TUFTED PUFFINS (*FRATERCULA CIRRHATA*) RESPOND TO PREDATION DANGER DURING COLONY APPROACH FLIGHTS

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Abstract.—In spite of their putative importance in the evolution of certain traits (e.g., nocturnality, coloniality, cliff nesting), the effects of aerial predators on behavior of adult seabirds at colonies have been poorly investigated. We hypothesized that Tufted Puffins (*Fratercula cirrhata*) respond to danger posed by aerial predators by modifying their behavior to mitigate danger. We observed Tufted Puffins making repeated colony fly-ins and departures and characterized (1) the timing of this behavior, (2) the activity rate (number of birds arriving or departing), and (3) the risk-level of activity, with respect to predation danger posed by Bald Eagles (*Haliaeetus leucocephalus*) and Peregrine Falcons (*Falco peregrinus*). As we predicted, we found that Tufted Puffins (1) dilute danger by synchronizing their fly-in and departure activities, (2) reduce fly-in and departure activity rates when predators are present, and (3) switch to lower-risk fly-in activities (e.g., staying over water where they have an escape route from an aerial attack) when predators are present. *Received 15 October 2004, accepted 5 January 2006.*

Key words: *Fratercula cirrhata*, predation, raptor, synchrony, Tufted Puffin, wheeling.

Réaction de *Fratercula cirrhata* au Danger de Prédation au cours des Vols d'Approche de la Colonie

Résumé.—Malgré leur importance putative dans l'évolution de certains caractères (e.g. nocturnalité, colonialité, nidification sur une falaise), les effets des prédateurs aériens sur le comportement des oiseaux de mer adultes dans les colonies ont peu été étudiés. Nous avons posé l'hypothèse que les Macareux huppés (*Fratercula cirrhata*) réagissent au danger que représentent les prédateurs aériens en modifiant leur comportement pour atténuer le danger. Nous avons observé des Macareux huppés effectuant des arrivées et des départs répétés et nous avons caractérisé (1) la synchronisation de ce comportement, (2) le taux d'activité (nombre d'oiseaux arrivant ou quittant la colonie) et (3) le niveau de risque de l'activité en relation avec le danger de prédation représenté par les Pygargues à tête blanche (*Haliaeetus leucocephalus*) et les Faucons pèlerins (*Falco peregrinus*). Comme nous l'avions prédit, nous avons trouvé que les Macareux huppés (1) diluent le danger en synchronisant leurs activités d'arrivée et de départ, (2) réduisent le taux d'activité lorsque les prédateurs sont présents et (3) reviennent à des activités d'arrivée à risque plus faible (e.g. restent sur l'eau où ils peuvent avoir une voie pour s'échapper en cas d'une attaque aérienne) lorsque les prédateurs sont présents.

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IN THE PAST, predator–prey research has primarily been concerned with the lethal effects of predators on their prey, but predators also have important nonlethal effects on their prey. There is a growing body of literature on the ecology of fear, and the effect that the perception of danger can have on the behavior, and ultimately on the life-history strategy and numbers, of a prey species (Brown et al. 1999). When animals perceive danger, they may modify their behavior to reduce that danger (Lima and Dill 1990, Lank and Ydenberg 2003), which in turn can affect life-history decisions made by an individual. Thus, consideration of fear is a critical component in understanding an animal's ecology, even when actual mortality events are rare.

Predation danger can alter an animal's foraging decisions (Lima and Dill 1990), migratory decisions (Lank and Ydenberg 2003), and even life history (Lima 1987). Seabird biology has focused on foraging and breeding, with relatively little consideration of the nonlethal effects of predators at the colonies (but see Finney et al. 2003). Predation danger may be an important factor affecting nest-site selection (Nettleship 1972, Finney et al. 2003), reproductive effort and provisioning (Harfenist and Ydenberg 1995), and general behavior in seabirds. Tufted Puffins (*Fratercula cirrhata*; hereafter "puffins") are highly wing-loaded (Livezey 1988) and tend to be awkward flyers and even more awkward landers (Piatt and Kitaysky 2002). Puffins face predation danger when flying into the colony, especially with a load of food for chick provisioning. While provisioning, they are at risk for kleptoparasitism (St. Clair et al. 2001) and aerial predation (Piatt and Kitaysky 2002).

