observations do not suggest that overflights among load-carrying puffins communicated foraging information or served in courtship (reviewed in Danchin and Wagner 1997). Overflights were diminished during high puffin arrival rates (Table 1) when colony activity was high and the potential for communication might be greatest. In addition, load-carrying individuals landed alone at individual burrows and typically entered their burrows immediately upon landing. However, a thorough assessment of this issue will entail data on how overflights affect the behaviour of other puffins. Puffins lacking food loads also performed overflights at our study site (GSB pers. obs.), indicating this behaviour may serve different purposes for puffins in different ecological circumstances (Addison et al. 2007).

The roles of predation and kleptoparasitism in the frequent breeding failures of Atlantic and tufted puffins (e.g. Harris 1984, Gjerdrum et al. 2003) are unclear, despite their association with decreased puffin survival (Harris 1980), recruitment (Finney et al. 2003), and reproductive success (Nettleship 1972), as well as altered nestling provisioning (Rice 1987). Cassady St. Clair et al. (2001) reported kleptoparasitism rates of 2–11% at Puffin Rock, concluding there was no evidence kleptoparasites limited reproductive success of tufted puffins. However, the impact of kleptoparasites might have been much greater without counter-tactics by puffins. Our results suggest that overflights are a counter-tactic employed by breeding tufted puffins at this site. Data are needed on the costs of kleptoparasitism avoidance to assess the affect of kleptoparasitism on breeding success. Lowered lifetime reproductive success, nestling growth, or recruitment at colonies with high levels of kleptoparasitism compared to ecologically similar sites lacking kleptoparasites would provide one form of support for the presence of kleptoparasite costs.

In conclusion, our study identifies several ecological indices of kleptoparasitism danger and supports the idea that load-carrying puffins use these or correlated cues to monitor and respond to this danger. Overflights appear to be associated with diminished kleptoparasitism when examined in their ecological context, suggesting they represent an effective evasion strategy that is integrated with the varying ecological conditions of each food delivery.

Acknowledgements – We thank Carl Schwarz and Michael Whitlock for statistical advice, and Judy Higham and Connie Smith for help with field camp logistics. We received ship and helicopter support from the Canadian Coast Guard. This research was funded by a grant from the Science Horizons program of Environment Canada to GSB, a grant from the Nestucca Oil Spill Trust Fund to Douglas F. Bertram and Gary W. Kaiser, Environment Canada and The Centre for Wildlife Ecology at Simon Fraser University.

References

Addison, B. A., Ydenberg, R. C. and Smith, B. D. 2007. Tufted puffins respond to predation danger during colony approach flights. – Auk 124: 63–70.

Brown, J. S. and Kotler, B. P. 2007. The ecology of fear. – In: Stephens, D. W., Brown, J. S. and Ydenberg, R. C. (eds). Foraging: behavior and ecology. Univ. of Chicago Press, pp. 437–480.

Caro, T. M. 2005. Antipredator defences in birds and mammals. – Univ. of Chicago Press.

Cassady St. Clair, C., St. Clair, R. and Williams, T. D. 2001. Does kleptoparasitism by glaucous-winged gulls limit the reproductive success of tufted puffins? – Auk 118: 934–943.

Creelman, E. and Storey, A. E. 1991. Sex differences in reproductive behaviour of Atlantic puffins. – Condor 93: 390–398.

Cresswell, W. 2008. Non-lethal effects of predation in birds. – Ibis 150: 3–17.

Danchin, E. and Wagner, R. H. 1997. The evolution of coloniality. – Trends Ecol. Evol. 12: 342–347.

Finney, S. K., Harris, M. P., Keller, L. F., Elston, D.A., Monaghan, P. and Wanless, S. 2003. Reducing the density of breeding gulls influences the pattern of recruitment of immature Atlantic puffins *Fratercula arctica* to a breeding colony. – J. Appl. Ecol. 40: 545–552.

Gaston, A. J. and Jones, I. L. 1998. The auks (Alcidae). – Oxford Univ. Press, New York.

