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.

[illegible]

[illegible]

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, 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.

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

[illegible]

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 [illegible] 2. [illegible]).

[illegible]	[illegible]	[illegible] (ß)	[illegible]	[illegible] (5% [illegible])
[illegible] 1	[illegible] 1			

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.

[illegible]

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.

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.