The dangers of approaching the colony make one particular behavior of puffins very puzzling: repeated fly-in behavior. Throughout the breeding season puffins can be observed circling toward and then away from the colony, tracing an ellipse over the nearshore water adjacent to the colony. Puffins appear to be repeatedly approaching the colony, as though with the intention of landing, and then aborting the attempt. The behavior is similar to the wheeling behavior of other alcid species (Gaston and Nettleship 1981, Harris 1984), except that it is often done by individuals or pairs, rather than large groups.

At Triangle Island, British Columbia, we observed puffins making repeated fly-ins to the colony slopes. We predicted that if puffins were sensitive to the danger posed by the presence of aerial predators, there would be a tendency for (1) fly-ins and departures to be clustered (or synchronized) rather than randomly distributed in time, that (2) higher rates of fly-in and departure activity would tend to be associated with periods of predator absence, and that (3) puffins would use lower-risk activities when predators were present. Therefore, we statistically tested these predictions against their equivalent null models using a data set consisting of measurements of the sequential time intervals between the landings of puffins at their burrows during three different and frequently observed (daily) regimes of predatory danger. We present data revealing that fear affects flight decisions by puffins, and use a novel statistical model to measure synchronicity in behavioral decisions.

METHODS

Study site.—In June and July 2002, during incubation and very early chick rearing, we observed puffins in the south bay of Triangle Island, British Columbia (50°52′N, 129°05′W) from a cabin located at the base of a long cliff in the eastern half of the bay. This cabin was ideally situated to observe the steep and high (194 m) south slope of Triangle Island characterized by grassy vegetation and a narrow band of flat cobble beach above the high-tide line. A pair of Bald Eagles (*Haliaeetus leucocephalus*; hereafter "eagles") nests at the west end of the slope and Peregrine Falcons (*Falco peregrinus*; hereafter "falcons") nest in the central part of the slope. Provisioning puffins are rarely observed on this slope, which is away from the main puffin colony; however, puffins made repeated fly-ins to these slopes as if prospecting for new nest sites, and so these puffins' response to predation danger is not influenced by a chick waiting in the nest.

Observations.—We made 84 standardized 5-min observations of a ~300-m-wide strip of the south slope and used a custom event-recording program to record all fly-ins and departures by puffins, as well as arrivals and departures of eagles and falcons in flight along or above the south slope. Observations were spread over all daylight hours (0530–2130 hours PST), and evenly throughout the study period, with the exception of a stormy week in the middle during which no observations were made. Several

5-min observations were done each day. There were always at least 5 min between observation periods. We attempted to record the timing of arrivals to the nearest second. We later organized the frequency distribution of arrivals into two-second intervals to minimize the influence of measurement error associated with observers' delayed reaction times being a significant fraction of a second.

Each flight toward the slope was classified as an "approach" if the bird turned back before the tide line (~30 m between slope and tide line). Each flight in which the bird crossed the tide line and came to within 30 m of the cliff was classified as a "close approach." For a flight to be classified as a "landing," the bird had to stand on the slope. On several occasions, birds came within a few centimeters of the slope and appeared to be preparing to land, but then turned back. These flights were classified as close approaches. We also logged "departures," because birds landing on the slope usually did not spend much time there, and subsequently continued repeated fly-in behavior.

Each fly-in was classified into one of three danger–risk categories. We classified a fly-in as occurring (1) when eagles were present, (2) when eagles had been present recently (within the observation period), or (3) during a predator-free period (no eagles present within the observation period). In the south bay of Triangle Island, it is not possible to separate the effects of eagle and falcon presence, because both raptor species almost always occur together. We rarely observed eagles flying in the bay without falcons chasing them, and we never saw falcons in the bay when eagles were not present. Eagle presence is therefore a surrogate for raptor presence, and is used in the analysis as a single "predator" value. By recording eagle presence only when eagles are visible in flight above the observer, we have used a conservative measure of predation danger, because some activities actually occurring during dangerous periods will be recorded as occurring in safe periods, thus diminishing the effect of eagle absence.