Gilchrist, H. G., Gaston, A. J. and Smith, J. N. M. 1998. Wind and prey nest sites as foraging constraints on an avian predator, the glaucous gull. – Ecology 79: 2403–2414.

Gjerdrum, C., Vallée, A., Cassidy St. Clair, C., Bertram, D. F., Ryder, J. L. and Blackburn, G. S. 2003. Tufted puffin reproduction reveals ocean climate variability. – Proc. Natl. Acad. Sci. USA 100: 9377–9382.

Grant, P. R. 1971. Interactive behaviour of puffins (*Fratercula arctica* L.) and skuas (*Stercorarius parasiticus* L.). – Behaviour 40: 263–281.

Harris, M. P. 1980. Breeding performance of puffins, *Fratercula arctica*, in relation to nest density, laying date, and year. – Ibis 122: 193–209.

Harris, M. P. 1984. The puffin. – T. and A.D. Poyser, Waterhouses.

Hosmer, D. W. and Lemeshow, S. 2000. Applied logistic regression. – Wiley, New York.

Kotler, B. P. and Brown, J. S. 2007. Community ecology. – In: Stephens, D.W., Brown, J. S. and Ydenberg, R. C. (eds). Foraging: behavior and ecology. Univ. of Chicago Press, pp. 397–434.

Lank, D. B. and Ydenberg, R. C. 2003. Death and danger at migratory stopovers: problems with "predation risk". – J. Avian Biol. 34: 225–228.

Lowther, P. E., Diamond, A. W., Kress, S. W., Robertson, G. J. and Russell, K. 2002. Atlantic puffin *Fratercula arctica*. – In: Pool, A. and Gill, F. (eds). The birds of North America. Vol. 18. The birds of North America Inc., Philadelphia, pp. 1–24.

Merkel, F. R., Nielsen, N. K. and Olsen, B. 1998. Clumped arrivals at an Atlantic puffin colony. – Waterbirds 21: 261–267.

Moore, J. 2002. Parasites and the behaviour of animals. – Oxford University Press, New York.

Nettleship, D. N. 1972. Breeding success of the common puffin (*Fratercula arctica*) on different habitats at Great Island, Newfoundland. – Ecol. Monogr. 42: 239–268.

Pennycuick, C. J. 1987. Flight of auks (Alcidae) and other northern seabirds compared with southern Procellariiformes: ornithodolite observations. – J. Exp. Biol. 128: 335–347.

Piatt, J. F. and Kitaysky, A. S. 2002. Tufted puffin *Fratercula cirrhata*. – In: Pool, A. and Gill, F. (eds). The birds of North America. Vol. 18. The birds of North America Inc., Philadelphia, pp. 1–32.

Pierotti, R. 1983. Gull–puffin interactions on Great Island, Newfoundland. – Biol. – Conserv. 26: 1–14.

Ratcliffe, N., Richardson, D., Lidstone Scott, R., Bond, P. J., Westlake, C. and Stennett, S. 1997. Host selection, attack rates and success rates for black-headed gull kleptoparasitism of terns. – Waterbirds 20: 227–234.

Rice, J. 1987. Behavioural responses of common puffins to kleptoparasitism by herring gulls. – Can. J. Zool. 65: 339–347.

Roberts, G. 1996. Why individual vigilance declines as group size increases. – Anim. Behav. 51: 1077–1086.

Spear, L. B. and Ainley, D. G. 1997a. Flight behaviour of seabirds in relation to wind direction and wing morphology. – Ibis 139: 221–233.

Spear, L. B. and Ainley, D. G. 1997b. Flight behaviour of seabirds in relation to wind speed and direction. – Ibis 139: 234–251.

Steele, W. K. and Hockey, P. A. R. 1995. Factors influencing rate and success of intraspecific kleptoparasitism among kelp gulls (*Larus dominicanus*). – Auk 112: 847–859.

Ydenberg, R. C., Butler, R.W. and Lank, D. B. 2007. Effects of predator landscapes on the evolutionary ecology of routing, timing and molt by long-distance migrants. – J. Avian Biol. 38: 523–529.