Statistics.—If fly-in and departure events are randomly timed, the expected probability distribution of inter-event intervals—in our case, the time interval from one fly-in or departure event to the next—follows an exponential distribution: the exponential distribution is a special case of the gamma probability distribution

having its standard deviation (σ) equal to its mean (μ) (Walpole et al. 1998). Alternatively, if these events tend to be clustered or synchronized in time, the gamma distribution will have $\sigma > \mu$; whereas if the timing of events tends to be regulated (spaced), $\sigma < \mu$. For our analyses, μ and σ estimate the mean time (in seconds) and standard deviation (in seconds) between sequentially arriving and departing puffins.

To test prediction (1), we coded the appropriate predictive models as VISUAL BASIC macros in EXCEL (Microsoft, Seattle, Washington). These models were used to statistically evaluate the observed frequency distribution of inter-event intervals (within two-second bin sizes) against the expected distribution of inter-event intervals calculated under the null hypothesis that arrivals and departures were randomly distributed. This evaluation was done for three independent hypotheses representing each of our three different predation-risk regimes (eagles present, eagles recently present, predator-free). We used the method of maximum likelihood as it applies to multinomial frequencies to solve for the best-fit gamma (μ and σ free) and exponential (forcing $\sigma = \mu$) distributions; we then used an information-theoretic approach (Burnham and Anderson 2002) to determine the model that was best supported by our data for each predator-presence regime. We used *t*-tests to judge the statistical significance of $\sigma \neq \mu$ (clustered) versus $\sigma = \mu$ (random, null).

To evaluate the quality of our model fits, we performed goodness-of-fit (GOF) randomizations of the best-fit distributions (Burnham and Anderson 2002), which in all cases were models with $\sigma > \mu$. Results of these GOF tests detected significant, but different, degrees of overdispersion in the distribution of puffins as they returned to the colony, as measured by the statistic $\hat{c}$ (Burnham and Anderson 2002). Note that this overdispersion is distinct from any non-independence (synchrony) of arrival–departure times that a gamma distribution ($\mu \neq \sigma$) might indicate. That is, if each puffin is making timing decisions independently of other puffins, then the GOF statistic $\hat{c}$ will be close to 1 (Burnham and Anderson 2002). If there is a statistical indication that puffins are making decisions in groups, then $\hat{c}$ is an estimate of the size of group in which puffins appear to be making joint decisions. For example, $\hat{c} = 2$ could be interpreted as indicating that puffins are behaving as pairs.

A statistical implication of $\hat{c} > 1$ is that effective sample size (*n*) decreases reciprocally to $\tilde{n} = n/\hat{c}$, which reduces statistical power. Our significant results yielded $\hat{c} > 1$ in all cases, so we used our estimated values of $\hat{c}$ to calculate QAIC (Akaike Information Criterion), QDeviance, and $\hat{c}$–corrected standard errors for our estimates of the ratio $\hat{\sigma} : \hat{\mu}$ (Burnham and Anderson 2002). This adjustment serves to control for the number of birds in a group, thus facilitating a comparable measure of arrival–departure synchronicity among each predator-presence regime.

We used a contingency table analysis (Walpole et al. 1998) to test predictions 2 and 3, that is, the effect of eagle presence on repeated fly-in and departure activity rate and risk level. If prediction 2 is supported, the count of each activity (approach, close approach, landing, and departure) will be lower when eagles are present than when they are absent. If prediction 3 is supported, the percentage of lower-risk activities (approaches) will increase, and the percentage of higher-risk activities (close approaches and landings) will decrease when eagles are present compared with when they are absent.

Results

We made a total of 84 5-min watches, totaling 420 observation minutes with 3,729 events. Predators were present for 21% of observation times, but only 10% of fly-in and departure events by puffins occurred when eagles were present. The activity rate (i.e., the number of fly-ins per observation second in each 5-min observation period) ranged from 0 to 1.7 ($\overline{x} = 0.6$), and the number of puffins making approaches to the colony at the beginning of each observation period ranged from 0 to ~100 ($\overline{x} = 7$). There was no consistent time-of-day pattern to activities of the puffins or the eagles, but puffin activity rates seemed highest in foggy weather.

As predicted (1), event timing was clustered, with more very short intervals and more long intervals than expected in a random distribution (Table 1). The GOF randomizations showed that nonindependent groupings of birds also occurred, with $\hat{c}$ being significantly greater than unity (1) when predators were absent ($\hat{c} = 5.9 \pm 1.9$). This is consistent with both the idea that arrival activity was happening in waves when eagles were not around and that activity rates would be expected to be high in relation to

when predators were present (see below). By contrast, birds tended toward smaller groupings, perhaps pairs, when eagles were present. The degree of clustering in arrival–departure times can be measured with the $\hat{\sigma} : \hat{\mu}$ ratio. Clustering was minimal when there were no predators ($\hat{\sigma} : \hat{\mu} = 1.44$), higher when eagles were recent but not present ($\hat{\sigma} : \hat{\mu} = 1.62$), and highest when they were present ($\hat{\sigma} : \hat{\mu} = 1.65$; Fig. 1). This suggests that the degree of synchrony of activities by the puffins tends to increase as the level of danger increases.

We predicted that puffins would also mitigate danger by (2) reducing their activity rate when danger was high and (3) switching to lower-risk activities when danger was high. We evaluated these predictions by measuring the number, and percentage of total, for fly-ins observed when predators were present versus absent. The clustering of activities detected when evaluating our first prediction (1) suggests nonindependence among observations. To reduce this possible influence, we excluded from the contingency table all observations for which the time since the previous activity was <5 s, because this value is greater than the mean interval (Table 1), which indicates that this interval is sufficient to ensure independence. The data confirm that puffins (2) lower their overall activity rates and (3) switch from close approaches and landings to approaches when eagles were present (*n* = 955 activity observations, $\chi^2 = 22.9$, df = 3, *P* < 0.001; Table 2). Departure activities were unaffected by the presence of eagles.

Discussion

We found that puffins modified their repeated fly-in behavior in three ways to reduce danger. (1) They synchronized activity to dilute the danger. Apparent synchrony of activity was attributable to two factors: sudden bursts, or waves, of activity after danger had passed (the eagles had left), and synchrony of activity during dangerous times (when eagles were present). They avoided eagles by (2) reducing activity rates; and (3) when eagles were present, they switched to lower-risk activities. The number of activities that took place when eagles were present was significantly lower than that expected if there was no effect of eagles. This effect was stronger for more dangerous activities, such

TABLE 1. Model-ranking results for four predatory regimes, the better-supported hypothesis for each regime having the lower ΔQAIC. The parameters $\hat{\mu}$ and $\hat{\sigma}$ estimate the mean time (in seconds) and standard deviation (in seconds), respectively, between sequentially arriving puffins. Significant ($P < 0.0001$; t-test with df = $\tilde{n} - 1$; Bonferroni-adjustment for $\alpha = 0.05$ and three trials yields $\alpha = 0.0167$) values for $\hat{\sigma}:\hat{\mu} > 1$ indicate that arrival events tended to be synchronized. For the better-supported model, $\tilde{n}$ represents the effective sample size after adjusting actual sample size n by $\hat{c}$, a measure of overdispersion, such that $\hat{c} > 1$ can be interpreted as indicating that puffins tend to make flight-synchrony decisions in group sizes of $\hat{c}$. See text for further explanation. Symbol k indicates the number of free parameters, ΔQAIC is the relative QAIC after correcting ΔAIC by $\hat{c}$, and ΔL and ΔQL are the relative deviance and quasi-deviance, respectively (Burnham and Anderson 2002).

| Regime (hypothesis)	n	$\tilde{n}$	k	$\hat{\mu}$	$\hat{\sigma}$	ΔL	ΔAIC	$\hat{c}$ (±1 SE)	ΔQL	ΔQAIC	$\hat{\sigma}:\hat{\mu}$ (±1 SE)	P
Eagles present ($\mu \neq \sigma$)	173	118	2	13.57	22.41	0.00	0.00	1.5 ± 0.3	0.00	0.00	1.65 ± 0.12	<0.0001
Eagles present ($\mu = \sigma$)	173		1	13.73	13.73	97.16	95.16	—	63.83	61.83	—	—
Eagles recent ($\mu \neq \sigma$)	650	239	2	4.58	7.43	0.00	0.00	2.7 ± 0.7	0.00	0.00	1.62 ± 0.10	<0.0001
Eagles recent ($\mu = \sigma$)	650		1	4.80	4.80	201.39	199.39	—	73.99	71.99	—	—
Predator-free ($\mu \neq \sigma$)	2847	482	2	4.02	5.79	0.00	0.00	5.9 ± 1.9	0.00	0.00	1.44 ± 0.07	<0.0001
Predator-free ($\mu = \sigma$)	2847		1	4.18	4.18	464.57	462.57	—	78.38	76.38	—	—
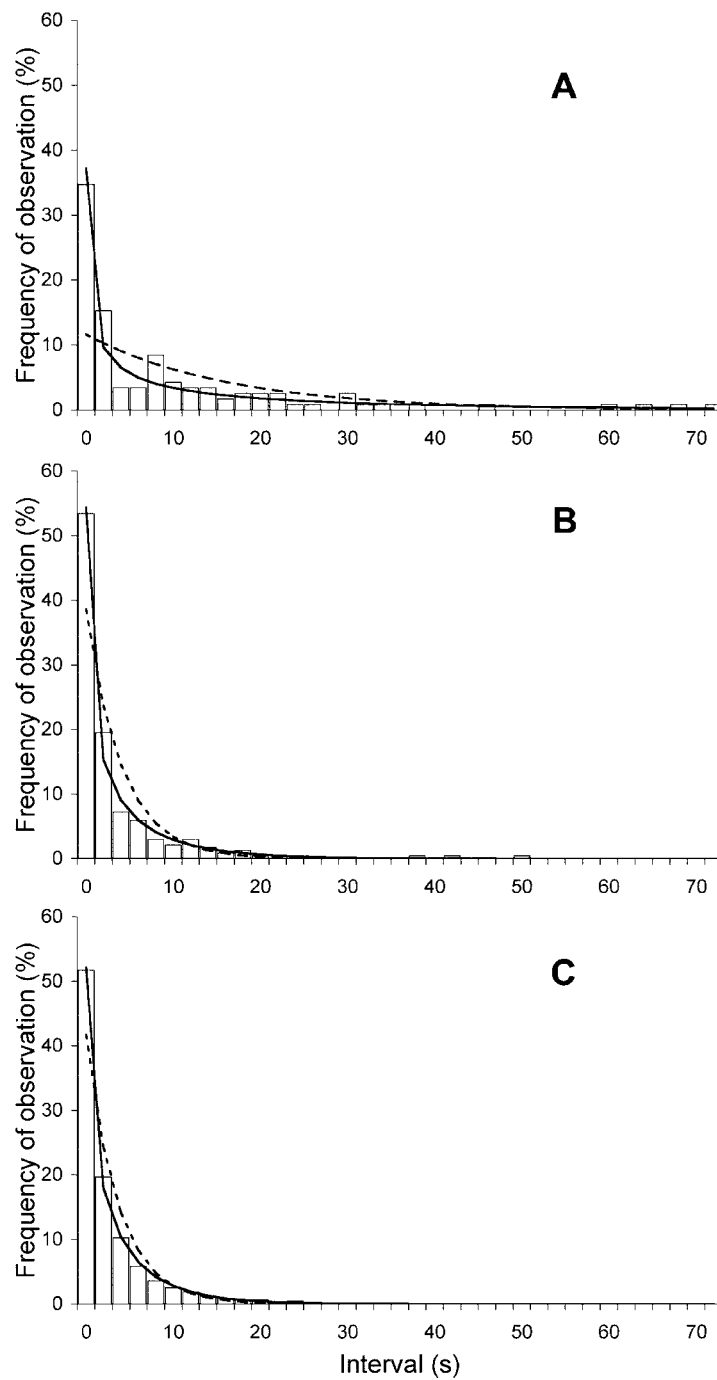
FIG. 1. Observed percentage (histogram) and best-fit gamma (solid line) and exponential (dashed line) distributions of fly-in and departure event intervals for (A) when eagles are present (n = 173), (B) when eagles have recently left (n = 650), and (C) when eagles are absent from the area for the observation period (n = 2,847). Events are more clustered when eagles are present (A) than when they have recently left (B) or are absent (C).

TABLE 2. Number (row percentage) of repeated approach activities observed when eagles were either present or absent. When eagles were present, puffins decreased their overall activity rates and decreased their close approach and landing activities in favor of safer approach activities.

Eagles	Approaches	Close approaches	Landings	Departures	Total
Absent	85 (10%)	420 (48%)	126 (14%)	241 (28%)	872
Present	24 (29%)	27 (33%)	9 (11%)	23 (28%)	83

as close approaches to the slope and landings, than it was for less dangerous activities, such as farther approaches to the slope and departures from the slope.

The higher activity rates and bursts of activity that occurred when predators were not present resulted in more birds circling, and thus larger group sizes, during these low-risk periods. This reflects temporal avoidance of predators by puffins but can make it difficult to distinguish synchrony of arrival times from a "group size" effect. Our GOF tests and subsequent $\hat{c}$ adjustments facilitated statistical partitioning of the effects of group size and arrival synchrony by identifying the degree to which birds tend to group together on arrival. The larger group size during low-risk periods results in a conservative test of our hypothesis of increased synchrony during high-risk periods when compared with low-risk periods, because more birds being engaged in this activity would tend to bias our data toward a decrease in the length of inter-event intervals.

A puffin is most vulnerable to attack on close approaches to, and landings on, the slope because a puffin over water has an available escape route if an attack occurs (Lima 1993). By switching to an approach over water when eagles are present, puffins retain an escape route and are able to continue their activity at a safe distance from potential danger. Also, puffins can evaluate danger levels by circling over water before attempting to land on the slope. Departing birds have the advantage of being able to assess danger from the burrow entrance before taking off into dangerous airspace and, furthermore, are flying directly to safety upon departure, and so may not need to alter this activity when eagles are present.

Mitigation of danger by synchronization of arrival times dilutes the risk of predation for the individual and may also "confuse" the predator, reducing the probability of an attack (Pitcher and Parrish 1993). Synchronization of activities has previously been demonstrated in seabirds. Murres (*Uria* spp.; Daan and Tinbergen 1979) and Atlantic Puffins (*F. arctica*; Stempniewicz and Iliszko 2002) synchronize timing of fledging, both within the fledging period and within the day, to dilute predation risk. Adult Atlantic Puffin appear to synchronize landings during food delivery to avoid kleptoparasitism (Rice 1987).

Raptor predators occasionally capture puffins (Gaston and Jones 1998, Piatt and Kitaysky 2002). Attacks on and captures of puffins by both eagles and falcons have been observed on Triangle Island (B. Addison pers. obs., M. Hipfner and J. Dale pers. comm.). This danger, however small, appears to alter their behavior. Despite the dangers of repeated-approach behavior, as evidenced by the arrival–departure synchronization adjustment by puffins, the birds continue to invest in it rather than abandoning the behavior in favor of safety on the water when predators are nearby. Investment in repeated-approach behavior is puzzling, because it does not appear to have a purpose, but the pay-off for this behavior may be undetectable to the casual observer. For example, if the behavior is nest-site prospecting, as it appears to be, this investment may have a future pay-off that is not easily measured. Predation and kleptoparasitism may be major factors in the evolution of life history and behavior of puffins. The nonlethal effects of predators deserve continued consideration.

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